# PRODUCTION OF ORGANIC MATTER IN THE OCEANS

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As on land, so in the sea, autotrophic plants are the basis of all life. Sessile plants live on a narrow fringe along coasts only, so, if we wish to consider the amount of matter produced by plants of the sea, we must confine our attention to planktonic algae, which are found everywhere in the upper oceanic water masses. It is the organic matter synthesized by phytoplankton out of purely inorganic substances by means of light which directly and indirectly serves as food for all organisms in the sea, from the smallest bacteria to the largest whale.

The first investigations of production of matter by phytoplankton in a coastal area were made 30 years ago by Dr. Atkins of the Plymouth Laboratory, England. He proceeded partly by determining the loss of carbon dioxide and partly by observing the loss of phosphate under one square meter of surface from the end of winter to the height of summer. Since the amounts of these substances which disappeared must have been used to build up vegetable matter, a minimum value for the production of matter in six months could be calculated from the values found. Atkins worked in the English Channel, and his method has been used in some other coastal waters too.

About 1930 the Norwegian planktonologist Gran introduced a direct method for measuring the production of matter by phytoplankton. In Gran's method, water samples from various depths are put into bottles and then placed at the different depths from which they were taken, normally for 24 hours. Oxygen production, which is an expression of photosynthesis, is determined by measuring the amount of oxygen present at the start and end of an experiment. The method has been used relatively little, since it is suitable only in areas with a large production of organic matter.

When the Danish GALATHEA Expedition put to sea in October 1950, one of the main items on its program was the investigation of organic productivity in all oceans. Since none of the methods mentioned seemed to be suitable for normal oceanic waters, it was important that the expedition be provided with equipment for determinations by a new method. This method, which has taken the radioactive carbon isotope $C^{14}$ into its service, proved applicable with equal certainty whether the productivity was high or low. A basis has now been established for an estimate of production of matter in the oceans, at least on broad lines.

Two slightly different modifications of the Carbon$^{14}$ method were used. In the first modification, samples of water taken from various depths in the photic zone were transferred to bottles with glass stoppers. Following addition of $C^{14}$ in the form of sodium bicarbonate, the bottles were suspended at the depth from which the samples were taken and left there for a definite time, for instance, from noon until sunset. At the end of this exposure period, the plankton was filtered off and the amount of $C^{14}$ assimilated was determined by measuring the $\beta$-radiation. To calculate the total carbon assimilated, it was necessary to multiply the amount of $C^{14}$ found by a factor corresponding to the ratio between $CO_{2(total)}$ and $C^{14}O_2$ in the water. In view of the fact that $C^{14}$ is not assimilated at quite the same rate as $C^{12}$, a correction for the isotope effect had to be made.

In the second modification, the bottles containing water samples from different depths were placed in a water bath which was illuminated by a definite light intensity. The penetration of light in the sea was determined at the time of collection. The production of matter beneath a unit surface was calculated by means of a formula derived from comparison of results from stations at which observations were made simultaneously by the two modifications. The first is the most accurate of the two modifications, but it takes about 20 times longer than the second.

On this occasion I will not discuss details of the method. Instead, I will give some of the main results obtained on the GALATHEA.

The most remarkable feature is a marked correlation between rate of production and hydrographic conditions. In the open sea, high productivity is found only in regions with a pronounced movement of water from deeper layers to the surface.

Fig. 1 gives the rates of organic production in a section from New Zealand to California. The direction of the route was northwestward to Honolulu, thence straight to San Francisco. The neritic station at the mouth of Hauraki Gulf, New Zealand and the last station in the coastal water outside San Francisco are included to give suitable contrast to the other stations, all of which are truly oceanic. These two neritic stations represent coastal areas with high productivity—about 0.6 g C/m$^2$/day.

The CARNEGIE's last cruise in 1929, together with the DANA's cruise in 1928–1930, gave valuable information on the hydrography

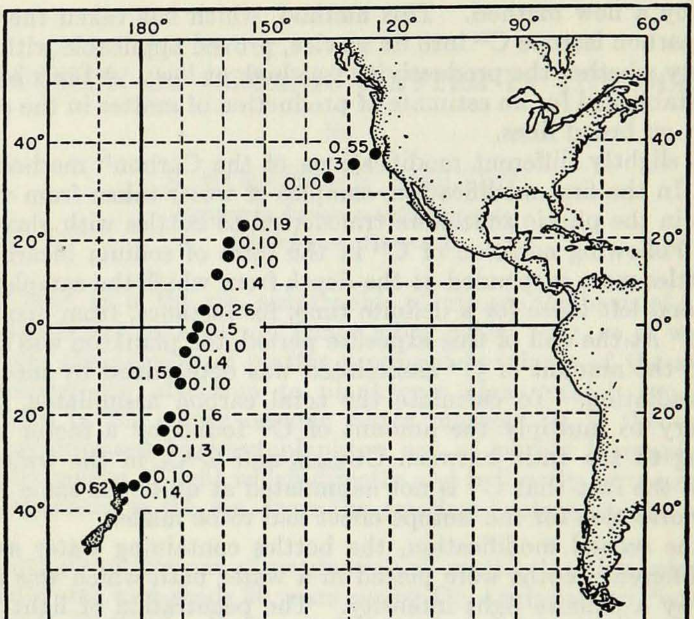


Figure 1

of this area. In the east, between the North and South Equatorial Currents, 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 is situated in the South Equatorial Current near the Equator, the other on the northern boundary of the Counter-Current. In these regions concentrations of slightly more than 0.4 $\mu$g-at P/l were found at the surface, and net catches of plankton were also rich here. Hydrographic and chemical conditions as found by the GALATHEA were rather similar to those found by the CARNEGIE.

The rate of organic production was fairly uniform at the GALATHEA's oceanic stations on this section. With the exception of stations near the divergences created by the Equatorial Counter-Current, the rate varied only between 0.10 and 0.19 g C/m$^2$/day. Only two stations were made in the region influenced by the divergences; the rates of production there were 0.26 and 0.5 g C respectively.

The thickness of the photosynthetic layer at the oceanic stations varied mostly between 95 and 120 m except for stations in or near the Counter-Current, where it was 78 and 85 m.

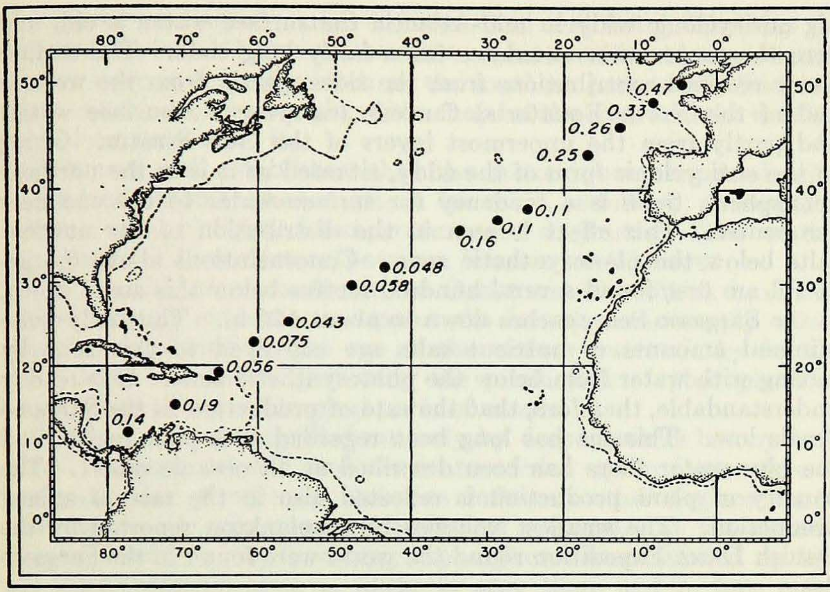


Figure 2

The oceanic surface water encountered on the Galathea section must be characterized as of medium age whereas that in the region near the mentioned divergences must be regarded as fairly new. An organic productivity of 0.10–0.19 g $C/m^2$/day is thus characteristic of tropical and subtropical regions having surface water of medium age. I am here using the term "age" of water in the manner originally introduced by Sverdrup and Allen.

Fig. 2 shows the rates of organic production on a section from Panama to the English Channel, which was run during May and June 1952. The first two stations are situated in the southern part of the Caribbean Sea, the next two in the Antilles Current (a westward continuation of the North Equatorial Current), three in the Sargasso Sea, six in the North Atlantic Current (the last one on the continental slope), and finally, one at the mouth of the English Channel.

The hydrographic conditions of the North Atlantic are well known. The surface water in the Caribbean Sea has its origin in the North Equatorial Current, which, at its western end, carries fairly old surface water. Organic productivity is 0.14–0.19 g C. Production in the Antilles Current is poor, being only 0.056–0.075 g C, which accords with the rather old age of the surface water.

About the lowest oceanic productivity found anywhere by the Galathea—0.043–0.058 g C—occurred in the Sargasso Sea. In this big anticyclonic eddy in mid-Atlantic the surface water is old, and here the same water circulates for a fairly long time. The surface water 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 form of the eddy, situated as it is in the northern hemisphere, there is a tendency for surface water to descend near the centre. This effect is seen in the distribution of the nutrient salts below the photosynthetic zone. Concentrations above 0.4 $\mu$g-at P/l are first found several hundred metres below this zone, which, in the Sargasso Sea, reaches down to about 120 m. Thus only quite minimal amounts of nutrient salts are conveyed to this zone by mixing with water from below the photosynthetic zone. It is readily understandable, therefore, that the rate of 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. The paucity of plant production is reflected also in the rate of animal production. The smallest volumes in zooplankton reported by the Danish DANA Expedition round the world were found in the Sargasso Sea.

The stations 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 gC. As one approaches the European continent organic productivity increases, probably due to the activity of eddies found there.

Finally, a productivity of 0.47 g C was found in the mouth of the English Channel. If production there occurs at that rate from March to June, then the result will be a productivity of the same order of magnitude as that estimated by the Plymouth Laboratory from the decrease of phosphate in spring until summer.

Fig. 3 shows the GALATHEA's results for the most productive area visited—the southern part of the Benguela Current, which is known to be one of the most productive areas in the oceans. This Current flows along the west coast of South Africa and is particularly conspicuous between the southern extremity of Africa and Lat. 17°–18° S. Under the influence of prevailing southerly and southeasterly winds, the surface layers are carried away from the coast and are replaced by upwelled water from moderate depths during most seasons of the year. These hydrographic conditions give rise to an enormously rich phytoplankton, since the upwelling water is rich in nutrient salts and establishes excellent conditions for plankton production. In the Benguela Current we find typically new surface water. According to the GALATHEA's measurements in the Current, the rate of organic production varied between 0.46 and 2.5 g C/m$^2$/day (in Walvis Bay, 3.8). However, we must expect considerable variation in productivity in a locality such as the southern part of the Benguela Current because, for example, of the shape of the coast and the weather conditions peculiar to it.

It is now well established that the factors governing production of phytoplankton in the sea are, in the main, as follows: a) supply of nutrient salts, b) light, c) temperature, and d) grazing. The relative importance of these factors, however, is not so well known.

The investigations made on the GALATHEA Expedition have furnished weighty evidence to support the fact that the supply of nutrients—manifested by the age of the surface water—is by far the most important factor governing the production of phytoplankton in the tropical and subtropical parts of oceans.

Nutrient salts are supplied not only by deeper waters but by horizontal currents as well, and nutrients carried up to the surface in one particular place may therefore influence other regions too if such regions are connected by horizontal currents. At the moment it is impossible to say how long a phosphorus atom carried up into the photosynthetic layer is likely to stay there and in how many phytoplankton cycles it may participate before being lost by sinking below this layer. Local variations will certainly occur. It can be demonstrated, however, that a particular surface water, rich in nutrients and therefore capable of high productivity, becomes poorer and poorer as it is transported by a horizontal current to regions where no other enrichment of the surface water takes place. The North Equatorial Current in the Atlantic offers a typical example. At the start of this Current, near the African coast, upwelling of water rich in nutrients takes place and organic production is rich. The western part of this Current (the Antilles) is characterized by low productivity, and the mid-Atlantic eddy, which is a further continuation of this Current, exhibits still lower productivity.

In planktonic algae as in all other autotrophic plants, variations in temperature strongly influence the rate of respiration and the rate of photosynthesis at a high light intensity. This does not necessarily mean, however, that the rate, measured per dry weight, is much lower in the arctic than in the tropics. In the arctic, a higher concentration of the enzymes that participate in respiration and photosynthesis may counteract the depressing effect of low temperature. In this respect marine phytoplankton has not been studied. Several authors have given examples of cases in which the rate of respiration of a given species, when subjected to the same temperature, is less for individuals collected from a warmer area than for those col-

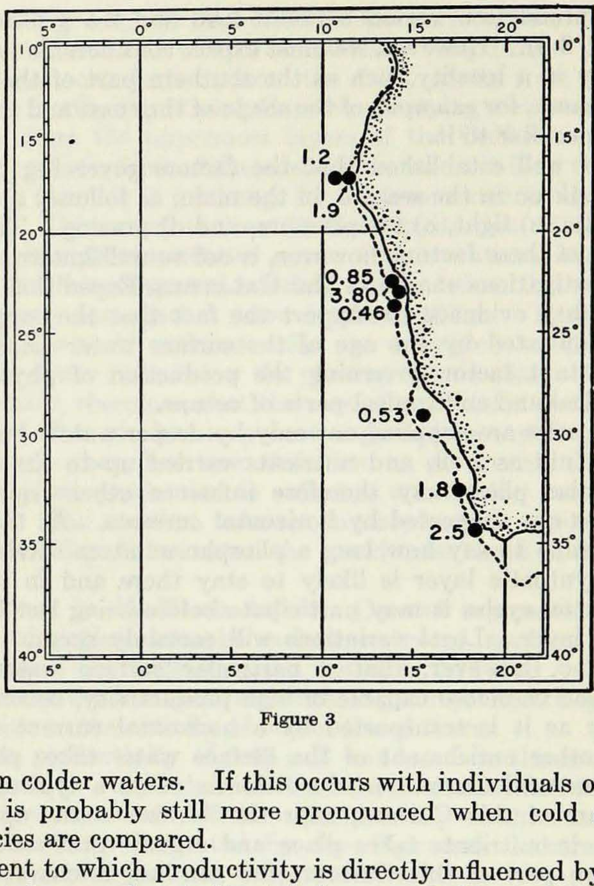


Figure 3

lected from colder waters. If this occurs with individuals of the same species it is probably still more pronounced when cold and warm water species are compared.

The extent to which productivity is directly influenced by temperature is not known, but indirect influence of this factor is perhaps the more important. Low temperature often seems to have a pronounced effect by inhibiting the activity of bacteria. Possibly an increase in temperature may accelerate regeneration of the nutrient salts with the result that organic production is also accelerated.

In highly productive regions having a rich supply of nutrient salts, light intensity is the most important limiting factor. It is also limiting in high latitudes during winter, in regions that lack stability of the water column, e.g., the Antarctic Ocean during spring. However, in tropical and subtropical areas, outside those localities with a pronounced upwelling, light intensity seems to be of little importance as a limiting factor.

Let us consider a tropical or subtropical station at which the depth

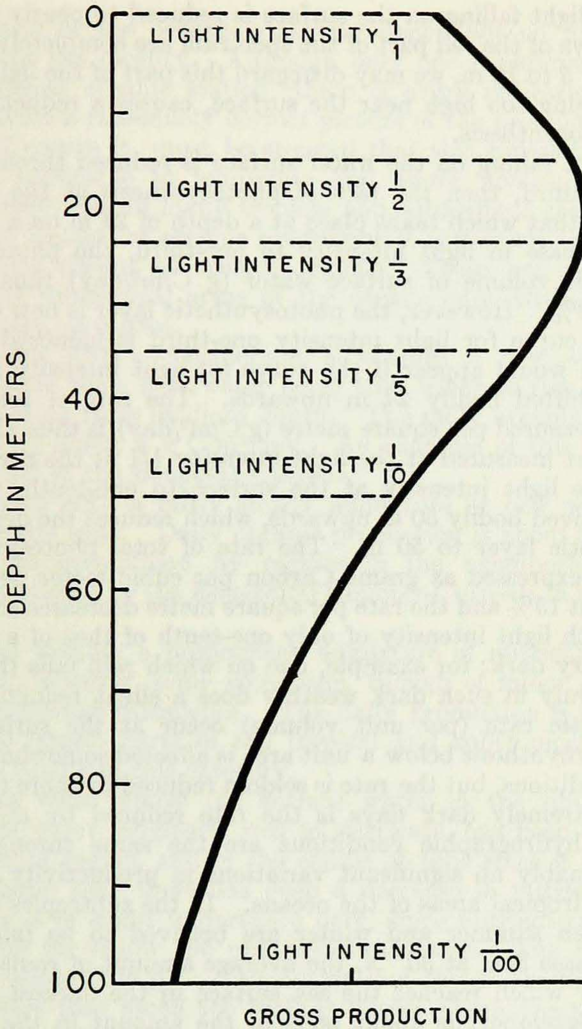


Figure 4

of the photosynthetic layer is 100 m. If the phytoplankton are evenly distributed in the layer and if the light absorption is the same at all depths, then we obtain the hypothetical curve shown in Fig. 4. This represents the daily relative rates of total photosynthesis at different depths on a clear day. The maximum rate is found at a depth of about 20 m, where the average of the blue and green part of the light falling on the surface is reduced to nearly one-third. Since the rays of the red part of the spectrum are completely absorbed in the upper 5 to 10 m, we may disregard this part of the light. 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 throughout the day to one-third, then the rate of photosynthesis at the surface is the same as that which takes place at a depth of 24 m on a clear day. With a decrease in light intensity to one-third, the photosynthetic rate per unit volume of surface water (g $C/m^3$/day) thus increases by nearly 50%. However, the photosynthetic layer is now only 76 m deep. The curve for light intensity one-third is identical with the curve which would appear if the curve for light intensity 1/1 at the surface 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 1/1 at the surface. By reducing the light intensity at the surface to one-tenth, the curve 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 expressed as grams Carbon per cubic meter per day decreases about 15% and the rate per square metre decreases about 75%.

A day with light intensity of only one-tenth of that of a clear day is in fact very dark; for example, one on which rain falls throughout the day. Only in such dark weather does a slight reduction of the photosynthetic rate (per unit volume) occur at the surface. The rate of photosynthesis below a unit area is affected somewhat more by weather conditions, but the rate is seldom reduced by more than 50%. On only extremely dark days is the rate reduced by about 75%.

If other hydrographic conditions are the same throughout the year, presumably no significant variations in productivity are to be expected in tropical areas of the oceans. In the subtropics the variations between summer and winter are believed to be fairly small. 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 the figure, assuming other factors equal, the rate of production per unit area in the darkest month is about 80% of that in the brightest month.

The effect of grazing will not be discussed here. However, various experiments were performed aboard the Galathea to obtain information regarding this factor. Grazing was found to be fairly important.

Investigations carried out during the Galathea Expedition have shown that the amount of organic production in tropical and subtropical parts of the oceans is strictly dependent on hydrographic conditions in the locality. Although only one experiment was performed at each oceanic station, there is every indication that the results provide a reasonably correct picture of the productivity of the region. Of course it must be stressed that this generalization is by no means applicable to temperate and arctic waters, nor does it apply in every case to many tropical and subtropical coastal waters.

From the amount of organic production it is possible to distinguish four different classes of oceanic regions. These are applicable to tropical and subtropical areas of the oceans only, with graduations between them, of course.

(1) Regions with a considerable admixture of new water to the photosynthetic zone, new water being that which is rich in nutrient salts originating from medium depth. The daily organic production is from 0.5 to about 3 g C/m$^2$/day. An example of this class is the southern part of the Benguela Current.

(2) Regions with a fairly steady admixture of new water to the photosynthetic zone. Daily organic production is about 0.2–0.5 g C. This may be exemplified by regions in the neighborhood of the divergences caused by the Equatorial Counter-Currents in the different oceans.

(3) Areas without a pronounced admixture of nutrient-rich water from below; however, some admixture, though of minor importance, may occur through turbulence. The daily production is 0.1–0.2 g C. By far the largest parts of the tropical and subtropical regions of the oceans belong in this category.

(4) Areas with typical old surface water in the photosynthetic zone. This water, originally rich in nutrients, has been transported from a distant region, and in the course of time since it entered the photosynthetic zone there has been a decrease in nutrient content. Turbulence is of slight importance only, since nutrient-rich water is present only far below the photosynthetic zone. The rate of production is about 0.05 g C. An example of this is the Sargasso Sea.

I am aware that much too little is known about the productivity of the arctic, antarctic, and temperate seas, where seasonal changes are pronounced, but nevertheless I have ventured to estimate the average daily gross production in all seas as about 0.15 g C assimilated per square mile. According to this, the net production for the whole hydrosphere is about $1.5 \times 10^{10}$ tons of carbon per year, which is the same as the general estimate for production on land.

On the GALATHEA Expedition a high rate of organic production was always found in conjunction with a shallow photosynthetic layer. In Walvis Bay (South Africa), where the highest rate of production was recorded (3.8 g C/m²/day), the photosynthetic layer was only 0.8 m deep.

The data for 184 GALATHEA stations are presented in Table I. The numbers are those from stations which fell within each category of production rate and depth. They 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 had a rate of production above 0.24. For a depth of 75–99 m, none had a rate above 0.49, the main part showing a rate between 0.11 and 0.24. For a depth of 50–74 m, none had a rate above 0.99, but about a quarter of the stations in this category showed rates between 0.05 and 0.99. For a depth of 25–49 m, a few stations had a rate of production above 1.0, but for the most part they were characterized by rates between 0.25 and 0.99. The stations with

TABLE I. CORRELATION BETWEEN THE VERTICAL EXTENT OF THE PHOTOSYNTHETIC LAYER AND THE RATE OF GROSS PRODUCTION

| *Rate of gross production (g C/m²/day)* | *Vertical extent of photosynthetic layer (m)* | | | | |
|---|---|---|---|---|---|
| | *0–24* | *25–29* | *50–74* | *75–99* | *100–120* |
| >1.00 | 7 | 3 | — | — | — |
| 0.50–0.99 | 6 | 15 | 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 shallowest photosynthetic layer (less than 24 m) belong essentially to the category with a rate of production above 1 g C/m²/day.

However, it must be borne in mind that some coastal stations may be characterized by a thin photosynthetic layer and an insignificant rate of organic production because of decreased light penetration due to suspended clay and other material. The stations off the mouth of the Congo River provide typical examples of this kind. But in general a marine area with a shallow photosynthetic layer is highly productive. On the other hand, if the photosynthetic layer is deep, the rate of production is always low. In the clearest ocean water, as in the Sargasso Sea where the depth of the photosynthetic layer is about 120 m, it is of considerable interest to estimate the rate of production which can be expected theoretically in such waters. This can be done by using the results from experimental plankton work.

In various countries during the last few years important work has been performed to determine the maximum possible rate of organic production by planktonic algae grown in large basins in a pilot plant under natural light conditions. In these experiments light intensity is almost the only limiting factor. All other factors, e.g., the concentration of nutrient salts, are made as optimal as possible. The most successful experiments yield a net production rate of slightly more than 10 g dry matter per square meter per day. This means a gross production of about 5 g $C/m^2$/day, which is about 30% more than that which occurs under natural conditions in Walvis Bay. The depth of the algal suspension in the basins is only a few centimeters, and the concentration of the algae (mostly *Chlorella*) is so high that nearly all the light that penetrates the surface is absorbed by the algae. The light absorption in the thin layer of water is without any importance.

In the ocean, however, when the depth of the photosynthetic layer is about 120 m, the algae absorb only a small part of the light and utilize it for the production of organic matter. Thus, most of the light is absorbed by the water itself. It would take too long to go through all the necessary computations, but briefly it can be stated that, theoretically, a maximum rate of production of only one-twelfth of the rate in the basin of the pilot plant is possible, that is 0.4 g $C/m^2$/day.

However, this value is still too high. The phytoplankton in oceanic regions of very transparent water grow under conditions far below the optimum that occurs in pilot plants. In the first place, the concentrations of nutrient salts are not optimal. If growth conditions were better, the increasing population of algae would soon render the water less transparent, thus diminishing the depth of the photosynthetic layer. Therefore, in oceans with a photosynthetic layer more than 100 m thick, it is not astonishing to find that the maximum rate of gross production is only 5% of the rate possible in the pilot plant and that the average rate is only about 2% of this rate. The waters of the Sargasso Sea are transparent because of the insignificant rate of organic production that occurs there as a result of the poor supply of nutrient salts.

In the foregoing, the rate of production has been stated per square meter of surface, since only in that way can the different regions of the sea be compared *inter se*. The rate of production however, as measured by volume, is also of considerable interest. Undoubtedly it is of importance to grazing animals whether plankton are concentrated in a shallow layer or dispersed through a deep layer. Moreover, although the planktonic algae are for the most part fairly evenly distributed throughout the photosynthetic layer, this is by no means always so.

Calculated per unit volume, the most productive station on the GALATHEA Expedition (Walvis Bay) yielded a rate of production at the surface which was 14,000 times the rate at the surface of the Sargasso Sea. Calculated per unit area, however, the rate at the Walvis Bay section is only 80 times higher. The differences in the depths of the photosynthetic zones, 0.8 and 121 m respectively, account for the differences in the rates.

From the GALATHEA investigations, it is possible to state that the laws governing organic productivity in tropical and subtropical parts of the oceans are not very complex. This does not mean, of course, that there is no reason to make further investigations in this field. Quite the opposite; it is an argument for intensifying such studies. It is important to possess detailed knowledge of organic productivity in the sea for all parts of the earth in order to understand better the conditions affecting the production of fish and other marine animals. Regions of primary interest to fisheries are mostly near the coasts, and organic production in coastal areas is often of a somewhat more complicated nature than that occurring in tropical and subtropical parts of the open oceans.

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