PRIMARY OCEANIC PRODUCTION

THE AUTOTROPHIC PRODUCTION OF ORGANIC MATTER IN THE OCEANS

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CONTENT

PREFACE

During the summer of 1949 the final plans were settled for sending a Danish naval ship round the world. Oceanographic investigations were to be the main task of the expedition. The senior author who had started his work as a planktonologist during another Danish expedition round the world by the "Dana" 1928-1930 was excited by the idea of attempting to measure the organic productivity in the sea. No method for such a determination was, however, available. The only method tried before in the ocean had given results which seemed to be in absolute disagreement both with measurements of the standing crop of phytoplankton in the ocean and with theoretical considerations concerning the background of oceanic productivity.

A new method therefore had to be developed. We were very fortunate in having just received in Denmark the first quantity of radiocarbon – ^{14}C. The availability of this tracer made it possible to develop a new technique. Although the time was rather short for such a work, there was no choice.

As neither of the present authors had worked with tracers before the successful development of the technique was greatly assisted by the help and instructions given by dr. Hilde Levi of the Zoophysiological Laboratory, University of Copenhagen.

Both authors took part in the expedition during the first three months after which the senior author returned home. Most of the field work has thus been done by the junior author. The phosphate determinations were made by Mr. I. Crossland, M. Sc. and Mr. U. Kläning, M. Sc.

Part I is written by the two authors together, Part 2 and 3 by the senior author.

We are greatly obliged to the Committee of the Expedition and the Royal Danish Navy for facilities on board. We offer our sincere thanks to A. F. Bruun, Ph. D., leader of the Expedition. Dr. Bruun had the most ungrateful job of administrating the available time, which was always too short. His keen interest in the work on productivity was a great help. Thanks are also due to the commanders of the "Galathea", during the first part of the Expedition, Kommandørkaptajn H. Madsen and later Kommandør S. Greve, and to all others on board the ship.

INTRODUCTION

Phytoplankton production is the biological basis of all life in the oceans. This was recognized early by oceanographers. The investigation of oceanic plankton in respect to quantity was started at the end of the last century. Most of the important pioneer work was done by Germans. First of all must be mentioned the "Plankton Expedition" 1899. HENSEN, the leader of the expedition, published (1911) in the concluding volume of the publications from the expedition a comprehensive treatise of the problems concerning oceanic productivity. The results were, however, in this respect not very satisfactory. The methods available for quantitatively estimating phytoplankton at the time of the expedition were rather inadequate, particularly for work in oceanic water. Silk nets were used.

Another German, Lohmann, must be recognized as the real father of oceanic quantitative phytoplankton science. During the "Deutschland" Expedition 1911 he used a method worked out by him at Kiel, whereby samples of water obtained from series of depths were centrifuged and the organisms counted in a living state. This method, although encumbered with systematic errors – cf. p. 115 – may still be recognized as one of the best for estimating the quantity of oceanic phytoplankton.

The route of the "Deutschland" Expedition covered representative parts of the subtropical and tropical parts of the North- and South-Atlantic. The general conclusions by LOHMANN 1920 about productivity in these waters must still be considered valid.

The work by Lohmann was continued by Hentschel during the "Meteor" Expedition, 1925-27. This expedition covered the whole of the South-Atlantic down into the Antarctic Ocean and parts of the North-Atlantic. The phytoplankton population was determined at more than 300 stations rather regularly scattered over the whole area in question.

The results which were published by HENTSCHEL 1932-1936 are in perfect agreement with Lohmann's work and because of the multitude of stations, give a still more instructive picture of the quantitative distribution of phytoplankton in an ocean. It is amazing to recognize how regular and simple is the

quantitative distribution of plankton algae in the oceans.

The standing crop of plankton was measured according to Lohmann's method. It is often pointed out, e. g. by HARVEY 1945 p. 142, that the evaluation of such counts can be interpreted only by an expert familar with the various species as they occur in the area in question. This view cannot, however, entirely be approved regarding the oceans. The variation in the cell size of the important phytoplankton organisms occuring in the open sea seems to be fairly constant from area to area. Further, it is rather moderate. The sum of the individuals of all organisms occuring gives a rather instructive picture of the quantity found, as convincingly shown, by both Lohmann and Hentschel. The pessimistic view on plankton counts seems to have been put forward by people acquainted primarily with coastal phytoplankton organisms taken with nets. The variation in size may here indeed be very great. It must, however, be pointed out that even in coastal waters the giants among the plankton algae only on rare occasions are of decisively quantitative importance provided that an artificial selection due to the net has not taken place. Furthermore the giants among the diatoms are not so important, most of the cell volume in these species being cell sap in contrast to the small sized species. When evaluating plankton counts from coastal waters it is mandatory to take the size of the algae into account. It is of course also necessary to estimate the different cell sizes when dealing with oceanic phytoplankton – see p. 115.

A measure of the standing crop of phytoplankton has been obtained by dissolving the plant pigments in acetone or alcohol and estimating either the mixed pigments or the chlorophyll. KREPS and VEJRBINSKAYA, 1930, were the first to use such a method. Net catches were originally used for these measurements. An important improvement was introduced by filtering a definite volume of the sea water from the different depths through paper (RILEY 1939) or better through a Cella-Filter (KREY 1939). Much faith in this method has been shown from nearly all sides. Recently, however, some doubts about the general reliability have arisen (GILBRICHT 1952) as it has been shown that a material part of the chlorophyll found sometimes may have nothing to do with living algae.

It is of great importance to know the size of the standing crop of plankton. It is, however, at least as important to obtain information about the daily production of organic matter by the plankton algae. Without such information it is impossible to estimate the food available for the animals. The word "production" is unfortunately used by different authors in very diverging senses. In this treatise we therefore use instead the more precise designation: primary "production of organic matter", which includes only autotrophic production due to photosynthesis and chemosynthesis. In coastal waters some investigations, although not too many, were made in the years after 1920 when ATKINS 1923 using indirect methods and GAARDER and GRAN 1927 using an experimental method started such work (for references see: STEEMANN NIELSEN 1952). In the open ocean indirect methods of measuring the organic production are only possible at higher latitudes, where an unproductive winter season and a productive summer season alternate. BOGOYAVLENSKII (1955) has used such methods in the most northern part of the Pacific. In oceanic waters of lower latitudes only investigations made by RILEY (1939) can be mentioned. As pointed out by STEEMANN NIELSEN 1952, 1954, 1955 the results of these investigations (Gaarder and Gran's technique) can hardly be considered realistic. It seems to be the reduction of the bacterial activity in the illuminated experimental bottles which was measured instead of the photosynthesis of the plankton algae. This reduction seems to be caused by antibiotics produced by the algae in the light; cf. the 1955 article.

For measuring oceanic productivity a much more sensitive method than the light-and -dark bottle oxygen method introduced in marine biology by Gaarder and Gran has to be employed. The availability of the radioactive tracer ^{14}C after the last war made it possible to develop the technique to be described in Part I.

PART I. THE METHODS

A. GENERAL INFORMATION ABOUT THE ^{14}C-METHOD FOR MEASURING ORGANIC PRODUCTIVITY IN THE SEA

The 14C-technique used on the "Galathea" Expedition has already been described by STEEMANN NIELSEN 1952. The main lines will, however, be reviewed here. Further, some important additional information will be given and the importance of some of the details, which may seem unimportant to some without further discussion, will be stressed.

In the 14C method the incorporation of the tracer in the organic matter of the plankton algae is used as a measure of the production. A definite amount of $14CO_2$ is added to the sea water the productivity of which is to be measured. The content of CO_2 (total) in this water must be determined or estimated (see p. 54). If we assume that $14CO_2$ is assimilated by the plankton algae only through photosynthesis (see, however, p. 55) and that $14CO_2$ is assimilated photosynthetically at the same rate as $12CO_2$ (cp. p. 56), by determining the content of 14C in the plankton after the experiment, we also determine the total amount of carbon assimilated. It is only necessary to multiply the amount of 14C found by a factor corresponding to the ratio between CO_2 (total) and $14CO_2$ in the water at the begining of the experiment. The amount of 14C assimilated is determined by measuring the β-radiation from the plankton, which is retained by a collodion filter.

As 14C has a half life of more than 5.000 years, samples with a definite content of $14CO_2$ could be prepared before the start of the expedition. 1 ml. samples of water were used which had nearly the same content of total CO_2 as normal sea water. The water had a content of NaCl a little lower than oceanic seawater; the pH was 9.5. The 14C-samples were kept in sealed glass containers (ampoules – Fig. 1). They were autoclaved at once after the preparation, as otherwise the possibility of bacterial growth and associated dark fixation of the tracer may cause trouble. The water used for preparing the $14CO_2$ solution has to be distilled immediately before the use as otherwise the bacteria count may be too high.

Fig. 1. Ampoule.

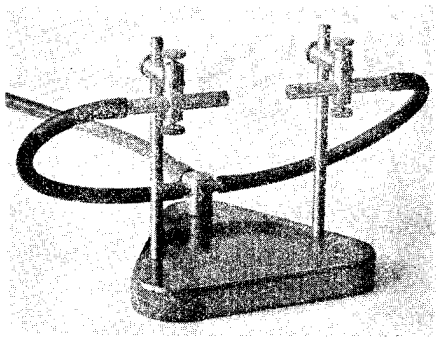


Fig. 2. Burner for sealing of ampoules (after JERMSTAD and SCHOU).

As the small ampoules are extremely difficult to clean on account of their narrow necks, previously sealed ampoules of jenafiolax glass were used. These were not only absolutely clean inside but were sterile, due to sealing during their manufacture. The ampoules were opened just before being filled. Presealed ampoules seem only to be manufactured and sold in Europe.

Whereas the filling of the ampoules may be done appropriately without difficulty the subsequent sealing may prove difficult. A special burner for this process – Fig. 2 – was used for the preparation of the glass containers for the "Galathea"-Expedition. It is to be recommended for workers not especially acquainted with pharmaceutical technique to autoclave the filled and sealed glass containers in a solution of methylene blue (0.1 %). On cooling, the blue solution is sucked into any glass containers which have not been effectively sealed. These are thus easily recognizable.

The $14CO_2$ solution in the ampoules must have no contamination of any kind. If any contamination was found at all in the "Galathea" ampoules it was minimal, in maximum 5 per cent. of the background.

According to a statement by RYTHER and VACARRO 1954, 1 ml of their solution had a rather variable contamination of radioactive particulate material averaging 200 per cent. of the background. They stated therefore that the lower limit of sensitivity of the 14C method was 1.3 mg C/m³. During the "Galathea" Expedition photosynthetic rates as low as 0.1 mg C/m³ could be measured to ± 10 per cent. If it had been necessary, still smaller rates could have been measured. According to a personal communication, Ryther and Vacarro are now able to prepare the tracer stock solution without contamination.

14C was supplied from Oak Ridge, U.S.A., in the form of $BaCO_3$ with 4.79 per cent. of the carbon in the form of 14C. As $BaCO_3$ is insoluble the CO_2 was converted into Na_2CO_3 as follows.

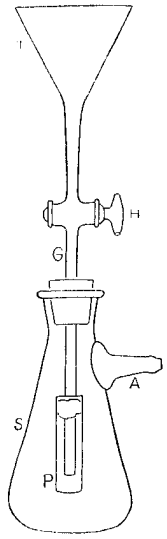


Fig. 3.
Vacuum line.

A specially constructed vacuum line was used (Fig. 3). A glass tube (G) carrying a funnel (T) and stopcock (H) is inserted in a pyrex glass suction flask (S) through the rubber stopper. A glass vessel (P) is attached to tube (G) by means of a cottonwool plug and a wire. $Ba^{14}CO_3$ and a suitable amount of normal $BaCO_3$ to act as a carrier is placed in the vessel (P). A solution of NaOH (generally 5 ml. 0.5 N) is placed at the bottom of the suction flask. Then HCl (generally 5 ml. 0.5 N) is poured into the funnel. After evacuation the suction flask is closed by a cock immediately outside the side tube (A). The cock (H) is now opened cautiously and the hydrochloric acid is run into vessel (P). This releases CO_2 which diffuses down to the NaOH solution, and is absorbed by it.

During the effervescence in vessel (P), some of the liquid will be thrown on to the cotton-wool, which must eventually be completely steeped in the hydrochloric acid in vessel (P) in order to ensure that the carbon dioxide in the barium carbonate which may have been thrown on to the cotton-wool is released. If the original quantity of hydrochloric acid is not sufficient, a little distilled water is added through the funnel (T).

Although experiments have indicated that essentially all the carbon dioxide in the barium carbonate is absorbed in the sodium hydroxide solution after 15 minutes, the apparatus is left to stand for a further 60 minutes. It is then opened and the stopper, together with tubes (P) and (G), funnel (T) and cock (H), removed. Then 200 ml. glass-distilled water is added; after shaking, 10 ml. is removed and titrated electrometrically with hydrochloric acid to pH 9.5. A corresponding amount of hydrochloric acid is added to the remaining 195 ml. and the 10 ml. are poured back. After checking that the pH is actually 9.5, a solid rubber stopper is placed in the mouth of the suction flask and the liquid is transferred to 1 ml. glass containers (Fig. 1) by means of a graduated (automatic) syringe. The liquid is withdrawn through the side tube (A) of the suction flask after the latter has been turned upside down. The glass containers are then sealed. The relatively high pH (9.5) prevents any appreciable loss of activity during the various manipulations. That this is really so appears from the fact that it is impossible to demonstrate any progressive reduction in activity from the glass container first filled to that last filled. In the subsequent addition of the contents of the ampoules to the water samples in which the photosynthetic activity is to be measured, it is also important that pH should be comparatively high.

For the "Galathea" Expedition 1 ml. ampoules of 4 different strengths were prepared. The different containers were made in series of 200, and were each wrapped in appropriately coloured tissue paper. Within series of the same calculated strength the correspondence was fairly close. In later calculations values for the particular series were always used. The series of the greatest strength contained 8 μC per ampoule, the series of the weakest strength, 0.2 μC.

For counting carbon dioxide was precipated as barium carbonate, which was then filtered off by the usual collodion filter or a smooth paper filter (3 sq. cm., see p. 54). Carrier was also added, and the weight per 3 sq. cm. was always about 20 mg.

In later work millipore-filters (Lowel Co, U.S.A.) have been used for measuring the activity of an ampoule instead of the ordinary collodion filters. These filters do not change weight if an aqueous solution is passed through. Regarding the determination of a self-absorption curve the reader is referred to CALVIN *et al.*, 1949 p. 31 and p. 104 f.f.; such a curve is presented in Fig. 4. By using Geiger tubes with windows of the same mass thickness identical curves were obtained. Some technical skill is necessary to make an adequate self-absorption curve.

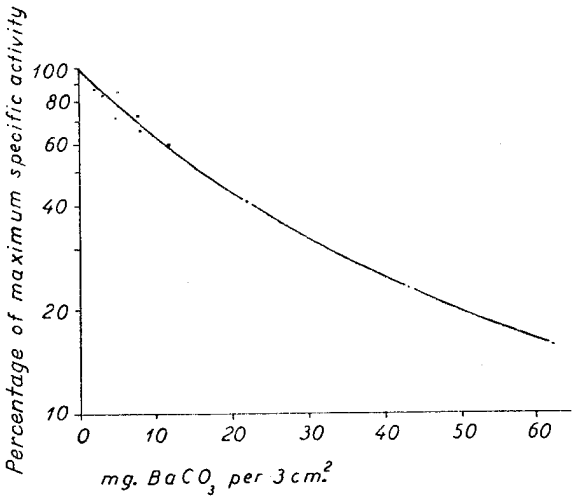


Fig. 4. Self-absorption correction curve.

B. THE DETERMINATION OF THE PHOTOSYNTHETIC ACTIVITY OF PLANKTON ALGAE

After the content of a ^{14}C ampoule has been added to a water sample containing plankton algae and the sample then has been exposed to light, part of ^{14}C is found in the organic matter of the plankton algae. If this quantity of ^{14}C is to be used as a measure of the photosynthetic intensity, we must know both the content of total CO_2 in the water and the ratio $\frac{^{12}C + ^{13}C + ^{14}C}{^{14}C}$ in the total CO_2 of the water. As a rule, however, we shall avoid using absolute amounts of ^{14}C, as only the activity of the experimental water and the activity of the plankton algae are to be determined. If, under identical conditions the activity of the experimental water is a, that of the plankton algae b, and the content of total CO_2 in the water c, then the total amount of CO_2 assimilated by the algae is $\frac{b \times c.}{a}$ This is on the assumption that $^{14}CO_2$ is assimilated at the same rate as $^{12}CO_2$ and that ^{14}C is not incorporated in the algae in any other way than through photosynthesis. In Section C this question will be discussed in detail.

If pH, titration alkalinity, and temperature are known, it is possible, according to BUCH (1945), to determine total CO_2 in fresh water provided that the titration alkalinity does not approach zero. In sea water it is also necessary to know the chloride content, which has partly a direct effect, partly an indirect effect through the boric acid, the concentration of which is proportional to the chloride concentration. In oceanic water the calculation of total CO_2 thus becomes slightly more complicated than in fresh water (see HARVEY 1945, pp. 52-73).

If Cl‰ is known, it is not necessary to determine the titration alkalinity A, as this is equal to 0.000123 Cl‰ expressed in equiv./l. With brackish water, as with fresh water, it is necessary to determine the titration alkalinity.

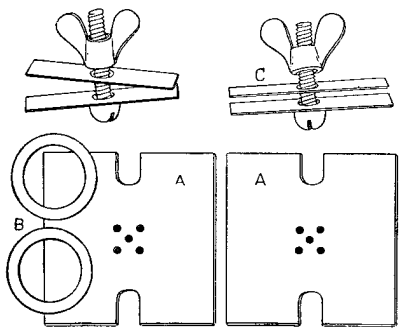


Fig. 5.
Special holder for collodion filters.

As pH varies so little in oceanic surface water, it is unnecessary to determine pH unless very high accuracy is aimed at. If it is put at 8.20, the error in total CO_2 will be 2 to 3 per cent. at the most. Normally for the present purposes it will be sufficient to put total CO_2 at 90 mg/l. for normal oceanic surface water.

The β ray activity of the plankton algae was measured after filtration through a collodion filter (membrane filter from Membranfiltergesellschaft, Göttingen). These filters are kept dry before use; this is a great advantage as compared with the prewar collodion filters, which had to be kept in water. Filtering was done by suction (in the "Galathea" a mechanical pump was used). The filtering surface was 3 sq. cm. Facilities for automatic filling were provided. The filtration device corresponds to that in CALVIN et al., 1949 fig. 40. In the "Galathea" 6 sets of this apparatus were placed so that they could all work at the same time. The filters used resemble closely the standard filter "mittel" of the factory. 300 ml. distilled water take about 20 minutes to pass through the filter. A considerable quantity of plankton reduces the rate materially; in these circumstances part of the sample is filtered. The maximum size of the pores is 0.5 μ. All marine autrophic plankton algae are retained. With most – perhaps all – waters it is possible to use filters with a slightly greater pore width (at most about 0.8 μ), so that it is possible to increase the rate of filtration materially.[1]

When filtration was completed, about 5 ml. of sea water free from activity was added for rinsing, etc. The filters were then placed in a special holder (fig. 5), dried in air for about 12 hours, and placed for 20 minutes in a closed container above fuming hydrochloric acid. This was done in order to remove carbonate to be found e.g. in coccoliths. Experiments have shown that all carbon in inorganic form is removed in this length of time, so that only ^{14}C in organic form, which is not destroyed by the process, is left. Immediately afterwards the filters must be dried in a desiccator – also containing some soda lime – and if they are not examined at once, kept there. If this is not done, the plankton sometimes may absorb water because calcium chloride is developed. Water containing organic matter with dis-

1. The firm has recently renamed their filters. We are now using filters "grob", Stufe 2.

solved ^{14}C may thus be sucked into the filter. Before the filter is finally dried, it is placed on a special mounting ring and base (CALVIN et al., 1949, fig. 41).

An end-window Geiger-Müller counter tube with a window radius of 7.5 mm. (made by Zerahn and Madsen, Copenhagen) proved most suitable for measurement of the radio-activity. For the "Galathea", Geiger tubes with a particularly thin window were selected. Care must be taken that the activity of a sample is about 10 times larger than the background.

A double counting unit made by Brüel and Kjær, Nærum, Denmark, was used. It has proved robust in all kinds of climate. The technicians of the Expedition were able to correct all faults that developed in the unit. A special 220- volt generator, unconnected to other circuits, supplied the current in the "Galathea".

As the geometry used in measuring the barium carbonate for determing the activity of the contents of the ampoules is identical with the geometry used in measuring the activity of the plankton, the two activities may be directly compared. As the weight of plankton was always below 0.1 mg. per 3 sq. cm. self absorption in the plankton may be disregarded.

At the start of an experiment, the contents of an ampoule are added, by means of an ordinary hypodermic syringe or a glass pipette, to the bottle with the sample in which the photosynthesis is to be measured. The container is rinsed with a little water from the sample.

A sample of elementary carbon containing ^{14}C, mounted on the same mounting ring and base as normal samples with the same area was always used as a standard.

C. IS THE AMOUNT OF ORGANICALLY BOUND ^{14}C A MEASURE OF THE INTENSITY OF PHOTOSYNTHESIS?

If the amount of organically bound ^{14}C in the plankton after an experiment is to give an absolute measure of the intensity of photosynthesis (the gross production) the following conditions must be present: – (1) No $^{14}CO_2$ must be incorporated in organic compounds except through photosynthesis, (2) the rate of assimilation of $^{14}CO_2$ must be the same as that of $^{12}CO_2$, (3) no $^{14}CO_2$ must be lost by the respiration which takes place simultaneoulsy with photosynthesis, (4) no organic matter must be lost by excretion.

None of these conditions are, however, quite fulfilled. Although the importance of each of them is only relatively slight at high light intensities and one of them has the opposite effect to the others it is necessary to introduce a correction (valid at high light intensities) covering them all.

As it is now generally known, both animals and plants have a dark interchange of CO_2 which has nothing to do with photosynthesis. Labelled CO_2 is in this way introduced into organic matter of both plants and animals. In a healthy culture of a plankton alga such a dark fixation of $^{14}CO_2$ is negligible compared with the fixation due to photosynthesis at a high light intensity as shown by BROWN, FAGER and GAFFRON 1949 and many others. In fig. 6 is presented the dependence of the length of the experimental time on the rate of dark fixation of $^{14}CO_2$ as given in per cent. of the photosynthetic fixation at optimum light intensity. *Chlorella pyrenoidosa* was used for these experiments. Compared with the fixation of $^{14}CO_2$ in the light the dark fixation was particularly low in the experiment presented in Fig. 6. The concentration of total CO_2 was much lower than in seawater. In experiments lasting four hours the dark fixation in water from the photic layer in the sea is mostly about 1-2 per cent. of the fixation at optimal light intensity. It may sometimes be as

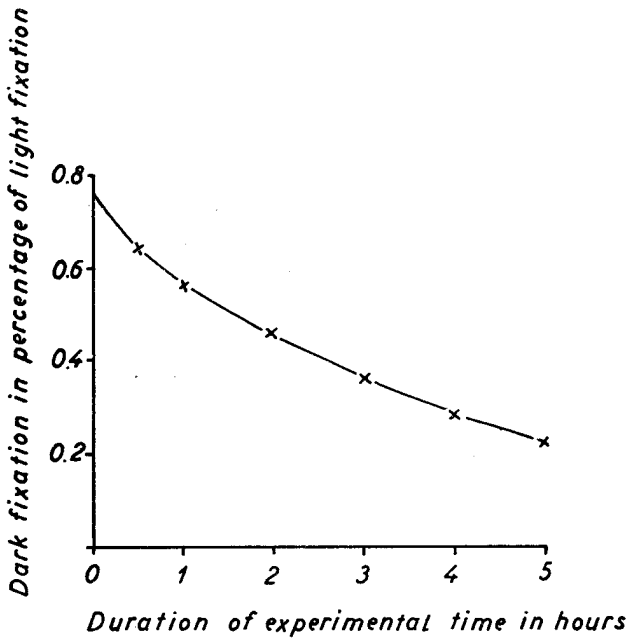


Fig. 6. Dark fixation of 14C in percentage of fixation in light. *Chlorella pyrenoidosa.*

high as 5 per cent. even in oceanic water. It must be remembered that the dark fixation by other organisms than the algae is included.

It was impossible during the "Galathea-Expedition" to make determinations of the dark fixation in all the water samples in which the rate of photosynthesis was determined. It was only done in part of them. The stock of the ampoules of the greatest activity was too small. The ampoules used for a normal determination of photosynthesis did not give the sufficient accuracy when used for measuring dark fixation, the rate of which was only a few per cent. of the rate of the fixation in light.

In more recent Danish investigations dark fixation has been measured in all water samples. For special investigations this is of importance. For normal measurements of the rate of photosynthesis it is unnecessary. If the autotrophic algae constitute only a minor part of the bio-mass present in the sea or if the photosynthetic rate is very low due to e.g. lack of light, dark fixation may be a more dominant part of the total fixation of $^{14}CO_2$. In polluted waters where huge quantities of bacteria are found, dark fixation may be of extraordinary importance. In the oceans it seems, however, never to be so if only a relatively high light intensity is employed and the experiments only have a duration of some few hours.

In agreement with Anderson and Libby 1951, it was theoretically estimated by STEEMANN NIELSEN 1952 that $^{14}CO_2$ should be photosynthesized 6 per cent. slower than $^{12}CO_2$. A recalculation of some experimental results obtained by van NORMAN and BROWN 1952 has shown that $^{14}CO_2$ is really assimilated about 5 per cent. slower than $^{12}CO_2$ (STEEMANN NIELSEN 1955). It was necessary to recalculate van NORMAN and BROWN's figure as, inter alia, they have paid no attention to the fact that about 50-70 per cent. of the CO_2 produced – or expected to be produced – by the respiration in some way or other is identical with CO_2 fixed during photosynthesis – STEEMANN NIELSEN 1955.

If it is assumed that the rate of respiration is about 10 per cent. of the photosynthetic rate at a high light intensity – cp. below – the interaction of respiration and photosynthesis will have the effect that the photosynthetic rate as measured by the ^{14}C method is about 6 per cent. too low. This correction was put at 4 per cent. by STEEMANN NIELSEN 1952.

If these three corrections are added together we get a total correction of $(+5+6-1)=+10$ per cent. The same total correction was used during the preliminary working up of some of the "Galathea" material (STEEMANN NIELSEN 1952).

The correction + 10 per cent. is only valid if the rate of photosynthesis is high as compared with the rate of respiration. If the rate of respiration is 5 % of the rate of photosynthesis, the correction should only be 7 %. If on the other hand the rate of respiration is 25 %, 50 %, or 100 % of the rate of photosynthesis, the correction should be about + 20 %, + 50 %, and + 155 % respectively. This means that measurements made with the C-14 technique at the compensation point would have to be multiplied with a factor of about 2.5 to obtain values for gross production. Therefore, it must be stated that the C-14 technique is only applicable with reservations if the rate of photosynthesis is not considerably higher than the rate of respiration. During the "Galathea" Expedition the normal measurements were made at a high intensity – about 18.000 lux cf. p. 60. The 12 experimental series made during the Expedition showing the dependence of the rate of photosynthesis on light intensity – cf. p. 101 – indicate for all kinds of surface water, that the rate of photosynthesis at 18.000 lux is high as compared with the rate of respiration – about 10 times as high. It is impossible to state any difference in the shape of these curves between the plankton from eutrophic and oligotrophic waters – cf. Figs. 32-36.

According to recent investigations in the North Atlantic by STEEMANN NIELSEN and HANSEN (under preparation) the ratio of rate of respiration to rate of optimal photosynthesis normally is less than $^1/_{10}$ in oceanic subsurface water.

The "in situ" experiments – cf. p. 57 and p. 67 – were only made during daytime, thus decreasing the influence of respiration by the factor 2. Finally these measurements were not carried on right down to the supposed compensation depth. Special corrections were made for the measurements from the lowest part of the photosynthetic layer. It should, however, be mentioned that even considerable deviations in the photosynthetic rates in the lowest part of the photosynthetic layer only slightly influence the size of organic production per surface unit.

No correction is made for organic material excreted by the algae. In the light of the modern knowledge concerning algal physiology there is no reason to consider such an excretion as being of any real importance in experiments of short duration at normal light intensities – cf. MYERS and JOHNSTON 1949.

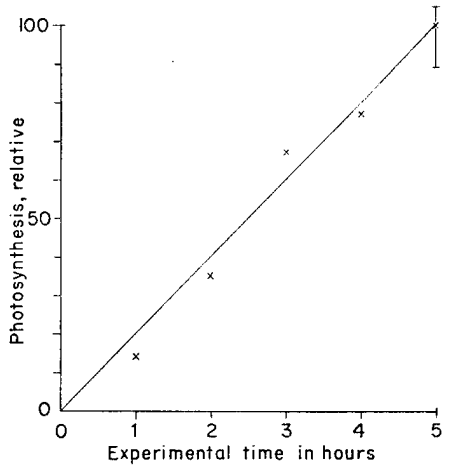


Fig. 6a. Dependence of the rate of photosynthesis on time. The variation is shown of five parallel experiments lasting 5 hours. St. 719a.

The duration of the normal experiments was 4 hours. The experimental series presented in Fig. 6a shows – like other similar series – that the rate of photosynthesis at a nearly optimum light intensity keeps constant at least during the first 5 hours. Surface plankton from the eastern part of the Pacific Ocean near Panama was employed illuminated at 18.000 lux. Identical water samples were illuminated for 1, 2, 3, 4, and 5 hours. 5 samples were illuminated for 5 hours. The rate of photosynthesis during the first hour was lower due to an after-effect of light inhibition - cf. p. 102.

It must always be considered wise to make the duration of experiments with natural plankton short. Firstly oceanic plankton algae are not able to stand the conditions in the experimental bottles for long periods – cf. p. 99. When using the ^{14}C-technique there is a special reason to keep the duration of the experiments short. If autolysis of the algae is taking place this technique gives very poor results as a material part of the organic matter containing the tracer will not be retained by the filter. Autolysis may easily take place due to photo-oxidation in experiments of long duration, particularly if there is no continuous stirring. As during the "Galathea" Expedition all experiments were of short duration and as effective stirring was employed, it is rather unlikely that autolysis played any serious rôle (see also p. 67). It is on the other hand likely that small amounts of water-soluble assimilates are lost during the filtration.[1]

The suppositions put forward by RYTHER 1955 regarding the use af the ^{14}C method in oligotrophic water are discussed by STEEMANN NIELSEN and AL KHOLY 1956. Furthermore, all evidence indicates that an absolute deficiency in P or in N is normally not found in nature – cf. p. 114.

It is possible that misleading results may be achieved in seawater with a very small concentration of plankton algae, if the duration of the ^{14}C-experiments is several days. The dark fixation of ^{14}C by the bacteria developing in huge quantities – cf. STEEMANN NIELSEN 1955 b – may completely outdo the fixation due to photosynthesis.

1. According to a personal communication from dr. G. E. Fogg, London, fixation of radiocarbon in filter-passing organic material in water from a eutrophic lake has been found to be only about 1 per cent of that in material retained on the membrane filter.

D. THE "IN SITU" METHOD FOR DETERMINING THE PRODUCTION PER SURFACE UNIT OF THE SEA

For determining the production of matter under 1 sq. m. of surface, a method resembling Gaarder and Gran's oxygen method can be used. Instead of measuring oxygen metabolism, the intensity of photosynthesis is determined by the ^{14}C method.

With an all-glass water-bottle (fig. 7, for a description see AABYE JENSEN and STEEMANN NIELSEN, 1952) 500 ml. of water is taken from the various layers of water in which photosynthesis is believed to take place. This may be decided by measuring the penetration of light into the sea (see p. 63). After a 300-ml. bottle (pyrex, with glass stoppers) has been filled and the contents of a ^{14}C ampoule introduced, the bottle is lowered to the depth from which the sample came. This is done either immediately before sunrise or when the sun is at its meridian altitude. The bottle is raised again, either in the first case when the sun is at its meridian altitude, or in the second case immediately after sunset. In both cases, the photosynthesis measured relates to half a day, and the value found has only to be multiplied by 2 to relate to the whole day. To estimate the total photosynthesis below 1 sq. m. surface of the sea the determinations from the single depth are presented graphically as e.g. in Fig. 8. The area to the left of the curve drawn represents the photosynthesis below the surface.

The "in situ" method was little used during the

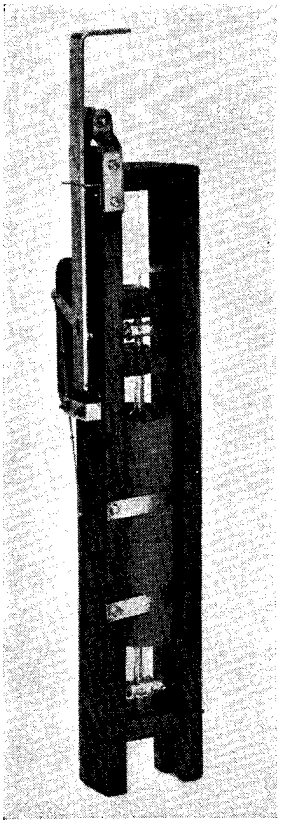


Fig. 7.
All-glass water-bottle.

"Galathea" Expedition. It is much too time consuming. It has, however, now been used regularly for some years both in Greenlandish and Danish waters. Light ships are particularly suitable for such studies. This work will be published elsewhere. Fig. 8 presents typical examples from all seasons from the Kattegat. The light conditions were in all cases favourable.

Five special "in situ" experimental series with surface water were made on the "Galathea" in order to investigate the dependence of the photosynthetic rate (real assimilation) on the light and to check the results obtained by the "tank" experiments. Four of these series are given in Fig. 9-12. All values are relative. The depth O = surface, the depth 100 is the depth at which an average of 1 per cent. of the green and blue light at the surface was found. The maximum rate of photosynthesis per day measured is put at 100 at the abscissa. The duration of the experiment was a half day – from noon to sunset. The curves would of course be identical if the duration of the experiments had been a whole day. It was bright weather during all series. The series shown in Figs. 9-11 were made in plankton-rich waters. The first mentioned was made with water from a depth of 10 m. off the coast of Angola – latitude 8°50'S – in December, the second was made in False Bay, South Africa – latitude 34°16'S – in January. Water from a depth of 4 m. was employed. The third series was carried out in the Gulf of Siam using water from a depth of 10 m. The depth showing 1 per cent. of the surface light (blue + green) was 43 m. in the first mentioned series, 18 m. in the second, and 60 m. in the third.

The experiment shown in Fig. 12, was made in clear oceanic water near Ceylon in the Indian Ocean. Water from a depth of 10 m. was used. The depth showing 1 per cent. of the surface light was 99 m.

As pointed out p. 56, the ^{14}C technique gives low values of the photosynthetic rate near the compensation point due to the intermixing of the respiratory and photosynthetic processes. The lower parts of the curves are corrected accordingly – dashed line. Dark fixation is not considered.

If the rate of respiration is put at 5-10 per cent. of the maximum rate of photosynthesis found, the compensation point during the day should be found at the dephts where 5-10 per cent. of the maximum photosynthetic rate is measured. The compensation point for 24 hours – a day and a night – is thus found at the depth at which 10-20 per cent. of the maximum

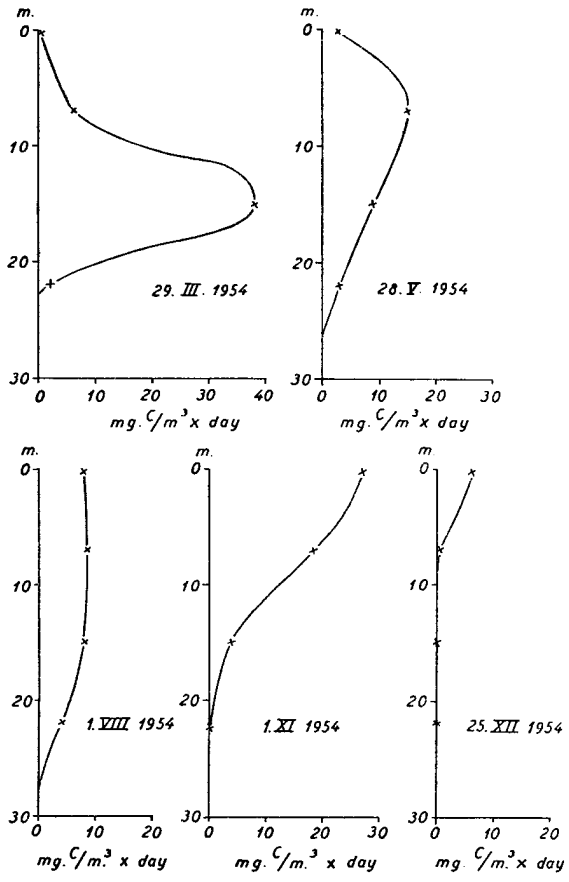


Fig. 8. Normal "in situ" experiments in the Kattegat.

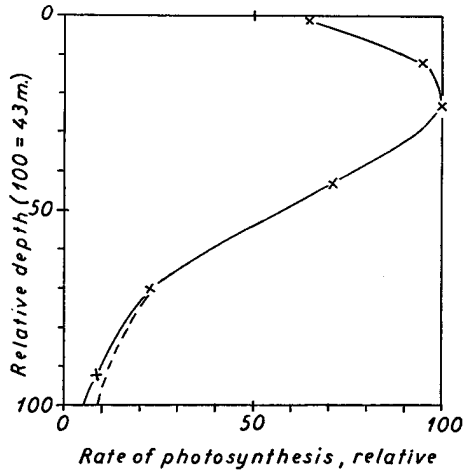


Fig. 9. Photosynthesis in water collected at 10 m. depth when exposed at different depths. St. 101.

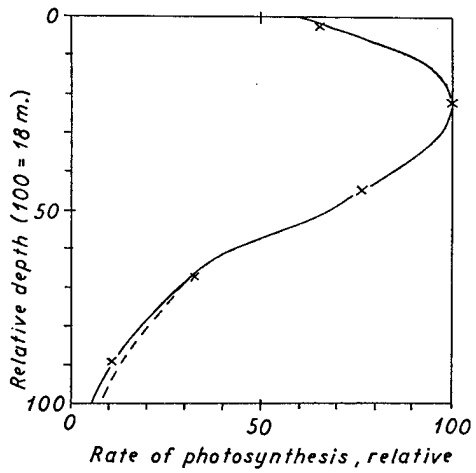


Fig. 10. Photosynthesis in water collected at 4 m. depth when exposed at different depths. St. 170.

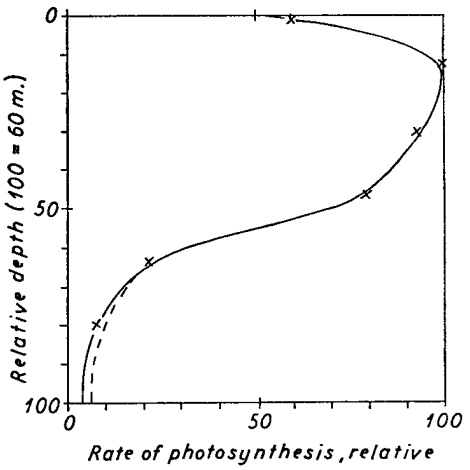


Fig. 11. Photosynthesis in water collected at 10 m. depth when exposed at different depths. St. 381.

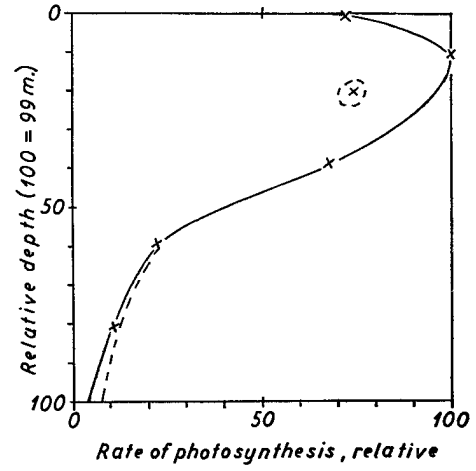


Fig. 12. Photosynthesis in water collected at 10 m. depth when exposed at different depths. St. 283.

photosynthetic rate is measured. As may be seen from Figs. 9-12 this depth corresponds approximately to the depth at which one per cent. of the surface light (blue + green) is found. Because of the intermixing of photosynthesis and respiration the compensation depth can only be presented with some reservation. This is, however, of only slight importance for the computation of the rate of photosynthesis per surface unit.

The areas to the left of the curves in Figs. 9-12 give the rate of photosynthesis below a surface unit. It is easily seen from all curves that this rate is practically identical with the rate at the "best depth" – the depth at which the highest photosynthetic rate is measured – multiplied with the depth at which 1 per cent. of the green + blue light is found, divided by 2. This formula is not only applicable in tropical and subtropical waters. It has also been shown with some modification to be valid in Danish waters (latitude 55°N) on bright days during summer – cp. STEEMANN NIELSEN 1951 Fig. 10. It is even possible to use the formula in arctic waters during summer as will be shown in a subsequent paper. The formula is the basis for computing the photosynthetic rate according to the "tank" method.

E. THE "TANK" METHOD FOR DETERMINING THE PRODUCTION PER SURFACE UNIT OF THE SEA

If only the "in situ" method could have been used during the "Galathea" Expedition only a few scattered observations on productivity could have been made. It is expensive to keep a big ship like the "Galathea" stationary for at least 6 hours – the duration of an "in situ" experiment in the Tropics. Furthermore, the program of the expedition was very extensive. The investigation of the organic productivity was only one of many topics of the expedition. A second, time-saving method for determining the production had therefore to be used.

With this method, water samples from the various depths, after addition of ^{14}C, are exposed to a definite light intensity in a water-bath at the same temperature as the sea. After 3 to 4 hours the plankton is filtered off and the photosynthetic intensity determined in the usual way. From the value of the photosynthetic intensity found for a given light intensity and temperature, the production of matter by photosynthesis through 24 hours can be calculated if we know firstly the dependence of photosynthesis on the light intensity, and secondly the light intensity at various times of the day at the depths from which the samples originate.

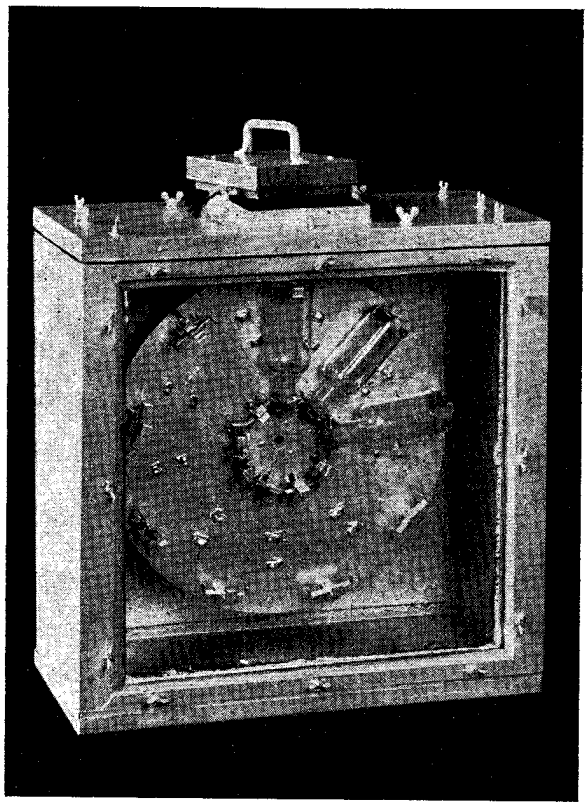


Fig. 13. Water-bath.

On account of the ship's movement at sea, the water-bath – Fig. 13 – is kept tightly closed. Through a trap-door in the middle of the top cover the bottles can easily be placed on the rotating disk in the middle of the bath, which can accomodate nine 300-ml. bottles. The spindle on which the disk rotates passes through the wall of the water-bath to a motor supplying the motive power. The whole front wall is glass, so that the experimental bottles can be illuminated by the twelve 20 W. tubular fluorescent lamps (Phillips 33a) which give a light with a spectral composition near that of the daylight. A mirror is placed behind the lamps. A ventilator was placed above the lamps.

Before the start of an experiment the temperature of the water in the water-bath is adjusted by adding ice, to about 1°C. below the temperature wanted. During a 4-hour experiment the temperature increases by 2°C. The increase in temperature is slight partly because the water-bath is very effectively insulated, and partly because tubular fluorescent lamps are used, which radiate very little heat. On the side of the water-bath facing the source of light partial insulation is provided by an extra pane of glass placed 1 cm. outside the pane in the bath.

All parts of the water-bath, including the rotating disk, are treated with silver-bronze, the light intensity thus being increased by about 50 per cent. With new fluorescent lamps the effective light intensity illuminating the water in the experimental bottles is about 20.000 international lux. This intensity, however, falls to about 18.000 lux in a comparatively short time. After a burning period of about 500 hours the light intensity is 14.000 lux: the lamp should be replaced before that stage is reached.

The idea behind the "tank" method is to expose the algae in the tank to a light intensity giving a photosynthetic rate identical with the average rate during a day in the sea at the "best" depth (Fig. 9). The production per surface unit may thus be found by multiplying the depth of the photosynthetic layer divided by 2. – according to the formula given on page 61.

Tank experiments made together with the "in situ" experiments given in Figs. 9-12 showed that the rate at the "best depth" during bright days was the same (about 90-110 per cent.) as in the tank if the light intensity which the algae received here was 18.000 int. lux.

The light intensity which the algae received in the tank could not be measured directly, as the algae received both the direct light and the reflected light particularly that from the rotating disk to which the experimental bottles were fastened. Instead the light intensity was measured indirectly. Light assimilation curves for surface plankton were produced using an open tank with the front window of glass for the higher light intensity. Facing this front window was placed an incandescent bulb able to produce sufficient high light intensities. The variation in light intensity in the open aquarium was produced by varying the distance of the experimental bottles from the bulb. The experiments at low light intensity were made in the normal tank without reflex light using filters to reduce the light intensity. The effective light intensity in normal tank experiments illuminated by the fluorescent lamps and with reflected light was put at the light intensity in the special experimental series giving the same photosynthetic rate as in the tank. In this way it could be stated that the reflected light in the tank increased the effective light intensity by about 50 per cent. At the same light intensity measured in the tank without reflected light, and in the special arrangement with incandescent light, the rate of photosynthesis was found to be practically identical. This was primarily caused by using overvoltage for the incandescent bulb- a special type designed for photographic use. Relatively much green and blue light was thus produced just as in the case of the fluorescent lamps. There is therefore no need for considering the different colour spectra of the two sources. The light intensities although measured in lux were only used relatively. The light-assimilation curves are discussed in detail in section III, C, 1.

If the light intensity in the tank measured without reflection was 12.000 lux and the effective light intensity thus 18.000 lux, no correction had to be made. If this was not the case, a correction to the measurements was made according to the curve shown in Fig. 14. The curve is drawn according to the experiments presented in section III, C, 1.

Samples from three different depths were collected, on a normal "Galathea" station: a) from the surface, b) from the depth at which the light intensity (blue + green) was 10 per cent. of the intensity at the surface, c) from the depth at which the intensity was 1 per cent.

If the temperature varied between the depths from which the three samples were collected, it was impossible to provide the right temperature for all

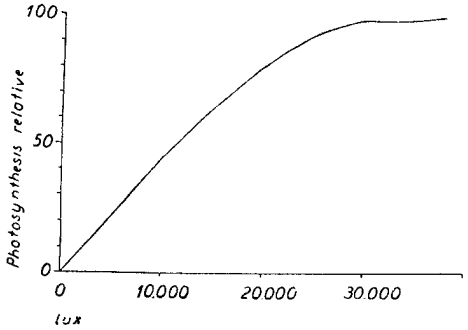


Fig. 14. Light intensity and rate of photosynthesis in tropical surface plankton.

samples. A correction for the photosynthetic rate therefore had to be made. The correction was put at 5 per cent. per degree Celsius. This correction was only of importance in some special areas.

The experiments shown in Figs. 9-12 in the previous section provided, as already mentioned, the necessary basis for deriving a formula for organic productivity.

Production of matter per sq.m. per 24 hours =

$$\frac{(2a+2b+c)\cdot d\cdot e}{5\cdot 2}\ \text{mg.C}$$

where a is the photosynthesis in mg. C per hour per cu.m. at 18.000 lux in surface water;
b is that in water from a depth with 10 per cent. of the surface light;
c that in water from a depth with 1 per cent. of the surface light;
d is the depth in m. at which the light is 1 per cent. of the total quantity of blue and green light at the surface; and
e is the number of hours from sunrise to sunset.

The "in situ" experiments and the light-assimilation experiments have been made with plankton from surface water (0-10 m. depth) exclusively. In section III, C, 1 will be shown that the algae from the lower parts of the photosynthetic zone must be supposed to show a somewhat deviating dependence on light from that of surface algae. It will be shown, however, that the formula presented above may also to a first approximation be used for the algae from the lower depth.

As the photosynthesis taking place in the deepest layers of the photosynthetic zone is of less quantitative importance than that taking place in the upper and middle layer, the value for photosynthesis at 18.000 lux in the water from the depth with 1 per cent. of the light is entered in the formula at half its value.

The formula applies to the tropics and subtropics.

In higher latitudes the formula may be used approximately during summer, but not during the other seasons. If the phytoplankton is not too heterogeneously distributed vertically it appears to be possible to determine the production of matter per surface unit by the "tank" method with an accuracy of about ± 20 per cent. (perhaps a little less accurate during the first month of the expedition), which should normally be quite sufficient. Greater accuracy may be obtained by taking samples from other depths exceeding the three mentioned above. In waters where the algae are very heterogeneously distributed vertically an augmentation of the number of samples is desirable.

The production of matter in the sea depends of course on weather conditions, although to a lesser degree than would be expected at first sight. The dependence on weather is discussed in section III, C, 3. It must, however, be mentioned that all values calculated for the production per area are reduced by 10 per cent. The values directly obtained by the formula given above correspond to absolutely bright weather. If 10 per cent. is subtracted average values for "normal" weather are obtained.

F. THE ACCURACY OF THE PRESENT MEASUREMENTS OF THE PHOTOSYNTHETIC RATE IN WATER SAMPLES

By choosing glass containers with sufficient ^{14}C and counting for a sufficiently long time, it is possible to determine the assimilation of ^{14}C with very great precision. Normally the activity is determined to an accuracy of ± 5 per cent. To aim at a greater accuracy would serve no purpose.

The experiments described in table 1 were made to discover to what extent the intensity of photosynthesis varies in parallel samples.

A large volume of surface water from two tropical localities was thoroughly mixed and distributed among seven to eight 300-ml. bottles. The contents of identical ^{14}C ampoules were added to each bottle.

Table 1.

Surface water Banda Sea imp./min.	Surface water Flores Sea imp./min.
108	60
115	53
115	48
126	61
110	60
106	56
108	61
117	
M = 113 ± 2	M = 57 ± 2
σ (single determination) = 6.1	σ (single determination) = 4.5

After illumination at 18.000 lux for 5 hours, the contents were filtered and the activity of the plankton determined. The variation between samples is greater than the inaccuracy in measuring the activity.

In addition to the two series presented here a multitude of observations during the Expedition gave further evidence concerning the accuracy of the measurements. The 12 series made to show the light dependence of the rate of photosynthesis – see p. 101 – the 5 series made to show the dependence of the photosynthetic rate on depth – see p. 59 – the 4 series to show the influence of addition of nutrients – p. 99, all indicate that the variation between parallel samples is of the magnitude given in table 1.

All the single samples of one of the above series were portions of a large homogenous volume of water collected at the same time and stirred. If the single samples are collected in the sea separately, a conformity nearly as high would be expected at high sea, due to the plankton concentrations here being very homogeneous – HENTSCHEL 1932-1936. In coastal waters a greater variation perhaps could be expected. Some investigations were made in the coastal waters of California. Table 2 presents the results.

Table 2. The variation in the rate of photosynthesis (relative) in surface samples, each collected at intervals of a few minutes.

	St. 705	St. 707	St. 708
A	110	90	97
B	89	79	102
C	102	133	102

The variations at the Stations 705 and 708 were of the same size as when portions of a single water sample are used. The variations were somewhat higher at St. 707.

G. MEASUREMENTS OF THE LIGHT PENETRATION INTO THE SEA

During the Swedish Deep-Sea Expedition 1947-48 on the "Albatross" very important studies on the submarine light in the oceans were made, JERLOV 1951, 1953, JERLOV and KOCZY 1951. The results reported on this subject previously were few.

Light measurements were made by the Swedish expedition only when the light conditions were absolutely favourable. In order to be able to present a physically indisputable picture of the light conditions in the oceans, measurements taken when conditions are not favourable must be rejected. Nevertheless it was possible to give a survey of the transparency in various ocean areas and to discuss the features of the horizontal and vertical variations of transparency. A relatively low penetration was observed in the upwelling areas west of South America and of Africa, whereas extremely clear water was encountered in the Sargasso Sea.

During the "Galathea" Expedition measurements of the light penetration into the sea were made at all stations where ordinary measurements of organic productivity were made. It was thus not possible to restrict the measurements to days when the light conditions and other weather conditions were absolutely favourable.

The ship was not very well fitted for measurements of submarine light. In a wind, the "Galathea" quickly gathered leeway on account of the very high superstructure. As a result, routine measurements could not be made further down than about 40-50 m, and for greater depths is was necessary to extrapolate. The measurements made during the "Albatross" Expedition made it possible to make such an extrapolation adequately. It must be stressed, however, that the measurements made on the "Galathea" by no means equal the measurements made on the "Albatross" in quality.

Fig. 15. Submarine photometer.

When the weather conditions were favourable the "Galathea"-measurements gave results which were practically identical with the "Albatross"-measurements in the same water. In the Sargasso Sea the Swedish Expedition made investigations at the two stations 372 and 377 – Jerlov 1951. Blue light (465 mμ) was found at a depth of 40 m. in percentages of 36 and 35 respectively of the intensity just below the surface. At three "Galathea"-stations in the Sargasso Sea the light conditions were favourable; 760, 762, 763. Blue light of practically the same wave length was observed at a depth of 40 m. in percentages of 38, 34 and 32 respectively of the intensity just below the surface.

Measurements had to be made also during much less favourable light conditions, however. The precision is therefore not always very high. However, the light measurements were only made with the purpose of determining the vertical extension of the photosynthetic layer. As no great precision was aimed at here – cf. p. 62 – the light measurements during the "Galathea"-Expedition may be considered adequate. The lower boundary of the photosynthetic layer was put at the depth at which the light is 1 per cent. of the total quantity of blue and green light at the surface – cf. p. 61. Only this depth is presented in table 20, as it may be considered misleading to publish all the details of the measurements.

For the measurement of light intensities the "Galathea" expedition used selenium photocells of a diameter of about 40 mm. which were manufactured by Evans Electroselenium Laboratory.

For submarine measurements the photocell was fitted in a watertight metallic casing provided with a thick glass window directly over the photocell – see Fig. 15. A rubber-insulated cable was introduced through a watertight stuffing box in the bottom of the casing and connected to the terminals of the cell. The casing was provided with three arms by means of which the photometer was connected through a crowfoot with three branches to the wire for lowering it into the sea. For measurements of light intensities above the surface of the sea, i.e. on deck, a photocell was fitted in a simple wooden mount which might be placed at any point where the

illumination remained undisturbed by irrelevant factors.

The submarine photometer as well as the deck-photometer were arranged so that light filters might be fitted over the photocells. The filters used were manufactured by Chance Brothers and had the following denotations: red OR1, green OGr1, and blue OB10. In addition one or more neutral filters of the type ON31 were used.

It is recommendable to place a diffusing opal glass above all filters. This, however, is not very important for relative measurements not aiming at a high precision.

The weak photo-currents were measured by means of a sensitive moving-coil ammeter. The moving coil of this instrument is carried on pivots, and there are three measuring ranges with full scale deflections corresponding to 0.0001 amp., 0.001 amp., and 0.01 amp. respectively. For all three measuring ranges the internal resistance of the instrument is 300 ohms.

In the measurements made with the described equipment it was not possible to keep within the ranges in which the deflection varies directly with the illumination of the photocell. It was therefore necessary prior to the departure of the expedition to plot correction curves for the photocells to be used in connection with the measuring instrument. From these curves it should be possible for every deflection of the instrument to read a value which is proportional to the luminous flux incident on the photocell. It was not necessary to provide the instrument with a graduation in definite units, e.g. lux, as relative measurements only were aimed at.

The correction curves were plotted as follows: by means of an incandescent lamp, placed perpendicular to and in front of the photocell, the instrument was caused to give a deflection I_1 sufficiently small to be safely inside the range in which illumination and deflection are proportional. A neutral filter was now inserted in front of the photocell and the resulting, somewhat smaller, deflection I_2 was read. The ratio of one deflection to the other is then equal to the "filter factor" of this filter in the set-up concerned.

$$f = \frac{I_1}{I_2}$$

By increasing the illumination, while leaving the filter in front of the photocell, the instrument was again caused to give the deflection I_1. The filter was now removed, and the resulting deflection I_3 was read. The filter was again brought into position, the deflection caused to increase to I_3, whereupon removal of the filter resulted in a deflection I_4.

We now have four different deflections with the corresponding "relative illuminations", as follows:

deflection	I_2	corresponds to	illumination		I_2
–	I_1	–	–	–	I_1
–	I_3	–	–	–	$f \times I_1$
–	I_4	–	–	–	$f^2 \times I_1$

By extending and repeating this procedure, a sufficiently large number of points were determined to enable the plotting of a curve representing the relationship between instrument deflections and relative illumination. In the case of deflections above 0.0002 amp. the curve shows a considerable deviation from linearity. The different photocells of the same type which were used for the measurements showed almost identical response, so that the same correction curve could be used for all of the photocells as long as they remained intact. During the work on board one photocell suffered slight damage necessitating special corrections subsequently to the few measurements made with this photocell.

The procedure applied during the measurements at the different stations was as follows: The measurements were made as near as possible to noon, and preferably in weather characterized by light air and thin clouds.

The vessel was stopped after having been manoeuvred into such a position that the stern with the rigged boom turned towards the sun.

The submarine photometer was fitted with colour filter and a suitable neutral filter ensuring that the instrument deflections were kept within the range covered by the correction curve. The deck-photometer was provided with the same filters and placed in full daylight. The submarine photometer was weighted with a 5 kg. lead weight and fastened by means of a shackle to the wire from a small hand winch at the boom. The photometer was now lowered into the sea, and measurements were made immediately below the surface and at four to six different depths down to 40 metres. On account of the considerable leeway it was only in few cases possible to make measurements at greater depths, because the wire angle became too large and the determinations of the depth consequently too inaccurate.

The rubber-covered cable from the photometer and the cable from the deck-photometer were both connected to the instrument on deck, the arrange-

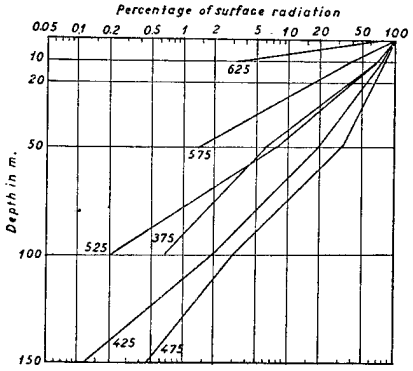


Fig. 16. Light penetration in the Sargasso Sea (After JERLOV).

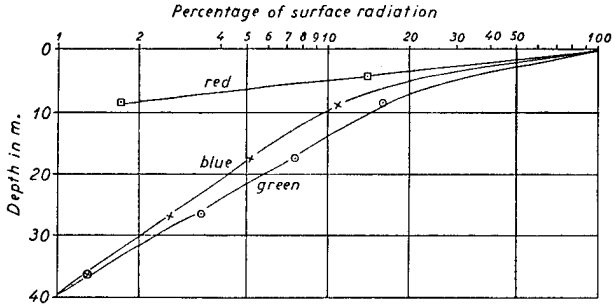


Fig. 17. Light penetration at St. 138. Benguela Current.

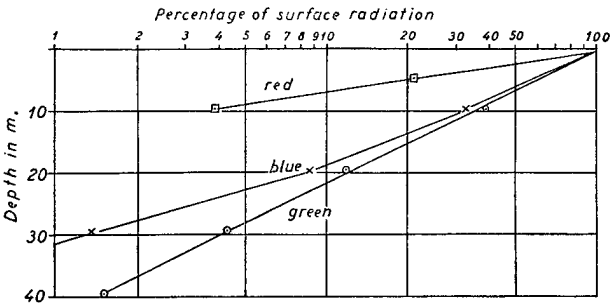


Fig. 18. Light penetration at St. 109. South Atlantic, off Angola.

ment being such as to enable a very rapid change-over of the instrument from one photometer to the other.

The following procedure was applied during the reading: at each depth the deflection produced by the deck photometer was first read and immediately afterwards the deflection produced by the submarine photometer. The readings were repeated with each of the three colour filters fitted, and this completed the actual photometric measurements.

Figures 16-18 show examples of the penetration of light into the sea in areas with different transparencies. The measurements are discussed in Part 2. With respect to the clearest water (in the Sargasso sea) Jerlov's measurements have been used, since the corresponding Galathea measurements have only been continued to a depth of 40 metres.

A consideration of the results obtained show that in very clear water blue light will penetrate farthest, while green light exhibits the greatest penetration in more turbid water. Red light proves in all cases, except one in water very rich in plankton (Walvis Bay, St. No. 139), to have a very low power of penetration compared to blue and green light.

In the calculation of the depth of the productive zone the red light has consequently been neglected at all stations of normal character. The limit of the productive zone has been defined as the depth at which the sum of the blue and the green light is equal to 1 per cent of the same sum measured at the surface of the sea.

To calculate this depth a method was used based on the direct measurements, the results of which were the following:

depth in metres	blue light, μamp		green light, μamp	
	in the sea	on deck	in the sea	on deck
a	i_{vba}	i_{dba}	i_{vga}	i_{dga}
b	i_{vbb}	i_{dbb}	i_{vgb}	i_{dgb}
c	i_{vbc}	i_{dbc}	i_{vgc}	i_{dgc}
etc.				

By means of the photocell correction curves the measured currents have been converted in to figures which denote the relative light intensities. The following table is obtained:

depth in metres	blue light		green light	
	in the sea	on deck	in the sea	on deck
a	i_{vba}	i_{dba}	i_{vga}	i_{dga}
b	i_{vbb}	i_{dbb}	i_{vgb}	i_{dgb}
c	i_{vbc}	i_{dbc}	i_{vgc}	i_{dgc}
etc.				

Now all of the measurements made in the sea are referred to the same intensity of light incident on the surface (measured on the deck).

This results in the following expressions for the relative intensities in the sea at the different depths:

depth in metres	blue light	green light
a	$I_{vba} = B_a$	$I_{vga} = G_a$
b	$I_{vbb} \times \frac{I_{dba}}{I_{dbb}} = B_b$	$I_{vgb} \times \frac{I_{dga}}{I_{dgb}} = G_b$
c	$I_{vbc} \times \frac{I_{dba}}{I_{dbc}} = B_c$	$I_{vgc} \times \frac{I_{dga}}{I_{dgc}} = G_c$
etc.		

The aim is now to determine the depth x which satisfies the following equation:

$$B_x + G_x = \frac{B_o + G_o}{100} \qquad \text{I}$$

The calculation is based on Beer's law:

$$\log \frac{I_a}{I_b} = k\,(b-a)$$

where I_a and I_b are the light intensities at the depths a and b, and k is the extinction coefficient. By substituting the intensities of blue light at the different depths, we find the extinction coefficients $k_{B(a,b)}$, $k_{B(b,c)}$, etc. In most cases these values do not differ much, and an extinction coefficient is consequently calculated by integration from the result of the uppermost measurement and that of the deepest measurement. The extinction coefficient thus found is denoted k_B. The extinction coefficient k_G for green light is calculated correspondingly.

The intensity of the green light and that of the blue light at the surface of the sea may be taken to be approximately identical. In order to find the total power of penetration of blue and green light we use a common extinction coefficient for light of these two colours which we calculate as follows:

$$k_{B+G} = \frac{k_B + k_G}{2} \qquad \text{II}$$

The result obtained by this method is not theoretically correct, and particularly when k_B and k_G differ much the result will be somewhat erroneous. For the purpose of the present measurements in which we do not aim at any very great accuracy the error is, however, negligible. The depth at which 1 per cent of the blue-green light is left can now be calculated from the following equation:

$$\log \frac{B_x + G_x}{B_o + G_o} = k_{B+G} \times x \qquad \text{III}$$

Combining this with equations I and II, we obtain

$$x = \frac{4}{k_B + k_G} \qquad \text{IV}$$

When blue and green light has been measured at the same depths a and b, we have:

$$k_B = \frac{\log \frac{B_a}{B_b}}{b-a} \quad \text{and} \quad k_G = \frac{\log \frac{G_a}{G_b}}{b-a}$$

and by substitution in equation IV we obtain

$$x = \frac{4\ (b-a)}{\log \frac{B_a \times G_a}{B_b \times G_b}} \qquad \text{V}$$

From this formula it is possible to calculate x directly from the corrected measurements. The depths a and b were determined by measuring the length of wire paid out by means of a meter wheel. At wind forces above 3 (Beaufort's scale) the leeway made by the vessel was sufficient to cause the wire angle to be considerable. In such cases the wire angle (the angle the wire rope makes with the vertical) was measured and the depth measurements corrected accordingly.

As already mentioned 40 metres was the maximum depth at which measurements of light intensities were made. However, at many of the stations the measurements of the extinction coefficients showed that the depth at which 1 per cent remains of the blue-green light considerably exceeds 40 metres. In these cases it has been necessary to extrapolate from the measurements made up to 40 m., the extinction coefficient being assumed to remain constant also at depths beyond 40 metres.

It has been shown, howewer, that this assumption is not correct. JERLOV (1951) has shown the absorption curves (in semilogarithmic representation) of clear sea water to display a break at about 40-50 metres, the extinction coefficient of the lower layers being higher than that of the upper layers.

This deviation is fairly high, and allowance was consequently made for it in the evaluation of measurements made in very clear water.

On the basis of Jerlov's measurements the following corrections have been calculated for all values of x from 60 metres and to 150 metres.

x (calculated) m.	correction %	x corrected m.
150	– 20	120
140	– 18	115
130	– 16	109
120	– 14	103
110	– 12	97
100	– 10	90
90	– 8	83
80	– 6	75
70	– 4	67
60	– 2	59

The calculation of the plankton production has been based on values of x calculated and corrected as described in the above.

H. LIMITATIONS AND PRECAUTIONS IN USING THE ^{14}C-TECHNIQUE

All methods have their limitations. Thus also the ^{14}C-method. Some important hints concerning the necessary precautions to be taken are repeated here:

(1) Because of the intermixing of photosynthesis and respiration it is only possible with reservations to make measurements if the rate of respiration equals the rate of photosynthesis. The latter rate must preferably at least be twice the rate of respiration, and the measurements are of a rather low quality even under this condition. A minimum ratio 4:1 is necessary in order to get a high accuracy. Therefore measurements by the ^{14}C-technique must be made at a high light intensity where natural phytoplankton normally shows a high ratio between the rate of photosynthesis and the rate of respiration, cf. p. 56. "In situ" measurements must be made during the day only and they must not be extended right down to the compensation depth.

(2) The measurements must be of short duration but not too short, due to a possible after-effect of light inhibition. "In situ" experiments must last only half a day, in the Tropics thus about 6 hours. At longer experimental times the quality of the measurements decreases.

With few exceptions all the water samples used in the experiments were collected in the period from about 2 hours before noon to about 2 hours after noon. At the start of the experiments with surface water we therefore must expect a more or less pronounced depression in the rate of photosynthesis. This is also seen in the experiments showing the dependence of the photosynthetic rate on the length of the experimental time. According to Fig. 6a, p. 57, the rate of photosynthesis was distinctly lower during the first hour as compared with the rate during the succeeding four hours. The experiment was started one hour after noon. It is suggested that the initial depression in the photosynthetic rate of surface samples is only of minor importance – although of some – if the duration of the experiments is four hours. The results of the experiments with surface water thus also seem to agree rather well with those in which water was used from the depth where only 10 per cent. of the surface light was found and where consequently no light inhibition was found. The slightly higher potential rate of photosynthesis often found at this depth as compared with that at the surface is primarily caused by the fact that the standing crop of phytoplankton is highest a little below the surface; cf. p. 110. Due to vertical mixing the effect of light inhibition at the very surface mostly is somewhat reduced.

(3) In laboratory experiments exceeding more than some few hours the experimental water must be stirred permanently as otherwise i.a. photo-oxidation may give trouble.

(4) When making tank experiments the temperature in the tank must be close to the temperature in the sea. Some plankton algae are sensitive to sudden changes in temperature.

(5) In waters with a relatively high content of bacteria and other heterotrophic organisms it is imperative to make control experiments in black bottles. A high ratio of the counts from the filters may under such conditions be due to dark fixation by the bacteria.

(6) The filters must be treated with fuming hydrochloric acid in order to get rid of possible inorganic carbon, e.g. in coccoliths.

(7) When measuring the organic production by placing the experimental bottles at the surface of the sea or in a tub on deck, it must be considered that the results may be very dependent on the weather conditions. In bright weather the rate of photosynthesis is lowest; cf. p 102.

I. COMPARISON BETWEEN RESULTS OBTAINED BY THE ^{14}C-TECHNIQUE AND BY OTHER TECHNIQUES. THE RATIO BETWEEN GROSS PRODUCTION AND NET PRODUCTION

STEEMANN NIELSEN 1952 compared results obtained by the carbon-14 technique with results obtained by using the ordinary light-and-dark bottle O_2-technique (Winkler titrations). The correction to be introduced in the carbon-14 technique was computed at the same time. A culture of *Scenedesmus quadricauda* was used. According to the basic composition of *Scenedesmus* cells and to the fact that in the culture solution nitrogen was added as nitrate, the oxygen method was regarded as giving a 33 per cent. greater yield than the carbon-14 method.

A multitude of experiments in which either algal cultures or natural plankton populations from Danish lakes were used have corroborated the original experiments. The same was the case in similar experiments made by RYTHER 1954, who writes, p. 134: "In general, agreement between the two techniques was extremely good. While photosynthesis values obtained by the ^{14}C method were consistently lower, they were always within 50-90 % of those obtained by light-and-dark bottle oxygen experiments." As RYTHER used a CO_2/O_2 exchange quotient of 1 and did not introduce any correction for ^{14}C-discrimination and for the intermixing of photosynthesis and respiration his experiences are in full agreement with those obtained in this laboratory.

MYERS and JOHNSTON 1949 found a CO_2/O_2 exchange quotient between 0.70 and 0.76 in photosynthesis of rapidly growing *Chlorella pyrenoidosa* with nitrate as the nitrogen source. They suggested that a value of 0.9 commonly reported from short-time manometric measurements is due to a temporarily increased carbohydrate synthesis when *Chlorella* is suddenly exposed to high light intensity.

As the basic composition of plankton algae from nature generally hardly deviates very much from that of *Scenedesmus* and *Chlorella* it seems reasonable to use a CO_2/O_2 exchange factor of 0.75 when expressing measurements obtained by the oxygen technique in equivalents of carbon.

As an example showing the extremely good agreement between the carbon-14 technique and the oxygen technique, measurements from a Danish Lake – Furesø – are presented. The rate of production is sufficiently high in this lake to produce measurements of a high quality by using the oxygen technique.

NYGAARD 1955 has presented measurements from the lake made during a whole year, 1950-1951. The gross production was 675 g. glucose per m^2 per annum. The maximum rate was 5.21 g. per m^2 per day. The ordinary oxygen technique was employed. The experimental bottles were suspended throughout the whole photosynthetic layer. During the year 1953-1954 similar measurements were made with the carbon-14 technique during all months in three localities in the Furesø. One of the localities corresponds to the locality where Nygaard had made his observations. The gross production there was 209 g. C per m^2 per annum. The maximum rate was 1.40 g. C per m^2 per day.

If Nygaard's measurements are converted to carbon and a CO_2/O_2 exchange quotient of 0.75 is used, we obtain a gross production of 204 g. C/m^2 per annum and a maximum rate of 1.56 g. C/m^2 per day. The two years were rather similar regarding weather conditions. It is, however, striking to find such an extremely good agreement.

Numerous measurements with the tracer technique in the Danish Waters and in the Arctic have in the same way shown a good agreement with previous measurements with other techniques. These will be published elsewhere.

In the present paper all production values have been given as gross production values. The main reason for converting the direct measurements obtained by the tracer technique – being intermediate between the gross and net production – into gross production instead of net production is the fact that the oxygen technique is only able to produce reliable gross production values because of the presence of animals and heterotrophic plants. It is of importance to be able to compare the results obtained by using the two different techniques.

Relying primarily on experiments with net plankton STEEMANN NIELSEN 1937 suggested that the maximum rate of photosynthesis in phytoplankton collected directly from the sea mostly is about 20 times the rate of respiration. The daily rate of respiration by the phytoplankton in the photosynthetic layer below a surface unit was on this basis put at 15 per cent. of the daily rate of photosynthesis below the same surface unit. In computing the net production for all oceans, RABINOWITCH 1945 also corrected for 15 per cent. respiration losses.

STEEMANN NIELSEN 1951 in presenting rather intensive studies on the production of organic matter in a Danish fjord discussed the matter again. It was concluded that the net production per surface unit on the average was 75 per cent. of the gross production. The same conversion was used for the oceanic production by STEEMANN NIELSEN 1952.

The present authors still believe that a rate of net production being 75 per cent. of the rate of gross production must be considered rather adequate for the oceans in general. None of the numerous experiments on the dependence of the photosynthetic rate on light intensity both made during the "Galathea" Expedition – cf. p. 101. – and in Danish and Arctic waters have been inconsistent with such a supposition. For formal reasons a slightly higher correction for the respiration losses has nevertheless been used in the present paper. If the rate of photosynthesis at optimum light intensity is 10 times the rate of respiration, the latter rate must be about 20 per cent. of the rate of photosynthesis per 24 hours at the depth where the rate of photosynthesis is highest. For the whole photosynthetic layer the rate of respiration therefore is about 40 per cent. of the rate of photosynthesis – cf. p. 89. The rate of net production per m^2 surface is thus 60 per cent. of the rate of gross production. With the exception of the winter season at high latitudes the correction for respiration losses just presented must be considered maximum.

PART II. THE MEASUREMENTS OF ORGANIC PRODUCTIVITY

A. GENERAL INFORMATION

The route of the "Galathea" around the world was from west to east. Investigations were made in all oceans. As one of the main objects of the expedition was to investigate the bottom fauna of the deep trenches found in the oceans, the route was planned so that as many of these trenches as possible could be visited. During the first part of the expedition a special task was stressed, namely to make quantitative investigations of the bottom fauna along the whole of the Atlantic coast of Africa. The range of action of the ship was somewhat limited. The size of the fuel tanks allowed only certain special ocean crossings.

The distribution of the oceanic stations at which measurements of organic productivity were made is thus far from being ideal. Important material was nevertheless gathered during the expedition. It must be kept in mind that the measurements were pioneer work.

B. THE ATLANTIC OCEAN

(The chart, fig. 19)

The Atlantic is the ocean by far best known concerning phytoplankton. In the subtropical and tropical parts of the ocean particularly the "Deutschland" Expedition and the "Meteor" Expedition have collected important material concerning the standing crop of the phytoplankton – cf. p. 50. The hydrographic conditions – including nutrient salts – in the Atlantic must be considered relatively well investigated also.

Although the "Galathea" investigations of organic productivity cover only rather limited parts of the ocean, it seems possible to give a rough, general picture of the production of organic matter in the ocean. The high correlation found between the standing crop of plankton, according to the counts made by Hentschel on the "Meteor", and the measurements of organic productivity made during the cruise of the "Galathea", makes it possible to use measurements of the standing crop for estimation of the rate of production – cf. p. 79.

An outline of the hydrographic conditions in the Atlantic is found in SVERDRUP et al. 1942. Only some scattered remarks will be given in the present work. The North Atlantic and the South Atlantic are both characterized by large circulating current systems; in the South Atlantic these run counterclockwise and in the North Atlantic clockwise. In the South Atlantic the Benguela Current is running in a northerly direction along the west coast of South Africa. It receives a material part of the water masses from subsurface layers. The upwelling of water from middle depth is of particular importance close to the shore. The mean temperature at the surface in February – the hottest month of the year – just outside the former harbour of Swakopmund (latitude 23°S) is only 17.1°C. Going further out into the current the temperature rises. It is, however, still relatively low thus showing the influence of the upwelling water.

The South Equatorial Current crosses the South Atlantic in a westerly direction just south of the Equator. A part of the current runs into the North Atlantic combining here with water masses from the North Equatorial Current. Another part – the Brazil Current – continues in a southerly direction along the coast of South America. The central part of the South Atlantic at middle latitudes constitutes a big anticyclonic counterclockwise eddy.

A similar anticyclonic eddy, the Sargasso Sea, is found in the North Atlantic. On the Northern Hemisphere, the direction is clockwise. The North Equatorial Current starts near Africa, where pronounced upwelling occurs off the coast. The current flows across the ocean and a part of it enters the Caribbean Sea; another part is the Antilles Current running just east of the West Indies. Between the North Equatorial Current and the South Equatorial Current a countercurrent running in an easterly direction is found. North of the central eddy the east-going Atlantic Current is found, a continuation of the Florida Current.

The "Galathea" Expedition started its work in the Atlantic. During October-December 1950 the ship worked along the whole of the African coast from south of Gibraltar to Cape Town. At more than 50 stations the rate of organic production was measured. The main work of the expedition during this period was to make comparative bottom inve-

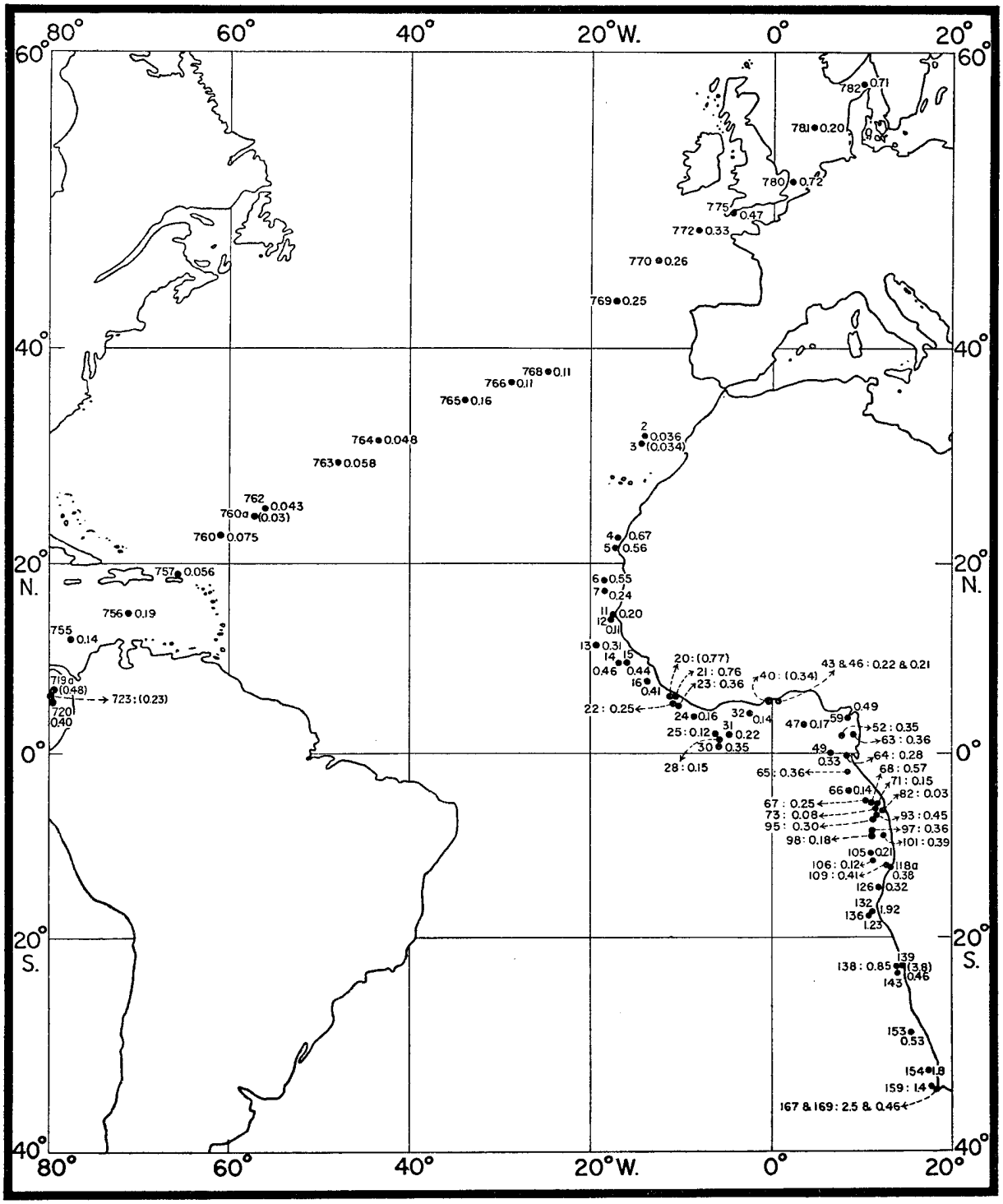


Fig. 19. Measurements in the Atlantic Ocean. Station numbers on the left, organic production (g.C per m.^{2} per day) on the right. The values are in brackets at stations where only measurements of surface water were made.

stigations near the coast. The route was therefore not specially suited for measuring oceanic productivity in the eastern part of the Atlantic. As the "Meteor" plankton counts present an excellent supplement to the productivity studies it seems nevertheless possible to give a not too bad picture of the organic production.

1. The Area off North Africa

Stations 2 and 3 north of Teneriffa represent the outskirts of the oligotrophic water found to the west but at least in autumn, reaching as far east as Teneriffa. The water was very transparent. The depth of the photosynthetic layer was more than 100 m.

The rate of production was accordingly low, about 0.04 g. C/m.²/day.

Stations 4 – 24 were situated in the eutropic area near the westcoast of North Africa. Some are found on the shelf, others over great depth until 200 miles off the shore. As may be seen clearly also from the investigations of the "Meteor" (HENTSCHEL 1933, Beilage I) the conditions for plankton production are somewhat complicated in the area in question. According to Hentschel the centre of the area with maximum concentration of plankton was found about 20°N, 20°W. The same centre was evidently found during the "Galathea" Expedition. It is rather likely however, that seasonal fluctations play at least some role. In general it may be stated that the area is very productive. This has also been stated concerning zooplankton, e.g. during the "Dana" Expedition (cf. JESPERSEN 1935, Fig. 27 and 28).

2. The Gulf of Guinea

In this gulf, Hentschel showed (cf. Fig. 20, p. 78) a characteristic quantitative distribution of the plankton. The Guinea Current (the most eastern part of the Equatorial Countercurrent) was easily recognizable as a relatively plankton-poor water mass. Less than 10.000 cells per litre in 0-50 m depth was counted here by Hentschel. To the South, the broad, so-called Congo tongue carrying relatively plankton-rich water (more than 10.000 cells per litre in 0-50 m depth) is found. It reaches far out into the middle of the ocean. The breadth of the tongue is about 5 latitudes. South of the tongue, relatively plankton-poor water approaches the coast of Africa. The tongue is comparable with the plankton-rich water just south of the Countercurrent in the eastern part of the Pacific – cf. pag. 88 – and is at least partly due to the divergence found.

The Guinea Current (Stations 24, 25, 28, 31, 32 and 47) is also recognizable as an area relatively poor in organic production. Per m.², the production varied from 0.12 to 0.22 g. C/day. At Station 30 just south of this area – i.e. in the Congo tongue – the production was 0.34 g. C/m.²/day. This station, however, has a common feature with the stations in the Guinea Current. The surface water is poor in organic production. At Station 30, the photosynthetic rate of surface water at 18.000 lux was 0.28 mg.C/m.³/hour. At the stations in the Guinea Current it varied between 0.14 and 0.26. In a water sample from a depth of 40 m., the rate at Station 30 (18.000 lux) was 1.1 mg.; at the stations in the Guinea Current in water from this depht, the corresponding rate varied between 0.39 and 0.70/m.³/hour.

In the lower part of the photosynthetic layer which extended downwards to about 70-80 m., and in the water-masses immediately below, high concentrations of phosphate were found everywhere. At a depth of 80 m. the concentration of phosphate varied between 1.0 and 1.8 μg.-atom P/L.

By the turbulence produced for example by the currents due to the internal waves – cf. p. 00 – nutrients are thus easily contributed to the photosynthetic layer. The water near the surface seems not to benefit much from this supply of nutrients however. Our knowledge about the mixing rates of the water-masses in the surface layers is unfortunately very limited. It is easy to understand however, that in areas of this kind where the mixing, for some reason or other, increases, the conditions for organic production improve too. The Congo-tongue represents according to all evidence such an area.

The stations over shallow depths in the Gulf of Guinea were characterized by a fairly moderate production rate. The highest value was found in the innermost corner at Port Victoria (0.49 g. C/m.²/day).

The coastal area outside the Gold Coast is characterized during a part of the year by upwelling water – see e.g. the chart, Beilage III, HENTSCHEL 1933 after Meyer, according to which such an upwelling is found in February. This must have a decisive influence on the production rate here at that time of the year.

3. The area outside the Congo-Estuary

The influence of the huge water-masses carried out by the Congo is distinctly to be seen far off shore both by the decrease in salinity and by the lowering of the transparency of the water – see table 4. Station 66, 210 miles off the coast and 260 miles north west of the mouth of the Congo, was thus characterized by a surface salinity of 32.59‰ and a depth of the photosynthetic layer of only 22 m. The low transparency was not due to a big standing crop of plankton. The production rate per m.²/day was only 0.14 g. C and the rate at 18.000 lux per m.³ of the surface water was only 1.23 mg. C/hour. The relatively low salinity at Stations 97 and 98 is presumably also caused by the Congo; it is hardly due to water coming from the Quanza River which de-

Table 4. Stations outside the Congo-Estuary.

Station no.	Distance in miles from mouth of the river	Salinity ‰	Depth of photosynthetic layer in m.	Production at 18.000 lux of surface water mg.C/m.³/hour	Production in the whole photosynthetic layer g.C/m.²/day
65	320	34.04	45	0.86	0.36
66	260	32.59	22	1.23	0.14
67	180	29.43	10	4.8	0.25
68	70	28.73	6	15.9	0.57
71	40	25.99	5	5.1	0.15
73	30	23.93	4	3.8	0.08
82	10	18.78	5	0.89	0.03
93	60	34.27	50	1.28	0.45
95	100	34.36	39	0.93	0.30
97	150	33.30	35	0.90	0.36
98	170	34.77	32	0.86	0.18

bouches just south of Loanda. Station 101 situated about 60 miles nearer the coast had a salinity of 35.05. If the relatively low salinity at Stations 97 and 98 should have been caused by water from the Quanza River, the influence at Station 101 should have been still more pronounced.

No investigations were made in the estuary proper. It must be supposed that the vertical turbulence here in connection with the opaqueness of the river water makes any production of organic matter by plankton algae practically impossible.

In the mixing area outside the river mouth the conditions are different. Although the water masses at least near the surface are very opaque the high degree of stabilization must prevent vertical turbulence rather effectively. Organic production is thus going on near the surface. At Station 82, where the lowest salinity – 18.78‰ S – was found, only a relatively low rate of photosynthesis was found in surface water illuminated by 18.000 lux. As the depth of the photosynthetic layer was only 5 m. the production per surface unity was extremely low – 0.03 mg. C/m.²/day. It is likely that one of the main reasons for the low potential photosynthesis of the surface water at Station 82 is the very recent formation of this water by the mixing of river water and surface sea water. Both kinds of water are poor in plankton algae. The freshwater species, if any, may further be considered unable to stand a salinity of 18‰. It takes some time for establishing a considerable plankton population. It was impossible to determine inorganic phosphates in the surface water due to the intense yellow colour. At a depth of 10 m. where the salinity was 35.50‰ S and thus showing no indication of any mixture with the river water, the phosphate concentration was 0.3 µg-atom P per litre. At stations 67,68, 71 and 73 the salinity at the surface varied between 29.43 and 23.93 ‰ S. The potential photosynthesis of surface water was relatively high. The rate at 18.000 lux varied between 3.8 and 15.9 mg.C/m.³/hour, the highest rate being found at a salinity of 28.73‰, the lowest rate on the other hand at Stations 73 at a salinity of 23.94‰. This is a further indication of the fact that it takes some time after the start of the mixing before a considerable stock of plankton algae is found. No inorganic phosphate was found at the surface at Station 73.

Due to the low transparency at all of the stations mentioned above the rate of production as measured per m.² surface is not particularly high with the exception of Station 68, where 0.57 mg. C/m.²/day was measured in spite of the photosynthetic layer being only 6 m. deep.

4. The area north of the Benguela Current proper

The rate of organic production in the area just north of the Benguela Current (North of latitude 15° S) was found to be much lower than in the Current proper. The area constitutes a natural continuation of the Benguela Current. However, no upwelling of subsurface water to the surface takes place here, at least at the time of the year – November – when "Galathea" visited the area. Stations 101-126 belong to this area. Stations 97 and 98 situated about 40 miles more to the west than St. 101 may be included too. Due to the influence of Congo-water which is distinct according to the surface salinity at both stations, they were treated jointly with the stations from the area outside the Congo-Estuary. With respect to the rate of organic production Stations 97 and 98 were in according with the other stations in the area just north of the Benguela Current. The rate varied between 0.12 and 0.41 g. C/m.²/day. The two stations with a relatively low production – Stations 105 and 106 – were situated about 50 miles from the coast over a depth of about 4000 m. The other stations were situated near the coast over a depth less than 1600 m.; Station 118 lay in the entrance to the Bay of Lobito where the depth was only 30 m.

The depth of the photosynthetic layer was fairly small at all stations – 34 – 43 m (21 m in the Bay of Lobito). The low transparency particularly at Sta-

tions 105 and 106 may seem a little astonishing considering the relatively low rate of production. No big standing crop of phytoplankton seems to have been present lowering the transparency to that extent. It must, however, be taken into account that the surface water of the area in question has its origin in more southern latitudes where a very high plankton production is going on constantly. Despite the relatively low standing crop of phytoplankton the water presumably contains much detritus and "Yellow substance" remnants from a previous very high production.

HENTSCHEL 1933 p. 90, has called attention to another similar phenomenon from the regions near the African coast. The areas here showing the highest concentration of the herbivoreous zooplankton organisms do not, according to the "Meteor" investigations, coincide absolutely with the areas where most phytoplankton was found but are displaced in the direction of the current; "so dass man versucht ist zu denken, dass eine stärkere Entwicklung des Metazoenplanktons auch räumlich auf die Hauptentwickling des Nannoplanktons folgt."

It seems perhaps reasonable therefore to assume that the rate of organic production in the area is controlled to a higher degree than normally by grazing. According to the hydrographic conditions a somewhat higher rate of photosynthesis could perhaps have been excepted. At a depth of 40 m., which is just in the lowermost part of the photosynthetic layer in the region, at least 1.7 μg-atoms P/l. (inorganic) was found at all stations. At a depth of 30 m. the concentration of inorganic phosphate varied between 0.1 and 0.4 μg-atoms P/l.

Seasonal fluctuations are presumably of importance in the present area. The hydrographic conditions indicate that even small variations may have a serious influence on the phytoplankton.

5. The Benguela Current

The Benguela Current is known to be one of the most productive areas of the oceans – cf. e.g. HENTSCHEL 1933. The current flows along the west coast of South Africa and is particularly conspicuous between the southern extremity of Africa and latitude 17° to 18°S (SVERDRUP et al., 1942, CLOWES 1950). Under the influence of the prevailing southerly and south-easterly winds, the surface water is carried away from the coast, and upwelling of water from moderate depths takes place in most seasons of the year. These hydrographic conditions

Table 5.

	Depth in m	S ‰	°C	μg-atom P/l	Production at 18.000 lux mg.C/m.³/hour
St. 138 depth of photosynthetic layer 39 m.	0	35.05	15.73	1.7	7.5
	15	35.10	12.48	2.3	0.92
	30	35.08	12.20	2.3	0.16
St. 143 depth of photosynthetic layer 37 m.	0	35.03	15.43	1.7	3.5
	15	35.01	13.73	1.7	1.1
	30	35.05	21.63	2.1	0.47

give rise to an enormously rich phytoplankton, since the upwelling water is rich in nutrient salts and establishes excellent conditions for plankton production.

According to the "Galathea"'s measurements at 9 stations (132-167), the rate of organic production varied between 0.46 and 2.5 g. C/m.²/day (in Walvis Bay 3.8 g. C). The lowest rate measured – 0.46 g. C – was found at Station 143 in the area where the highest rate of upwelling was demonstratted. Station 138 – organic production 0.85 g. C/m.²/day – was situated in the same area. In table 5 the data about hydrography and production are presented.

At both stations a high, although not extremely high, potential photosynthesis was found at the surface. A similar high potential photosynthesis was not demonstrated below the surface. At a depth of 15 m. where the light conditions must have been excellent – cp. Fig. 17, p. 65 – such a high rate could have been expected. The low temperatures at depths of 15 and 30 m. at both stations indicate very recent upwelling of water masses from medium depths. The surface temperatures of 15-16 °C., on the other hand, is an indication that some heating has occurred, and some time must have elapsed since the water just at the surface rose. Water masses in the photosynthetic zone can be too "new"; it takes some time before a considerable population of plankton algae develops in the water masses brought up to the euphotic zone from the aphotic zone below (cf. SVERDRUP and ALLEN 1939).

Fig. 17, p. 65 showing the percentage of surface radiation at the different depths at Station 138 indicates clearly that the subsurface water is much more transparent than the plankton-rich upper layer.

At Station 143 the same light conditions in the sea were found.

The position of Stations 138 and 143 is in the innermost part of the especially plankton-rich area called "die Südwestafrikanische Zunge" by HENTSCHEL 1933. This area stretches about 1000 miles out into the ocean. The richness in plankton is due to the upwelling immediately on the coast. It is therefore interesting to note that in the very place of upwelling the organic production is not particularly high. It was a pity that the time did not allow the "Galathea" to make a section out in the ocean at this latitude.

Fig. 18 from Station 109 gives a strikingly different picture. This is in accordance with the fact that the water from the subsurface is at least as plankton-rich as that from the surface; cf. Table 20, p. 125.

Another area with plankton-rich water stretching far out into the ocean was found by Hentschel near the southern limit of Africa – and called "die Kap-Zunge "by him. At two "Galathea"-stations near the coast in this area organic production was measured (Stations 154 and 167).

Per surface area, both stations had a high rate of organic production – 1.8-2.5 g. C/m.²/day. In the centre of the upwelling area outside Cape Town a third station is found – Station 159. Due to insufficient recording of the measurements at the station it is only possible to state the rate of production with some reservation.

The observations made at only 9 stations in the entire area of the Benguela Current do not allow any detailed description of the organic production. Measurements during all seasons of the year are necessary in order to present a detailed picture.

6. Walvis Bay.

Walvis Bay (latitude 23 °S.) is known as a place where an enormous fish mortality often occurs (cf. e.g. COPENHAGEN 1953). This question will be thoroughly discussed by R. Spärck in another "Galathea" Report. The fish mortality is often – although not always – described as being due to red water i.e. a mass occurence particularly of naked peridinians. When the "Galathea" dropped anchor in Walvis Bay in order to celebrate Christmas Eve December the 24th, 1950, a fish mortality had occurred some days before. Red water – or better "khaki" water as a local man said – was found in the bay.

Only the water masses near the surface could, however, be called "khaki" or red. At midnight the water at a depth of 3,5 and 6 m. was quite clear, at 2 m. nearly clear, at 1 m. rather stained and at the surface very coloured. The colour was due to huge amounts of a little naked dinoflagellate which was handed over to Professor Braarud, Oslo, who has examined the alga and described it as a new species: *Gymnodinium Galathea* Braarud (see Braarud 1957).

Some other phytoplankton species – peridinians – were present without being of quantitative importance at all, however.

Light measurements at noon showed that 1 per cent. of the total green and blue light at the surface was found at a depth of about 0.8 m. Experiments with surface water yielded a gross production of 3.8 g. C. assimilated per square metre of the surface per day. This enormously great production took place in a water layer of 0.8 m. only.

In Table 6 the hydrographic data from the anchorage in Walvis Bay are shown. The observations were made just before and after midnight.

Table 6. Hydrographic observations at the anchorage Walvis Bay. 24.12.50 (started 23 h 30'). Depth 6 metres.

Depth in metres	°C	S ‰	"O_2" ml./l.	Inorganic Phosphate µg-atom P/l.
0	19.80	35.26	0.86	> 2
1	18.03	35.14	1.44	> 2
2	17.93	35.10	2.34	> 2
3	17.03	35.07	2.94	2.3
5	16.66	35.05	2.33	2.1

The temperature at the surface was distinctly higher in the bay than just outside. At Station 138 just outside the bay thus a temperature of only 15.73°C. was found at the surface. The salinity at the surface was also higher in the bay – 35.26 S‰ here against 35.05‰ at Station 138 – indicating a rather high evaporation in the bay.

Oxygen was determined in the usual way by means of the Winkler-method The 0.86 ml./l. at the surface apparently shows a distinct undersaturation. This can hardly be correct, however, as the intense photosynthesis in the surface layer produces enormously great quantities of oxygen, establishing in all probability a definite supersaturation of oxygen.

According to the measurements of photosynthesis, more than 10 ml. O_2/litre was produced by the surface water during the day whereas less than 1 ml. O_2 must be supposed to have been used during the respiration going on from sunset to midnight when

the O_2-determinations were made. The great quantity of phytoplankton does not seem to allow the use of the Winkler-method. The present determination gives a striking example of the inexpediency of using the Winkler-method as a standard method in very eutrophic water.

In the present case it is presumed that a part of the iodine produced corresponding to the amount of free oxygen is absorbed by fatty oils in the algae. Fatty oils having double bonds will loose these in the presence of iodine. For each double bond two atoms of iodine will be absorbed.

Considerable concentrations of inorganic phosphate were found at all depths. In the surface-layer 0-2 m. the amounts are given as minimum values, as an exact determination was impossible because of the enormous amounts of plankton present. At least 2 μg-atom P/l. were present at the surface. If the ratio P: C is put at 0.02 (COOPER 1937), and the assimilation of the 3.8 g. C per square metre is assumed to have taken place in the uppermost metre (0.8 m. according to the measurements of the submarine light), presumably more than 2 μg-atom P/l. must have been taken up during the last day. At least 4 μg-atom P/l. must thus have been present on the morning of December the 24th, if no P has been added to the surface layer during the day. As the great plankton production had been going on for at least some days already, constantly using phosphate, a considerable quantity of this salt must be available in the bay.

Rivers from land will only sporadically convey considerable water masses to the bay. At the moment of the investigation this had not happened for a very long time. The sewage from the settlement in Walvis Bay is insignificant and cannot provide any phosphate enrichment of real importance in the bay.

From the bottom sediments amounts of phosphate are undoubtedly conveyed to the free water masses just as in similar localities. Due to bacteria, phosphate is regenerated from organic compounds in the bottom sediment. Such a contribution of phosphate cannot, however, without specifications, be the real source for the surface layer, since in this case a significant increase in phosphate from the surface where the algae are found exclusively, to the bottom should have occured. If anything, the opposite is observed. It is, however, possible that large quantities of phosphate are produced only at very shallow depths, thus affecting only the very surface water.

The water from the depth in the eastern part of the South Atlantic has a phosphate content of about 3 μg-atom P/l. at the most (see THOMSEN 1937). During the cruise of the "Galathea", a phosphate content above 1.7 μg-atom P/l. at the surface was not observed. The red water in Walvis Bay can decidedly not have been due only to deep water being brought to the surface in the Benguela Current outside the bay. Such water would only have had phosphate enough for one or two days at the most when the uptake of P is about 2 μg-atom P/l. per day. As more than 2 μg-atom P/l. was "left" at the moment of investigation another explanation for the red water in the bay must be looked for.

A possible explanation besides that offered above seems to be phosphate supply through the guano given off by birds. During our visit, enormous swarms of sea birds were seen over the bay. It must be assumed that they had been fishing outside the bay at the rich fishing grounds there and were on their way back to their nests. December falls during the nesting time of the sea birds of this region. It is therefore explained at the same time why the red water in Walvis Bay always seems to occur at this time of the year.

The tide being about one metre in Walvis Bay will daily wash a considerable amount of guano from the beach at the places where the birds have their nests, thus presumably giving rise to a considerable concentrations of nitrate and phosphate in the surface water of the bay.

In calm weather as during the visit of the "Galathea" to Walvis Bay the population of the *Gymnodinium* is found only just at the surface down to about 1 m. If this alga produces a poison responsible for the fish mortality, this poison should thus be found only near the surface. During rough weather the wind will effect mixing of all water layers in the shallow bay however and thus give rise to a poisoning of all water masses in the bay. It may possible be assumed that such a mixing of the water masses is necessary in order to effect a real mass mortality of fishes. It is difficult by using the hydrographical material obtained during the stay of the "Galathea" in Walvis Bay to determine when the last vertical mixing of the water masses, if any, had occurred.

7. The Section across the North Atlantic Ocean.

Fig. 19 shows also the rates of organic production on the section from Panama to the English Channel. The section was run during May and June 1952. The first two stations – 755 and 756 – are situated in the

southern part of the Caribbean Sea; Stations 757 and 760 in the Antilles Current, which is a westward continuation of the North Equatorial Current. Stations 762-764 are in the Sargasso Sea; Stations 765-772 in the North Atlantic Current, the last of the stations mentioned being situated on the continental slope. Station 775 lies at the mouth of the English Channel.

As may be seen e.g. from the excellent survey given by SVERDRUP *et al.* 1942, the surface water in the Caribbean Sea has its main origin in the North Equatorial Current, which at its western end carries fairly "old" surface water.[1] The main eddies in the Caribbean Sea affecting vertical mixing of the water masses are situated more to the north. In the southern part of this region oceanic productivity may therefore be expected to be of normal size. The rate was 0.14-0.19 g. C. per square metre per day.

The production of organic matter in the Antilles Current is poor, being only 0.056-0.075 g. C, which is in accord with the rather old "age" of the surface water.

About the lowest oceanic productivity anywhere found by the "Galathea" – 0.043-0.058 g. C per square metre per day – occurred in the Sargasso Sea. In this big anticyclonic eddy in mid-Atlantic the surface water is "old", and the same water circulates here for a fairly long time. The surface water of the eddy receives contributions from the sides, partly from the western end of the North Equatorial Current (carrying "old" surface water) and partly from the uppermost layers of the Gulf Stream. Owing to the anticyclonic nature of the eddy, which is situated in the northern hemisphere, there is a tendency for the surface water to descend near the centre (see fig. 7 – BÖHNECKE et al., 1930). This effect is to be seen in the distribution of the nutrient salts below the photosynthetic zone. Concentrations above 0.4 μg-atoms P per litre are first found several hundred metres below this zone, which in the Sargasso Sea reaches down to about 120 m. (see Table 12, p. 94 and "Dana" Stations 3540-3544 – THOMSEN, 1937). Thus only quite minimal amounts of the nutrient salts are conveyed to this zone by mixing with water from below the photosynthetic zone.

It is therefore readily understandable that the rate of organic production in the Sargasso Sea is low. This sea has long been regarded as a poor region, and the blue water there has been described as an oceanic desert. KALLE 1939 has shown that the content of suspended particles, according to the Tyndall effect in water samples, is exceedingly low in the surface water of the Sargasso Sea indicating a very low content of plankton algae such as shown by LOHMANN 1920 and HENTSCHEL 1933 by the use of a centrifuge. The paucity of the plant production is reflected also in the rate of animal production. The smallest volume of oceanic zooplankton reported by the Danish "Dana" Expedition round the world was found in the Sargasso Sea (see JESPERSEN, 1935). (The findings of Riley, who believes the Sargasso Sea to be a productive area, are discussed by STEEMANN NIELSEN 1954, 1955).

Stations 765-768, in the North Atlantic Current, represent a region of typically subtropical oceanic surface water of medium "age". The rate of organic production varied between 0.11 and 0.16 g. C per square metre per day. In the northwestern part of the Sargasso Sea near the border of the Gulf Stream similar conditions are possibly found during a part of the year due to seasonal fluctuations in the admixture of Gulf Stream water to the area. As one approaches the European continent, organic productivity increases – probably due to the activity of the eddies found here. At Station 772 the production rate was 0.33 g. C per day.

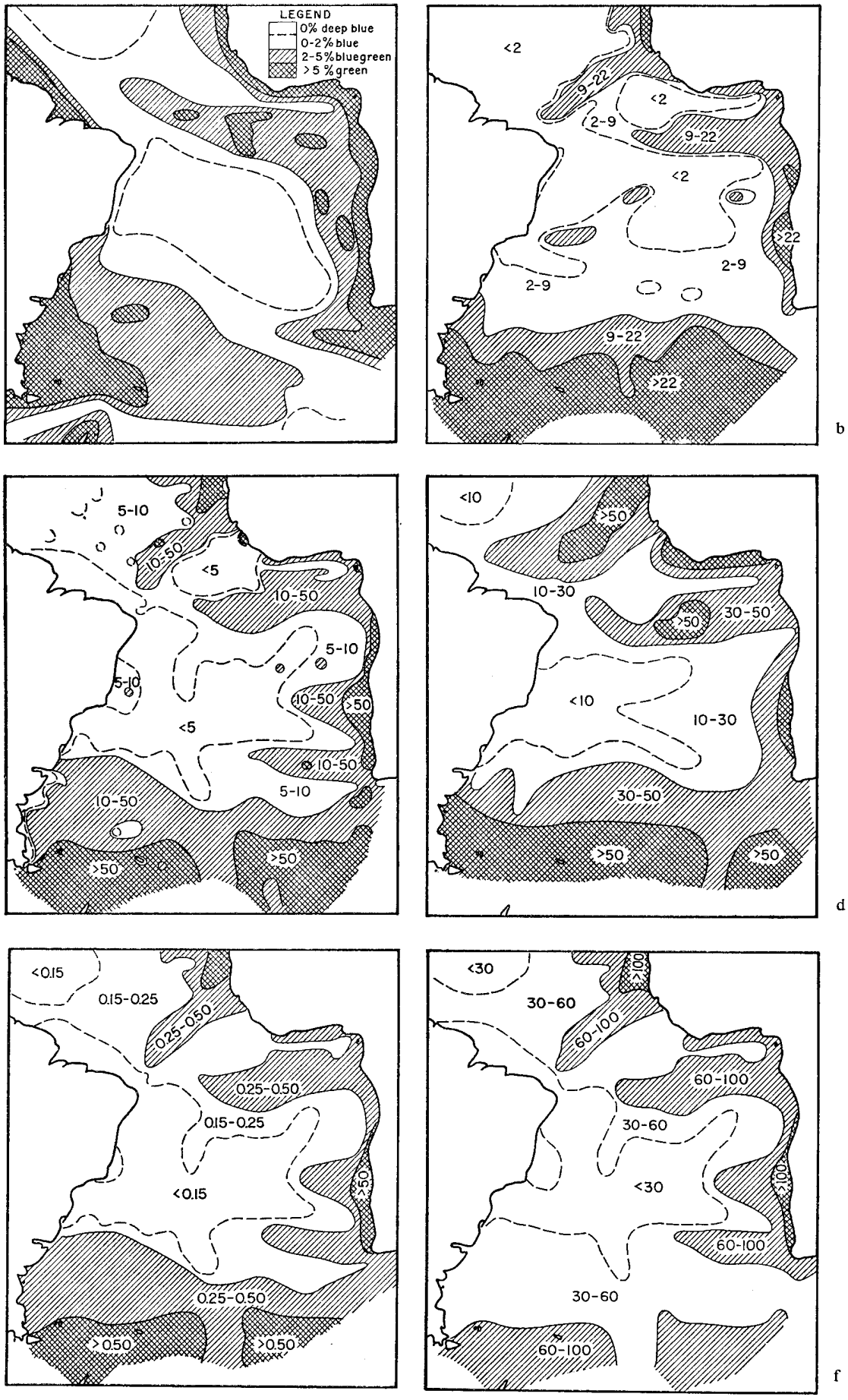
Finally, a productivity of 0.47 g. C per square metre par day was found at Station 775, in the mouth of the English Channel. If production occurs here at this rate throughout the months of March to June, the result will be a productivity of the same order of magnitude as was estimated by the Plymouth Laboratory from the decrease of phosphate from spring to summer (ATKINS, 1923).

The "Galathea" continued to make observations in the English Channel and in the North Sea – cf. table 20. These observations will be discussed in another publication in connection with observations from later Danish cruises.

8. A survey of the Atlantic Ocean

The Atlantic Ocean is the most thoroughly investigated ocean in all respects. Because of the "Meteor"-Expedition the South Atlantic is particularly well known concerning the quantitative distribution of plankton. As the "Galathea" measurements on organic production are too few to permit the construction of a survey chart dealing with a whole ocean, the "Meteor" counts have been used as a supplement for designing such a chart. The very

1. The "age" of surface water is explained on p. 89.


LEGEND
0% deep blue
0-2% blue
2-5% bluegreen
>5 % green
a
<2
9-22
2-9
>22
b
5-10
10-50
<5
>50
c
<10
10-30
30-50
d
<0.15
0.15-0.25
0.25-0.50
>0.50
e
<30
30-60
60-100
>100
f

← Fig. 20. A series of charts of the South Atlantic Ocean. a, distribution of colour of the sea (after SCHOTT); b, distribution of phosphate in mg per m.^{3} in the upper 50 m. layer; c, distribution of plankton organisms, thousands per litre, in the upper 50 m. layer (after HENTSCHEL and WATTENBERG 1930); d, distribution of zooplankton (metazoa), numbers per 4 litre in the upper 50 m. layer (after HENTSCHEL 1933); e, distribution of organic gross production in summer (g. C per m.^{2} per day; f, distribution of annual net production (g. C per m^2).

high correlation found between the standing crop of plankton algae and the production of organic matter – as will be shown in Part 3, – makes such a combination of data of different origin not only possible but quite obvious.

In Fig. 20 e a chart of the South Atlantic is presented showing the rates of organic gross production per day and per m^2 of the surface in the different areas. Whereas the rates presented for the tropical and subtropical parts of the ocean must be considered more or less representative for the whole year, this is not so for the areas outside the Tropics and Subtropics. The rate given for the areas south of Latitude about 35°S correspond only to the conditions during the middle of summer, when the maximum production is going on in these waters. For the whole year, the average rate of production is presumably only about $^1/_3$ of the rates found during the height of summer. Certainly the rate of annual organic production in the Atlantic Ocean is considerable, but not nearly as high as would appear by taking only the summer conditions into account.

In Fig. 20 f a chart of the South Atlantic is presented showing the annual net production per m^2 of the surface in the different areas. Although many assumptions are necessary in order to estimate the annual rates outside the Tropics and Subtropics, the chart most likely may be considered satisfactory as a first approximation. In principle all other oceans are supposed to resemble the South Atlantic Ocean.

According to Fig. 20, b and c, we find an extraordinarily high correlation between the standing crop of plankton and the concentration of phosphate near the surface. The latter may on the other hand easily be correlated with the general hydrographic conditions. High concentrations of phosphate near the surface are only found in areas where a considerable addition of subsurface water to the surface takes place. The central part of the ocean – the big anticyclonic eddy – is on the other hand characterized by a downward movement of the surface water. Very little inorganic phosphate is therefore here at the disposal of the plankton algae, the concentration of which consequently is low.

The charts presented in Fig. 20 are discussed in detail in Part III.

C. THE INDIAN OCEAN

(The charts, Fig. 21 and Fig. 26)

Previous investigations of importance for evaluating the productivity of the Indian Ocean have been made particularly by the "Dana" Expedition 1928-1930, the "John Murray" Expedition 1933-34, the "Swedish Deep-Sea Expedtion" 1947-48 and the "Discovery" Expedition 1934. GILSON 1937 has used the nitrate determinations from the "John Murray" Expedition for estimating the production of organic matter in the Indian Ocean. He arrived at a production rate of 14.4 g./m.^{2}/day (wet weight of algae). It is, however, hardly realistic to use the method employed by this author for estimating organic productivity. The value will not be considered in the present treatise.

The main lines of the hydrography of the Indian Ocean may be found in SVERDRUP *et al.* 1942. In general terms they may be sketched as follows. During all seasons there is found a typical South Equatorial current starting at Australia and flowing across the Ocean south of the Equator. On reaching Africa, a part of it turns south and follows the African coast. The most southerly continuation is called the Agulhas Current. In the southernmost part of the Ocean a current starts south of Africa and is going in an easterly direction towards Australia. In the center of the currents metioned is found an anticyclonic eddy, similar to the eddy found, e. g., in the South Atlantic.

North of the Equator is found in parts of the year the westgoing North Equatorial Current; this, however, is neutralized when the South West Monsoon is blowing, or is substituted by an eastgoing current. Between the North Equatorial Current and the South Equatorial Current a Counter Current is found. The southern boundary of this current is found between 9°S and 5°S. Off the African coast the northern boundary is situated at about 4°S. "The Swedish Deep-Sea Expedition" made special investigations regarding the Equatorial Currents and the Counter Current in the Indian Ocean (JERLOV 1953).

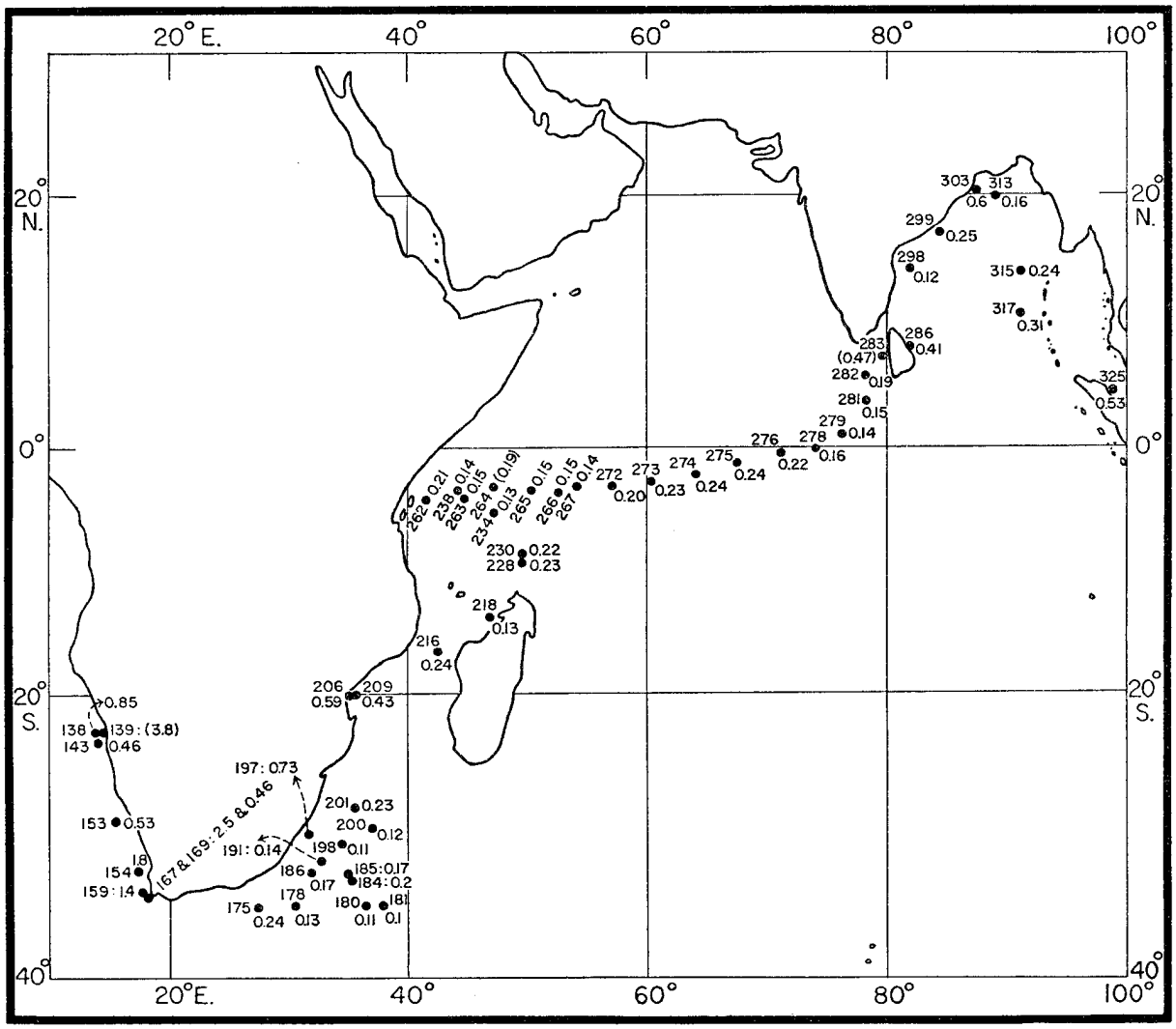


Fig. 21. Measurements in the Indian Ocean. Station numbers on the left, organic production (g. C per m.^{2} per day) on the right. The values are in brackets at the stations where only measurements of surface water were made.

1. The western part of the ocean

According to the investigations of the "Discovery" in the western part of the ocean, the distribution of phosphate in a very instructive longitudinal section in the Indian Ocean is given – Fig. 22 after CLOWES 1938. The values are corrected for salt error according to COOPER 1937. In lower latitudes only a shallow surface layer poor in inorganic phosphate is found. In middle latitudes – 20°-35°S – this surface layer poor in nutrients is vertically extended. Whereas in the lower latitudes water rich in nutrients is found in the lower part of the photosynthetic zone giving rise to an important photosynthetic capacity here, in middle latitudes nutrient rich water is first found well below the lower boundery of the photosynthetic zone. The "Dana" investigations covering both nitrate and phosphate, and the phosphate observations made during the "Galathea" Expedition, confirm the "Discovery" investigations fully (cf. THOMSEN 1937 and fig. 24 and fig. 25). In identical subsurface water the P observations by the "Dana" and the "Discovery" are fairly identical. The P values given by the "Discovery" in the most P-rich intermediate water are about 10 per cent. lower than

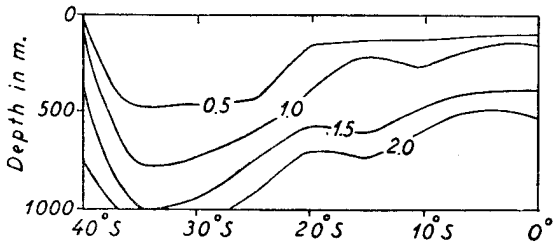


Fig. 22. The distribution of phosphate (μg-atom P/l) in a longitudinal section in the western part of the Indian Ocean (after CLOWES 1938).

those presented by the "Dana". No investigations on the distributions of nutrient salts and plankton have been made in the central part of the Indian Ocean at middle latitudes. The big anticyclonic eddy situated here must be supposed to resemble the similar eddy in the South Atlantic in respect to the vertical distribution of the nutrient salts. Due to the descending of surface water in these anticyclonic eddies nutrient rich water is first met far below the lower boundery of the photosynthetic zone – cf. p. 77.

It is thus to be expected that a section out from Africa at middle latitudes should show the smallest rate of production to the east. The "Galathea" section along latitude 35°S – Stations 175, 178, 180, 181, illustrates this clearly. The production rate at Stations 181 – the most easterly station – was 0.097 g. C/m.²/day. It was the lowest value found in the Indian Ocean by the "Galathea", although it is nearly the double of the values found in the centre of the corresponding eddy in the North Atlantic. Station 181 is, however, only situated near the boundary of the eddy.

All the "Galathea" stations at middle latitudes in western part of the Indian Ocean outside the continental shelf were characterized by a production rate between 0.1 and 0.2 g. C/m.²/day, the value normally found in tropical and subtropical oceanic regions in abscence of any pronounced admixture of nutrient-rich water from below.

On the shelf itself, a pronounced ascent towards the surface of relatively nutrient-rich water from middle depth is found without, however, giving rise to any real upwelling of water to the very surface. The surface temperature was high everywhere. Station 197 off the coast of Natal gives a typical example. As on the "Galathea" only hydrographic observations were made in the photosynthetic zone, the Fig. 23 will be presented instead. It shows the distribution of P-PO_4 in a section off Africa at about latitude 28°S. The two stations located over the shelf are "Dana"-stations from January. The most eastern station is from the "Discovery" section (April) presented in Fig. 22. The ascent of subsurface water over the shelf is very significant. It is, however, not as considerable as in the Equatorial region of the Indian Ocean where, at least in the divergences, 1 µg-atom P is met with in a depth of 40-100 m. – cf. Fig. 22. Near the coast in the latitudinal section at 28°S, 1 µg-atom P/1. was found between 400 and 500 m.

The lower boundary of the photosynthetic layer was at a depth of 30 m. at Station "Galathea" 197.

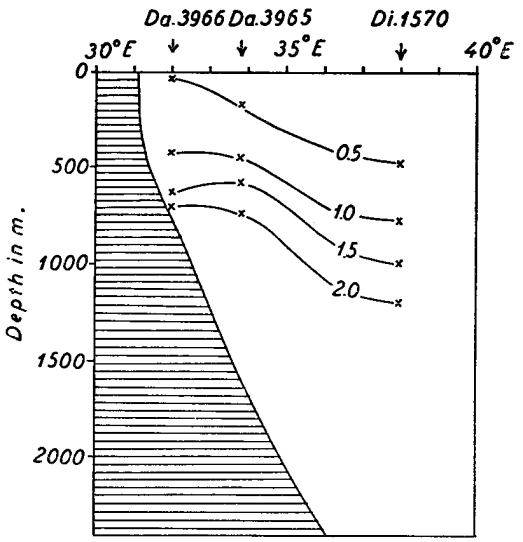


Fig. 23. The distribution of phosphate (µg-atom P/1) in a section off Africa at about latitude 28°S.

Nutrient-rich water is thus conveyed into the photosynthetic layer – as also distinctly seen from the measurements at Station 197 – cf. Table 20. The high rate of photosynthesis in the surface water – 5.0 mg. C/m.³/hour at 18.000 lux – shows that considerable amounts of the nutrients must be supplied rather constantly to all water masses in the photosynthetic layer. However, only small amounts of the nutrients are found at the very surface. 10 degrees more to the north at 20°S, similar conditions for the production of organic matter are found on the shelf-Stations 206 and 209. The rates were 0.59 and 0.43 g. C/m.²/day respectively.

On the Agulhas Bank at the southern limit of the continent, a really considerable admixture of nutrient rich subsurface water to the surface was shown. Nitrate was found in concentrations up to 25 µg N-NO_3/1 at the surface – "Dana" Station 3972. The strength of the south-going Agulhas Current, the continuation of the South Equatorial Current, has apparently the effect that the ascent of deeper water masses already takes place above rather considerable depth. Thus at the "Dana" Station 3971 at 35°49'S, 23°09'E, where the depth was 1980 m 5 µg-atom N-NO_3/1 and 0.3 µg-atom P/1 was found at a depth of 75 m. At the "Galathea" Station 175 situated more to the east and over a depth of 4500 m., a distinct ascent of nutrient rich water into the photosynthetic layer was observed. The lower boundary of this layer was found at a depth of 81 m.; 1.7 µg-atom P/1 was measured at a depth of 75 m. Water from 80 m. had a photosynthetic rate of 0.88 C/m.³/hour when illuminated by

18.000 lux. This is a rather high value, $3^1/_2$ times as high as the corresponding rate of the surface water, which was of the same size as found elsewhere east of Africa at these latitudes.

2. The Equatorial part of the ocean

Rather intensive investigations of organic productivity were made by the "Galathea" in the Equatorial part of the Indian Ocean. First of all a section from Mombasa to Ceylon was made. A preliminary survey of this section was already published during the expedition – STEEMANN NIELSEN 1952. As already pointed out in the text of the article mentioned, the values given in the accompanying Fig. were about 30 per cent. too low owing to an exchange of the special Geiger-tubes used.

As shown by JERLOV 1953, the hydrographic conditions are complicated in the region in question. The vertical inhomogenity of the photosynthetic layer contributes further to complicate the measurements of organic productivity. Whereas the photosynthetic rate if, measured at 18.000 lux, mostly is rather uniform throughout the whole of the photosynthetic layer in the tropical and subtropical parts of the ocean, this is not quite true in the area in question. Photosynthetic rates up to 3 times the rate of surface samples at the same light intensity are often met with. Nutrient-rich water is found in the lower part of the photosynthetic layer, which in the area in question may have a vertical extension down to about 90 metres. The distribution of inorganic P and $N\text{-}NO_3$ at the 4 sections across het equatorial currents – Fig. 24 and Fig. 25 – shows this clearly.

The depth of the photosynthetic layer e.g. at Station 276 was 92 metres. The rates at 18.000 lux of water samples from 0, 40 and 80 metres were 0.24, 0.60 and 0.52 mg. C/m.^{3}/day respectively. The influence of the nutrients at the lower depths is obvious. In areas of the present kind it is preferable to take samples from more depths than three if a high accuracy is aimed at. It must further be expected that the extrapolations for the whole photosynthetic layer of the light measurements, which on the "Galathea" were made only down to 40 m. must be considered as being rather inexact in the area in question. The light measurements made during the "Swedish Deep-Sea" Expedition – cf. JERLOV 1951 – shows that in the area in question ("Albatross" Stations 201, 206, 227) the transmission of light is definitely decreased below a depth of about 30 m. (Fig. 23 of the paper mentioned). The vertical extension of the photosynthetic layer is therefore presumably estimated a little too high, hardly, however, more than 10 per cent. No attempts at making any corrections have been made. The accuracy when using the tank-method is less in this sort of water than normally. The order of magnitude of the determination, the really important matter during a pioneer work like the present, is of course not influenced.

The direction of the section of the "Galathea" across the Indian Ocean is not very suitable for in-

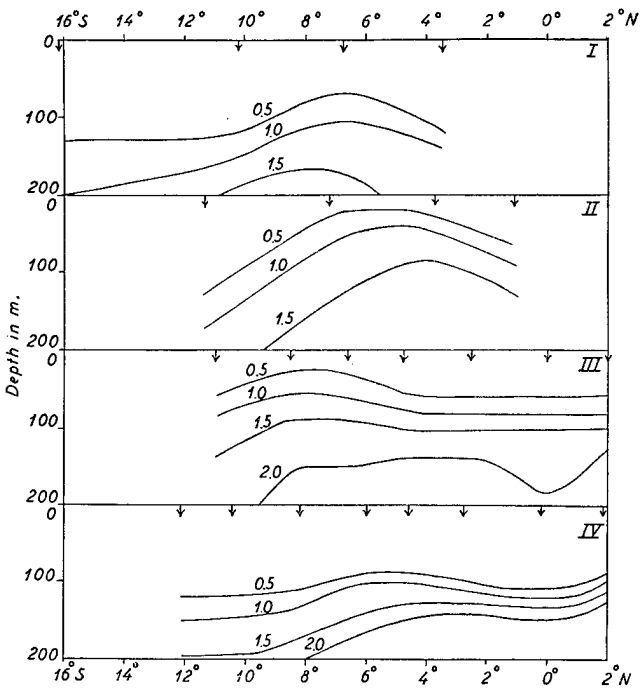


Fig. 24. The distribution of phosphate (μg-atom P/l) in four sections across the Equator (Indian Ocean). Section I at about longitude 40°-45°E. (Dana), Section II at longitude 50°-60°E. (Dana). Section III near 88°E. (Swedish Deep-Sea Expedition), Section IV near latitude 95°E. (Dana).

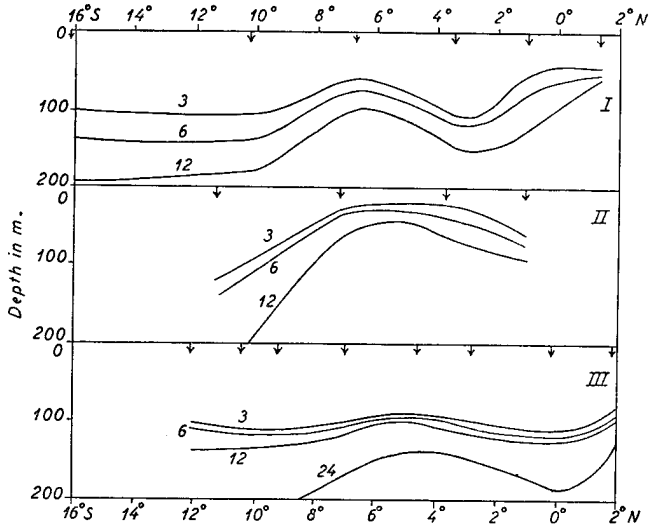


Fig. 25. The distribution of nitrate (μg-atom N/l) in three sections across the Equator (Indian Ocean). Section I at about latitude 40°-45°E., Section II at latitude 50°-60°E., Section IV near latitude 95°E.(Dana).

vestigating the details concerning the influence of the hydrographic conditions. The lack of data from depths below the photosynthetic layer must also be mentioned.

4 sections across the equatorial currents in the Indian Ocean are presented instead showing the vertical distribution of $P\text{-}PO_4$ and $N\text{-}NO_3$ in the upper water layers – see Fig. 24 and Fig. 25. Section I near Africa follows longitude about 40°-45°E. It is drawn according to the observations of the "Dana" – Dec.-Jan. 1929/1930. The nitrate data from the most northern part of the section not visited by the "Dana" are, however, taken from the "John Murray" Expedition, Dec. 1933 – GILSON 1937. The same method for determining nitrate was used on both expeditions. At some stations more to the east covered by both expeditions the results were conformant.

Section II is made according to the "Dana" observations between 50°E and 60°E. This section could not be extended to the north using data from the "John Murray" expedition. The nearest station was more than 8 latitudes more to the north than the most northern "Dana" station. 2 stations taken during the first mentioned expedition were situated in the middle part of the "Dana" section – about lat. 2°-3°S.

Section III near 88°E is from the "Swedish Deep-Sea" Expedition, JERLOV 1953 b. Only phosphate determinations were made. Section IV near 95°E originates from the "Dana".

The "Discovery" longitudinal section from the western part of the Indian Ocean presented in Fig. 22 crosses the Equator between Section I and Section II. In principle it is very similar to the other sections.

The shape of the isolines both for phosphate and nitrate shows for all sections at least one distinct divergence, where phosphate – and nitrate-rich water is found relatively near the surface. In Section 1 a divergence was found at about 7°S. 1 μg-atom $P\text{-}PO_4$ and 12 μg-atom $N\text{-}NO_3$ per liter were determined in the water from a depth of about 100 m. Another divergence was demonstrated at about 2°N according to the nitrate observations. No phosphate data are available from the northern part of the section. The southern divergence is found near the boundary of the South Equatorial Current and the Counter Current. The northern divergence must represent the northern boundary of the Counter Current. At about 3°S a convergence was demonstrated, 1 μg-atom $P\text{-}PO_4$ and 12 μg-atom $N\text{-}NO_3$ being found in a depth of about 150 m. Although the isolines for N and P are found at a somewhat greater depth in the convergence compared with the conditions in the divergences, they are nevertheless localized at a definitely higher level than, e. g., in the southern part of the South Equatorial Current. At 16°S the 1 μg-atom P/l. isoline was found at a depth of 200 m.

In section II only a southern divergence at about 5°S could be demonstrated. No observations were available in the area where a northern divergence could be expected. The descending of the isolines north of latitude 4°S indicates presumably the existence of a convergence just south of the Equator. 1 μg-atom P/l. and 12 μg-atom N/l was found at a depth of 40 m. in the centre of the divergence.

In Section 3 according to Jerlov 1953 one divergence is found near 8°S. Another should be found near the Equator and a convergence should be located at 4°S. According to the phosphate observations only the southern divergence is conspicuous. 1 μg-atom $P\text{-}PO_4$/l. was here found at a depth of 60 m.

In Section 4 a southern divergence is found at about 5°S. Another is found about 2°N with a very inconspicuous convergence lying between. In the divergences the isolines for 1 μg-atom $P\text{-}PO_4$/l. and 12 μg-atom $N\text{-}NO_3$/l. were found at a depth of 100 m.

From the 4 Sections showing the distribution of phosphate and nitrate it is obvious that nutrient-rich water is found rather near to the surface in the whole of the equatorial region of the Indian Ocean. This is true not only in the divergences but also in the convergences. In the central part of the ocean – see Sections 2 and 3 – this water is approaching nearest to the surface. The lower part of the photosynthetic layer must be supposed to provide good conditions for the plankton algae with respect to nutrients. The upper part of the photosynthetic layer may also profit by this nutrient-rich water just below. It must, however, be mentioned that a very high temperature gradient is found. In the centre of the divergence found in Section 2, the surface temperature was 8°C higher than that at a depth of 50 m.

The stations on the "Galathea" Section from Mombasa to Ceylon show a pronounced maximum of production between 57°E and 72°E. The reason for the smaller rate of production west of this region – Station 262 over the shelf is an exception of course – is apparently found in the decisively less ascent towards the surface of water rich in nutrient salts in the most western part of the ocean, as shown in section 1, Fig. 22 and Fig. 23. At Stations 228 and 230 in the South Equatorial Current just south of the divergence a relatively high production rate – 0.22-0.23 g. C/m.²/day was found.

The four stations from the most easterly part of the Mombasa-Ceylon Section – 278-282 – are situated in the North Equatorial Current. Nutrient-rich water is still found rather near the surface. The 0.5 μg-atom P curve is found at a depth of about 50 m., a little higher up than in the Counter Current – cf. Sections 2 and 3, Fig. 24. The rates of production found were, however, a little lower than the rates in the Counter Current. Station 283 at the coast of Ceylon – depth 820 m. – had a production rate of 0.47 g. C/m.²/day. As always in the Tropics, the production rate over the shelf increases.

According to SCHOTT, 1935, the Counter Current bends south at about 100°E and follows the coast of Java, its southern boundary not crossing 10°S until at 115°S. The "Galathea" Stations 466, 472, 475 were located here (fig. 26). At Stations 472 and 475 the rate of production was very high, 0.70 and 0.59 g. C/m.²/day. Such high values were not found elsewhere in the tropical currents of the Indian Ocean. The photosynthethic layer was shallow, 34 and 40 m. respectively. Relatively cold water was found rather near the surface – cf. table 20, p. 125 –. The temperature was 23.4°C at a depth of 30 m. at Station 472. Thus an important conveyance of surface water into the productive zone explains the high rate of production. The topography of the bottom is presumably the most important factor causing the ascent of deeper water layers in this area. The depth at the two stations mentioned was about 2500 m. At Station 466, which was located 4 degrees further to the west, the depth was more than 7000 m. The rate of productivity was here only 0.17 g. C/m.²/day. The lower boundary of the photosynthetic layer was, however, at a depth of 59 m, indicating that productive water was found not far away. The extension of this layer was reaching much deeper at the tropical stations in the western part of the Indian Ocean.

Summarizing all of the "Galathea" measurements in the equatorial current systems of the Indian Ocean, it seems reasonable to state that the rate of production is moderately high in the whole region. Only in locally very restricted areas was a very high production rate found.

3. The Bay of Bengal

The Bay of Bengal is a proper part of the Indian Ocean. Through supply of freshwater, the salinity is relatively low – about 33-34‰ at the surface. 4 stations were taken by the "Galathea" outside the shelf in this area. The production was on the avarerage 0.19 g. C/m.²/day (0.12-0.24), a little more than usually found in tropical oceanic water.

Subsurface water rich in nutrients was found rather near to the surface at the two most northern stations. 3 μg atom P/l. was thus found at a depth of 80 m. at Station 299, and at a depth of 40 m. the concentration was 1.3 μg-atom P/l. The thickness of the photosynthetic layer was only 45-66 m. at the two western stations. At the two stations in the eastern part of the bay the lower boundary of the photosynthetic layer was at 84 and 99 m. respectively. Organic and inorganic material conveyed by the Ganges is presumably the reason for the relatively low transparency of the water in the western part of the Bay. The low transparency decreases the rate of photosynthesis as measured per surface area.

The three stations located on the shelf – 286, 303,

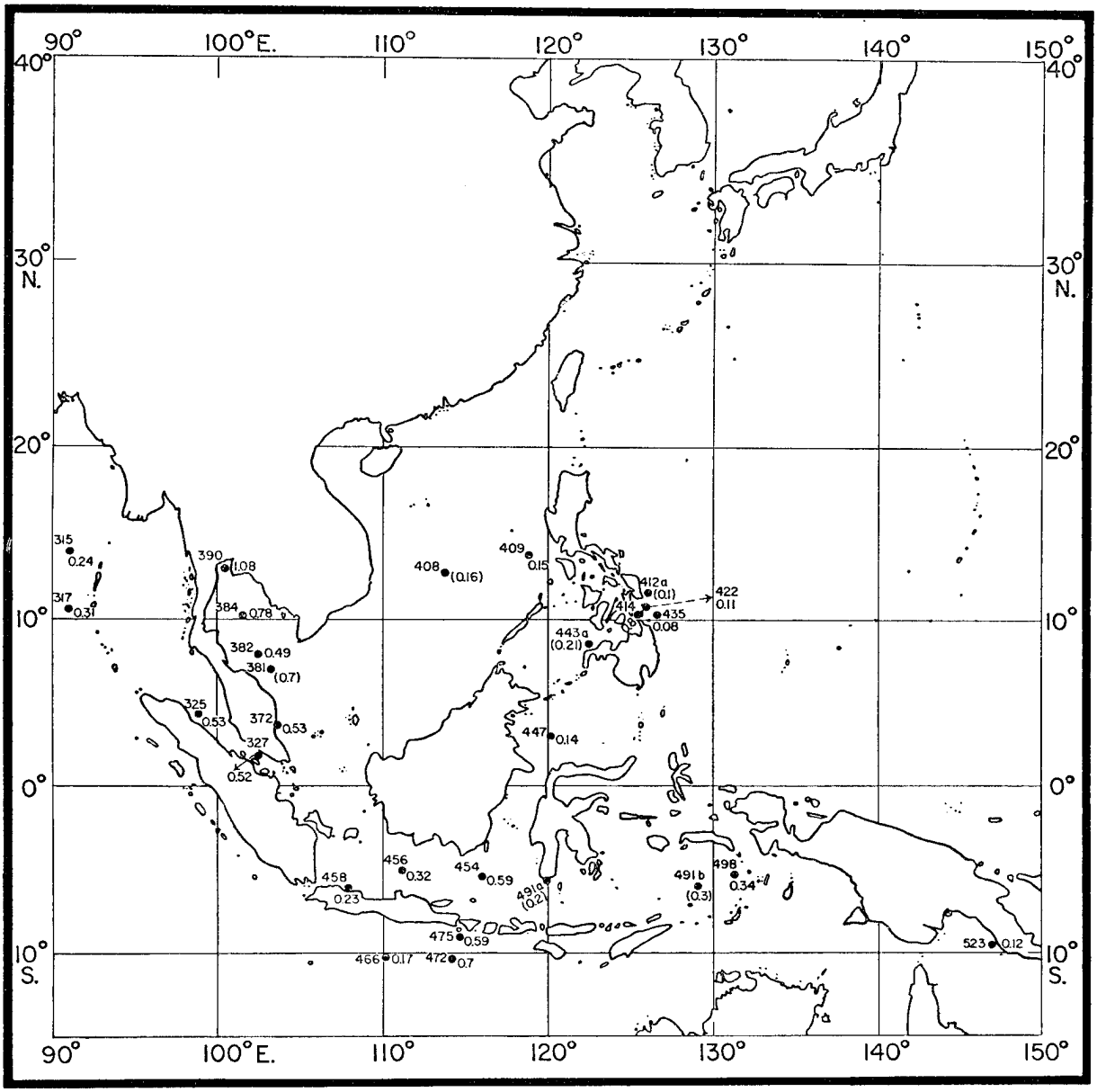


Fig. 26. Measurements in the Indo-Malayan Waters. Station numbers on the left, organic production (g.C per m.^{2} per day) on the right. The values are in brackets at stations where only measurements of surface water were made.

315 – were all characterized by a high rate of production.

We may assume that the Monsoon shift has some influence on the rate of production in the Bay of Bengal. Extensive investigations during the different seasons are necessary in order to give a true picture of the production of organic matter.

4. The Indo-Malayan Waters

(The chart, Fig. 26)

Measurements of the rate of production in this huge area were made at altogether 13 complete stations and in addition at 4 surface stations. It is therefore possible only to give a very rough sketch of the conditions. The measurements were, however, rather instructive. Two of the three complete stations located over great depth – Station 409 in the northern part of the East China Sea and Station 447 in the Celebes Sea, resemble in all respects normal stations in the open oceans. The rate of production was 0.15 and 0.14 g. C/m.^{2}/day respectively. The depth of the photosynthetic layer was 98 and 90 m. respectively. Really nutrient-rich water was not found in the lower part of the photosynthetic zone. At a depth of 100 m. a concentration of 0.2 μg-atom P/l/day was found at Station 409. At Station 447 the concentration was 0.4. The results from "surface

Stations" 408 and 443a resembles in all respects those from the complete stations from the same area.

Station 498 in the Banda Sea – depth 7465 m. – was very different from the four stations just mentioned. 1.3 µg-atom P/l. was found at a depth of 60 m. The depth of the photosynthetic layer was 42 m. The rate of production was 0.34 g. C/m.²/day (the same rate was found at the surface station 491 b. The position of Station 498 was practically identical with "Dana" Station 3676 – cf. THOMSEN 1937. – Although this stations was taken in March and the "Galathea"-station in September the vertical distribution of nutrient salts is very alike. As the positions of the two stations are very near to the 1000 m. curve in the northwestern part of the Banda Sea, the conditions here are perhaps somewhat locally conditioned. The macroplankton-samples from the two "Dana"-stations from the Banda Sea, JESPERSEN 1935, indicate a not very high, but at least a somewhat higher production here than in the Celebes Sea and in the northern part of the East China Sea.

All of the 10 stations taken over shallow depth in the whole of the Indo-Malayan region were characterized by a high rate of production varying between 0.24 and 1.08 g. C/m.²/day. On the average the rate was 0.61 g. C/m.²/day. It was found during the expedition that the rate of organic production is high practically anywhere in the Tropics in shallow water.

D. THE PACIFIC OCEAN

(The charts, Fig. 26 and Fig. 27)

The investigations by the "Galathea" include scattered measurements in the most western part of the ocean, measurements in the Tasman Sea and the water around New Zealand, a section across the whole of the ocean from New Zealand to San Francisco and a section along the American Continent from San Francisco to Panama.

Despite the fact that the few "Galathea"-observations cover only a very small part of the big Pacific Ocean and despite the fact that the hydrography of just this ocean is but little known – cf. SVERDRUP *et. al.* 1942. – the measurements represent a not too bad introduction into the exploration of the organic production of this ocean. A few general rules may at least be laid down if the information from the other oceans is used as a supplement.

Stations 422 and 435 are located near the Philippines, Fig. 26, the first over the submarine slope-depth 2200 m., the other above the Philippine trench – depth 10.026 m. The rate of production was low at both stations, 0.11 and 0.08 g. C/m.²/day respectively. The low rate of production is in accordance with the considerable vertical extension of the photosynthetic layer. The area in question may perhaps be compared with the area of the Antilles Current in the Atlantic Ocean, where a similar low rate of production was found – cf. p. 77.

West and south of New Guinea, measurements of the production were made on three normal stations and on four "stations" where only the rate of photosynthesis in surface samples was measured. The rate of production varied between 0.11 and 0.32 g. C/m.²/day. Because of the Solomon Islands to the west and other islands, the hydrography of the area presumably must be rather complicated. It is not astonishing that both regions with a low productivity rate and regions with a decisively higher rate were found. The "Galathea" material is, however, quite inadequate for a closer study.

Three stations were taken in the coastal waters of Australia, Station 538 outside Queensland, Station 553 in the Bass Strait and 564 in the Great Australian Bight. Only in the Bass Strait was a really high rate of production measured (0.42 g. C/m.²/day). It is, of course, impossible to say much about the productivity of the Australian coastal waters on the basis of this meagre material.

In the offshore waters of the Tasman Sea between Australia-Tasmania and New Zealand measurements were made at three stations. At Station 550 near the northern border of the Tasman Sea a rate of production of 0.15 g. C/m.²/day was measured. This moderate rate is in accordance with the hydrographic conditions. No phosphate determinations were made at this station by the "Galathea". But according to the measurements of the "Dana" from January-February 1929, 0.5 µg-atom P/l. was first found at a depth of about 200 m. at the most western stations ("Dana" 3659 and 3663) of the section Auckland-Sidney. At the more eastern stations of the section, 0.5 µg-atom P/l. was found already at a depth of 75-100 m. – cf. THOMSEN 1937. According to the zooplankton measurements of the "Dana" – JESPERSEN 1935, Fig. 11 – a very distinct

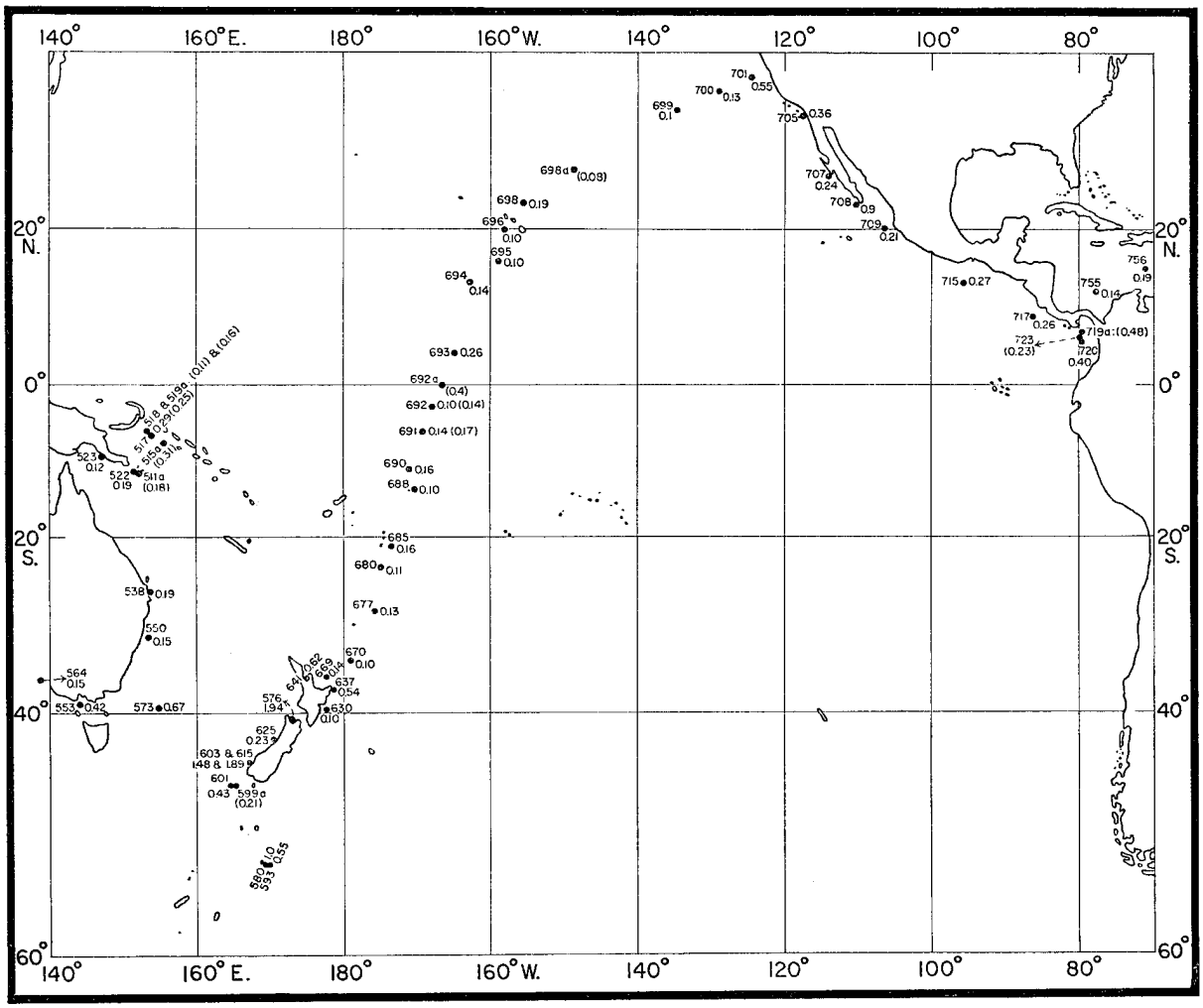


Fig. 27. Measurements in the Pacific Ocean. Station numbers on the left, organic production (g.C per m.^{2} per day) on the right. The values are in brackets at the stations where only measurements of surface water were made (St. 691 and St. 692 cf. Table 20, p. 134).

decrease in plankton volume in hauls with 50-100 metres wire, – $1^1/_2$ m. stramin net – is found going from east to west in this section.

Stations 573 and 601 were located more to the south in the Tasman Sea, the former at 39°25'S, surface temperature 17.5°C, the latter at 45°51'S, surface temperature 12.7°C. Throughout the photosynthetic layer phosphate was present only in a concentration of 0.1 µg-atom P/l. at Station 573. Below the photosynthetic zone no phosphate determinations were made. The rate of organic production was high – 0.67 g. C/m²/day. There is reason to believe that the rate of production is seasonally conditioned. The station was worked on December 17th. In the middle of June-corresponding to the middle of December on the southern hemisphere – in the open Atlantic south of Iceland a dense phytoplankton is found. The spring maximum here starts during May – cf. STEEMANN NIELSEN, 1935 and 1943 – after the commencement of stabilization due to the summer heating. There is reason to believe in at least some resemblance to the conditions in the temperate part of the Tasman Sea.

Station 601 was worked a month later in the south eastern part of the Tasman Sea. 0.4 µg-atom P/l. was found throughout the photosynthetic layer. The north-going current originating here from the adjacent Antarctic Ocean, where high phosphate concentrations are found at the surface during the summer (cf. CLOWES 1938), indicates that a high rate of production presumably is going on here throughout the whole summer.

The "Galathea" measured the organic production in the waters near Campbell Islands south of New Zealand. One station was worked in the fjord Perseverance Harbour and one outside the fjord at a depth of 110 m. The rate of production was high on

both stations – 1.0 and 0.55 g. C/m.²/day respectively. This is in accordance with the concentration of phosphate found, 1.3 μg-atom P/l. at all depths in the photosynthetic layer.

In the shallow water around the coasts of New Zealand 7 productivity stations were worked by the "Galathea" in the period 21. December – 27. January. The rate of production was high everywhere, in the Cook Strait and in the fjord Milford Sound even extremely high. The coastal waters as well as the open waters around New Zealand are without doubt very productive. The zooplankton investigations by the "Dana" – cf. JESPERSEN 1955 Fig. 5 – also indicate this clearly. It must, however, be emphasized that investigations during all seasons must be made in an area like the present in order to obtain a correct picture of the productivity.

The section across the Pacific has already been discussed by STEEMANN NIELSEN 1954. Fig. 27 gives the rate of organic production in the section from New Zealand to California. The direction of the route was northwestward to Honolulu. From there the "Galathea" continued straight on to San Francisco. All stations were made between the beginning of March and the beginning of April, with the exception of Station 641, made at the end of January. This neritic station, at the mouth of Houraki Gulf, New Zealand and the last station of the section, Station 701, in the coastal water outside San Francisco, give a suitable contrast to the other stations of the section, which are all truly oceanic. The two neritic stations represent coastal areas with a high organic productivity – about 0.6 g. C per square metre per day.

The "Carnegie"s last cruise in 1929, together with the "Dana"'s cruise, in 1928-1930 and the Swedish Deep-Sea Expedition 1947-1948 gives valuable information on the hydrography of the area in question (see SVERDRUP et al., 1942). The work done by the Fish and Wildlife Service at Hawaii in recent years has added much to our knowledge – cf. KING 1954, CROMWELL 1954, AUSTIN 1954. Between the North and South Equatorial Currents, in the east, there lies the remarkably well developed Equatorial Counter Current. The "Carnegie" found two regions of divergence in which the ascent of water from medium depths to the surface could be clearly recognized. One of these regions is situated in the South Equatorial Current near the Equator and the other on the northern boundary of the Counter Current. In these regions concentrations of slightly more than 0.4 μg-atoms P per litre were found at the surface. Net catches of plankton (GRAHAM, 1941) were also rich here.

The "Albatross" section – Stations 80-94 situated more to the East showed the same two divergences – JERLOV 1953, a, b. The "Galathea"'s section is further westward than the "Carnegie"'s. According to SVERDRUP *et. al.* (1942, Fig. 197) the depth of the discontinuity surface near the equator increases from east to west. This indicates perhaps a less pronounced admixture of water from medium depths on the "Galathea" section than on the "Carnegie" section. On the latter, between 8°S and 3°N concentrations of 0.4 μg-atom P per litre at the surface were found. On the "Galathea" section a phosphorus concentration of 0.3-0.7 μg-atom P per litre was, however, found at the surface at all stations between 6°S and 4°N. According to the 172° longitudinal section presented by CROMWELL 1954 0.5-0.8 μg-atom P per litre was found between 5°S and 5°N – February, March.

The rate of organic production was fairly uniform at the "Galathea"s unfortunately relatively few stations on this section. With the exception of the stations near the divergence between the Counter-Current and the South Equatorial Current found just north of the Equator, the rate varied only between 0.10 and 0.19 g. C per square metre per day.

Only two stations were made by the "Galathea" in the region directly influenced by the divergence in question. The rates of production were 0.26 and about 0.4 g. C per square metre per day respectively. The last value is unfortunately not very exact. Only the productivity of the surface water was measured, since unfortunate circumstances made it impossible to carry out intensive investigations in this interesting locality. No influence on organic production of a possible divergence at the northern border of the Counter-Current was observed. This is in accordance with KING 1954 – cf. p. 118. JERLOV 1953 a, Fig. 8 states a divergence near 10°N at his western section (Stations 124-138). The influence on the phosphate distribution was, however, very limited.

The thickness of the photosynthetic layer at the oceanic stations of the "Galathea" section was found to vary between 95 and 120 m., with the exception of the stations near the Equator, where a depth between 78 and 85 m. was found. The layer was 77 m. deep at Station 700. The latter station is in the approaches to the Californian coast.

No straight dependence of the rate of production on the concentration of phosphate is seen in the tropical part of the section in question. *A priori* this

is not to be absolutely expected – cf. p. 93, where the influence of phosphate is discussed. Thus at Station 692 near the Equator where the phosphate concentration at all depths of the photosynthetic layer was 0.7 μg-atom P/l. a much higher rate than observed, 0.14 g. C/m.²/day, could have been expected. Certainly the high phosphate-concentration may not have been accompanied by equally high nitrate-concentrations. Available N was very likely the real limiting factor for organic production. As will be shown in Fig. 28, p. 93 the surface water of the South Equatorial Current about the longitude in question, according to the "Dana" observations showed a characteristic minimum in nitrate whereas phosphate was relatively abundant.

The effect of a divergence on the plankton production is, in all probability, not restricted to the precise location of the divergence. Through the horizontal currents a bigger area is positively affected. Without the help of really extensive observations, an area like the equatorial region of the Pacific cannot be treated in much detail.

The section from San Francisco to Panama along the American coast will only briefly be presented. All stations were located in water either very productive or at least rather productive. It is to be expected that an extensive series of observations from all seasons will be available in the near future through productivity work made at the Scripps Institution of Oceanography. It would thus be premature to try to use the present scant data for any detailed study.

Besides Station 420 in the Golf at Panama, where the rate of production was measured in the normal way in water from 3 different depths, determinations of the production in surface water samples were made at two other stations, giving a rate somewhat less than at Station 420.

E. THE PRODUCTION OF ORGANIC MATTER IN THE HYDROSPHERE AS A WHOLE

Investigations on a much greater scale than was possible during a single circumnavigation of the globe are of course needed to get exact figures for the production of matter in the seas.

In previous publications – STEEMANN NIELSEN 1952 and 1954 – the senior author has estimated the average annual gross production of matter in all seas to be 55 g. C/m.². This estimate is perhaps a little too low. The rate of production in antarctic waters was perhaps a little underestimated. No observations at all are available. The average annual gross production for all seas exceeds, however, hardly 70 g. C/m.². If we use a value of 55-70 g. C/m.² and reckon on a 40 per cent. loss through respiration (my previous figure, 25 per cent., is presumably too small) and a sea area of 361×10^6 sq. km., we obtain a total net production per year in the sea of $1.2\text{-}1.5 \times 10^{10}$ tons of carbon. This figure is practically the same as that estimated by SCHROEDER 1919 for the production on land. Before many more observations are available it is pointless to try to obtain a better estimate of the production of matter in the hydrosphere. Investigations carried out during the "Galathea" Expedition have shown that the amount of organic production in the tropical and subtropical parts of the oceans is strictly dependent on the hydrographic conditions. Although experiments were made only once at each station there is every indication that the results obtained in the main provide a reasonably correct picture of the productivity of the region. It must of course be stressed that this is by no means applicable to temperate and arctic waters, and only partly to some tropical and subtropical waters.

It is possible to distinguish four different classes of oceanic regions according to amounts of organic production. These are applicable only to tropical and subtropical parts of the oceans. Graduations between them are found of course.

(I) Regions with a very considerable admixture of "new" water to the photosynthetic zone. "New" water is water rich in nutrient salts originating from medium depth. The daily organic production is from 0.5 to about 3 g. C per square metre. An example of this class is the southern part of the Benguela Current.

(II) Regions with a fairly steady admixture of "new" water to the photosynthetic zone. The daily organic production is about 0.2-0.5 g. C per square metre. This may be exemplified by the regions in the neighbourhood of the divergences caused by the Equatorial Counter-Currents in the different oceans.

(III) Areas without a pronounced admixture of nutrient-rich water from below. Some admixture –

although of minor importance – may occur, however, through turbulence. The daily organic production is 0.1-0.2 g. C per square metre. By far the largest parts of the tropical and subtropical regions of the oceans belong to this category.

(IV) Areas with typically "old" surface water in the photosynthetic zone. This water, originally rich in nutrients, has been transported from a distant region, and the lapse of a long time has resulted in decrease in nutrient content since the water entered the photosynthetic layer. Turbulence is of only slight importance, since nutrient-rich water is present only far below the photosynthetic zone. The rate of organic production is about 0.05 g. C per square metre per day. An example of this is the central part of the Sargasso Sea.

As a general rule it may be stated that the organic production is high in the shallow coastal regions of the Tropics. It may be supposed that the high temperature of the bottom material during the whole year gives rise to a fast decomposition rate of organic material producing considerable amounts of the nutrient salts – cf. p. 86.

According to the Fishery statistics (F.A.O.) the annual yield of all of the marine fisheries is at present 2.4×10^7 tons of fresh weight. If this is converted into carbon it indicates that about 0.01 per cent. of the carbon annually fixed in the plankton algae in all seas is taken every year by the fishermen.

0.01 per cent. does not seem to be very much. But it must be kept in mind that fishing is not going on at all in most parts of the oceans. Unfortunately fishing in many of these areas will hardly ever be economically possible.

In eutrophic coastal areas at higher latitudes – as e.g. the North Sea – about 0.2-0.3 per cent. of the carbon annually fixed by the plankton algae is taken every year by the fishermen. There is every indication that such a high percentage of the yield is possible only in eutrophic areas where further a material part of the fish caught is represented by species like the herring. Mostly only one link is found in the food chain between plankton algae and herring. The problems will be discussed in detail in another publication dealing with the recent Danish investigations on production of organic matter in the northern seas.

PART III.
THE GENERAL BACKGROUND OF OCEANIC PRODUCTIVITY

A. INTRODUCTION

It is now rather well established (see e.g. SVERDRUP *et al.*, 1942) that the main factors governing the production of phytoplankton in the sea are the following: A) the supply of nutrient salts, B) light, C) temperature, D) sinking, E) grazing by animals. Other factors like hormones and antibiotics produced by the phytoplankton itself or by other organisms are undoubtedly also of importance. At present, however, we know little about the effects of such factors in the open ocean. LUCAS 1947 discussed the whole matter. It is very likely that external metabolites have at least some influence on the production rate of phytoplankton even in the open ocean – cf. p. 114.

The investigations made on the "Galathea" Expedition have furnished considerable evidence that the supply of nutrients – manifested by the "age" of the surface water in the sense used by SVERDRUP and ALLEN 1939 – is by far the most important factor governing the production of phytoplankton in the tropical and subtropical parts of the oceans. Subsurface water recently ascended to the surface is called "new". The concentrations of the nutrient salts are high in such water. In "old" surface water the nutrient salts are exhausted due to the activity of the plankton algae.

Nature has normally established an equilibrium between all the factors governing phytoplankton production; it is only occasionally possible at any given time to describe one of the factors as the absolutely limiting one. Any change in one of the factors mentioned above will normally influence the other factors as well and establish a new equilibrium. All of these factors should therefore be treated as inseparable. However, in the interest of clarity in this chapter, only attempts in this direction will be made in the main sections; in conclusion a comprehensive survey of the whole complex will be given.

B. SUPPLY OF NUTRIENT SALTS

1. Nitrate versus Phosphate

The two elements nitrogen and phosphorus often become limiting for the production of organic matter in the oceans. In oceanic water it seems never to have been definitively stated that other elements such as iron may act in the same way. A survey of these problems may be found in SVERDRUP *et al.* 1942.

Whereas inorganic phosphate is easily determined, it is not quite so with the inorganic nitrogen sources which are assimilated by plankton algae. In coastal water the difficulties are particularly great, since both ammonia, nitrite and nitrate may be found in nearly equally important quantities – cf. STEEMANN NIELSEN 1951. The determination of nitrate in coastal water was till recently often inexact. The reduced strychnine method, originally introduced by HARVEY 1928, may be inadequate in productive water of that kind.

In the open ocean, the difficulties are much fewer. According to the experiences obtained during the "Dana" Expedition 1928-1930, the reduced strychnine method seems to give reasonably reliable measurements of nitrate in oceanic water having a normal content of plankton. In very plankton-rich water it may be different.

In recent years only the concentration of phosphate has been measured in most investigations – for example during the "Galathea" Expedition, where the determinations were made according to WATTENBERG 1937 and corrected for salt error according to COOPER 1938.

Apparently there seems to be good reason for determining only phosphate. According to REDFIELD 1934, the ratio of phosphorus as inorganic phosphate to nitrogen as nitrate is nearly constant in the oceans. In the Atlantic he found essentially a constant ratio down to the smallest concentrations of both elements; thus these should be exhausted simultaneously due to the activity of the plankton algae.

COOPER 1937, 1938, has also discussed the N: P ratio in the sea. In principle he agrees with Redfield. He gives (1938) an "ideal" ratio of 15 when the concentrations are expressed as μg-atom/l. and the phosphate determinations are corrected for salt error. He showed, however, that anomalies in the

N: P ratio may be found. In oligotrophic areas of the Mediterranean the ratio was much above the "ideal" value. He used the phosphate and nitrate observations made during the "Dana" Expedition 1928-1930 in the Mediterranean to prove this statement. These observations were published by THOMSEN 1931. In the same paper some scattered observations from the Atlantic, the Pacific and the Indian Ocean were published out of the great number of observations made during the expedition. REDFIELD 1934 made use of these few published observations.

HARVEY 1945 noted that the N: P ratio was abnormally low in certain waters of the South Atlantic. He suggested that it may be due to the direct regeneration of phosphate being more rapid than the indirect regeneration of nitrate in such water. RILEY *et. al.* 1949 p. 18 refer to the same suggestion but mention in addition, that "it might also be implied that nitrogen is the more important limiting factor, particularly in the southern areas".

THOMSEN 1937 has published the entire observations from the "Dana" Expedition 1928-1930, unfortunately, however, without any accompanying text. Some characteristic features from this valuable collection of observations will be presented here. No attempt will be made to treat these numerous observations in detail. In Part II some of the "Dana" observations have already been used. The phosphate determinations have been corrected for salt error according to COOPER 1938.

Whereas a N: P ratio of about 15, as given by Cooper, is adequate for the Northern Atlantic, the ratio seems to be smaller in most other parts of the oceans. This is also the case in deep water, where it mostly is about 12-14. Particularly low ratios are found in the eastern part of the South Pacific. The "Dana" Station 3563 may be used as an example – Table 7.

Table 7. Nitrate and Phosphate at "Dana" Station 3563 7°45'S, 131°22'W. 29. 9. 1928.

depth in m.	μg-atom $N\text{-}NO_3$/l.	μg-atom $P\text{-}PO_4$/l.	N:P
0-50	2.8	0.5	5.6
75-100	2.8	0.6	4.8
150	3.6	0.6	6.0
200	10.7	1.1	9.8
300	19.6	1.7	11.5
400	19.6	1.7	11.5
500	25.0	2.4	10.5
600	28.6	2.4	11.9
1.000	26.8	2.9	9.3
1.500	26.8	3.0	9.0
2.000	28.6	2.9	9.9
3.000	28.6	2.4	11.9
4.000	28.6	2.4	11.9
4.500	26.8	2.4	11.2

The concentrations of both nitrate and phosphate were sufficiently high at all depths to allow the compution of a fairly exact: N: P ratio. The highest ratio found at any depth was 11.9. On the average it was definitely lower. The very low ratios varying between 4.8 and 6.0, found in the water layers between the surface and 150 m. are of special interest in this connection.

Let us suppose that deep water from "Dana" Station 3558 originally was brought up into the photosynthetic layer. Station 3558 was the most eastern station in the South Equatorial Current situated near a centre of real upwelling (0°18'S, 99°07'W). The nitrate concentration in this deep water was 35.7 μg-atom N/l., the phosphate concentration was 3.0 μg-atom P/l. The plankton algae have now assimilated both nitrate and phosphate during the westward drift of the surface water. According to determinations by Fleming cited in SVERDRUP *et. al.* 1942 p. 236, the ratio of N: P in plankton diatoms may be put at 16, in good agreement with the ratios presented by REDFIELD 1934 and COOPER 1937. If therefore the nitrate concentration due to the assimilation by the phytoplankton is reduced to 2.8 μg-atom/l. (the actual concentration found in the photosynthetic layer at Station 3563), 32.9 μg-atom/l. is thus assimilated; if the ratio assimilated N: assimilated P is put at 16, 1.9 μg-atom P/l. is thus consumed, leaving 0.9 μg-atom in the water. This is in good agreement with the 0.5 μg-atom P actually found in the surface layer 0-50 m. at Station 3563. The low N: P ratios near the surface are thus easy to explain.

If all the nitrate had been assimilated, theoretically we should still have expected about 0.8 μg-atom P/l. In order to demonstrate the decrease in the N: P ratio, the nitrate and phosphate concentrations near the surface (0-50 m.) from a section of the "Dana" following the South Equatorial Current in the South Pacific from the Galapagos Islands to north of New Zealand are presented. The N: P ratio found is also given and finally the theoretical ratio is presented. The latter was derived on the assumption that the $N\text{-}NO_3$ and $P\text{-}PO_4$ concentrations prior to any assimilation by the plankton algae were 35.7 and 3.0 μg-atom/l. respectively (the values at Station 3558 in the deep water).

Table 8. The average concentrations of $N\text{-}NO_3$ and $P\text{-}PO_4$ and the actual and "theoretical" N:P ratio in the uppermost 50 m. of the South Equatorial Current in the Pacific. Observations at depths of 0, 10, 25 and 50 m.

Station No.	Position	µg-atom $N\text{-}NO_3$/1.	µg-atom $P\text{-}PO_4$/1.	actual ratio N:P	"theoretical" ratio N:P
3558	0°18'S-99°07'W	11.6	1.25	9.3	7.8
3561	4°20'S-116°46'W	5.7	0.85	6.7	5.2
3563	7°46'S-131°22'W	2.8	0.5	5.6	3.1
3573	17°36'S-149°42'W	0.1	0.6	(0.2)	0.1
3577	18°49'S-153°10'W	0	0.2	–	–
3580	18°53'S-163°02'W	0.1	0.2	(0.5)	0.1
3624	28°17'S-177°01'W	0	0	–	–
3626	27°00'S-177°41'W	0	0	–	–

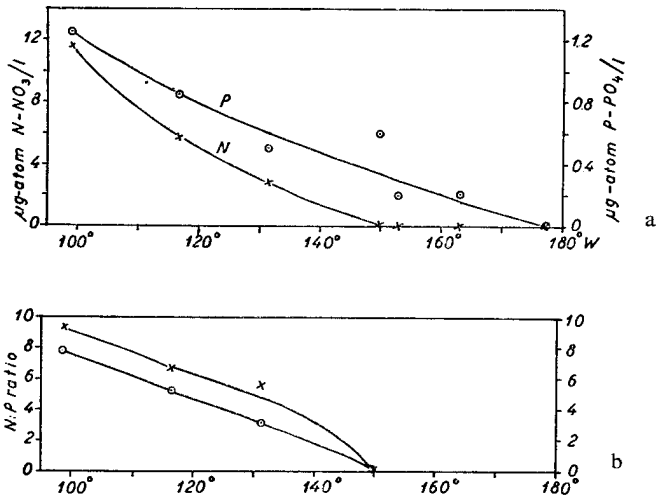


Fig. 28a and b. The observations and calculations given in Table 8 are graphically presented.

In Fig. 28a and b, the observations and calcualtions are presented graphically. In the whole section the actual and the "theoretical" ratios agree very well. In the South Equatorial Current in the Pacific about 150°W, relatively high concentrations of phosphate are found although nitrate is almost completely exhausted. During the "Galathea" Expedition, a section was made across the current at approximately this longitude. The relatively high phosphate concentrations found in the photosynthetic layer at Stations 691 and 692, Table 20, may thus not neccessarily be a symptom of excellent growing conditions for the plankton algae. The relatively low rates of organic production found in this region may thus be explained.

The facts presented are a memento; it may sometimes be wrong to assume that excellent nutrient conditions follow from relatively high phosphate concentrations if determinations of this nutrient only have been made.

As shown above, the low N: P ratios in the photosynthetic layer of the South Equatorial Current in the Pacific was ascribed to the relatively low ratio in the deepwater ascending to the surface in the easternmost part of the current. As the ratio assimilated N: assimilated P was definitely higher, the ratio present N: present P decreased when the concentrations of the nutrient decreased.

Table 9. The average concentrations of $N\text{-}NO_3$ and $P\text{-}PO_4$ and the N:P ratio off the Atlantic coast of North Africa. Observations at depths of 0, 10 and 25 m.

Station No.	Position	µg-atom $N\text{-}NO_3$/1.	µg-atom $P\text{-}PO_4$/1.	N:P
4007	18°22'N-18°14'W	10.1	0.9	11.3
4005	13°31'N-18°03'W	7.0	0.6	11.7
4003	8°26'N-15°11'W	4.8	0.5	9.6

In the eastern part of the North Atlantic off the coast of North Africa a similar upwelling of deep water occurs. The N: P ratio in this water of about 15 – Cooper's ideal ratio – has the effect that the ratio decreases only slightly when the nutrient salts are assimilated by the phytoplankton. Table 9 which gives the nitrate – and phosphate concentrations and the N: P ratio in the uppermost 25 m. at three representative "Dana" stations, shows this clearly.

Other comments on the N:P ratio in oceanic water may be made. As shown in Table 8, both nitrate and phosphate are fully exhausted in the photosynthetic layer at the last two stations of the section along the South Equatorial Current in the Pacific – Stations 3624 and 3526. It could be supposed that this situation was caused by a high N: P ratio for "new" surface water. The surface water at these stations should hence originate not in the more eastern part of the current, but should consist mainly of water from deeper levels at the location. This water originally should have had a high N:P ratio. The N:P ratio in the subsurface water at these stations is, however, by no means high – Table 10.

We are thus forced to assume that when surface water, in which nitrate is fully exhausted but phosphate is not, becomes still "older", it also becomes exhausted with respect to phosphate. This may be explained in several ways, as e.g., by a faster regeneration rate of nitrate (including ammonia and

Table 10. Nitrate and phosphate at "Dana" Station 3626-27°00'S, 177°41'W.

Depth in m.	μg-atom $N\text{-}NO_3$/l.	μg-atom $P\text{-}PO_4$/l.	N: P
0-50	0	0	–
65-100	0.1	0.15	(0.7)
200	1.4	0.3	4.7
300	3.6	0.4	9.0
400	7.1	0.6	11.9
500	10.7	0.9	11.9
1.000	26.8	2.2	12.2
2.000	39.2	2.9	13.5

nitrite) in the photosynthetic layer or by addition of nitrate from rainwater or by assimilation of elementary nitrogen by blue-green algae. No marine plankton species having this ability are known, however.

The supply of nitrate in rainwater due to electrical fixation in the atmosphere is hardly of any decisive importance for the entire photosynthetic layer. Even if, according to BENECKE-JOST 1924, we take the greatest supply found in the Tropics – 0.6 g $N\text{-}NO_3$/m.²/year – this would correspond only to 0.09 g. $P\text{-}PO_4$/m.². If the photosynthetic layer is 100 m. deep, it would further correspond only to 0.9 mg. P/m.³ = 0.03 μg-atom $P\text{-}PO_4$/l.

For the actual surface on the other hand, the nitrate from rainwater may be of some importance. A high percentage of the "Dana" stations in the parts of the oceans (primarily the Indian Ocean), where nitrate was found to be lacking in the photosynthetic layer, but where phosphate was still present, showed an absolute phosphate depletion in the actual surface; on the other hand, small concentrations of nitrate sometimes were found there. The contribution of nitrate to the actual surface makes it possible for the algae to utilize the remaining quantity of phosphate. The "Dana" Station 3850, Table 11 presents a typical example.

Table 11. Vertical distribution of $N\text{-}NO_3$ and $P\text{-}PO_4$ at "Dana" Station 3850. 6°01'S, 93°12'E.

depth in m.	μg-atom $N\text{-}NO_3$/l.	μg-atom $P\text{-}PO_4$/l.
0	0.1	0
10	0	0.2
25	0	0.2
50	0	0.2
75	0	0.2
100	14	1.0

Table 12. Nitrate and phosphate at "Dana" Station 3542 – 24°52'N, 44°40'W.

Depth in m.	μg-atom $N\text{-}NO_3$/l.	μg-atom $P\text{-}PO_4$/l.	N: P
0-100	0.1	0	–
150	0.3	0	–
200	2.5	0.15	17
400	11.7	0.3	39
600	23.2	0.5	47
800	25.0	0.85	29
1.200	26.8	0.65	41
1.500	23.3	0.55	42

If nitrate is regenerated faster than phosphate, we must expect a high N: P ratio in the water masses just beneath the photosynthetic layer in areas of descending surface water. Nitrate and phosphate found here must originate chiefly from organic matter produced in the surface layers. Such areas are mostly extremely oligotrophic. Using the "Dana" observations, COOPER 1937 has already shown that such conditions are found in the eastern Mediterranean, where just such a descent of surface water takes place. A similar area is found in the North-Atlantic eddy- the Sargasso Sea. RILEY *et. al.* Fig. 8 presented the vertical distribution of the ratio at a station from the northwestern border of this area. In Table 12, the vertical distribution of the concentrations of nitrate and phosphate are presented together with the ratio from a "Dana" station located in the centre of the Sargasso Sea where particularly high ratios are found.

It may be supposed that the regeneration rate of nitrate probably mostly is faster than that of phosphate. In quite "new" surface water, the amounts of the salts regenerated may be considered to be relatively small compared to the primary amounts present. They are thus of little importance for the N:P ratio. When the original nitrate is used the regeneration rate becomes important. In the long run, the greater amounts of nitrate regenerated in the photosynthetic layer cause all the phosphate to be used by the plankton algae. In very "old" surface water both nitrate and phosphate are thus exhausted.

It was shown above that in areas where surface water descends, the N: P ratio in the water layers immediately below the photosynthetic layer has a very high N:P ratio. According to the "Dana" observations positive anomalies were also found just beneath the photosynthetic layer near the divergence at the northern boundary of the South Equatorial Current in the Indian Ocean. A N:P ratio

Table 13. Nitrate and phosphate at "Dana" Station 3925 – 7°13'S, 52°22'E.

Depth in m.	μg-atom $N\text{-}NO_3$/1.	μg-atom $P\text{-}PO_4$/1.	N : P
0	0.3	0.1	–
10	0	0.2	–
25	2.1	0.5	4.2
50	16.1	0.75	21.4
75	23.2	1.15	20.1
100	28.5	1.15	24.8
150	30.4	1.6	19.0
200	30.4	1.7	17.8
400	30.4	2.1	14.5
1.000	43.0	3.15	13.7
2.000	43.0	3.15	13.7

of 20.6 was found at a depth of 150 m. at "Dana" Station 3848 of the section 4 – cf. Fig. 24 and p. 84 The "Dana" Station 3925 from the section 2, Fig. 24 gives the best illustration, Table 13. "Dana" Station 3585 located about 450 miles south of the corresponding divergence in the Pacific (but about 100 miles north of the "Dana" section presented in Fig. 25, p. 83) had a N:P ratio of 19 and 21 in depths of 400 and 500 m. respectively.

It seems at present impossible to give any absolutely convincing explanation of the high N:P ratio found at depths between 50 and 200 m. in these particular areas. It is perhaps an indication of an especially high regeneration rate of the nutrient salts at these depths. Such high N: P ratios are rarely found below the photosynthetic layer in eutrophic regions.

It is rather obvious however, that differences may be expected between the various regions. A quantitative knowledge of all of the processes going on would be necessary for a real understanding. We do not by far possess such a knowledge today.

Whether nitrogen or phosphorus is the real limiting factor for the organic production varies from area to area. At present it is possible to say that generally speaking nitrogen is the most important limiting factor in areas where the replenishment of the nutrients is due particularly to a supply originally brought up near the surface by subsurface water. In areas in which the replenishment is due primarily to a direct regeneration, either in the water of the photosynthetic layer or at the bottom in contact with this layer, phosphorus particularly becomes limiting – cf. the conditions in the Danish Isefjord, STEEMANN NIELSEN 1951.

2. The replenishment of nutrients

As clearly pointed out for example by KETCHUM 1947, "it is the rate of replenishment, and not the concentration observed at a given time, which determines the fertility of an aquatic environment. This replenishment is provided by the two processes of decomposition and water circulation."

Neither of these processes is too well known – the best, however, being the water circulation. The nutrient salts are brought into the photosynthetic layer by turbulence, including eddy diffusion, and by upwelling. The latter requires special hydrographic conditions. It is therefore found only at special places – as in the South Atlantic near the coast of Africa. As subsurface water containing a relatively high concentration of the nutrient salts is transported up to the surface during upwelling, the influence of this process is very pronounced on the replenishment of the nutrients and thus on the organic productivity.

The influence of turbulence is less than upwelling on the one hand. On the other, it is of a more universal occurrence. Whereas turbulence may be investigated quantitatively in some waters without great difficulty (see JENSEN 1940), the problem seems at present to be rather difficult to handle in most oceanic areas. Turbulence, as will be used in the present section, may be described as the process by which the photosynthetic layer interchanges water masses with the layers just below it. It is therefore of immense importance for the transport of nutrient salts, how the concentrations of these are in the water layers just below the lower boundary of the photosynthetic zone.

The concentration of inorganic phosphate at a depth of say, 50 m. below the lower boundary of the photosynthetic zone may therefore often provide a usefue indication of the influence of turbulence on the transport of the nutrient salts into the photosynthetic layer. Although phosphate determinations below the photosynthetic zone were only sporadically made on the "Galathea", sufficient material is available from other expeditions for most of the areas investigated. The degree of stability of the water masses must be assumed to have a comparably strong influence on the transport of the nutrient salts into the photosynthetic layer. It is therefore not possible to use the concentration of nutrients just below the photosynthetic layer as an index of potential nutrient supply without reservations.

At present it is possible to investigate only indi-

rectly the problem of the regeneration of the inorganic phosphate from soluble organic phosphate and from particulate, "dead" phosphate. The same is the case with nitrogen. Because of the enormous development of bacteria on bottling a sample of natural water no experimental investigation of regeneration under natural conditions seems possible at present.

The regeneration of e.g., phosphate could be measured indirectly by investigating the rate of photosynthesis if sufficient knowledge of the importance of vertical mixing of the water masses were available. It may be supposed that roughly 1 mg. P is assimilated for every 40-50 mg. C – cf. e.g. REDFIELD 1934. In one of the least productive areas of the oceans – the Sargasso Sea – the rate of photosynthesies is about 0.5 mg. C per m.^{3} per day near the surface – cf. Table 20. The rate of phosphate assimilitation may thus be estimated to be about 0.01 mg. P per m.^{3} per day. This is apparently about 1 per cent. of the concentration of inorganic phosphate normally found here – cf. Table 20.

As fairly phosphate-rich water in the Sargasso Sea first is found several hundred meters below the photosynthetic zone (cf. Table 12), and as the water masses show a tendency of descending, turbulence must be assumed to be of very little importance here for the phosphate replenishment in the photosynthetic zone. Assuming stable conditions, the daily regeneration rate of inorganic P may thus be estimated to be about 0.01 mg. P/m.^{3}.

For comparison, another marine area may be mentioned where the same phosphate concentration as in the Sargasso Sea was found during a period of the summer. During 3 series of investigations in the very productive Danish Isefjord (STEEMANN NIELSEN 1951) in the period August-September 1941, the phosphate concentration (inorganic) was about 1 mg. P per m.^{3} The organic productivity in this period varied between 250 and 520 mg. C per m^3. per day at the surface. P-assimilation may thus be estimated to be about 5-10 mg. per m.^{3} per day. The amount assimilated daily is thus about 5 times the amount present at any given time. It may therefore be stated that the inorganic phosphate present in solution at any moment in a water mass may represent from 1 to 500 per cent of the amount taking part in the daily metabolism. According to all evidence available inorganic phosphate must be assumed to be present in greater quantities than those indicated by the determinations of phosphate in solution. At the low P-concentrations found in Nature, a relatively considerable adsorption of phosphate must be expected to take place at all surfaces – for example at the surfaces of detritus. As the phosphate in solution must be in equilibrium with the phosphate adsorbed, the latter may very likely often represent an important P-reserve.

Paradoxically the phosphate supply apparently seems to be most secure for the algae in the oligotrophic water from the Sargasso Sea where the amount of inorganic phosphate in solution present at any moment is sufficient for the normal consumption during a long period. It could be supposed that the few algae present here hardly ever suffer a really pronounced phosphate deficiency. This is true in spite of the fact that the scarcity of algae and the low rate of organic productivity found is caused ultimately by poverty in phosphate and other nutrients. This puzzling problem is discussed further on p. 113.

In the shallow Danish fjord where the water masses are without stratification and are in constant contact with the bottom, the regeneration of the nutrient salts – presumably taking place primarily at the surface of the bottom deposits – represents virtually the only way in which the nutrients are supplied. The dependence of organic productivity on temperature – cf. STEEMANN NIELSEN 1951 – indicates that this factor affects the regeneration of the nutrient salts very pronouncedly.

In open waters quite another picture is obtained. KETCHUM 1947 discusses the problem in a very instructive article. He deals with the Gulf of Maine. The total assimilation of phosphate during the production period is calculated as 8 g. PO_4 (= 2.7 g. P) per m.^{2}. Of this, only 2 % originated from the inorganic phosphate originally present in the photosynthetic layer, 73 % was brought to the surface by vertical transport and – "estimated on meager grounds" as Ketchum states – 25 % was supplied by decomposition within the surface layer. The calculated daily total utilization of 14 mg. P per m.^{2} per day corresponds to 560 mg. assimilated C per m.^{2}, a production rate to be expected during the summer season in the Gulf of Marine.

It is unfortunately rather improbable that the conceptions concerning regeneration of inorganic phosphate in coastal waters and in freshwater lakes can be directly used for marine areas of another kind. Not even a knowledge of the concentration of organic phosphate and of detritus containing P would necessarily give any real information about the rate at which inorganic phosphate may be re-

generated at a certain temperature.[1] Soluble organic phosphates may be of a different nature; some easily accessible for attack, some not so easily. It is possible that in "new" surface water a higher proportion of both the soluble organic phosphate and the P in the detritus (besides the adsorbed phosphate) may be relatively rapidly regenerated into inorganic phosphate, whereas in "old" surface water an accumulation has taken place of material more difficult to decompose. It seems very likely that the regeneration of the nutrient salts takes place rather slowly in the water masses of the photosynthetic layer, at least in ologiotrophic oceanic areas. The same seems to be the case in the water masses below the photosynthetic layer. At the two "Dana" stations in the Sargasso Sea – 3543 and 3545 – at a depth of 200 m. – i.e. about 100 m. below the compensation depth – a phosphate concentration of only 0.1 mg.-atom P/m.[3] was found. As the consumption of phosphate must be supposed to be zero at this depth the rate of regeneration is low.

It is usually assumed that the demineralization of the salts containing N and P is due to the activity of bacteria. This is true concerning the sea bottom according to all evidence.

The mineralization occuring in the free water masses on the other hand may be due not predominantly to the activity of bacteria, but to enzymes found in the water. Because of antibiotics produced by the phytoplankton in light, the activity of most species of bacteria seems to be rather restricted near the surface – STEEMANN NIELSEN 1955b.

KREPS 1934 has presented weighty evidence that enzymes catalyse chemical reactions such as NO_3-production in samples of sea water, poisoned with $HgCl_2$, or filtered through an ultrafilter. The enzymes have their origin in plants, animals or bacteria and they are presumably released in the water due to the death of the organism.

Kreps writes: "It is highly probable that bottom deposits and bottom water layers, which contain most of the organic matter originating from dead animals and plants, planktonic as well as bottom living, are especially rich in various enzymes increasing the rate of various chemical reactions. Liberated in the bottom strata, these enzymes may be involved in the vertical mixing, and are so brought up in the whole water mass, exerting everywhere their catalytic action".

1. The procedure of measuring total phosphorus in surface waters such as stressed by KETCHUM *et. al.* 1955 must, however, be considered an important improvement.

In oceanic surface water enzymes may presumably also be liberated into the water particularly from algae, which have been eaten by the zooplankton. It must, however, be supposed that the concentration of these enzymes is very low in oligotrophic oceanic surface water. This would be in accordance with the apparently slow rate of P- and N-regeneration in such areas.

The hydrolysis of most of the phosphorylated organic compounds is very likely proceeding at a measurable speed without the presence of enzymes. Inconsiderable enzyme concentration should thus be sufficient to account for the rather slow rate of regeneration of inorganic phosphate from soluble organic phosphate found in oceanic water.

3. Concentration of nutrients and rate of organic production in the different oceans

It is at present impossible to compare the rates of organic production in the different oceans. The available data are too few and too scattered. In broad outline, the different oceans do not seem to vary much in this respect. Some differences may, however, be expected.

The distribution of nitrate and phosphate is at least an indication of a possible difference in organic

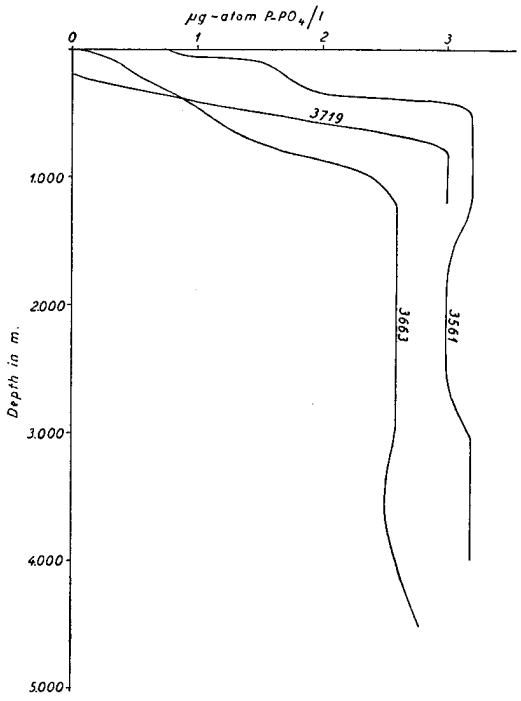


Fig. 29. The vertical distribution of phosphate (µg-atom P/l) at three Dana stations in the Pacific Ocean. St. 3561 – 4°20′S, 116°46′W. St. 3663 – 33°33′S, 154°04′E. St. 3719 – 20°48′N., 124°49′E.

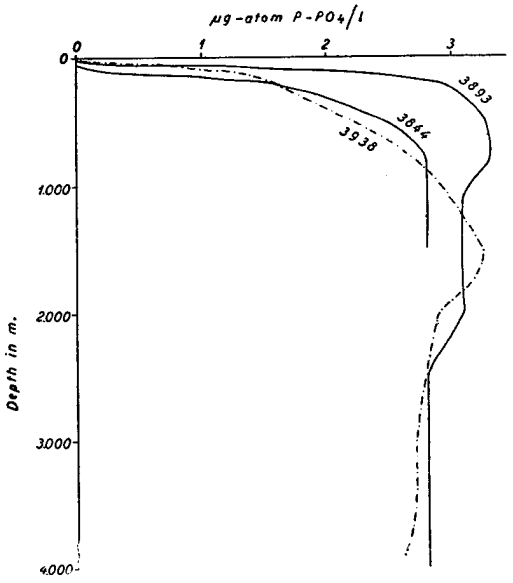


Fig. 30. The vertical distribution of phosphate (μg-atom P/l) at three Dana stations in the Indian Ocean. St. 3841 – 12°05′ S., 96°44′E. St. 3893 – 5°59′N., 92°29′E. St. 3938 – 9°10′S., 45°17′E.

production. According to the distribution of these salts the North Atlantic could be expected to be somewhat less productive than the oceans in general. On the average the water masses particularly of the North Atlantic but also of the South Atlantic contain less phosphate and nitrate than the oceans in general. This fact is well known – cf. SVERDRUP *et. al.* 1942.

In Fig. 29-31 the vertical distribution of phosphate is presented for three representative stations in each ocean. The data originate from the "Dana" – THOMSEN 1937.[1] Whereas all stations from the Pacific and the Indian Ocean are generally similar the stations from the Atlantic give quite another picture if the upper water masses are disregarded.

Station 3998 from the eastern part of the South Atlantic resembles (for the water-layer from the depths about 200-1,000 m.) Station 3561 from the eastern part of the South Pacific or Station 3893 from the eastern part of the Indian Ocean. The maximum P-concentration in the Atlantic at these depths is 3.0 μg-atom P/l. and 3.2-3.3 in the Indian Ocean and the Pacific respectively. Below a depth of about 1,000 m., at the Atlantic station, deep water is found showing a P-concentration of about 1.8 μg-atom/l. In the deep water found at the two stations in the other oceans, the P-concentration is about 3.0 μg-atom/l. The origin of the water masses found in the South Atlantic Ocean – a survey is given by SVERDRUP *et. al.* 1942 p. 625 ff. – explains the vertical distribution of phosphate.

At Station 3998 the intermediate water rich in phosphate is of Antarctic origin, whereas the deep water with the exception of a thin bottom layer-originates from higher latitudes on the Northern hemisphere.

According to SVERDRUP *et. al.* Table 76 the following water masses are transported across the equator towards the north: 6×10^6 m.^{3}/sec. upper water, 2×10^6 m.^{3}/sec. intermediate water and 10^6 m.^{3}/sec. bottom water. In the southerly direction, 9×10^6 m.^{3}/sec. deep water are transported. The amounts of nutrient salts being transported in either direction must be the same. If the average P-concentration of the deep water is put at 1.8 μg-atom/l., 16 kg. P/sec. are transported northwards. If the P-concentration in the intermediate water is put at 3.0, and that in

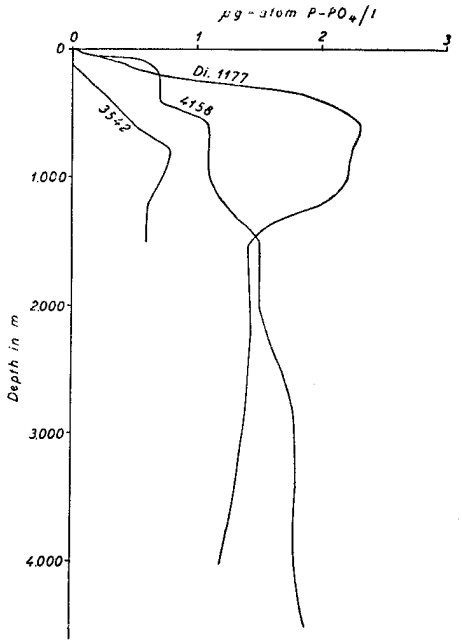


Fig. 31. The distribution of phosphate (μg-atom P/l) at three stations in the Atlantic Ocean. St. Discovery 1177 – 19°S., 1°30′W. St. Dana 4158 – 46°28′N., 8°01′W St. Dana 3542 – 24°52′N., 44°40′W.

1. The curve for the South Atlantic originates, however, from the "Discovery" – CLOWES 1937. Whereas for all other areas of the oceans the P-observations from the "Dana" agree very well with observations obtained during other expeditions, this is not so in the South Atlantic.

   The "Dana" observations are about 35 per cent. higher than the "Discovery" observations (both corrected for salt error). Unpublished observations from the "Meteor" – kindly provided by Professor J. Krey, Kiel – agree with the "Discovery" observations. It is only possible now to guess about the failure of the "Dana" in the South Atlantic. During the section northwards from Cape Town, the wrong determinations seem first to start at St. 3980 (23°26′ S, 3°56′E). At St. 3978 (30°15′S, 13°15′E), the "Dana" and the "Meteor" observations agree.

the bottom water at 2.0 μg-atom/l., 6+2 = 8 kg. P/sec. is transported northwards by these water masses. 8 kg. P/sec. must thus be transported by the upper water. This means that the P-concentration must be 1.3 μg-atom/l. on the average. The real concentration of dissolved inorganic phosphate is decidedly lower. In making a computation of the present kind we have, however, to use the values for total P. Particulate P and dissolved organic P must be included. An average concentration of about 1.3 μg-atom total P/l. seems rather likely for the upper water. In the other water masses, practically all of the P is in the form of inorganic phosphate in solution.

Because the total amount of inorganic P below a surface unit in the North Atlantic Ocean is only about 50 per cent of that in the other oceans, this does not necessarily mean that the amount of P annually used by the phytoplankton below a surface unit is much lower in the North Atlantic than elsewhere on the average. Other instances are also of importance. In the North Atlantic including the Arctic waters, it may thus be stated that in broad outline all phosphate conveyed up into the photosynthetic layer is used by the algae. This is in contrast to the conditions in the Antarctic Ocean. The high concentrations of phosphate and nitrate found at all seasons in these waters indicate that some factors – chiefly the lack of an effective stabilization of the water masses – do not allow the nutrients to be fully utilized.

The Mediterranean presents an example of a reduction in the amount of nutrients of quite another order of magnitude compared to the North Atlantic Ocean. In the eastern part of the Mediterranean only about 7 per cent. of the phosphate normally found in the oceans (depth 0-4,000 m.) was measured by the "Dana" – THOMSEN 1937. According to the quantitative zooplankton investigations – JESPERSEN 1935, the eastern part of the Mediterranean is extremely poor in plankton. If the productivity of the North Atlantic is influenced by the reduced amounts of phosphate found in the watermasses as a whole, this reduction must be assumed to be rather limited.

4. Experiments with ocean water to which nutrient salts are added

It is a well known fact that it is possible to increase the growth of phytoplankton in a sample of coastal water enclosed in clear glass bottles and exposed to light, if the concentrations of the nutrient salts are increased. This procedure seems, however, not to be possible in true oceanic water. HENTSCHEL 1932 refers to such experiments made on the "Meteor" Expedition.

Table 14 (after HENTSCHEL 1932).

	Initial count, bottle a	Initial count, bottle b	Count after 26 hours, bottle c, phosphate added	Count after 26 hours, bottle d, no phosphate added	Count after 37½ hours, bottle e, phosphate added
diatoms	244	237	132	99	6
coccolitho-phorides	672	938	249	165	66
dinoflagellates	996	1405	297	650	369

At the "Meteor" Station 254 in the Southern Atlantic near the Equator, surface water was enclosed in 2 litres bottles which were suspended near the surface for either 26 or 37½ hours. Phosphate was added in 2 bottles but not in a third. The plankton was counted at the start of the experiment and after 26 and 37½ hours. Table 14 shows the results.

It is obvious that the plankton cannot tolerate enclosure in the glass bottles for 26-37 hours. Under these circumstances it is impossible to see any effect of added phosphate. During the "Dana" Expedition the culturing of oceanic phytoplankton in glass bottles was similarly found to be impossible – unpublished observations by the senior author.

During the cruise of the "Galathea", four series of experiments were made with addition of various nutrients to surface water from the ocean. In order to avoid damage of the plankton algae due to a prolonged stay in the bottles, experimental times from 4 to 5 hours only were employed. It was impossible to discern any effect in any of the four series. The experiments were made in the illuminated tank. Two of these series are presented below. The experiments given in Table 15 were made with ocean water poor in plankton collected about 600 miles northeast of Hawaii. The experiments given in Table

Table 15. Experiments in the illuminated tank with addition of nutrients to surface water enclosed in bottles. 31. March 1952. Position 148°32'W, 26°52'N. Experimental time 5 hours.

	Addition in mg. per litre		Relative rate of photosynthesis
	phosphate -P	nitrate-N	
A	0	0	100
B	0.1	0	97
C	0	0.1	107
D	0.1	0.1	90

16 were made with rather plankton-rich water collected 140 miles South of Panama.

In both series the variation in the rate of photosynthesis is of the same order of magnitude as in the parallel samples – cf. p. 62. Hence no influence of the addition of nutrients could be observed. This, is however, by no means an indication that the nutrients already were present in optimum concentrations in the surface water used for the experiments. This was perhaps the case in the series given in Table 16 but not so in the other series (Table 15). It seems impossible to increase the photosynthetic rate by addition of nitrate and phosphate either momentarily or in the course of a few hours, even if nitrate or phosphate is the absolutely limiting factor – cf. STEEMANN NIELSEN and AL KHOLY 1956. Experimental times of much longer duration would be necessary. As already stated, oceanic plankton does not seem to tolerate such a treatment.

Table 16. Experiments in the illuminated tank with addition of nutrients to surface water enclosed in bottles, 10. May 1952. Position 79°30′W, 6°52′N. Experimental time 5 hours.

	Addition in mg. per litre		Relative rate of photosynthesis
	phosphate -P	nitrate-N	
A	0	0	100
B	0.1	0	103
C	0	0.1	89
D	0.1	0.1	105
E	0.3 ml. distilled water added per bottle (300 ml.)[1]		101

1. The same amount of distilled water was added to each bottle together with nitrate and phosphate in B, C, D. This special experiment was made in order to prove that the distilled water was not poisonous.

C. INFLUENCE OF LIGHT

The light dependence of photosynthesis in cultures of plankton algae has been rather intensively studied during recent years – cf. RABINOWITCH 1949. The growing of algae in large scale cultures or even in pilot plants has also furthered our present knowledge – see BURLEW 1953. Howewer, plankton growing under natural conditions in the sea shows light dependant features of photosynthesis which cannot be satisfactorily investigated in the laboratory. In spite of all the work already done, our knowledge of the influence of light on phytoplankton production in nature still remains incomplete. During the "Galathea" Expedition an attempt was made to remedy this deficiency to some extent.

At higher latitudes the instability of the water-masses may be an important factor regulating or even impeding the growth of plankton algae – cf. BRAARUD and KLEM 1931, STEEMANN NIELSEN 1935 and SVERDRUP 1953. Under such conditions plankton algae are unable to utilize the light energy penetrating the surface. The duration of the stay of a single cell in the euphotic layer is too short. In none of the areas investigated by the "Galathea" was the instability of the surface water-masses of importance, at least during the time of the year when the expedition visited the area. Discussion of the important question of the influence of instability is hence inappropriate here.

1. Experiments on the dependence on light intensity in marine plankton algae

A knowledge of the dependence on light intensity in the photosynthesis of the marine plankton algae is a necessary background for understanding organic production in the sea. Laboratory experiments using cultures of algae are of only limited importance. The photosynthetic mechanism in algae is highly unstable, and depends on the special conditions during the cultivation. Very few investigations have been made previously on the light dependence in plankton algae just collected in the sea- PETTERSON *et. al.* 1934, STEEMANN NIELSEN 1937. No investigations concerning oceanic plankton have been published previously.

Altogether 12 experimental series with surface water having the normal content of phytoplankton were made during the "Galathea" Expedition. These were made in order to investigate the dependence of the rate of photosynthesis on light intensity. Nine of these series were made with tropical ocean water. As some of the bottles containing the sea water were placed in an open aquarium during the experiments, these could be made only in calm weather. The experimental time was 4 hours for all the twelve series. The experimental procedure is described on p. 61. The temperature was the same as that of the surface water.

Figs. 32-35 show light assimilation curves from

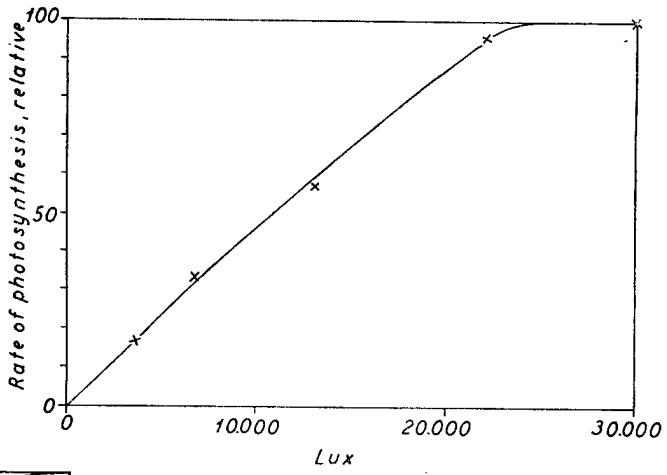


Fig. 32. Light intensity and rate of photosynthesis in oceanic tropical surface plankton (St. 518). Maximum rate = 0.29 mg. C per m.^{3} per hour.

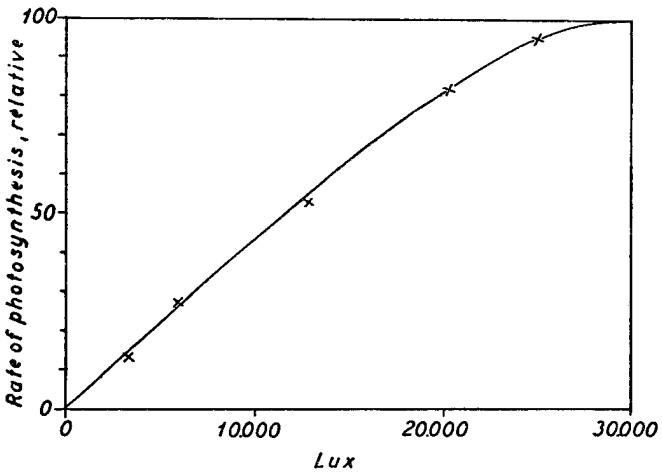


Fig. 33. Light intensity and rate of photosynthesis in oceanic tropical surface plankton (St. 511 a). Maximum rate = 0.52 mg. C per m.^{3} per hour.

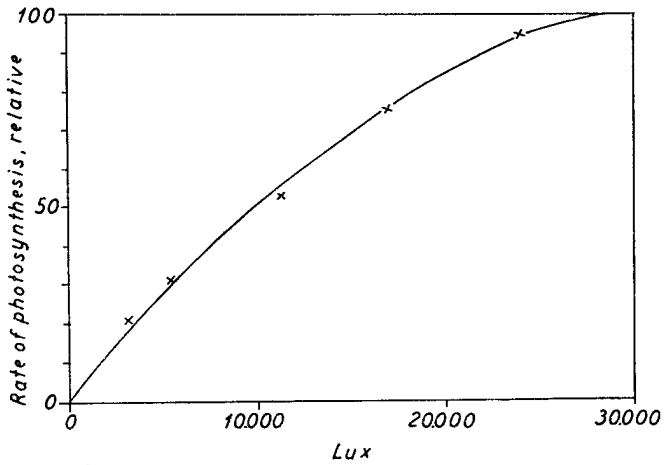


Fig. 34. Light intensity and rate of photosynthesis in oceanic tropical surface plankton (St. 515 a). Maximum rate = 0.88 mg. C per m.^{3} per hour.

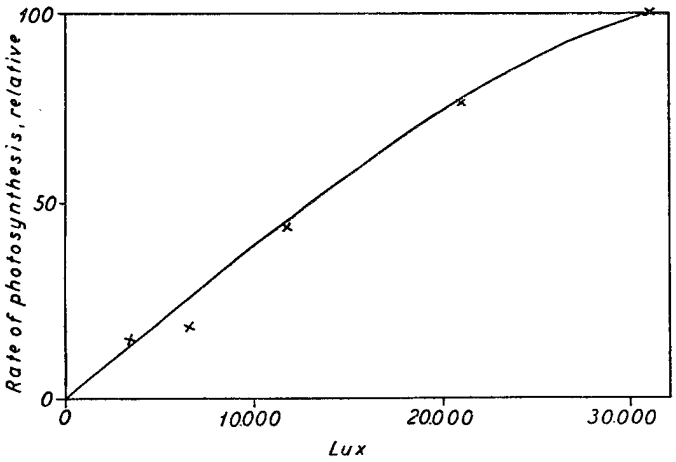


Fig. 35. Light intensity and rate of photosynthesis in oceanic tropical surface plankton (St. 519 a). Maximum rate = 0.41 mg. C per m.^{3} per hour.

four of these experiments with tropical ocean water. The maximum photosynthetic rate was put at 100 per cent. in all experiments. The single measurements are given directly without corrections. The correction factor for C-14 discrimination is without importance for a relative curve, as all single measurements has to be multiplied with the same factor. The rate of dark fixation was not measured in these series. But according to all the measurements of dark fixation in oceanic water the rate varies between about 1 and about 5 per cent. of the rate in optimal light. As the ratio rate of respiration to rate of optimal photosynthesis otherwise would be extremely low, it is better to assume that the rate of dark fixation in the present series was maximum. If the dark fixation is put a 5 per cent, the curves drawn in Figs. 32-35 has to be displaced downward by 5 relative units. To get the curves for net production we have to take into account that about 60 per cent. of the respiratory CO_2 is identical with CO_2 just assimilated (cf. p. 56.). If the ordinate and the curve corrected for 5 % dark fixation would intersect at a point – 5 below zero – as it approximately would do in the experiments presented in Figs. 32-35, the curve for net production and the ordinate would intersect at a point $-\frac{5 \cdot 100}{60} = -8$. The whole curve has to be displaced downwards by another 3 units. The rate of respiration is thus about 8 per cent. of the rate of optimal photosynthesis. If the curve corrected for dark fixation instead has to be corrected to gross production it has to be displaced 5 units upward. This curve is thus identical with the curve drawn according to the original measurements. The curves presented in Figs. 32-35 thus illustrate gross production.

The experiment made at Station 518 (Fig. 32) illustrates the most oligotrophic water investigated by the "Gålathea". According to the experiments, the rate of photosynthesis under natural conditions at the surface was 1.5 mg. C per m^3 per day. The curves from all the four experimental series presented in Figs. 32-35 are very similar. They can therefore be treated together. There is found no indication that the curves from very oligotrophic water should deviate materially from those from more normal water – cf. RYTHER 1954.

The slope of the lower linear part of the relative curves was practically the same in all the series where tropical ocean water was employed; 50 per cent. of the maximum rate of photosynthesis was found at light intensities varying between 10.000 and 13.000 lux. The maximum rate of photosynthesis was reached at about 25.000-30.000 lux. It was impossible with the equipment available to make experiments on board the "Galathea" at higher light intensities than 30.000 lux. The "in situ" experiments – cf. p. 58 ff, Figs. 9-12 – give information about the photosynthetic rate at really high light intensities. According to these experiments, the average rate of photosynthesis at the surface during a day is only about 60 per cent. of the average rate at the "best" depth – i.e. the depth showing the highest rate of photosynthesis. The photosynthetic rate at the "best" depth during the day is 70-80 per cent of the maximum rate on the average. It may thus be said that the average photosynthetic rate at the surface in bright weather during the whole day is about 50 per cent. of the maximum rate. During the middle of the day, the rate must be decidedly lower than 50 per cent. The light intensity may be estimated to be about 100.000 lux during the middle of the day. A considerable light inhibition was thus found at this light intensity.

The shapes of the curves (Figs. 32-35) indicate that light inhibition already is of importance at about 30.000 lux. The curves could not be adequately described by the equation of SMITH, 1937, 1938:

$$K\,I = p/(p^2max\text{-}p^2)^{1/2}$$

in which K is a constant that locates the curve on the I axis, I is the light intensity, p is the rate of photosynthesis at I, and p_{max} is the asymptotic maximum rate of photosynthesis. The equation holds at the lower light intensities but not at the higher. While the theoretical curve continues to ascend, the actual values fall off, indicating the onset of processes other than photosynthesis.

Light inhibition is found near the surface on bright days not only in the Tropics but also in temperate waters during summer – see e.g., STEEMANN NIELSEN 1951. Even in the high Arctic – 70°N – such a light inhibition may occasionally be observed at the surface – unpublished results by the senior author. Working with freshly collected late-autumn plankton from the Sound, Denmark, STEEMANN NIELSEN 1937, in one of the three series under laboratory conditions found a distinct reduction of the photosynthetic rate at the relatively low intensity 23.000 lux, the highest light intensity employed.

The light inhibition directly observed at high light intensities cannot be due to chlorophyll inactivation – cf. STEEMANN NIELSEN 1952 a. The maximum rate

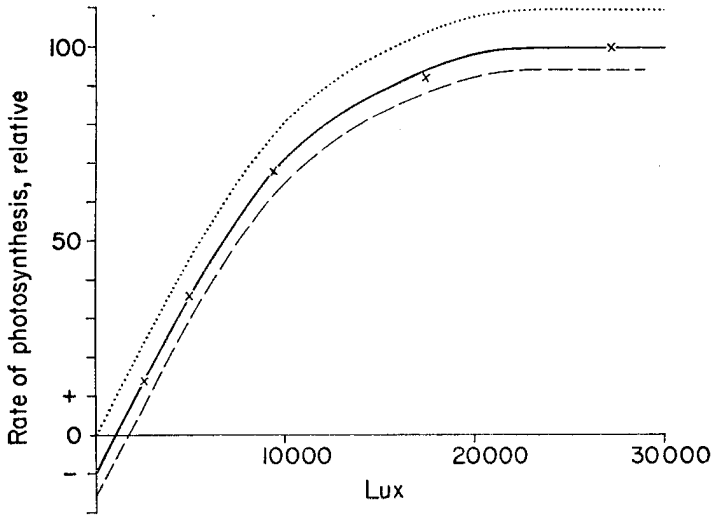


Fig. 36. Light intensity and rate of photosynthesis in the Tasman Sea (St. 599a). Maximum rate = 0.74 mg. C per m.^{3} per hour. Dashed line = net production, dotted line = gross-production.

of photosynthesis is independent of chlorophyll concentration. A chlorophyll-activated decomposition or inactivation of some enzymes of importance in photosynthesis very likely takes place. If the algae showing light inhibition is transferred to a lower, but still saturated light intensity, the rate of photosynthesis gradually regenerates, which shows that the enzymes in question must be re-activated or reproduced; cf. STEEMANN NIELSEN 1949, Fig. 13.

In Fig. 36, a relative light-assimilation curve is presented from an experimental series with surface plankton from the Tasman Sea – 46°S – during the middle of the southern summer. The measurements corrected for dark fixation (1 %) are given directly. If 60 per cent. of the CO_2 given off during respiration is identical with CO_2 just assimilated, the dashed curve represents net production (relative) and the dotted curve gross production (relative).

The rate of respiration is 14 per cent. of the optimal rate of photosynthesis. The compensation point is found at 1.700 lux. The curve for gross production resembles those made with tropical plankton. There is a distinct difference to be seen, however. Half of the optimal rate was achieved at 6.000 lux (10.000-13.000 lux in tropical plankton). In arctic surface water during summer, it is found at about 5.000 lux; cf. STEEMANN NIELSEN and HANSEN under preparation.

In contrast to the "Galathea" Expedition, incandescent light, however, was used. Lux is a measure of light without much sense if the sensibility of the human eye is not taken into consideration. A comparison of results after use of light sources with different spectral composition is in fact meaningless.

It was intended to make experiments during the expedition with plankton from the lower depths of the photosynthetic zone. Owing to other work these experiments were indefinitely postponed. During recent investigations in the North Atlantic and in Arctic waters a considerable number of light assimilation curves has been obtained using water collected at all depths of the photosynthetic layer (STEEMANN NIELSEN and HANSEN). Fig. 37 presents such a typical curve from the lower part of the photic layer in the Atlantic water south of Iceland. As the dark fixation of C-14 was measured it was possible to construct approximate curves for both net and gross production – the dashed line presents net production. The compensation point was found at about 700 lux. Half of the optimal rate of photosynthesis was achieved at 4.000 lux. The rate of respiration was about 10 per cent. of the rate of optimal photosynthesis. Most of the light assimilation curves of water collected in the lower part of the photic layer have shown a slightly lower ratio of

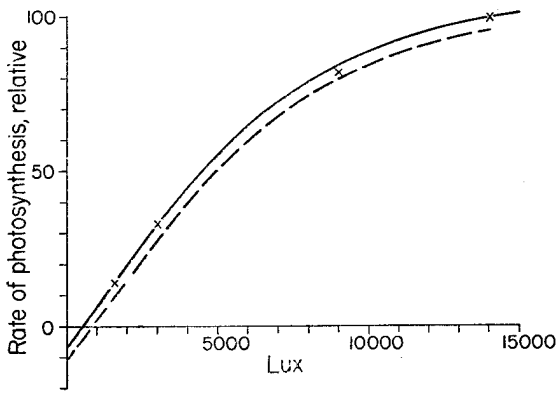


Fig. 37. Light intensity and rate of photosynthesis in plankton from the North Atlantic south of Iceland (latitude 62°N) in the begining of july. Plankton from a depth near the compensation point. Dashed line = netproduction (after STEEMANN NIELSEN and HANSEN, under preparation).

respiration to photosynthesis. At most stations the ratio for subsurface water was somewhat lower than the ratio for surface water. This is also theoretically to be expected.

It seems reasonable to conclude that maximum rate of photosynthesis in plankton from the lower depths of the photosynthetic zones in tropical and subtropical waters is achieved at a slightly lower light intensity than in the surface plankton investigated (Figs. 32-36). At 18.000 lux (the light intensity normally used in tank experiments), the maximum rate of photosynthesis was therefore probably often more or less achieved in the plankton originating from the depth where 10 and 1 per cent. of the surface light (blue + green) was measured.

When using the measurements at 18.000 lux with sub-surface plankton to estimate the productivity per surface area according to the formula presented on p. 61, it must be remembered that the formula is derived from experiments with surface plankton. In Nature, the sub-surface plankton receives only the lower light intensities, where the light dependence must be supposed to be more or less concordant both in surface and in sub-surface plankton. It is unimportant that the rate of photosynthesis of sub-surface plankton, contrary to that of surface plankton, possibly does not increase at light intensities above 18.000 lux. Under natural conditions, sub-surface plankton never receives light of such high intensities. As an approximation, the method of calculating the productivity per surface unit may be considered adequate. It must further be taken into account that about three quarters of the total photosynthesis as measured per surface area takes place above the depths where 10 per cent. of the surface light (blue + green) is found. Only about one quarter takes place below this depth – cf. Figs. 9-12.

The light assimilation curves given in Figs. 32-36 are only relative, but the maximum rate per volume of water is also given (gross production). It is of considerable interest to recalculate the curves in terms of photosynthetic rates both per amount of organic matter and per chlorophyll content in the algae.

It seems possible to make the latter recalculation although no special chlorophyll measurements were made during the "Galathea" Expedition. It may be concluded that the initial slope of a light assimilation curve is solely determined by the light absorbed by the active chlorophyll. As the rate of photosynthesis at low light intensities is determined by the rate of the photochemical processes, factors like temperature are without importance. As an approximation only chlorophyll is considered capable of transforming light energy. In thin layers of dilute suspensions of algae it may be concluded that the light absorbed by the chlorophyll is proportional to the content of chlorophyll. Even in leaves of higher plants where the absorption of light is rather complicated due to reflection within the leaf with its numerous airfilled intercellular spaces, GABRIELSEN 1948, Fig. 15, was able to show such a proportinality between light absorption and chlorophyll concentration at low chlorophyll concentrations in the leaves.

Some few light assimilation curves for plankton algae are available, where the chlorophyll concentration is known. We may as an standard use an assimilation curve of *Chlorella pyrenoidosa* grown at 6.000 lux, presented by WINOKUR 1948. In such a culture no chlorophyll is found outside the cells and all chlorophyll inside the cells is most likely in an active state. *Chlorella pyrenoidosa* as grown by Winokur contains 12 μg chlorophyll per mm^3 cells (KOK in BURLEW 1953, p. 65), a statement in accordance with experiences from other laboratories. If a CO_2/O_2 exchange factor of 0.75 is used, 0.36 mg. C is assimilated per mg. chlorophyll per hour at an illumination of 1000 lux.

For comparison we may use an assimilation curve with surface water from the extremely eutrophic Wessling See in Germany presented by GESSNER 1944, p. 725. The stabilization of the water layers in this windprotected lake is so effective that "dead" chlorophyll (i.e. chlorophyll outside living cells) hardly constitutes any important part of the total chlorophyll. If a CO_2/O_2 exchange factor of 0.75 is used, 0.41 mg. C is assimilated per mg. chlorophyll per hour at 1000 lux. This is in accordance with the value obtained by using Winokurs measurements.

Using the standard 0.36 mg. C/mg. chlorophyll per hour at 1000 lux, it is possible to determine the concentration of active chlorophyll in the water used for the experiments presented in Figs. 32-36. They are presented below. Unfortunately these values can hardly be correct. Whereas Winokur and Gessner used incandescent light, fluorescent light was used on the "Galathea". The values of lux thus are not strictly comparable – cf. p. 103. The values presented below should very likely be increased by at least 50 per cent.

Station No.	Fig.	mg. active chlorophyll/m.^{3} surface water
511a	33	0.07
515a	34	0.15
518	32	0.04
519a	35	0.05
599	36	0.16

In comparing chlorophyll directly measured with an ordinary technique and chlorophyll computed from the initial slope of a light assimilation curve, it should be remembered that only active chlorophyll in living algae is included in the latter technique, whereas all chlorophyll is included in the direct measurements. As the plankton used in the present experiments was collected from the surface during the middle of the day some of the chlorophyll may have been inactive. The experiments were of short duration; cf. STEEMANN NIELSEN 1949 and 1952a. The initial slopes of the curves presented in Figs. 32-36 would possibly have been a little steeper, if the experiments had been performed during night, thus showing a higher concentration of active chlorophyll.

It is only possible, approximately – and with reservations – to recalculate the curves (Figs. 32-36) in terms of photosynthetic rate per amount of organic matter in the algae. If using the values for the photosynthetic rate per chlorophyll content, it is necessary to know the relation between the amount of chlorophyll and the amount of organic matter in the algae. No measurements of this kind were made during the expedition. It is a well-known fact that the chlorophyll concentration is low in tropical surface plankton. An analysis during summer of plankton from Dry Tortugas – about 25°N. – yielded a carbon pigment ratio of 0.045, while this ratio averaged about 0.017 at Georges Bank – 42°N., RILEY, STOMMEL and BUMPUS 1949. The pigment was unfortunately given in Harvey units, the conversion of which into chlorophyll seems to be variable (cf. Atkins and Parke 1951). As an approximation Harvey's original ratio 1000 H.U. = 0.3 mg. chlorophyll has been used. Using this ratio and assuming the weight of algae to be half that of the total plankton we obtain for Dry Tortugas 5 μg chlorophyll per mg. organic matter in the algae and for Georges Bank 14 μg, values which seem to be in accordance with other experiences.

It is assumed that the plankton from the tropical Pacific water (the light-assimilation curve of which is presented in Fig. 32) has an organic matter: chlorophyll ratio equal to the Dry Tortugas plankton. If the curve is converted to the basis of mg. organic matter produced per hour per mg. organic matter in the algae, the lower curve in Fig. 38 is obtained. The upper curve represents the experimental series from the Tasman Sea (Fig. 36) converted in the same way. The organic matter: chlorophyll ratio is assumed to be the same as at Georges Bank.

As stressed before, the curves presented in Fig. 38 should only be accepted as a first approximation. They are, however, hardly too far from the truth. They would otherwise hardly agree so well with results obtained by determining the organic matter in the plankton by measuring cell volumes – cf. p. 115.

According to the experiment with oligotrophic, tropical waters presented in Fig. 38 (lower curve), the rate of photosynthesis (real assimilatation) is $0.0735 \times 12 = 0.88$ mg. organic matter per mg. organic matter in the algae per day at 18.000 lux, corresponding to the conditions at the "best depth" – cf. p. 60. If the net production per 24 hours at the best

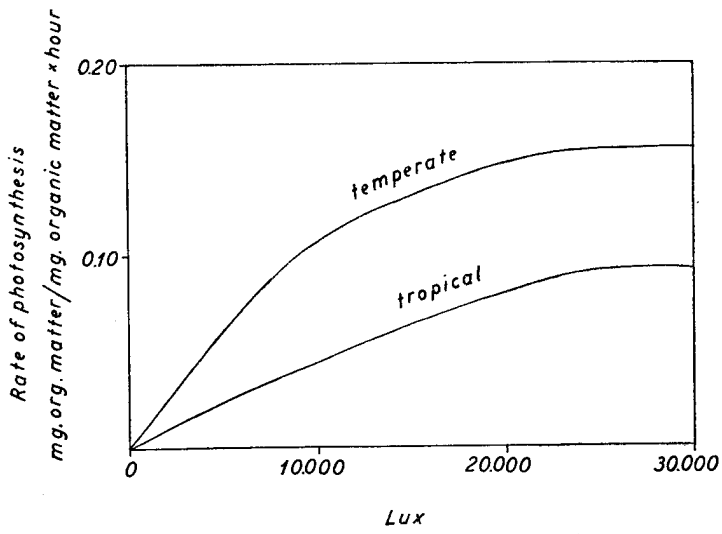


Fig. 38. Light intensity and rate of photosynthesis (mg. organic matter per mg. organic matter in the algae per hour). Upper curve: Tasman Sea St. 599a, lower curve: oceanic tropical oligotrophic surface plankton (St. 518).

depth is put at 0.80 of the gross production we obtain a daily increase here of $\frac{88 \times 80}{100}$ = about 70 per cent., assuming no losses due to grazing and sinking. For the whole photosynthetic layer the corresponding increase would be $\frac{88}{2} - \frac{88 \times 20}{100}$ = about 25 per cent. If the population of algae has to remain constant, one quarter of the population in the photosynthesis zone has to be lost every day by grazing and sinking.

According to the Tasman Sea experiments (Fig. 38, upper curve), the rate of photosynthesis (real assimilation) is $0.14 \times 15 = 2.10$ mg. organic matter per mg. organic matter in the algae per day at the "best depth". If the net production per 24 hours is put at 0.80 of the gross production we obtain a daily increase here of 168 per cent., assuming no grazing or sinking, For the whole photosynthetic layer, the corresponding increase would be about 60 per cent. on the average. An increase of this size seems to be rather likely for a productive temperate ocean area during the summer. It seems also to be probable that the increase in oligotrophic tropical parts of the oceans is less than half this size. The values are only approximate of course; but they must, at least be supposed to be of the right order of magnitude. It is nevertheless to be hoped that future investigations may produce more exact values.

2. The utilization of the light penetrating the sea surface by the algae

Compared to the light energy penetrating the surface of the sea only a small amount is utilized by the algae. According to KIMBAL 1928 the average daily light energy at a sea level during a year may be put at about 300 gram calories per cm.^{2} in the tropics and subtropics. Half of the energy is in the visible part of the spectrum. This part is practically identical with that used in photosynthesis. The average daily production of organic matter here may be put at 1.5×10^{-5} g. carbon in the organic matter per cm.^{2} – cf. p. 89, corresponding to 0.06 gram calories per cm.^{2}. This is a utilization of only 0.02 per cent of the total energy and about 0.04 per cent. of the energy in the visible part of the spectrum.

When growing under light of very low intensity, both algae and terrestrial higher plants may utilize as much as 20 per cent. of the incident energy in the visible part of the spectrum under optimal conditions. When they are growing in full sunlight, the maximum conversion is reduced to 2-3 per cent. of the visible part of the spectrum – BURLEW 1953, Chapt. 1 and 5. In the sea a conversion of nearly the same size may occasionally be found – Walvis Bay, cf. p. 75.

The reason why the marine plankton algae normally utilize only a small fraction of the light energy falling on the surface of the sea is, according to all evidence, not due to a poor utilization of the light energy absorbed by the pigments in the algae. In spite of the low chlorophyll content in plankton from the tropical parts of the oceans, the production rate of organic matter per unit of organic matter in the algae is high at optimum light intensity. According to Fig. 38 (lower curve) dealing with algae from an oligotrophic tropical habitat, the maximum rate is 0.09 mg./hour per mg. in the algae. According to the measurements by WINOKUR 1948, the corresponding value in *Chlorella pyrenoidosa* grown at 6.000 lux is 0.17 mg. The Tasman Sea plankton – Fig. 38 upper curve – yielded a value of 0.16 mg. Due to the low chlorophyll content, tropical surface plankton on the other hand utilize the light of low intensities rather poorly.

The reason why only a minimal percentage of the incident light normally is utilized by the algae in the oceans is to be found predominantly in the fact that only a minimal percentage of the light is absorbed by the pigments of the plankton algae. The rest is absorbed mainly by the water but also to some degree by particulate death material and by coloured dissolved organic matter – e.g. "Yellow Substance".

A high utilization of the incident light is possible only if the plankton algae are concentrated in a shallow photosynthetic layer. The light absorption by the water is thus minimised. In the basins of the pilot plants used for growing algae, a daily yield of up till 6 g. C per m.^{2} surface has been obtained, BURLEW 1951. The depths of the water is only a few cm. in these basins. The depth of the photosynthetic layer was only 0.8 m. in Walvis Bay where, as mentioned above, the highest rate of photosynthesis was measured during the "Galathea" Expedition – 3.8 g. C per m.^{2} per day.

The investigations of organic productivity during the expedition shows clearly that the rate per m.^{2} is inversely proportional to the depth of the photosynthetic layer. The data for 184 "Galathea"stations are presented in Table 17. These reveal a marked negative correlation between the vertical extent of the photosynthetic layer and the rate of organic production. For a depth of 100-120 m. none of the stations has a rate of production exceeding 0.24 g. C.

Table 17. Correlation between the vertical extent of the photosynthetic layer and the rate of gross production.

Rate of gross production in g.C/m.²/day	The vertical extent of the photosynthetic layer in metres				
	0–24	25–49	50–74	75–99	100–120
> 1	7	3			
0.50–0.99	6	13	12		
0.25–0.49	6	15	17	9	
0.12–0.24	2	6	15	37	12
0.0– 0.11	2	1		9	12

(The numbers within the table are numbers of stations.)

For a depth of 75-99 m. none has a rate above 0.49, the bulk showing a rate between 0.11 and 0.24 g. C. For a depth of 50.-74 m. none of the stations has a rate of production above 0.99 g. C but about a quarter of the stations in this category show rates between 0.50 and 0.99 g. C. For a depth of 24-49 m. a few stations have a rate of production above 1 g. C., but for the most part they are characterized by rates between 0.25 and 0.99 g. C. The stations with the shallowest photosynthetic layer – less than 24 m. – belong essentially to the category with a rate of production above 1 g. C.

All "Galathea" stations were divided into classes according to the depths of the photosynthetic layer: (1) depth 0-10 m.; (2) depth 11-20 m.; (3) depth 21-30 m.; etc. From every class the station showing the highest rate of production was selected. In Fig. 39 these stations are presented; the ordinate gives the rate of production and the abscissa the depth of the photosynthetic layer. The curve drawn thus shows the maximum rate of production found at every thickness of the photosynthetic layer. This curve illustrates even better than the correlation diagram, Table 17, that the rate of production per m.² of the surface is inversely proportional to the thickness of the photosynthetic layer. If the depth of the photosynthetic layer is more than 50 m. a rate of production higher than about 1 g. C/m.² cannot be expected. If the depth of the layer is more than 100 m., a rate of production higher than 0.25 g. cannot be expected.

If the rate of production per m.² is definitely lower than the curve values, the intransparency of the water must be due primarily to causes other than living plankton-algae. Here must be mentioned *inter alia* clay brought out by rivers. The stations in the Atlantic in the neighbourhood of the Congo Estuary – as far as 300 miles away, Table 4, p. 73 –

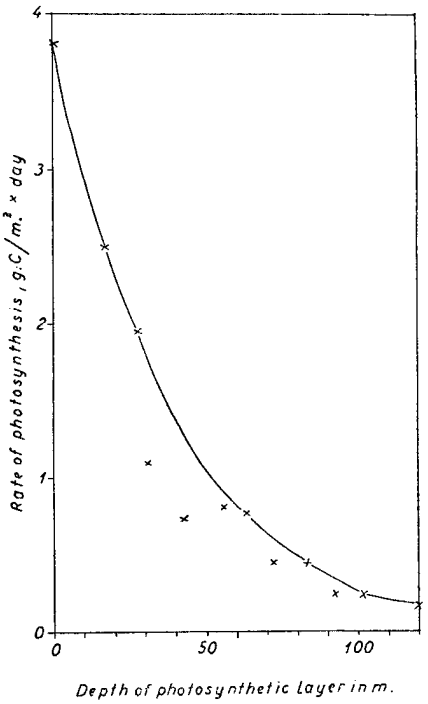


Fig. 39. Depth of photosynthetic layer and maximum rate of photosynthesis per m.² surface.

provide typical examples of this kind. Remnants from a considerable production which has been found previously in the water – "yellow matter", detritus – are able to decrease the transparency of the water in the same way. Such an influence may be found at the same place where the high productivity has taken place – such as found after a spring maximum at higher latitudes – or the influence may be found at another place due to transport of the water. A typical example of the latter was found in the area of the Atlantic immediately north of the Benguela Current proper, cf. p. 73.

The water colour is dependent on the transparency of the water. Therefore, the distribution of the water colour in the open ocean outside the influence of land must be closely similar to the quantitative distribution of plankton algae. The charts presented in Fig. 20, p. 78, show this to be true.

STEEMANN NIELSEN 1954 p. 320 ff., has shown that due to the light absorption by the water a high rate of organic production must be considered impossible with a depth of the photosynthetic layer such as occurs in the clearest ocean waters.[1] As the whole matter is obvious, it seems to be pointless to repeat the

1. In a hypothetic ocean free of any particles and dissolved organic matter 1 per cent of green light (525 mμ) and blue light (475 mμ) is found at depths of 90-95 and 160-165 meters respectively. Personal communication by dr. Jerlov. The depth of the photic layer would be about 140 meters.

calculations here. It was shown that in the clearest oceanic water a rate of production higher than about 0.4 g. C/m.^{3}/day must be considered theoretically impossible, and that such a high rate would require in addition absolutely optimum conditions for the algae. This is far from being fulfilled here.

If the depth of the photic layer is considerable, red light must be considered without importance for photosynthesis or even injurious. Red light under such conditions is only found in water layers where the light intensity is supra-optimal – cf. Figs. 9-12. Red light includes about $^1/_3$ of the photosynthetically active light.

3. The influence of weather conditions and of seasons on the rate of organic productivity

The light reaching the surface of the sea varies according to both the season and the weather conditions. In the present work, only the conditions in the Tropics and Subtropics will be discussed. Considerable information concerning organic productivity in temperate and arctic seas has now been collected from Danish sources. This material is to be presented in a special publication.

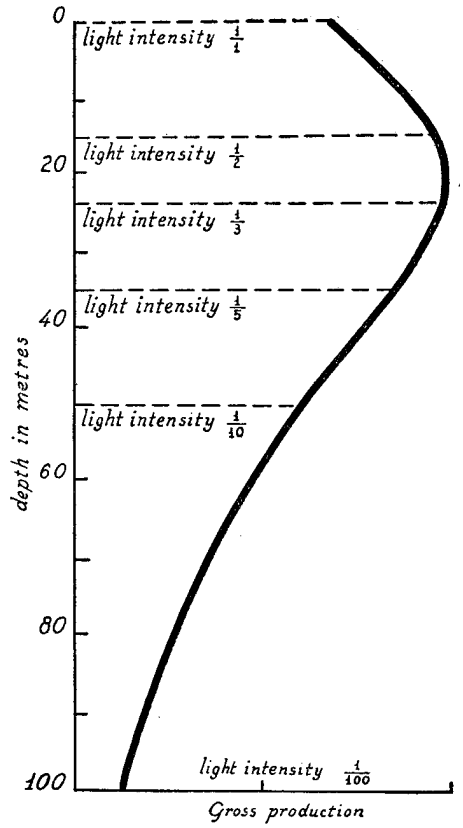


Fig. 40. Light intensity and rate of gross production at the different depths – cf. the text.

It is in fact a matter of convention to speak about limiting factors for organic production. In one way light may always be considered a limiting factor, since a reduction of the light reaching the surface will reduce the organic productivity per area in all cases momentarily as will be shown below. The whole matter is much more complicated however. All factors affecting organic productivity must be regarded as complex. A series of factors may apparently all appear as limiting and they are really so under the normal steady state conditions found in Nature.

If, however, one of these factors – e.g., light – would be permanently changed, the whole mosaic of factors would create a new equilibrium. It is thus quite likely that a permanent reduction of the light intensity at the surface (to e. g. 50 per cent. of its normal value without the other factors being affected – a rather improbable condition in Nature) in the long run would have very little influence on the organic productivity as measured per surface area. The considerations given below thus concern only the instantaneous effects which influence organic productivity by reducing the light reaching the surface.

Let us consider a tropical station at which the depth of the photosynthetic layer is 100 m. If the plankton algae are evenly distributed in the layer – and the light absorption is the same at all depths – we obtain the hypothetical curve shown in Fig. 40. This represents the daily relative rates of total photosynthesis at the different depths on a clear day. The maximum rate is found at depth of about 20 m., where the average of the blue and green parts of the light falling on the surface is reduced to nearly one-third. As the rays of the red part of the spectrum are completely absorbed in the upper 5 to 10 m., for the sake of clearness although not correctly we may disregard this part of the light. The light intensity being too high near the surface causes a reduction in the rate of photosynthesis.

If the light falling on the water surface is reduced through-out the day to one-third, the rate of photosynthesis at the surface is the same as that taking place at a depth of 24 m. on a clear day. With a decrease of the light intensity to one-third, the photosynthetic rate per unit volume of surface water (g. C/m.^{3}) thus increases by nearly 50 %. However, the photosynthetic layer is now only 76 m. deep. The curve for a light intensity of one-third is identical with that (Fig. 40 light intensity $\frac{1}{1}$ at the surface) which would be obtained if the curve is shifted

bodily 24 m. upwards. The rate of total photosynthesis measured per square metre (g. C/m.²/day) is thus about two-thirds of that measured at the light intensity $\frac{1}{1}$ at the surface. By reducing the light intensity at the surface to one-tenth, the curve (Fig. 40) has to be moved bodily 50 m. upwards, which reduces the depth of the photosynthetic layer to 50 m. The rate of total photosynthesis at the surface as g. C per cubic metre per day decreases about 15 % (or less-because of the red light) and the rate as g. C per square metre per day decreases to about 25 % of the rate at light intensity $\frac{1}{1}$ at the surface.

A day with a light intensity of only one-tenth of that on a normally clear day is in fact a very dark one, for example on which rain falls throughout the day. Only in such very dark weather does a slight reduction of the photosynthetic rate occur (per unit volume) at the surface.

The rate of photosynthesis below a unit area is affected somewhat more by the weather conditions, but the rate is seldom reduced by more than 50 %. On extremely dark days only, the rate is reduced by about 75 %.

If other hydrographic conditions are the same throughout the year, no important variations in organic productivity are presumably to be expected in the tropical parts of the oceans. In the subtropical parts the variations between summer and winter are believed to be fairly small. According to Table 25 in SVERDRUP *et. al.* (1942), in the Sargasso Sea at 30°N the average amount of radiation from sun and sky which reaches the sea surface in the darkest month of the year (December) is about 50 % of the amount in the brightest month (August). According to Fig. 40 with the other factors assumed to be the same, the rate of organic production per unit area in the darkest month is about 80 % of the rate in the brightest month. In this calculation no consideration is taken of the fact that a seasonal change being a long term change will try to create a new permanent equilibrium, thus reducing the influence of the variation of a single factor – cf. above.

D. INFLUENCE OF TEMPERATURE

Variations in temperature strongly influence the rate of respiration and the rate of photosynthesis at a high light intensity. This is true both for plankton algae and for all other autotrophic plants. It does not necessarily mean that the rate – measured per dry weight – is lower in the Arctic than in the Tropics. On the contrary, the two curves from a tropical and a temperate ocean area, presented in Fig. 38, p. 105, seem to indicate just the opposite, a result of the higher concentration of chlorophyll in the algae from the latter environment. A higher concentration of the enzymes participating in respiration and photosynthesis may counteract the depressant effect of the low temperature in the Arctic. Marine phytoplankton has not been studied in this respect. Several authors – e. g., SPÄRCK 1936 – give examples of cases in which the rate of respiration of a specific animal species is less at the same temperature for individuals which have been collected from a warmer environment than for individuals collected from colder waters. If this occurs with individuals of the same species it is probably even more pronounced when cold- and warm-water species are compared. There is no reason to believe that in this respect plants are different.

The extent to which organic productivity in the sea is directly influenced by temperature is not known.[1] The indirect influence of this factor is most likely the more important. Low temperature often seems to have a pronounced effect through inhibiting the activity of bacteria. An increase in temperature may perhaps particularly accelerate the regeneration of the nutrient salts, with the result that organic production is also accelerated.

The reason why areas in the Tropics with shallow depths practically all show a rather high rate of organic production must be ascribed primarily to the high temperature at the top of the bottom-sediments; thus a high regeneration rate of the nutrient salts is caused. By diffusion and other mechanisms the nutrient salts are transferred into the water layers above and have an almost immediate effect on the organic production of the phytoplankton. The bacteriological decomposition in the surface water of the open oceans seems to be rather limited in scope. The supply of nutrient salts seems to be effected mainly in other ways. A high temperature of the surface layers must be supposed to be of only little importance for the organic production here. The production rates measured in the open sea seem to confirm this supposition.

1. Recent investigations in the North Atlantic and in the Arctic seem to indicate that the direct influence of temperature on the rate of organic production is rather limited.

E. INFLUENCE OF SINKING AND GRAZING BY ANIMALS

The importance of grazing for the production of plankton algae was already mentioned by early investigators, thus by LOHMANN 1908 in his outstanding treatise on the plankton near Kiel. Later, HARVEY *et. al.* 1935 have contributed to the problem. FLEMING 1939 published some important theoretical considerations. CUSHING 1955 has given an interesting contribution concerning the conditions in plankton patches found in the North Sea.

As shown so convincingly by HENTSCHEL 1932-1936, the concentration of phytoplankton is extremely constant in the different areas of the Atlantic in tropical and subtropical latitudes. The phytoplankton is, however, constantly growing. According to the experiments concerning the light dependence of production presented on p. 101, the growth rate must be rather substantial even in the oligotrophic parts of the oceans.

If the lower curve given in Fig. 38 is taken as the standard for the oligotrophic tropical parts of the ocean, 0.89 mg. organic matter is produced per 12 hours at 18.000 lux per mg. organic matter in the algae. This is the gross production. 12 hours at 18.000 lux correspond to 12 hours at the "best" depth" – cf. p. 60. The daily average for the whole photosynthetic zone is thus $0.5 \times 0.89 = 0.45$ mg. per mg. of the algae. If the respiratory rate for 24 hours is put at 40 per cent of photosynthesis, the average daily net production per mg. algae organic matter is 0.25 mg. If no loss of algae took place, the algal concentration would be doubled in about 4 days. As this does not happen, there must be a simultaneous loss of algae amounting to about $^1/_4$ of the algae daily, on the average.

This loss may be due to 1) sinking below the photosynthetic layer, 2) grazing by animals and 3) death and decay of the algae. The last possibility will not be discussed here as it must be assumed to be of minor importance only. No real information is available. CUSHING 1955 uses the percentage of empty diatoms as a measure. Empty diatoms may, however, result from their consumption and excretion.

Sinking, on the other hand, must be assumed to be of considerable importance. The vertical plankton distribution in the South Atlantic according to the "Meteor" gives very instructive information. HENTSCHEL 1936, Abb. 68, has shown that according to the whole material from the expedition the concentration of total plankton at a depth of 100 m. is less than $^1/_{10}$ of the concentration at the surface. At 200 m. depth it is less than $^1/_{100}$. This figure is a little misleading, however, as the coastal stations with a shallow photosynthetic layer and a high concentration of plankton tend to reduce the relative concentrations at the depth of 100 m., 200 m. and more.

We have therefore taken the 25 stations from the central minimum area of the South Atlantic – profiles VI, VII and VIII – and computed the average plankton concentrations at the different depths 0-1000 m. We have taken only the sum of coccolithophorides, diatoms and dinoflagellates, thus including all the important producers of organic matter. The distribution of plankton is rather homogeneous in this area.

As the depth of the photosynthetic layer is a little more than 100 m. in the area in question, it is seen that the concentration of phytoplankton at a depth of 200 m., i.e. at a depth less than 100 m. deeper than the lower boundary of the photosynthetic layer, is decreased by a factor of 10; cf. Table 18.

In the next 200 m. the phytoplankton concentration drops only by a factor of about 5; per 100 m. thus by a factor of only 2.2; in the next 300 m. by a factor 1.5 per 100 m. and in the next 300 m. by a factor 1.1 per 100 m. If the sinking rate is the same in all these water layers – a supposition which, however, by no means has to be correct – it means that the rate of grazing must be considerably higher in and near the photosynthetic layer than further below. This is, however, not surprising. It must be assumed that there is a lower concentration limit for phytoplankton below which the grazing animals cannot afford to work. Unfortunately the whole matter of grazing is only little investigated (cf. e.g. GOULD 1951). We can, however, from the presence

Table 18. The vertical distribution of phytoplankton (coccolithophorides, diatoms, dinoflagellates) in the central minimum area of the South Atlantic (calculated after Hentschel).

Depth in m.	Number of cells per liter
0	2600
50	3600
100	2400
200	287
400	60
700	16
1.000	13

of grazing animals in the oligotrophic parts of the ocean, conclude that it is possible to collect sufficient food by eating plankton algae at least in the photosynthetic layer and a little further down, although considerably more work must be done by the zooplankton compared to the work necessary in more plankton-rich water.

In the photosynthetic layer, the highest plankton concentration is found at a depth of 50 m. Both at the surface and at a depth of 100 m. the concentration is considerably lower. This vertical distribution is in rather good agreement with the vertical distribution of potential productivity as found in areas of the same kind during the "Galathea" Expedition.

An attempt was made to obtain information on grazing by experiments on the "Galathea". Very little faith was put in these experiments however. It is far from certain that the grazing animals behave normally when enclosed in a rotating bottle as was used in these experiments. Further, only 300 ml. water samples could be used, a quantity very far from being representative of an open ocean in respect to the grazing organisms. According to Hentschel, less than 10 metazoes were found per 4 litres in the upper 50 m. layer in the oligotrophic parts of the Atlantic – cf. Fig. 20d. p. 78. The experiments were made at 56 stations altogether, all during the latter part of the expedition.

These were made by taking water from the surface and illuminating three 300 ml. samples in the tank for 4 hours. One sample was filtered through finest bolting silk (No. 25) before the start of the illumination, one was filtered in the same way after the end of the illumination, and one was not filtered at all. The difference between the photosynthetic rate of the first and the second of these samples should theoretically represent a measure of grazing; other explanations may be given, however. The phytoplankton from the open ocean often seems to suffer somewhat by being filtered through the silk. At the majority of the stations a slightly higher photosynthetic rate was found in the samples filtered after the experiments than in the samples filtered before, thus indicating a damage of the photosynthetic capacity by filtering.

At some few stations "grazing" was possibly observed experimentally. However, it seems safest not to put any stress on these observations.

As shown on p. 106 the daily loss of phytoplankton in the photosynthetic layer in the tropical oligotrophic parts of the ocean amounts to about 25 per cent. – equal to the daily increase due to photosynthesis. The lower curve (Fig. 38) was taken as a standard. In temperate parts of the ocean on the other hand, the rates of both processes are pronouncedly higher. If the daily increase in organic matter in the Tasman Sea – see the upper curve Fig. 38 – is treated in the same way as done for the station given in the lower curve the daily increase of organic matter in the whole photosynthetic layer amounts to 60 per cent. The daily loss due to sinking and grazing therefore may be expected also to be about 60 per cent. The daily increase of organic matter is very likely somewhat higher in really eutrophic areas both in the Tropics and at higher latitudes.

Without a mathematical treatment it is difficult to estimate how much of the losses in the photosynthetic layers are due to sinking and how much are due to grazing. If we consider all water layers as a whole, however, most of the plankton which is lost in the photosynthetic layer ultimately seems to be eaten by animals. The vertical distribution of phytoplankton normally found indicates that a considerable rate of grazing must take place in the water layers immediately below the photosynthetic zone. It would otherwise be difficult to understand how the phytoplankton concentration drops by a factor 10 per 100 m. in the first 100 m. below the lower limit of the photosynthetic layer, whereas it only drops by a factor varying from 1.6 to 1.1 per 100 m. between 400 and 1000 m. – cf. Table 18 p. 110. It may be supposed that about 95 % of the algae consumed daily is eaten in the uppermost 200 m.

In the Appendix 2, Mr. K.P. Andersen, M. Sc. has treated the "Meteor" counts presented in Table 18 mathematically. By means of some simple assumptions and the rates published in the present work regarding the production of organic matter in the oligotrophic tropical-subtropical parts of the oceans, the rate of the grazing going on at the different depths and the sinking velocity are computed. The latter (about 11 m per day) is comparable with the velocity for such areas given by other workers, RILEY, STOMMEL and BUMPUS 1949. According to Mr. Andersen's calculations 99 per cent. of the algae consumed is eaten in the uppermost 200 m. The sinking velocity is most likely estimated somewhat too high. This is mainly due to a specific oligophotic plankton being found first of all at a depth of 50-100 metres.

The rates of grazing offered by Mr. Andersen in the appendix 2 in terms of number of algae eaten

have been converted into mg. carbon per m.^{3} and day. The total grazing has been put at $60 \times 0.75 =$ 45 mg. carbon/m^2 $\times$ day (= net production). As mean values for grazing in the central, tropical + subtropical, oligotrophic areas of the oceans we obtain the following mean values.

depth in m.	grazing (mg. carbon/m.^{3} per day)
50 – 0	0.24
100 – 50	0.35
200 – 100	0.14
400 – 200	0.01
> 400	< 0.01

We may thus conclude that the animals eating phytoplankton seem to be able to handle the grazing effectively even in the oligotrophic parts of the ocean. How they manage to deal with the considerable volume of water necessary is another problem not yet adequately solved – cf. CUSHING 1955. It must, however, be supposed to cost a considerable amount of energy to collect the necessary food in oligotrophic water, as already pointed out on p. 110. Whereas the major part of the food digested may be used for growth if food is plentiful, only a minor part may be supposed to be available for growth if food is scarce, the major part being used for the production of energy necessary for collecting food. It could therefore be expected that the mean lifetime for the single individuals of zooplankton animals is much longer in oligotrophic areas than in eutrophic areas. Although the production of these animals is low, the standing crop may be relatively higher. In Section H some indications of this will be presented.

One of the last links in the food cycle – the fishes – according to all evidence are scarce in the extremely oligotrophic parts of the oceans. This is presumably a necessary condition for the existence of a relatively high – although in reality nontheless low – standing crop of zooplankton. It may perhaps be concluded that a certain minimum concentration of zooplankton is necessary for most fish species. Below that concentration fish cannot exist at all; at least only a few especially adapted species. The concentration of zooplankton in the most oligotrophic parts of the oceans is thus probably too low for maintaining a real stock of many fish species, although this zooplankton has a higher concentration – higher standing crop – than expected according to its production. It may be mentioned that oceanic birds, which also are dependent on the zooplankton, are practically absent in the very oligotrophic parts of the oceans like the Sargasso Sea – cf. JESPERSEN 1937.

From certain quarters – cf. HARVEY 1955 – the idea is continually put forward that a harmonic balance is unlikely to occur in nature, where the animals enjoy alternating periods of overeating and starvation and where the equilibrium between standing crop of plants, herbivores and carnivores is continually passing in and out of balance.

Against this assumption it may be mentioned that those investigations which technically may considered by far the most reliable present evidence of just a very significant and constant balance between the phytoplankton and the zooplankton. The investigations in the Baltic near Kiel by LOHMANN 1908 and by HENTSCHEL 1932-1936 in the Atlantic must be mentioned particularly. The present investigations give further evidence from the oceans, just as unpublished recent investigations in Danish Waters and in Danish Lakes. The problem is discussed further in Sections F and H.

F. THE INTERACTION OF THE FACTORS LIMITING OR CONTROLLING THE PRODUCTION OF ORGANIC MATTER IN THE SEA

In the introduction to this section it was stressed that the different factors influencing the organic production hardly can be treated separately. In spite of this, these factors were discussed separately. Due attention was paid to the indirect influence by other factors. An attempt at synthesis will now be made.

Taking all seas as a whole, it may be stated – as an approximation at least – that the replenishment of the nutrients in the productive surface layers is the essential factor determining the size of organic productivity. The amounts of nutrients – particularly nitrate and phosphate – which annually are made available for the plankton algae by upwelling, turbulence and regeneration, determine the total productivity of all oceans. For instance if we knew exactly the annual replenishment of phosphorus in the surface layer of all seas we could compute the total productivity measured as carbon by multiplying the phosphorus content by a factor of 40-50, as was done for certain special areas.

Generally speaking, it may be stated that light as a whole is available in sufficient quantity to provide

the energy necessary for a production equivalent to the annually available P and N in the surface layers. In certain areas or at certain times of the year, light energy is insufficient locally or temporarily. In areas with upwelling, the whole amount of nutrient salts conveyed to the surface is mostly not utilized at that place; the nutrients are distributed over a much wider area by horizontal currents. At high latitudes during winter, light is insufficient for a production utilizing all of the nutrient. During the spring maximum however this takes place. Integrated over the whole year and for all seas, light energy is sufficient to keep in step with the replenishment of the nutrient salts. Some parts of the Antarctic must probably be excluded, because of too strong vertical mixing affecting too poor light conditions for the single algae, leading to a decrease in the organic production. The phytoplankton is not able to utilize the light during the summer to the extent that all phosphate and nitrate near the surface is assimilated (GRAN 1931).

As a theoretical possibility it could be supposed that the light intensity reaching all sea surfaces would be increased by e.g. 50 per cent. The total annual organic production would then be supposed to increase in the sea. However, the main reason for this increase would, not be primarily the direct effect of the increase in light intensity on photosynthesis, but mainly the more indirect effect due to an increased water circulation in the oceans together with a faster regeneration of the nutrient salts due to an increased temperature in the seas.

On p. 108 the effect of a temporary variation of the light intensity on the organic production was discussed. It was also shown here that the two factors, light intensity and nutrient supply, mostly are matched in such a way that apparently they both seem to act as limiting factors at the same time. If nutrient supply is high, the depth of the photosynthetic layer is shallow due to absorption of light by the big standing crop of algae. A considerable part of the light is thus used for photosynthesis. If, on the other hand, the nutrient supply is scanty, the depth of the photosynthetic layer is considerable, since the population of algae absorbs only a small proportion of the light and utilizes it for photosynthesis. The major part of the light is thus absorbed by the water. In both cases a temporary decrease of the light intensity due to weather conditions influences the organic production. As the light intensity during a clear day is superoptimal for algal photosynthesis near the surface, the decrease in productivity on dark days is only rather limited (see p. 109).

In section D the idea was stressed that the influence of temperature on organic production primarily is indirect. An increase in temperature increases the bacterial and enzymatic regeneration rate of the nutrient salts. The influence of the last mentioned factor, grazing, seems to be of a much more complicated nature. Grazing certainly is of importance for the regeneration of the nutrient salts, since the first steps in these regenerations consist mostly of processes going on in the grazing animals after the algae have been eaten by them.

The influence of grazing is much more intricate, however. Regeneration of the nutrients can take place without the help of the animals eating the algae, although grazing certainly is of importance in this respect. At least as important, however, is the influence of the grazers in maintaining the stock of plankton algae at a level suitable for the available growth conditions. Whereas the supply of nutrient salts and partly light energy may be characterized as the limiting factors for the organic production, grazing may be better characterized as the controlling factor. Without grazing, organic production by the plankton algae could not be maintained under the static conditions mostly found in Nature. The consumption of algae by zooplankton has the effect that plankton algae in Nature rarely are found in a state where their growth is absolutely limited by deficiency in nutrient salts.

When growing plankton algae in cultures under laboratory conditions, quite another picture than that normally seen in nature is mostly obtained. In the laboratory, lack of nutrients – e.g., those containing N and P – in a very short time produce an absolute deficiency of these elements, – cf. AL KHOLY 1956. The algae are transferred into a state where they are not growing at all. The respiratory rate is more or less unaffected, while the rate of photosynthesis is much reduced. After a renewed supply of the lacking nutrient, it takes a considerable time – in *Chlorella* thus more than 24 hours – before growth is starting again – AL KHOLY 1956. The rate of photosynthesis is unaffected for at least many hours – cf. STEEMANN NIELSEN and AL KHOLY 1956.

If no grazing animals were found, e.g., in the oligotrophic, tropical parts of the oceans, we should very likely expect short periods with relatively much plankton alternating with long periods when practically no algae were found. Hentschel's investigations during the "Meteor" Expeditions have indisputably shown that on the contrary the standing crop of algae is exceedingly constant here both in regard to

place and time. If no grazing animals were present, a population of plankton algae would be assumed to absorb completely the nutrient salt being most pronouncedly in the minimum. The algae would continue growth until the element in question would be in absolute minimum also in the cells of the algae. Growth would thereafter stop completely and the population would slowly but steadily sink into deeper water layers. As the replenishment of the nutrient salts is a slow process in the area in question, it would probably take a considerable time before new production of algae could be started.

The presence of the grazing zooplankton alters the picture completely. The development of an algal population able to utilize the nutrients completely and to produce absolutely deficient algae, is prevented. The result is the existence of a small but rather stable population of plankton algae. The growth rate is certainly reduced compared to the rates found when a higher supply of the nutrient salts is available. A daily growth rate of about 25 per cent. per day on the average in the photic zone may be estimated for these oligotrophic areas – cf. p. 106. This growth rate is identical with the daily loss due chiefly to the grazing by the zooplankton. Remarkably stable populations of algae and animals are thus found, as was shown by HENTSCHEL 1933.

According to the important contribution by FISH 1954 concerning the zooplankton in the northern Sargasso Sea, there seems to be a rather marked biological cycle here. Short periods of relatively high – although in fact low – zooplankton concentrations alternate with periods of very low concentrations. It must, however, be kept in mind that because of the rather coarse silk used for the nets, such as also mentioned by Fish, nauplia and the early stages of the small copepods were not caught. Per cubic metre only about 200 metazoa on the average – mostly copepods – were found. In the central part of the South Atlantic Eddy – comparable with the Sargasso Sea – HENTSCHEL 1933 using a technique applicable also for animals of small size, found at least 5 times as many metazoa per $m.^3$ on the average. No marked fluctuation – neither seasonally nor locally – in the total number of metazoa was indicated in the South Atlantic Eddy as Hentschel otherwise scarcely would have been able to demonstrate such an even distribution of zooplankton.

It seems thus rather likely that in waters like the Sargasso Sea no great variations in the total amount of "grazers" are found. The fluctation found by Fish seems principally to be explained by sequences of periods with a maximum of adult organisms alternating with periods where the zooplankton mainly consists of juvenile animals not caught by the nets employed. The short period numerical fluctuations in adult animals shown by Fish are nevertheless of principal importance.

The station worked by Fish in the Sargasso Sea was located as high to the north as latitude 35°N, where the annual fluctuation in the temperature of the upper water masses is far from negligible. The conditions for the zooplankton differ thus markedly between summer and winter. However, in the really tropical part of the oceans rather similar fluctuations in the zooplankton probably occur. These fluctuations, as in the Subtropics, would concern principally the composition in species and age groups, not the total number of grazers.

As static conditions seems to be found in most tropical parts of the oceans, the size of the standing crop of zooplankton must be assumed to be directly dependent on the size of the algal production, or better perhaps on the growth rate of the algae under static conditions.

The detailed mechanisms of this very complicated and intricate interrelation between zooplankton production and phytoplankton production are at present beyond our knowledge. We must be content with admiring Nature. It seems rather likely that external metabolites excreted by animals and plants at least have som influence on the growing rates of the plankton algae and the animals, and thus also on the establishment of an equilibrium between the plants and animals – cf. LUCAS 1947, RICE 1954.

In the northern latitudes, growth conditions for the plankton algae may often suddenly shift from being very poor to being exceedingly favourable. In the North Atlantic south of Iceland, a calm period during May thus has the effect that the water masses become stabilized due to the heating of the surface layer – cf. STEEMANN NIELSEN 1935. The low standing crop of algae – a consequence of the lacking stability – increases immediately and very quickly. At first very little grazing takes place. After the establishment of a big standing crop of phytoplankton, the grazing rate increases rapidly preventing an unlimited further growth of the algae. In some way or other, the breeding of the zooplankton in these waters must get started due to the phytoplankton production. According to MARSHALL and ORR 1952, the egg production by the hibernating specimens of the zooplankton is affected by a growing phytoplankton.

Not even Nature always seems to function perfectly. From northern latitudes, e.g., patches of the brown flagellate *Phaeocystis Pouchetia* are known. It seems that quantities of this flagellate under certain conditions exclude the zooplankton. This again seems to have the effect that the flagellates grow without control – cf. HARDY 1936b.

In all probability in some areas with special hydrographic conditions the standing crop of zooplankton occasionally may be temporarily or locally too big in comparison with the growth rate of the phytoplankton. Overgrazing will thus occur, but it seems to be on the whole without much importance in the oceans – see further p. 117.

G. STANDING CROP OF PHYTOPLANKTON AND ORGANIC PRODUCTIVITY

As already pointed out in the Introduction, the agreement in the oceans between the standing crop of algae as measured by plankton counts after centrifugation and the organic productivity by the algae seems to be surprisingly high. The quantitative picture of an ocean on the basis of the counts made during the "Deutschland" and the "Meteor" Expeditions seems to be identical in all respects with the picture to be drawn according to the measurements of organic productivity made during the "Galathea" Expedition. In most freshwater lakes a high correlation is also found between the concentration of chlorophyll and the production – cf. GESSNER 1944.

It is of considerable interest to try to transform the plankton counts into organic matter. For the most oligotrophic parts of the Atlantic Ocean, the volume of all counted algae per m.^{3} surface water according to relative abundance and size of the different species (HENTSCHEL 1932) has been estimated to be about 3.5 mm.^{3}. According to Hentschel about 3000 cells per litre were counted. If, according to WINOKUR 1948, a factor $\frac{1}{10}$ is used for converting volume in mm.^{3} to carbon in mg. about 0.35 mg. carbon bound in the autotrophic algae is thus found per m.^{3} surface water. If the light-assimilation curve from the oligotrophic oceanic surface water is used (the lower curve, Fig. 38), a rate of photosynthesis of about 0.025 mg. carbon per hour per m.^{3} at 18.000 lux should be expected. The surface water at the three "Galathea" stations in the Sargasso Sea (762, 763, 764) gave on the average a photosynthetic rate per hour of 0.069 at this light intensity. The measured production rates are thus nearly 3 times the rates computed according to Hentschel's plankton counts. It must, however, be taken into account that his centrifugation technique caused a rather considerable underestimation of the number of cells present. Comparative studies using at the same time another established method have indicated that in oceanic water about $^2/_3$ of the plankton cells may escape enumeration in the technique used by Hentschel (cf. STEEMANN NIELSEN 1933, SCHMIDT-RIES 1936 and BERNARD 1953). The statement by BALLANTINE 1953 that about 100 per cent. correct plankton counts may be obtained by a similar centrifugation technique concerns only the special conditions used by her. The plankton which was found in relatively high concentrations was concentrated by her only by a factor 10 – as against a factor 1000 used in normal plankton work.

As another example, an area of quite a different kind may be chosen. In the very plankton-rich water off the coast of Africa between 15°S and 25°S, HENTSCHEL 1932 found a plankton concentration of about 300.000 cells per litre. If the cell volume of counted algae is put at 350 mm.^{3} per m.^{3} and the loss of cells due to the technique is put at $^2/_3$, the total volume per m.^{3} is 1000 mm.^{3}, which again is equal to 100 mg. carbon per m.^{3}. By using the Tasman Sea curve – the upper curve, Fig. 38 – the photosynthetic rate at 18.000 lux is 14 mg. carbon/m.^{3}/hour. The photosynthetic rate at 18.000 lux of surface water at the four "Galathea" stations in this area (132, 136, 138, 143) varied between 3.5 and 18 mg. C/m.^{3}/hour (on the average 11 mg. C).

It can thus be stated that the measurements of the standing crop of algae investigated by the "Meteor" Expedition and the measurements of organic productivity during the "Galathea" Expedition are in rather good agreement, both in the most oligotrophic and in the most eutrophic part of the ocean. In the tropical parts of the Atlantic where the life conditions for the phytoplankton must be assumed to be very stable, variations from seasons to season and from year to year most likely are small only. There should be no reason not to compare the plankton from the "Meteor" and the "Galathea" expeditions although nearly 25 years lay between the two expeditions.

It is of course always better to compare the stand-

ing crop of plankton algae measured simultaneously with the determination of the organic productivity. At higher latitudes this is a condition *sine qua non*. From Danish waters, a multitude of such simultaneous observations is now available, which will be published elsewhere.

In the Danish investigations the plankton counts are made with Utermöhl's method (inverted microscope) – using formalin-preserved material. Such a procedure is mostly adequate, but not always. If diatoms predominate, the technique is excellent. Sometimes, however, the main bulk of algae consists of fragile flagellates which disintegrate when preserved with formalin.

Therefore, as an example of the correlation between the organic production and the standing crop of algae computed by counting the algae and measuring their cell volumes, some comparative studies made in two Austrian lakes together with Professor F. Ruttner, Lunz, will be quoted instead. The plankton counts and the determinations of cell volumes were made by Professor RUTTNER by means of fresh material. In the table presented above the gross production in mg. C per m.^{3} per day from the water layer showing the optimum light conditions for photosynthesis is compared with the standing crop of algae expressed as mg. C/m.^{3}. It is supposed – as done elsewhere in this treatise – that 1 mm.^{3} algae is equivalent to 0.1 mg. C.

	Gross production mg.C/m.^{3} per day	Standing crop mg.C/m.^{3}	Gross production (mg.C/m.^{3} per day in percentage of standing crop) mg.C/m.^{3}
Lunzer Untersee 21.7.53	18.5	14.6	127
– – 27.7.53	14.2	10.9	130
Lunzer Obersee 25.7.53	66	47	140

If the chlorophyll concentration at a maximum is put at 4 per cent. of the organic matter in the algae, we may at a maximum expect 1.5 mg. chlorophyll per m.^{3} in the Untersee at the 21th of July and 1.1 mg. at the 27th of July. According to GESSNER 1944 2 mg. chlorophyll was found per m^3 in the Lunzer Untersee in July 1941. The maximum rate of photosynthesis at an optimum light intensity may for the 21th July be estimated at about 7.5 mg. CO_2/m.^{3} per hour. The assimilation number is thus about 5 at minimum, which is in accordance with the assimilation numbers given for plankton from similar lakes, e.g. by GESSNER 1944. It may be mentioned that the assimilation numbers stated when the oxygen technique is used for measuring the rate of photosynthesis, mostly must be considered about 25 per cent. too high if a CO_2/O_2 exchange factor of 1 is used – as done by Gessner.

Theoretically, chlorophyll concentration would not seem to be very suitable for measuring the standing crop of phytoplankton. The chlorophyll concentration is first of all a factor of importance at low light intensities; cf. GABRIELSEN 1948. It has, however, been shown from many sides (e.g. by GESSNER 1944) that the amount of chlorophyll mostly – but not always – presents a relatively good measure of the standing crop of autotrophic algae. A high correlation is mostly found between the rate of photosynthesis at optimum light intensity and the concentration of chlorophyll.

During a cruise of the German Research ship "Südfall", Institut für Meeresforschung Kiel, in Danish waters in April 1956 chlorophyll measurements were made by Professor J. Krey in 24 water samples taken at a number of stations. At the same time the optimum rate of photosynthesis was measured in the same water samples by the senior author. The carbon-14 technique was employed, a water bath and optimum illumination being used. The assimilation number was normally about 5-8. A considerably lower assimilation number was found for certain water samples from relatively great depths, where the concentration of chlorophyll was extraordinarily high, in all probability due to the presence of "dead" chlorophyll, i.e. chlorophyll outside living cells.

Dr. R. W. Holmes, Scripps Institution of Oceanography, University of California, has kindly allowed us to quote some simultaneous measurements on chlorophyll a and organic production from the Pacific Ocean. The carbon-14 technique was employed. Surface water samples were trailed astern of the vessel from sunrise to noon. In the oligotrophic eastern part of the North Pacific Gyral observations were made at three stations:

Station No.	In situ production, mg.C/m.^{3}/day	Computed optimum rate of production, mg.C/m.^{3}/hour	Chlorophyll a, mg./m.^{3}	Assimilation number
TransPac 6	1.12	0.25	0.168	5.4
– – 7	0.58	0.13	0.143	3.3
– – 12	0.68	0.15	0.102	5.4

The rates of production were practically the same as found by the "Galathea" in the same area. The position of St. TransPac 6 was 36°09.2'N, 133°20'W,

that of St. TransPac 7 36°21.8'N, 134°53'W and that of St. TransPac 12 40°26.9'N, 143°32'W.

The assimilation number – i. e. mg. CO_2/mg. total chlorophyll per hour at optimum light intensity – is very near to those presented both for eutrophic and oligotrophic lakes; cf. i. a. GESSNER 1944. They are also near to those found in Danish Waters.

The concentration of chlorophyll in the photosynthetic layer in the oceans seems to vary between about 20 and about 0.1 mg./m.^{3} or a little less. When the concentration is highest the depth of the photosynthetic layer is only about $^1/_{10}$ of the depht found when the concentration of chlorophyll is very low. If the assimilation number always was the same, we would expect the rate of production to be about 20 times higher in the most eutrophic areas of the oceans compared with that in the really oligotrophic areas. According to the measurements made during the "Galathea" Expedition the organic production per surface unit was about 40 times higher in the most productive areas compared with the most unproductive areas of the oceans.

If using chlorophyll for estimating the standing crop of autotrophic algae, it must always be kept in mind that a considerable part of the chlorophyll possibly may be "dead". It seems rather likely that this normally is the case in the water masses below the photosynthetic zone. But it may be true even in surface water. At Georges Bank off the Atlantic coast of U.S.A. RILEY 1941 thus in June at St. 3961 found a O_2-production at the surface of 1.12 g./m.^{3} per day. The chlorophyll concentration was 7.0 mg./m.^{3}. At the same concentration (6.4 mg./m.^{3}) at St. 3965, also from June, the O_2-production was only 0.04 g./m.^{3}.

H. STANDING CROP OF ZOOPLANKTON AND ORGANIC PRODUCTIVITY

The zooplankton measurements in the South Atlantic – counts of metazoa in 4 l. samples – by the "Meteor" Expedition gave a distributional picture practically identical with that obtained by the phytoplankton counts – HENTSCHEL 1933. In Fig. 20, p. 78, Hentschels counts of metazoa and algae in the South Atlantic (0-50 m) are shown side by side. In the same figure the organic production per m^2 surface, the phosphate concentration and the colour of the sea are presented. In all instances the same distribution is observed. The plankton volumes from the "Dana" Expedition (JESPERSEN 1935), similarly show a striking resemblance to the measurements of productivity obtained during the cruise of the "Galathea", for the areas visited by both expeditions – cf. p. 86 and below. As the production of zooplankton must be more or less dependent on the amount of food – i.e., the phytoplankton production – this relation is quite obvious.

It is apposite to compare the present measurements of organic production at the longitudinal section in the Pacific from Samoa to Hawaii with the measurements of zooplankton volumina made by the Fish and Wildlife Service, Hawaii – KING 1954. For the phytoplankton, the correlation between the standing crop and the production is high – as shown in the section above. For the standing crop of zooplankton we must therefore expect a high correlation with both the standing crop and the production of phytoplankton.

Under special circumstances an inverted relation between quantities of phytoplankton and zooplankton may be found. At the very start of a phytoplankton bloom during spring in northern waters this seems to be normal, as the zooplankton production is delayed compared to that of the phytoplankton – STEEMANN NIELSEN 1937. Further under unstable conditions due e.g., to a concentration of zooplankton caused by currents or to the start of the dark season at higher latitudes, such an inverted relation undoubtedly occasionally may be found. Overgrazing in the sense of HARVEY *et al.* 1935 should thus be the reason for the poverty of phytoplankton, although probably many – but not all – of the cases given in the literature are artefacts only, due to the use of nets for measuring the phytoplankton crops, a method which is often very inadequate or even completely misleading – cf. GESSNER'S (1944) criticism. In coastal waters huge localised quantities of plankton larvae of bottom animals occasionally may be found decimating the crop of plankton algae – STEEMANN NIELSEN 1951. Animal exclusion in the sense of HARDY 1936 may or may not sometimes be of importance. It must also be mentioned here that practically all the observations used for demonstrating animal exclusion are based on investigations employing nets for measuring phytoplankton quantities. Normally, animal exclusion probably is of no importance at all. An inverted relation between quantities of phytoplankton and zoo-

plankton is the exception. As a rule a very clear direct relation is found if adequate sampling techniques are used such as shown for the open ocean by Hentschel.

In the early plankton literature, there was a severe controversy between those regarding oceanic plankton to be patchy in its distribution and those regarding it to be relatively evenly distributed. Hentschel's results on the "Meteor" finally proved the latter theory to be true regarding the phytoplankton in the Tropics and Subtropics. HARDY 1936c on the other hand, has given some evidence that the opposite view holds for the zooplankton.

Although the total amount of grazers does not seem to show any pronounced patchiness, as shown by HENTSCHEL 1933, Abb. 46, the local occurence of species and age groups very likely is subject to fluctuations. Such fluctuations would be comparable with the seasonal fluctuations found by FISH 1954 in the Sargasso Sea.

If the relation between the standing crop of zooplankton and organic production is considered, it is important to include only areas which can be strictly compared. Oceanic areas may not be strictly comparable to coastal areas – cf. below.

In JESPERSEN'S 1935 survey of the quantities of zooplankton from the "Dana" Expedition, only real oceanic stations, with a few exceptions, were included. It is thus possible to compare organic productivity and zooplankton volumes from all the parts of the oceans investigated by the "Dana" and the "Galathea".

Table 19.

Area	Volume in cc./per one hour haul (average) (50-300 m. wire)	g.C/m.²/ day produced by algae	Zooplankton (cc./hour): phyto-plankton (g.C/m.²/ day)
Sargasso Sea-Antilles Current	219	0.06	3.800
Indian Ocean off Africa 20°-35°S	240	0.14	1.700
Indian Ocean between Mombassa and Madagascar	389	0.16	2.400
Carribean Sea	424	0.17	2.500
Indian Ocean between Madagascar and Ceylon (Station 3924 and Station 3926 omitted)	455	0.20	2.300
North Atlantic off North Africa – 10°-25°N	1630	0.40	4.100

According to Jespersen, Fig. 27, and corresponding measurements by the "Galathea", the Table 19 is obtained. In the first column is given the mean volume of macroplankton per hour from horizontal hauls in the upper layers (50-300 m. wire, corresponding to depths from about 25-150 m.) using a 2 m. stramin net; in the second column is given the average production in g. C/m.²/day according to the "Galathea" measurements. No volumes from hauls from the Pacific are included, as the "Dana" unfortunately used a $1^1/_2$ m. stramin net for all depths in this ocean, whereas a 2 m. net was used in the upper layers in the other oceans.

The areas are taken according to those used by Jespersen with the exception that the North-Atlantic area off Africa, instead of extending from 35°-10°S, extended only from 35°S-20°S. Two of the 17 "Dana" stations from the area between Madagascar and Ceylon are omitted. These stations – 3924 and 3926 – showed rather special conditions. Vast quantities of salps were locally found here.

Although certainly too few areas are treated, and in spite of the fact that the relative zooplankton volumes from horizontal hauls are far from being an ideal measure of zooplankton quantities, the interrelation is clear. A similar interrelation could have been shown using instead the volumes of horizontal hauls from deeper layers – 1000-5000 m. wire out, depth about 500-2500 m. A net with a diameter of $1^1/_2$ m. was used here. The volumes are thus not directly comparable with those from the upper layers where the diameter of the net was 2 m. It may be mentioned that the mean volume of the hauls from the deeper layers was 291 ml./hour in the very eutrophic area of the North Atlantic off North Africa and 68 ml./hour in the very oligotrophic Sargasso Sea (including the Antilles Current). The influence of the production of organic matter by the plankton algae is thus as conspicious in the volume of zooplankton from the deeper layers as in those from the upper layers.

In Fig. 41, the "Galathea" measurements of organic production from the longitudinal Pacific section between Samoa and Hawaii (14°S-24°N) are compared with quantitative measurements on zooplankton given as cm.³ per 1000 m.³ made during a cruise of a research vessel from the Fish and Wildlife Service, Hawaii (KING 1954). Two sections were made, one at 170°W, one at 160°W. The time of the year was February-March (1951). The "Galathea" made the section during March 1952. To the south, the "Galathea" section was identical with the 170°

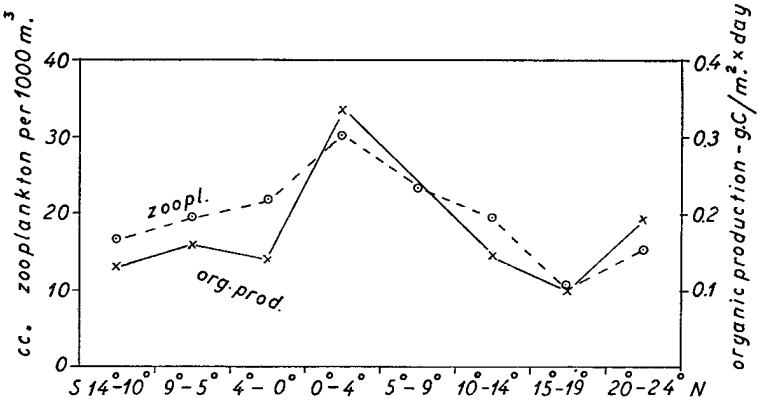


Fig. 41. Rate of organic production (Galathea) and volumn of zooplankton (after KING 1954) on a longitudinal section across the Equator, 160°-170°W during February-March. All values given are averages for 5 degrees of longitude.

W-section, to the north with the 160°W-section. In comparing the zooplankton volumes with the organic production, the 170°W-section was used south of the Equator. Between Equator and 5°N the average of the two section was used and north of 5°N only the 160°W-section. The zooplankton material as used for the comparison consisted of altogether 64 hauls, distributed nearly evenly along the section. Averages for 5 latitudes were employed.

The two curves in Fig. 41 are very similar, both showing a pronounced maximum just north of the Equator coincident with the divergence near the southern boundary of the Counter Current.

In the section p. 110 dealing with grazing, the idea was put forward that the mean life of the grazers in the most oligotrophic areas probably must be considered to be somewhat longer than elsewhere. The cause should be due to the limited food supply resulting in a slower development. The relation of the standing crop of zooplankton to the organic matter produced by the algae should thus be relatively high in very oligotrophic areas (cf. last column in Table 19). If the Sargasso Sea (+ Antilles Current) area is compared with the three areas presented immediately below, some evidence for the hypothesis may be found. The ratio of the volume of zooplankton to the rate of organic production is also high (according to Table 19) for the truly eutrophic area off the coast of North Africa. It may be assumed that this high ratio is caused at least partly by the route of the "Dana" being further offshore than that of the "Galathea". According to Hentschel 1933, Beil. 1, the concentration of phytoplankton is decidedly higher here some hundred miles off the shore than nearer to the coast. A rather attractive object for future research should be the investigation of the relation between the standing crop of zooplankton and the organic production using more adequate methods.

RILEY and GORGY 1948 have estimated the zooplankton in the northwestern part of the Sargasso Sea from quantitative hauls between a depth of 400 m. and the surface as 1-2 g. dry weight below each m^2. This would seem to agree rather well with an estimate based on Hentschel's zooplankton counts in the most oligotrophic areas of the Atlantic. The phytoplankton standing crop per $m.^2$ surface may be estimated to be about 0.5 g. dry weight according to the measurements by the "Galathea" in the Sargasso Sea (– cf. p. 77). The weight of the standing crop of zooplankton being about 3 times the weight of phytoplankton seems to be rather adequate for a region of the present kind. The daily food available for the zooplankton corresponds to the net production of phytoplankton. As shown p. 77, it is 0.04 g. C = 0.15 g. dry weight. It represents about 10 per cent. of the dry weight of the zooplankton. As a minor part of the zooplankton is carnivorous the daily diet of the herbivorous plankton animals most likely must be a little more than 10 per cent. of their own body weight. Unfortunately we do not know how much of the assimilated food is used for respiration and how much for growth and reproduction in oligotrophic areas. If food is plentiful, it has been shown for copepods that by far the most of the assimilated organic matter is used for growth and reproduction. Experiments by RILEY and GORGY 1948 in the Sargasso Sea showed that immediately after capture a crustacean zooplankton looses about 12 per cent. daily. This would mean a loss of the same size as the daily intake of food. Such experimentally found values are, however, certainly too high for the conditions in the sea. Evidence shows that the crustaceans increase their rate of respiration when enclosed in experimental bottles.

If it is assumed that in extremely oligotrophic tropical areas at least 80 per cent. of the assimilated food in the herbivorous zooplankton is used for re-

spiration, the average lifetime of such an animal would be about 50 days. This is undoubtedly a long time compared with the lifetime in more eutrophic areas at the same temperature. According to the literature survey by CUSHING 1955, the lifetime in the North Sea during spring is about 80 days for the relatively big copepod *Calanus finmarchicus*. There is, however, no reason to expect that lifetimes have to be short due to a high temperature. A high temrature may, e.g., be counteracted by a low concentration of some of the enzymes taking part in the processes going on in the cells of the animals.

According to the studies by FISH 1954 a life time of about 50 days for the Oithona species in the Sargasso Sea would seem rather appropiate. The genus Oithona includes the most abundant copepod species in this area.

In eutrophic areas the daily food of the zooplankton has been found to be considerably more than 10 per cent. of their own weight. Although the reproduction of the algae is faster here than in oligotrophic areas, the relation: weight of standing crop of zooplankton to weight of standing crop of phytoplankton, may thus be supposed to be lower than in oligotrophic areas.

It must be noted, however, that a considerable part of the organic matter in the phytoplankton in a eutrophic coastal area is not digested by the zooplankton but is either directly eaten by the bottom-living fauna or is contributed in the form of more or less undigested faecal pellets to the bottom. In the oligotrophic parts of the oceans such undigested pellets are hardly produced in any quantity by the zooplankton. With the exception of the minor part of algae lost by sinking into the abysses – cf. 110 – nearly all of the organic matter produced by the algae is presumably digested here by the zooplankton.

APPENDIX 1. THE INFLUENCE ON THE PRODUCTION RATE OF THE FILTRATION OF SEA WATER THROUGH FINEST BOLTING SILK

When at the beginning of this century Lohmann introduced the centrifuge for quantitative measurements of marine phytoplankton, he was able to show – see e.g. LOHMANN 1908 – that the fine silk net retained only a small part of the plankton algae. Despite this fact, silk nets have been used by many for estimating phytoplankton quantities and they are still in use in many countries. Warnings – such as by STEEMANN NIELSEN 1938 and by GESSNER 1944 – seem to have had only a very limited effect. It should indeed be unnecessary to give additional experimental evidence for the unsuitability of nets for quantitative phytoplankton estimations.

Some experiments on the effectiveness of nets were nevertheless made during the expedition. The reason for this was to provide a refutation of an argument often advanced by the workers still using nets; this argument is that although the bulk of the algae are lost through the nets, larger species retained are the main producers of organic matter.

As mentioned on p. 111, some special experiments were made at 56 stations during the latter part of the expedition. Surface water was used. One sub-sample was filtered through finest bolting silk (No. 25) before the start of the illumination, one was filtered in the same way after the end of the illumination and one was not filtered through the silk at all. The three samples were used for ordinary productivity measurements in the tank. They were illuminated for 4 hours. Whereas the difference between samples one and two theoretically should give information about the rate of grazing, the difference between samples 2 and 3 tells how much of the organic productivity is due to algae which are retained by the silk.

Fourteen coastal stations (depth less than 300 m.) gave an average photosynthetic rate of 82 per cent. of that of unfiltered samples if the water was filtered through bolting silk before being filtered by the membrane filter. The total variation was between 31 and 102 per cent. Only two stations from Milford Sound, New Zealand, showed a really important decrease after filtering through the bolting silk. If these two stations are omitted, the average rate of the filtered samples is 89 per cent. This means that net samples generally would have given values of about 10 per cent. of the real values.

Thirty six oceanic stations had an average photosynthetic rate of 94 per cent. if the water was filtered through bolting silk. The difference varied between 78 and 115 per cent. As the standard deviation for a single determination of a series of parallel determinations is about 6 per cent – cf. p. 62 – a difference between two parallel determinations amounting to more than 15 per cent. may be easily found.

Little stress need therefore be laid on the individual differences between the filtered and non-filtered samples. The average for the difference at all the stations must, on the other hand, be considered valid. Net samples from oceanic water must thus be supposed to give about 6 per cent. of the bio-mass of photosynthezising algae on the average. If the numbers of algae are determined instead, the difference between net samples and real quantitative samples is much higher. The big cells exclusively retained by the nets have a much higher rate of photosynthesis per cell than the average plankton algae found.

APPENDIX 2. AN ATTEMPT TO DETERMINE THE ORDER OF MAGNITUDE OF THE SINKING VELOCITY OF ALGAE, WITH INFORMATION ON THE RATE OF GRAZING AT THE DIFFERENT DEPTHS

By K. P. ANDERSEN

Let us assume that we have an ocean with a stationary number of algae per m.^{3}, and let this number A(z) be a function of the depth z alone. We assume further that the sinking velocity v m. per 24 hours is constant, that the organic production per m.^{3} 24 hours p(z), and the grazing per m.^{3} 24 hours g(z) are functions of z alone. The stationary condition makes it possible to find a relation between A(z), v, p(z) and g(z).

If we consider a water column with a cross section of 1 m.^{2} there will be A(z)dz algae between z and z + dz. During a time dt, v · A(z) dt algae will pass through a cross section at z, and vdt A(z + dz) will pass through at z + dz. During the same time dt we will have an organic production of p(z) dzdt and a grazing of g(z) dzdt between z and z + dz. This means that the number of algae between z and z + dz after a time dt will be:

A(z) dz + vA(z) dt – vA(z + dz) dt + p(z) dzdt – g(z) dzdt.

The stationary condition now gives:

A(z) dz = A(z) dz + vA(z) dt – vA(z + dz) dt + p(z) dzdt – g(z) dzdt

As A(z + dz) = A(z) + A'(z) dz we get after dividing by dt:

$$p(z)\,dz - A'(z) \cdot v \cdot dz - g(z)\,dz = O \qquad (1)$$

Hentschels Data from the "Meteor" Expedition – cf. table 18 – give us some values of A(z):

A(0)	$= 2.800 \cdot 10^6$	A(400)	$= 0.060 \cdot 10^6$
A(50)	$= 3.600 \cdot 10^6$	A(700)	$= 0.016 \cdot 10^6$
A(100)	$= 2.400 \cdot 10^6$	A(1000)	$= 0.013 \cdot 10^6$
A(200)	$= 0.287 \cdot 10^6$		

From these figures and Fig. 41 in the present treatise corrected to net production it is possible to determine p (z) under the assumption that the total production per 24 hours in the productive layer (0-100 m.) is 25 % of the total number of algae in this layer.

In this way we find:

p(0)	$= 0.82 \cdot 10^6$	p(60)	$= 0.63 \cdot 10^6$
p(10)	$= 1.19 \cdot 10^6$	p(70)	$= 0.36 \cdot 10^6$
p(20)	$= 1.42 \cdot 10^6$	p(80)	$= 0.20 \cdot 10^6$
p(30)	$= 1.37 \cdot 10^6$	p(90)	$= 0.09 \cdot 10^6$
p(40)	$= 1.17 \cdot 10^6$	p(100)	$= 0.00 \cdot 10^6$
p(50)	$= 0.91 \cdot 10^6$		

(1) can be transformed to

$$\int_o^z p\,(z)\,dz - v \cdot A\,(z) - \int_o^z g\,(z)\,dz = 0 \qquad (2)$$

For z → o (2) gives

v · A(0) = 0

As A(0) ≠ 0 this means v = 0 at the surface. It is in this way clear that v cannot be independent of z. But it is probably not too far from reality to assume that v is independent of z for z ≧ 30 m. (1) is in this way only valid for z ≧ 30 m.

From the given A(z) it seems very reasonable to put $A(z) = A_{max.}$ for z = 45; this means A' (45) = 0 and (1) gives with z = 40 and dz = 10

p(45) · 10 – g(45) · 10 = O

or

$g(45) = p(45) = 1.04 \cdot 10^6$

To determine v it is necessary to make an assumption about g(z) and this assumption is very essential for the whole problem. We will assume that g(z) is constant from 40 m. to 60 m. We now put z = 50 and dz = 10 in (1) and get:

$$p(55) \cdot 10 - v \cdot \frac{A(100) - A(50)}{50} \cdot 10 - g(45) \cdot 10 = 0$$

or $0.77 \cdot 10^7 + 0.24 \cdot 10^6 - 1.04 \cdot 10^7 = 0$

and finally

v = 11 m/24 hours

Having determined v it is now possible to estimate g(z).

(1) may written as

$$\int_{z_1}^{z_2} p(z)dz + A(z_1) \cdot v - A(z_2) \cdot v - \int_{z_1}^{z_2} g(z)dz = O$$

$z_1 = 50$ and $z_2 = 100$ gives:

$$\int_{50}^{100} g(z)dz = 30.9 \cdot 10^6 \qquad \text{mean } g(z) = 0.62 \cdot 10^6$$

$z_1 = 100$ and $z_2 = 200$ gives:

$$\int_{100}^{200} g(z)dz = 23.8 \cdot 10^6 \qquad \text{mean } g(z) = 0.24 \cdot 10^6$$

$z_1 = 200$ and $z_2 = 400$ gives:

$$\int_{200}^{400} g(z)dz = 2.5 \cdot 10^6 \qquad \text{mean } g(z) = 0.02 \cdot 10^6$$

For $z > 400$ we find $g(z) \simeq O$

As

$$\int_0^{1000} g(z)dz = \int_0^{1000} p(z)dz - v \cdot A(1000)$$

we have

$$\int_0^{50} g(z)dz = \int_0^{100} p(z)dz - v \cdot A(1000) - \int_{50}^{1000} g(z)dz = 19.6 \cdot 10^6$$

mean $g(z) = 0.40 \cdot 10^6$

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Table 20. The observations.

St No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.³ per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.² in g.C. per day
2	29.10.50	32°08′5 N	0	21.26	36.76		106	0.053	0.036
	Depth 4320 m.	14°00′ W	20	21.26	36.76			0.081	
			40	21.23	36.76			0.075	
3	29.10.50	31°17′ N	20	21.53	36.78		abt. 100	0.065	0.034
	Depth 4320 m.	14°20′ W							
4	2.11.50	21°30′0 N	0	19.93	36.40			9.10	
	Depth 62 m.	17°05′0 W	10	19.80	36.40		15	7.8	0.67
5	2.11.50	21°30′0 N	0	19.57	36.31		40	4.00	0.56
	Depth 62 m.	17°08′7 W	15	18.54	36.26			1.2	
6	3.11.50	18°20′5 N	0	26.83	35.03		abt. 60	1.9	0.55
	Depth 3000 m.	18°21′5 W	20	26.83	35.03		60	1.4	
			40	24.65	35.65			2.0	
7	3.11.50	17°10′2 N	0	26.84	35.08			0.64	
	Depth 3200 m.	18°30′0 W	20	26.33	35.35		62	0.61	0.24
			40	17.33	35.70			0.74	
11	7.11.50	14°30′0 N	0	27.33	34.60		51	0.72	
	Depth 94 m.	17°30′ W	20	21.77	35.59			0.70	0.20
			40	17.13	35.59			0.12	
12	7.11.50	14°08′5 N	0	27.67	34.97		47	0.39	
	Depth 1000 m.	17°46′ W	20	26.16	35.43			0.62	0.11
			40	18.26	35.61			0.55	
13	8.11.50	11°34′9 N	0	28.04	34.58			1.1	
	Depth 4750 m.	19°34′2 W	20	28.27	34.97		68	0.58	0.31
			40	20.91	35.53			0.88	
14	9.11.50	9°30′ N	0	27.81	34.83		84	1.1	0.46
	Depth 820 m.	17° 0′ W	20	27.71	34.92			1.1	
			40	23.43	35.53			0.89	
15	9.11.50	9°30′ N	0	28.25	33.73		63	1.4	
	Depth 290 m.	16° W	20	27.13	34.72			1.5	0.44
			40	20.59	35.55			0.96	
16	10.11.50	7°29′ N	0	28.44	31.20		65	1.1	
	Depth 340 m.	13°44′ W	90	15.83	35.57			0.24	0.41
20	13.11.50		0				28	10.00	0.77
	3 sm W off Monrovia, Liberia harbour								
	Depth 26 m.		8					2.6	
21	13.11.50		0					6.2	0.76
	500 m off entrance of Monrovia harbour		10				21	7.2	
	Depth 15 m.								
22	14.11.50	6°01′7 N	0	28.37	33.69	0.0	72	0.31	0.25
	Depth 220 m.	10°50′8 W	40	20.53	35.57	0.6		1.0	
			80	16.74	35.59	1.7		0.47	
23	14.11.50	5°31′0 N	0	27.88	34.40	0.1	79	0.44	
	Depth 2080 m.	10°42′0 W	40	19.90	35.66	1.0		1.6	0.36
			80	16.11	35.61	1.4		0.24	

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.³ per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.² in g.C. per day
24	15.11.50	3°54′ N	0	27.41	34.67	0.0	45	0.31	
	Depth 3200 m.	8°22′ W	40	22.80	35.26	0.4		1.0	0.16
			80	17.09	35.66	1.7		0.14	
25	16.11.50.	2°06′ N	0	26.45	35.39	0.0		0.17	
	Depth 5050 m.	5°58′ W	40	24.83	35.64	0.0	65	0.59	0.12
			80	16.23	35.61	1.7		0.18	
28	17.11.50	1°47′5 N	0	26.19	35.48	0.2		0.16	
	Depth 5150 m.	5°49′5 W	40	25.16	35.59	0.0	68	0.67	0.15
			80	15.99	35.61	1.5		0.37	
30	18.11.50	0°42′ N	0	25.77	35.46	0.1		0.31	
	Depth 5160 m.	5°59′ W	40	25.43	35.48	0.2	75	1.2	0.35
			80	19.49	35.68	1.1		1.2	
31	19.11.50	1°56′ N	0	26.05	35.39	0.0		0.24	
	Depth 4930 m.	4°37′ W	40	24.84	35.46	0.0	81	0.77	0.22
			80	15.13	35.57	1.5		0.48	
32	20.11.50	4°05′ N	0	27.81	34.79	0.0		0.16	
	Depth 2100 m.	2°13′ W	40	26.93	35.07	0.0	89	0.45	0.14
			80	16.27	35.61	1.3		0.25	
40	25.11.50 Anchorage Accra Depth 7 m.		1				6	10.5	0.34
43	26.11.50	5°37′ N	0	27.21	34.69	–	57	0.64	0.22
	Depth 30 m.	0°44′ E	20	27.28	34.74	–		0.78	
46	26.11.50	5°36′ N	0	28.44	34.63	0.1	28	0.36	
	Depth 280 m.	0°48′ E	15	27.13	34.72	0.1		1.6	0.21
			30	26.34	34.99	0.3		1.8	
47	27.11.50	2°54′ N	0	27.95	33.66	0.1	86	0.29	0.17
	Depth 4160 m.	3°50′ E	40	25.82	35.62	0.1		0.43	
49	29.11.50	0°00′	0	26.43	34.11	0.0	41	1.5	0.33
	Depth 42 m.	6°32′ E	10	26.47	34.22	0.0		1.5	
52	30.11.50	1°42′ N	0	26.54	28.12	0.0	61	1.6	
	Depth 2550 m.	7°51′ E	40	19.44	35.61	0.9		0.53	0.35
59	1.12.50	4°00′ N	0.5	28.04	19.13	–	6	22.0	
	Depth 9 m.	9°11′ E	5	26.18	30.88	–		8.3	0.49
63	2.12.50	2°00′ N	0	27.15	21.27	–	30	2.2	0.36
	Depth 1250 m.	9°14′ E	20	26.99	28.28			2.2	
			40	20.27	35.50			0.45	
64	3.12.50	0°16′ S	0	26.98	32.36	0.0	43	1.3	
	Depth 2240 m.	8°12′ E	20	26.30	33.96	0.2		1.7	0.28
			40	19.93	35.75	1.1		0.11	
65	4.12.50	2°17′ S	0	26.43	34.04	0.0	45	0.95	
	Depth 2610 m.	8°10′ E	20	24.83	34.94	0.1		1.9	0.36
			40	22.78	35.41	0.1		1.6	
66	5.12.50	4°00′ S	0	26.98	32.59	0.0	22	1.4	0.14
	Depth 4020 m.	8°25′ E	20	24.57	35.64	0.2		1.0	
			40	18.06	35.53	0.9		0.14	

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.³ per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.² in g. C. per day
67	6.12.50	5°00′ S	1	26.69	29.43	0.1	10	0.53	0.25
	Depth 2830 m.	9°15′ E	10	26.66	29.69	0.3		3.9	
68	6.12.50	5°19′ S	1	26.83	28.73	0.0	6	17.5	
	Depth 1840 m.	10°55′ E	10	26.10	30.93	0.4		8.6	0.57
71	7.12.50	5°23′ S	1	25.43	25.99	0.0	5	5.6	0.15
	Depth 880 m.	11°28′ E	10	25.36	34.83	0.3		4.6	
73	7.12.50	5°41′ S	1	25.33	23.93	0.0	4	4.2	
	Depth 430 m.	11°26′ E	10	25.25	34.94	0.2		4.7	0.08
82	8.12.50	5°53′ S	1	24.99	18.78			9.8	
	Depth 25 m.	12°04′ E	10	22.89	35.50	0.3	5	1.1	0.03
93	10.12.50	6°38′ S	0	25.74	34.27	0.0	50	1.4	
	Depth 685 m.	11°32′ E	20	25.63	34.42	0.1		2.3	0.45
			40	21.63	35.55	0.4		0.74	
95	10.12.50	6°51′ S	0	26.91	34.36	0.1	39	1.0	
	Depth 1120 m.	11°15′ E	20	26.34	34.49	0.1		1.8	0.30
			40	18.45	35.79	0.4		1.3	
97	10.12.50	8°22′ S	0	26.98	33.30	0.0	35	0.71	
	Depth 2680 m.	11°08′ E	20	22.95	35.81	0.4		3.2	0.36
			40	16.21	35.66	2.0		0.14	
98	10.12.50	8°52′ S	0	26.83	34.74	0.2	32	0.74	0.18
	Depth 2750 m.	11°09′ E	20	19.80	35.77	0.5		1.4	
			40	16.51	35.70	1.8		0.40	
101	12.12.50	8°50′ S	0	25.84	35.05	0.2	43	1.2	
	Depth 975 m.	12°32′ E	20	25.28	35.50	0.2		3.5	0.39
			40	19.80	35.62	1.1		5.9	
105	18.12.50	10°45′ S	0	25.63	36.06	0.1		0.29	0.21
	Depth 3980 m.	11° 3′ E	20	23.65	36.06	0.1	43	1.3	
			40	16.80	35.81	2.0		0.97	
106	18.12.50	11°24′ S	0	25.83	35.82	0.1	41	0.42	0.12
	Depth 3660 m.	11°15′ E	20	23.08	35.79	0.2		0.59	
			40	16.46	35.64	2.2		0.27	
109	19.12.50	12° 6′ S	0	26.99	34.94	0.2		0.57	
	Depth 1170 m.	13°08′ E	20	21.79	35.21	0.4		3.4	0.41
			40	18.36	35.64	1.7	38	1.04	
118 a	20.12.50	12°20′ S	0	24.5		0.4		5.4	
		13°40′ E	10	21.0		1.5	21	1.5	0.38
126	21.12.50	14°35′ S	0	24.03	35.55	0.3	34	1.6	
	Depth 1930 m.	12°06′ E	20	19.49	35.64	1.2		1.31	0.32
132	22.12.50	17°13′ S	0	16.77	35.52	1.7		18.0	1.92
	Depth 200 m.	11°27′ E	15	16.72	35.52	1.7		15.4	
			30	16.70	35.55	2.0	19	17.7	
136	22.12.50	17°13′ S	0	17.53	35.57	1.3		15.3	
	Depth 960 m.	11°12′ E	15	17.52	35.57	1.4	16	8.4	1.23
138	24.12.50	22°45′ S	0	15.73	35.05	1.7		7.5	
	Depth 80 m.	14°15′ E	15	12.48	35.10	2.4	39	0.92	0.85
			30	12.20	35.08	2.4		0.16	

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.³ per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.² in g. C. per day
139	24.12.50	Walvis Bay	0	19.80	35.26	2.2	0.8	780	abt. 3.8
	Depth 6 m.								
143	25.12.50	23°16′ S	0	15.43	35.03	1.7	37	3.5	
	Depth 150 m.	14°02′ E	15	13.73	35.01	1.7		1.1	0.46
			30	12.63	35.05	2.2		0.47	
153	27.12.50	29°00′ S	0	16.74	34.97	0.4		3.0	
	Depth 182 m.	15°29′ E	15	16.73	34.96	0.4	27	3.1	0.53
154	28.12.50	32°37′ S	0	13.48	34.88	0.2		22	
	Depth 255 m.	17°25′ E	15	12.63	34.94	0.4	11	26	1.8
159	2.1.51.	33°58′ S	0	10.61	34.76	1.1	40		1.4
	Depth 100 m.	18°09′ E							
167	3.1.51	34°16′ S	0	15.45	35.19	0.7		22	
	Depth 50 m.	18°32′ E	15	15.36	35.17	0.4	18	19	2.5
169	3.1.51	34°11′ S	0	18.3	–	–		3.7	
	Depth 20 m.	18°27′ E	15		–	–	20	3.1	0.46
175	21.1.51	35°00′ S	0	21.46	35.61	0.2		0.27	
	Depth 4330 m.	27°22′ E	40	21.17	35.59	0.1		0.41	
			80	19.97	35.57	1.7	81	0.97	0.24
178	23.1.51	35°07′ S	0	21.94	35.64	0.2		0.22	
	Depth 4630 m.	30°35′ E	40	21.10	35.64	0.2		0.21	
			80	19.98	35.57	0.3	101	0.16	0.13
180	25.1.51	34°56′ S	0	21.27	35.57	0.2		0.25	0.11
	Depth 5220 m.	36°31′ E	40	19.71	35.57	0.1		0.21	
			80	18.60	35.59	0.3	80	0.17	
181	26.1.51	34°54′ S	0	22.09	35.73	0.1	92	0.17	
	Depth 5380 m.	38°02′ E	40	20.96	35.73	0.1		0.14	
			80	19.30	35.68	0.1		0.21	0.1
184	29.1.51	33°06′ S	0	23.60	35.50	0.1		0.35	
	Depth 1470 m.	35°21′ E	80	21.74	35.52	0.1	94	0.32	0.2
185	30.1.51	32°31′ S	0	22.72	35.55	0.2		0.35	
	Depth 1680 m.	35°01′ E	40	22.72	35.53	0.2	85	0.30	0.17
186	31.1.51	32°33′ E	0	23.53	35.55	0.2	79	0.31	0.17
	Depth 3620 m.	32°01′ E	40	23.02	35.55	0.2		0.36	
			80	21.00	35.53	0.5		0.33	
191	4.2.51	31°49′ S	0	23.30	35.48	0.1		0.22	
	Depth 3510 m.	32°52′ E	40	22.93	35.52	0.1	96	0.22	0.14
			80	21.22	35.44	0.3		0.24	
197	14.2.51	29°57′ S	0	24.39	35.44	0.1	30	5.5	0.73
	Depth 605 m.	31°26′ E	20	23.10	35.37	0.2		3.2	
			40	21.15	35.34	0.7		3.2	
198	15.2.51	30°32′ S	0	24.63	35.55	0.2	86	0.2	0.11
	Depth 2690 m.	34°27′ E	40	24.20	35.55	0.2		0.21	
			80	20.30	35.50	0.2		0.28	
200	17.2.51	29°39′ S	0	24.58	35.59	0.1	105	0.18	0.12
	Depth 5050 m.	37°01′ E	40	23.16	35.57	0.1		0.19	
			80	20.00	35.50	0.2		0.24	

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.³ per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.² in g.C. per day
201	20.2.51	28°04′ S	0	27.08	35.48	0.2	101	0.36	0.23
	Depth 2110 m.	35°25′ E	40	26.00	35.55	0.2		0.42	
			80	22.21	35.41	0.2			
206	24.2.51	20°01′ S	0	28.45	35.82	0.0	23	4.4	0.59
	Depth 30 m.	35°10′ E	15	28.40	35.82	0.0		4.2	
209	24.2.51	20°08′ S	0	29.15	35.35	0.2	72	1.1	0.43
	Depth 75 m.	35°33′ E	30	26.65	35.41	0.2		1.3	
			60	19.00	35.32	0.9		0.32	
216	26.2.51	16°24′ S	0	27.77	34.34	0.2	102	0.51	0.24
	Depth 2760 m.	42°29′ E	40	28.10	34.81	0.2		0.35	
218	28.2.51	13°41′ S	0	27.47	34.25	0.1	83	0.32	0.13
	Depth 3300 m.	46°40′ E	40	26.93	34.99	0.2		0.33	
			80	22.23	35.28	0.3		0.11	
228	5.3.51	9°31′ S	0	28.48	34.92	0.2	91	0.30	0.23
	Depth 5050 m.	49°29′ E	40	26.34	34.97	0.0		0.64	
			80	21.14	35.21	0.0		0.44	
230	7.3.51	9°02′ S	0	29.16	34.92	0.2	87	0.28	0.22
	Depth 4950 m.	49°27′ E	40	26.39	35.21	0.3		0.77	
			80	19.30	35.23	1.1		0.2	
234	10.3.51	5°25′ S	0	29.21	35.50	0.3	101	0.25	0.13
	Depth 4830 m.	47°09′ E	40	25.70	35.34	0.3		0.31	
			80	18.60	35.32	1.3		0.63	
238	13.3.51	3°23′ S	0				87	0.3	
	Depth 3970 m.	44°04′ E	40					0.32	0.14
262	23.3.51	4°16′ S	0	28.02	35.55	0.3		0.31	
	Depth 2720 m.	41°33′ E	40	26.56	35.59	0.3	88	0.61	0.21
			80	25.59	35.64	0.4		0.3	
263	24.3.51	4°14′ S	0	29.90	35.34	0.2	86	0.33	0.15
	Depth 4650 m.	44°52′ E	80	24.90	35.59	0.4		0.33	
264	25.3.51	3°12′ S	0	30.27	35.28	0.2	90	0.35	abt. 0.19
	Depth 4920 m.	47°01′ E	40	27.50	35.35	0.2		0.52	
			80	19.38	35.32	0.9			
265	26.3.51	3°30′ S	0	30.63	35.53	0.2	87	0.21	0.15
	Depth 5340 m.	50°20′ E	40	27.90	35.44	0.2		0.34	
			80	26.02	35.44	0.2		0.52	
266	27.3.51	3°38′ S	0	29.72	35.30	0.2	86	0.26	0.15
	Depth 4720 m.	52°43′ E	40	27.45	35.35	0.3		0.39	
			80	24.41	35.39	0.4		0.24	
267	28.3.51	3°07′ S	0	30.15	35.32	0.3	85	0.23	
	Depth 4150 m.	54°09′ E	40	27.00	35.39	0.3		0.45	0.14
			80	19.75	35.32	0.3		0.12	
272	2.4.51	3°20′ S	0	29.30	35.41	0.4	88	0.28	0.20
	Depth 4110 m.	57°16′ E	40	28.81	35.46	0.3		0.62	
			80	25.24	35.44	0.3		0.32	
273	3.4.51	2°54′ S	0	29.20	35.35	0.4	107	0.24	0.23
	Depth 4320 m.	60°26′ E	40	29.07	35.41	0.4		0.48	
			80	28.31	35.46	0.3		0.49	

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.³ per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.² in g. C. per day
274	4.4.51	2°04′ S	0	29.10	35.25	0.4		0.24	0.24
	Depth 4485 m.	64°00′ E	40	28.55	35.41	0.3		0.67	
			80	24.30	35.39	0.5	94	0.50	
275	5.4.51	1°15′ S	0	28.72	35.19		93	0.48	0.24
	Depth 2410 m.	67°25′ E	40	28.58	35.23			0.51	
			80	24.91	35.48			0.38	
276	6.4.51	0°42′ S	0	29.38	35.14	0.3	92	0.24	0.22
	Depth 4630 m.	71°07′ E	40	28.59	35.16	0.3		0.60	
			80	24.96	35.52	0.5		0.52	
278	7.4.51	0°10′ S	0	29.03	35.05	0.3	94	0.17	0.16
	Depth 2640 m.	74°02′ E	40	28.29	35.14	0.2		0.38	
			80	24.75	35.46	0.5		0.46	
279	8.4.51	1°00′ N	0	28.75	34.69	0.3		0.22	
	Depth 4300 m.	76°17′ E	40	28.62	35.03	0.3	94	0.29	0.14
			80	24.08	35.48	0.9		0.29	
281	10.4.51	3°38′ N	0	29.51	34.72		92	0.22	0.15
	Depth 3400 m.	78°15′ E	40	29.26	34.97			0.26	
			80	28.40	35.17			0.56	
282	11.4.51	5°32′ N	0	29.70	34.25	0.3		0.23	
	Depth 4040 m.	78°41′ E	40	28.58	34.67	0.3	86	0.62	0.19
			80	25.56	34.69			0.23	
283	12.4.51	7°05′ N	10	29.55	34.05	0.2	85	0.94	0.47
	Depth 820 m.	79°37′ E							
286	20.4.51	7°50′ N	0	29.70	34.16	0.2	60	1.8	0.41
	Depth 28 m.	81°43′ E	10	28.77	34.27	0.2		1.0	
			20	28.28	34.20	0.2		0.6	
298	23.4.51	14°20′ N	0	29.40	33.75	0.1	66	0.29	0.12
	Depth 3240 m.	82°00′ E	40	28.12	33.91	0.2		0.40	
			80	26.67	34.40	+		0.25	
299	24.4.51	17°10′ N	0	28.52	33.96	0.2	45	1.2	0.25
	Depth 2860 m.	84°30′ E	20	24.70	34.70	1.3		0.87	
			40	18.29	34.90	3.2		0.52	
303	26.4.51	20°37′ N	0	27.28	34.02		51	1.9	0.6
	Depth 62 m.	87°33′ E	20	27.10	34.00			2.2	
			40	25.48	34.29			2.7	
313	2.5.51	19°53′ N	0	29.20	32 65	0.0	84	0.37	0.16
	Depth 1400 m.	89°05′ E	40	27.53	33.28	0.0		0.38	
			80	24.47	34.63	1.7		0.27	
315	4.5.51	13°58′ N	0	30.19	32.54	0.1	99	0.31	0.24
	Depth 3000 m.	91°03′ E	40	28.12	33.62	0.2		0.55	
			80	25.61	34.20	0.4		0.50	
317	5.5.51	10°32′ N	0	29.89	32.66	0.2	85	0.55	0.31
	Depth 850 m.	90°59′ E	40	29.22	32.99	0.2		0.89	
			80	22.49	34.40	2.0		0.42	
325	10.5.51	4°20′ N	0	30.17	30.72	0.0	36	3.6	0.53
	Depth 46 m.	98°54′ E	20	29.90	31.24	0.1		2.0	
			40	29.32	32.56	0.3		2.1	

St No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.³ per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.² in g. C. per day
327	11.5.51	1°55′ N	0	30.16	30.73	0.2	19	6.2	0.52
	Depth 45 m.	102°27′ E	10	30.05	30,75	0.2		4.7	
			20	30.04	30.72	0.2		3.5	
372	6.6.51	3°48′ N	0	29.30	32.72	0.2	50	1.6	0.53
	Depth 25 m.	103°40′ E	10	28.79	32.74	0.2		2.0	
			20	28.77	32.72	0.2		2.3	
381	8.6.51	7°0′ N	10	30.08	31.51		60	2.2	abt. 0.7
	Depth 54 m.	103°18′ E							
382	9.6.51	7°57′ N	0	30.30	31.40	0.0	69	0.73	0.49
	Depth 78 m.	102°32′ E	40	28.87	31.73	0.2		2.0	
			68	26.91	33.08	0.7		1.0	
384	10.6.51	10°11′ N	0	29.73	31.51	0.1	64	2.0	0.78
	Depth 72 m.	101°37′ E	30	29.40	31.67	0.2		1.7	
			68	27.40	32.86	1.4		3.6	
390	11.6.51	13°02′ N	0	29.82	31.78		31	6.0	1.08
	Depth 22 m.	100°33′ E	10	29.82	31.74			7.1	
			20	29.82	31.73			5.0	
408	4.7.51	12°56′ N					abt. 100	0.28	abt. 0.16
	Depth 4330 m.	116°11′5 E							
409	5.7.51	13°44′ N	0	28.88	33.08	0.9	98	0.15	0.15
	Depth 3780 m.	118°56′ E	50	28.92	33.35	0.2		0.42	
			100	23.03	34.29	0.2		1.1	
411a	11.7.51	12°41′ N							
		123°27′ E						0.098	
412a	12.7.51	11°38′ N					abt. 120	0.15	0.1
		126°11′ E							
414	17.7.51	10°20′ N	0	28.03	34.34	+	56	2.6	0.8
	Depth 40 m.	125°32′ E	15	28.02	34.33	0.1		2.2	
			30	27.84	34.34	0.1		2.5	
422	24.7.51	10°47′ N	0	29.95	34.34	0.4	118	0.12	0.11
	Depth 2150 m.	126°02′ E	60	28.75	34.36	0.3		0.21	
435	8.8.51	10°20′ N	0	29.19		0.5	119	0.10	0.08
	Depth 9790 m.	126°41′ E	60	28.28		0.3		0.14	
			120	25.62		0.4		0.15	
443a	17.8.51	8°22′8 N					abt. 90	0.43	0.21
		122°26′4 E							
447	20.8.51	3°05′ N	0	30.00	34.04	0.1	90	0.37	0.14
	Depth 4660 m.	120°10′ E	50	27.61	34.47	0.2		0.24	
			100	23.80	34.79	0.4		0.17	
454	25.8.51	5°23′ S	0	27.79	34.18	0.0	63	1.8	0.59
	Depth 60 m.	116°02′ E	25	27.65	34.04	0.0		1.5	
			50	25.11	34.04	0.7		2.1	
456	26.8.51	5°00′ S	0	28.08	33.46	0.1	50	0.9	0.32
	Depth 60 m.	111°11′ E	25	27.83	33.75	0.1		1.3	
			50	27.74	33.86	0.1		1.5	
458	27.8.51	6°08′ S	0	28.25	31.18	0.1	21	1.9	0.23
	Depth 20 m.	107°57′ E	15	27.73	31.09	0.1		2.2	

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.³ per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.² in g. C. per day
466	6.9.51	10°21′ S	0	26.09	34.34	0.2	59	0.43	0.17
	Depth 7130 m.	110°12′ E	34	25.85	34.34	0.1		0.53	
			60	25.48	34.36	0.2		0.64	
472	10.9.51	10°24′ S	0	25.29	23.23	0.1	34	3.7	0.7
	Depth 2470 m.	114°07′ E	15	24.60	34.23	0.2		4.3	
			30	23.44	34.27	0.4		2.9	
475	11.9.51	9°02′ S	0	25.60	34.14	0.2	40	3.4	0.59
	Depth 2750 m.	114°48′ E	15	25.58	34.14	0.2		2.7	
			30	24.40	34.16	0.3		1.3	
491a	17.9.51	5°45′ N					abt. 60	0.63	abt. 0.2
		119°59′ E							
491b	19.9.51	6°16′5 S					abt. 50	1.2	abt. 0.3
		129°05′ E							
498	24.9.51	5°18′ S	0	26.68	34.60	0.3	42	1.8	0.34
	Depth 7280 m.	131°06′ E	30	26.30	34.59	0.4		1.6	
			60	23.11	34.52	1.3		0.66	
511a	4.10.51	11°42′ S					abt. 80	0.43	0.18
		152°16.5′E							
515a	10.10.51	7°47′ S					abt. 80	0.73	0.31
		155°40.5′E							
517	12.10.51	6°31′ S	0	28.09	34.69	0.4	80	0.56	0.29
	Depth 8920 m.	153°58′ E	40	28.22	34.63	0.4		0.53	0.25
			80	28.05	35.23	0.5		0.67	
				+					
518	14.10.51	6°11′ S					abt. 100	0.21	0.11
	Depth 8860 m.	153°31′ E							
519a	16.10.51	5°59′ S					abt. 100	0.30	0.16
		153°27′ E							
522	18.10.51	11°27′ S	0	27.22	35.17	0.3	83	0.40	0.19
	Depth 2600 m.	151°48′ E	40	26.25	35.16	0.4		0.53	
			80	25.10	35.16	0.4		0.33	
523	19.10.51	9°35′ S	0	25.75	35.08	0.2	94	0.18	0.12
	Depth 1200 m.	147°05′ E	50	25.30	35.12	0.2		0.21	
			100	24.95	35.17	0.3		0.39	
538	5.11.51	26°27′ S	0	22.44	35.48	0.3	63	0.44	0.19
	Depth 55 m.	153°27′ E	20	22.20	35.48	0.3		0.65	
			40	22.19	35.48	0.3		0.44	
550	12.11.51	31°27′ S	0	21.24	35.61		63	0.37	0.15
	Depth 4410 m.	153°33′ E	40	20.80	35.57			0.26	
			80	20.20	35.62			0.56	
553	4.12.51	39°03′ S	0	14.75	35.39	0.1	62	0.78	0.42
	Depth 84 m.	144°04′ E	30	14.00	35.39	0.2		0.99	
			60	13.94	35.39	0.2		1.5	
564	6.12.51	36°18′ S	0	18.34	35.71	0.1	83	0.36	0.15
	Depth 60 m.	138°29′ E	25	16.21	35.68	0.1		0.22	
			50	15.45	35.75	0.1		0.25	

St No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.³ per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.² in g.C. per day
573	17.12.51	39°00′ S	0	17.53	35.55	0.2	abt. 60	1.3	
	Depth 4500 m.	154°57′ E	30	17.30	35.55	0.1		2.2	0.67
			60	16.64	35.52	0.1		1.2	
576	21.12.51	40°31′ S	0	15.44	34.65	0.2	28	12.0	1.94
	Depth 60 m.	173°20′ E	15	15.33	34.69	0.3		12.0	
			30	12.21	35.07	1.1		2.8	
					abt.				
580	3.1.52	52°33′ S	0	8.90	34.18	1.3		8.3	
	Depth 30 m.	169°08′ E	20	8.39	34.25	1.3	28	1.1	1.0
593	4.1.52	52°35′ S	0	8.59	34.31	1.3	62	1.3	0.55
	Depth 110 m.	169°14′ E	25	8.39	34.29	1.3		1.1	
			50	8.33	34.41	1.3		0.97	
599a	13.1.52	45°58′ S					abt. 55	0.55	0.21
		165°10′ E							
601	14.1.52	45°51′ S	0	12.71	34.81	1.3	55	1.1	0.43
	Depth 4400 m.	164°32′ E	25	12.20	34.76	0.4		1.1	
			50	12.08	34.78	0.4		1.3	
603	16.1.52	44°37′ S	0	14.84	20.59	0.1	18	6.2	1.48
	Depth 30 m.	167°55′ E	15	12.45	33.26	0.4		17.9	
615	19.1.52	44°37′ S	0	13.34	16.65	0.0	24	10.7	1.89
	Depth 293 m.	167°53′ E	10	12.92	33.26	0.1		7.8	
			20	12.68	33.96	0.1		20.5	
625	20.1.52	42°08′ S	0	15.85	33.05	0.3	63	0.26	0.23
	Depth 595 m.	170°20′ E	25	14.94	35.04	0.3		0.67	
			50	14.31	35.06	0.3		0.76	
630	25.1.52	39°45′ S	0	18.28	35.21	0.1	64	0.28	0.31
	Depth 320 m.	177°41′ E	30	17.43	35.31	0.1		0.84	
			60	15.76	35.33	0.3		1.6	
637	26.1.52	37°28′ S	0	18.63	35.25	0.1	55	1.7	0.54
	Depth 1400 m.	178°18′ E	25	18.29	35.27	0.2		1.4	
			50	16.58	35.35	0.4		1.6	
641	27.1.52	36°34′ S	0	19.00	35.21	0.2	51	2.3	0.62
	Depth 45 m.	174°59′ E	20	18.90	35.24	0.2		2.3	
			40	14.79	35.19	1.3		1.8	
669	29.2.52	36°10′ S	0	21.28	35.50	0.2	97	0.17	0.14
	Depth 2490 m.	177°50′ E	40	20.58	35.58	0.2		0.26	
			80	17.85	35.53	0.3		0.44	
670	1.3.52	34°07′ S	0	21.75	35.34	0.1	82	0.22	0.10
	Depth 4000 m.	179°20′ W	40	19.76	35.41	0.2		0.33	
			80	15.93	35.44	0.7		0.065	
677	4.3.52	28°38′ S	0	24.02	35.64	0.1	106	0.26	0.13
	Depth 9190 m.	175°53′ W	50	abt. 22	35.58	0.1		0.21	
			100	17.92	35.55	0.2		0.16	
680	7.3.52	23°24′ S	0	27.17	35.03	0.1	102	0.22	0.11
	Depth 7800 m.	175°01′ W	60	25.30	35.23	0.1		0.21	
			120	22.28	35.32	0.2		0.17	
683a	9.3.52	21°12′ S						2.5	
		174°41′ W							

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg.C per m.³ per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.² in g.C. per day
685	10.3.52	21°06′ S	0	26.51	35.53	0.2	95	0.31	0.16
	Depth 9820 m.	173°33′ W	60	26.36	35.61	0.2		0.27	
			120	24.30	35.63	0.2		0.39	
688	15.3.52	13°42′ S	0	29.60	35.28	0.3	120	0.19	0.10
	Depth 4720 m.	170°37′ W	60	28.07	36.04	0.3		0.17	
			120	25.00	36.22	0.3		0.077	
690	16.3.52	11°01′ S	0	29.58	34.99	0.2	120	0.19	0.16
	Depth 600 m.	171°07′ W	60	29.48	35.01	0.2		0.21	
			120	26.59	35.97	0.5		0.39	
691	17.3.52	6°00′ S	0	29.45	35.19	0.3	113	0.19	0.14
								(0.38)[1]	(0.17)
	Depth 5790 m.	169°17′ W	60	29.22	35.35	0.3		0.28	
			120	27.59	35.97	0.7		0.17	
692	18.3.52	2°47′ S	0	27.80	35.35	0.7	78	0.24	0.10
								(0.48)[1]	(0.14)
	Depth 5570 m.	167°41′ W	60	27.70	35.41	0.7		0.24	
			120	27.86	35.62	0.7		0.26	
692a	19.3.52	0°02′ S					80	0.95	abt. 0.4
		166°29′ W							
693	20.3.52	4°00′ N	0	28.02	35.08	0.4	81	0.60	0.26
	Depth 5260 m.	164°48′ W	40	27.80	35.08	0.4		0.62	
			80	27.63	35.10	0.4		0.51	
694	22.3.52	13°00′ N	0	26.30	34.40	0.2	85	0.32	0.14
		162°42′ W	50	26.21	34.45	0.2		0.28	
			100	26.18	34.42	0.2		0.34	
695	23.3.52	16°00′ N	0	24.74	34.40	0.2	100	0.18	0.10
		159°00′ W	50	24.19	34.63	0.2		0.18	
			100	24.11	34.69	0.2		0.21	
696	24.3.52	19°57′ N	0	24.02	34.83	0.1	101	0.20	0.10
		158°10′ W	60	23.95	34.82	0.1		0.18	
			120	23.57	35.01	0.1		0.17	
698	29.3.52	23°00′ N	0	22.63		0.2	105	0.31	0.19
	Depth 4700 m.	155°25′ W	60	22.50	35.16	0.1		0.34	
			120	22.50	35.12	0.1		0.39	
698a	31.3.52	26°52′ N					100	0.08	abt. 0.08
		148°32′ W							
699	3.4.52	33°37′ N	0	14.60	33.57	0.2	97	0.11	0.1
	Depth 5260 m.	134°53′ W	60	14.56	33.71	0.2		0.24	
			120	15.38	34.11	0.2		0.21	
700	4.4.52	35°45′ N	0	13.43	33.10	0.4	77	0.27	0.13
	Depth 4755 m.	129°10′ W	40	12.20	32.94	0.5		0.32	
			80	11.63	32.86	0.4		0.39	
701	5.4.52	37°16′ N	0	11.50	32.86	0.3	63	0.89	0.55
	Depth 4755 m.	124°36′ W	30	11.06	32.88	0.5		0.76	
			60	11.04	32.97	0.4		0.47	
705	22.4.52	32°50′ N	0	16.37	33.24	0.3	23	2.1	0.36
	Depth 16 m.	117°32′ W	10	15.41	33.28	0.4		3.3	

1. A mistake in recording seems to have been made. The value in brackets is most likely correct.

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.³ per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.² in g.C. per day
707	24.4.52	26°00′ N	0	17.01	33.60	0.3	67	0.59	0.24
	Depth 1600 m.	113°31′ W	30	16.40	33.66	0.4		0.59	
			60	15.40	33.71	0.5		0.52	
708	25.4.52	22°50′ N	0	18.34	34.38	0.5	34	3.5	0.9
	Depth 800 m.	110°06′ W	25	17.15	34.31	1.0		7.7	
			50	14.21	34.18	2.4		0.25	
709	26.4.52	20°00′ N	0	23.53	34.81	0.4	55	0.59	0.21
	Depth 3600 m.	106°12′ W	25	20.30	34.63	0.8		0.86	
			50	17.03	34.56	2.3		0.28	
715	4.5.52	13°00′ N	0	29.62	34.16	0.2	80	0.73	0.27
	Depth 4600 m.	95°48′ W	40	21.22	34.42	2.6		0.71	
			80	13.91	34.85	2.6		0.012	
717	7.5.52	8°41′ N	0	29.10	33.48	0.3	52	0.63	0.26
	Depth 3310 m.	86°12′ W	25	23.20	34.33	1.3		1.4	
			50	18.79	34.81	2.6		0.46	
719a	10.5.52	6°52′ N					60	1.4	0.48
		79°30′ W							
720	11.5.52	5°36′ N	0	26.72	33.78	0.4	60	1.9	0.40
	Depth 3000 m.	79°31′ W	30	21.38	34.43	1.7		0.99	
			60	16.60	34.90	2.6		0.31	
723	12.5.52	6°00′ N					60	0.72	0.23
	Depth 3230 m.	79°54′ W							
755	22.5.52	11°52′ N	0	28.63	35.99	0.1	90	0.21	0.14
	Depth 3960 m.	77°41′ W	50	26.93	36.42	0.1		0.30	
			100	24.01	36.76	0.1		0.41	
756	24.5.52	15°00′ N	0	28.06	35.97	0.1	63	0.51	0.19
	Depth 4200 m.	71°06′ W	40	27.70	35.97	0.2		0.64	
			80	26.94	35.95	0.2		0.44	
757	30.5.52	18°33′ N	0	27.70	36.00	0.1	100	0.12	0.056
	Depth 960 m.	65°36′ W	50	25.93	36.31	0.1		0.085	
			100	24.20	36.78	0.1		0.098	
760	2.6.52	22°43′ N	0	26.87	36.09	0.1	119	0.079	0.075
	Depth 6170 m.	60°54′ W	60	24.82	36.55	0.1		0.17	
			120	22.51	36.89	0.1		0.067	
760a	3.6.52	24°23′ N					120	0.045	abt.0.03
		57°04′ W							
762	4.6.52	25°03′ N	0	26.00	36.92	0.1	108	0.059	0.043
	Depth 6200 m.	56°06′ W	60	22.79	36.74	0.1		0.064	
			120	21.14	36.74	0.1		0.12	
763	6.6.52	29°27′ N	0	22.22	36.64	0.1	94	0.091	0.058
	Depth 4700 m.	47°53′ W	60	20.13	36.62	0.1		0.15	
			120	18.57	36.49	0.1		0.079	
764	7.6.52	31°35′ N	0	22.71	36.94	0.1	121	0.057	0.048
	Depth 3730 m.	43°31′ W	60	21.46	36.96	0.1		0.069	
			120	19.82	36.74	0.1		0.11	
765	9.6.52	35°16′ N	0	21.13	36.24	0.1	76	0.16	0.16
	Depth abt. 2000 m.	33°50′ W	40	18.34	36.20	0.1		0.70	
			80	16.34	36.7	0.2		0.17	

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.³ per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.² in g. C. per day
766	10.6.52	36°50′ N	0	19.90	36.29	0.0	87	0.11	0.11
	Depth 3200 m.	28°50′ W	50	17.15	36.17	0.1		0.43	
			100	16.07	36.11	0.2		0.10	
768	14.6.52	37°53′ N	0				92	0.25	0.11
	Depth 2030 m.	24°45′ W	40					0.20	
			80					0.18	
769	16.6.52	43°10′ N	0	17.32	35.73	0.1	44	0.89	0.25
	Depth 4450 m.	17°04′ W	20	17.23	35.71	0.1		0.71	
			40	14.90	35.71	0.1		1.2	
770	17.6.52	45°53′ N	0	17.00	35.64	0.1	60	0.67	0.26
	Depth 4900 m.	12°27′ W	30	15.00	35.62	0.1		0.73	
			60	12.10	35.62	0.4		0.61	
772	18.6.52	48°00′ N	0	15.31	35.29	0.1	41	1.22	0.33
	Depth 1520 m.	8°18′ W	20	15.00	35.59	0.2		1.4	
			40	13.25	35.59	0.3		1.1	
775	19.6.52	49°37′ N	0	14.70	35.17	0.1	49	1.4	0.47
	Depth 80 m.	4°35′ W	20	14.30	35.16	0.1		2.1	
			40	11.53	35.23	0.3		0.55	
780	25.6.52	51°10′ N	0	13.71	35.05	0.1		2.1	0.72
	Depth 44 m.	1°41′ E	15	13.70	34.97	0.1		2.3	
			30	13.70	34.97	0.1		2.1	
781	26.6.52	54°50′ N	0	12.13	34.63	0.1	45	0.56	0.20
	Depth 45 m.	4°28′ E	20	11.93	34.60	0.1		0.59	
			40	< 8.	34.67	0.3		0.53	
782	28.6.52	57°43′ N	0	12.40	33.24	0.1	34	2.2	0.71
	Depth 16 m.	10°11′ E	10	12.35	33.28	0.1		3.0	

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