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PRIMARY PRODUCTION IN TROPICAL MARINE AREAS

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Most studies of marine primary production have been carried out in temperate or arctic water. The location of most marine institutes, together with the sites of the world's biggest fisheries, is of course one of the main reasons for this fact. It would be wrong, however, to assert that the tropical parts of the open oceans are particularly little known concerning primary production. These regions are in fact those best understood at present. The German Expeditions during the first third of this century—the *Deutschland* and the *Meteor* Expeditions—provided the fundamental knowledge concerning the size of the standing stock of phytoplankton in these waters. These were followed by the Danish *Galathea* Expedition in 1950-52 where the organic productivity was measured by means of the carbon-14 technique. In recent years the work in the open oceans has been greatly intensified.

In this article only the primary production by the marine phytoplankton will be discussed. The production caused by sessile microscopic and macroscopic plants living near the coast generally follows the rules valid for the phytoplankton. The carbon-14 technique (Steemann Nielsen, 1952) has rendered it possible to measure the rate of organic production by the phytoplankton, whether it is high or low.

It is always problematical to generalize about the magnitude of the primary production in the sea. It would at least be rather difficult to establish well-defined regions according to temperature. Cold marine areas may be either very productive or very unproductive. The same is true of the really warm regions of the sea.

Temperature as such can thus hardly be a factor of general decisive importance for the size of primary production. We shall provide evidence that the influence of temperature on the size of primary production is indirect. A high temperature may be the real cause of a rich production in some areas, whereas it is of very little importance in other areas.

Another characteristic of tropical marine areas is the ordinary high intensity of light penetrating the surface. If the light intensity were the ordinary limiting factor for marine organic productivity, all tropical marine areas would be very productive. However, only a small and varying part of the light reaching the sea surface is transformed into chemical energy by the plants. The major part of light is ordinarily not absorbed by the plants but by the water itself, by suspended dead organic and inorganic particles and by dissolved matter.

Generally the principal factor limiting the magnitude of organic production in the sea is the replenishment of the nutrients in the productive euphotic layer (*cf.* for example Steemann Nielsen and Aabye Jensen, 1957). The replenishment of the nutrients—primarily phosphate and nitrate (or ammonia) is provided by the two processes of decomposition and water circulation.

In general, it may be stated that in the open deep ocean replenishment by water circulation is by far the most important process, whereas in such coastal areas where the water in the photic zone is more or less regularly in contact with the bottom, microbiological decomposition of organic matter is the most important factor. Due to this decomposition, the salts containing phosphorus and nitrogen are regenerated. In the open ocean and in shallow water, organic productivity is thus governed in a different way.

The Production in the Open Oceans

Sverdrup (1955, Fig. 2) has presented a schematic picture of the probable relative productivity of ocean areas, based entirely on theoretical considerations. In the areas where either intensive measurements of the standing stock of phytoplankton have been made, such as in virtually the whole of the Atlantic ocean, or where measurements of the primary production have been made, a remarkable agreement with Sverdrup's theoretical picture is found. Sverdrup's theoretical considerations were based on the idea that the size of the primary production in the open ocean is dependent primarily on the rate of replenishment of the nutrient salts through the supply of subsurface water to the photosynthetic zone, as was shown convincingly in the South Atlantic by the *Meteor* Expedition (Hentschel and Wattenberg, 1930).

A common feature, especially obvious in the tropical and subtropical parts of the oceans, is the low range of variations of the values obtained within areas which are hydrographically uniform. This is true both for the plankton counts, carried out on a very big scale by the German expeditions—(*cf.* Lohmann, 1920 ; and Hentschel, 1933-36), and for the measurements of organic production as carried out in the later years by means of the carbon-14 technique.

It is possible to give a hydrographical outline corresponding, in general terms, to the conditions found in all oceans (for details *cf.* Sverdrup *et al.*, 1942). All oceans are characterized by large circulating current systems. In the South Atlantic, the South Pacific and the Indian Ocean these run counterclockwise. An anticyclonic eddy is found in the center of the currents. The current in each ocean flowing across the oceans south of Equator from East to West is called the South Equatorial Current. In contrast to the oceans of the southern hemisphere the anticyclonic eddies in the North Atlantic and in the North Pacific are clockwise. The North Equatorial Currents are thus also running from East to West.

In all oceans an eastgoing Counter Current is found between the North Equatorial and the South Equatorial Currents, both running in a westerly direction. Due to the shape of the Indian Ocean the current system in the northern part only partly resembles those found in the North Atlantic and the North Pacific. The west-going North Equatorial Current is found only during part of the year. It is neutralized or substituted by an eastgoing current when the South West Monsoon is blowing.

Theoretically a low productivity is to be expected in lower latitudes in the central part of the anticyclonic eddies. Here the surface water is slowly sinking downwards thus preventing any admixture of subsurface water to the photic zone. The renewal of the plant nutrients in the surface water takes place by decomposition *in situ* of organic matter or by lateral influx of surface water, already impoverished with regard to nutrient salts. On the other hand, high productivity is found in localities where upwelling takes place, for example, associated with diverging surface currents. At the boundary between the South Equatorial Current and the Countercurrent in the eastern parts of all three oceans, especially well developed divergences are found.

According to Brandhorst (1958), in tropical oceanic waters there is an inverse relationship between the depth of the thermocline and the size of the standing crop of zooplankton—and thus also with the magnitude of the primary production. In the tropical ocean, outside areas with upwelling, a strong thermocline is found throughout the year. As ordinarily no seasonal turnover of the water column takes place, the availability of the nutrient salts to the plants—the factor governing the size of the primary production—is dependent largely upon the depth of the thermocline.

The depth of the thermocline varies much within tropical oceanic waters. Accordingly the rate of the primary production also varies a great deal. Whereas the daily rate is about 50 mg. C/m.^{2} near the centres of the anticyclonic eddies corresponding to a depth of the thermocline of more than 100 metres, it increases in other parts of the oceans to values about 500 mg. C/m.^{2}. Near true upwelling, the rate may be considerably higher (*cf.* Steemann Nielsen and Aabye Jensen, 1957).

The simplest way to estimate oceanic production is by means of the colour of the sea. The deep blue water is the most unproductive water. The transparency of the water is, of course, a better indication of productivity. The more transparent the water, the greater is the depth of the photosynthetic layer and the smaller is consequently the part of the incident light which is absorbed by the plankton algae. The clearest, deep blue water with a very small stock of algae behaves in this respect virtually like distilled water.

It is possible at present to outline the general pattern of oceanic primary production in the tropics. The details, however, are still missing. A lot of work must be done before these become known. If investigations on primary production are to be used as a basis for evaluating the possibilities, for example, of a commercial fishery, it is absolutely necessary to know the details. Special parts of the oceans, such as the Bay of Bengal and the Arabian Sea in the Indian Ocean especially demand intensified studies, not only because of the influence of the monsoon shift in such areas but also because of the special importance of increasing the fishery here.

The Production in Tropical Coastal Areas

Much too little is known concerning the organic production in tropical coastal areas. It is nevertheless possible to present some general outlines. Whereas in the open ocean the replenishment of the nutrients and thus productivity is governed primarily through admixture to the photosynthetic zone of nutrient-rich subsurface water in which the regeneration of the salts has taken place long ago, in coastal waters the replenishment is first and foremost due to regeneration taking place simultaneously.

Present knowledge seems to indicate that the regeneration of the nutrient salts in coastal waters takes place primarily in the surface of the bottom sediments. If the depth is inconsiderable the water masses of the photosynthetic zone will be in more or less continual contact with the bottom and the replenishment of the nutrient salts will be easy. If a layer of discontinuity of some kind is found, the admixture of the nutrients to the surface layer becomes somewhat more complicated. All available evidence suggests that the regeneration rate of the nutrient salts is dependent on temperature. The higher the temperature, the higher the rate. This is in accordance with the fact, that the regeneration is due primarily to microbiological processes. The rate of metabolism in bacteria is dependent on temperature.

As demonstrated during the *Galathea* Expedition. (Steemann Nielsen and Aabye Jensen, 1957) a relatively high rate of organic production was found at practically all coastal stations in the tropics. This is in agreement with the theoretical considerations presented above. The only exception was found near the mouth of the Congo River where the low transparency of the water masses due to the silt brought down with the river water caused very poor light conditions for the phytoplankton and thus a very low production rate.

The seasonal variation of the primary production in coastal waters in the temperate zone provides additional evidence for the thesis that temperature is the most important factor governing the size of primary production in water masses in contact with the bottom. In Danish waters a large number of such localities have now been investigated all of which show a close correlation between the rate of primary production and temperature (*cf.* for example, Fig. 6 in Grøntved and Steemann Nielsen, 1957). For one area where regular investigations have been carried out during several years it has been possible to correlate the rate of primary production during the summer with the temperature (Steemann Nielsen, 1958).

Even close to the coasts of isolated islands in the tropical parts of the oceans a relatively high rate of organic production is ordinarily found. Doty and Oguri (1957) have shown this to be true for the Hawaii Islands, which are situated in an oligotrophic part of the Pacific.

Details of coastal productivity in the Tropics are still lacking. We may perhaps suggest that they are as varied as those found in similar areas at higher latitudes.

Temperature and the Production of Organic Matter in Plankton Algae

Enzymatic processes are dependent on temperature. In plankton algae respiration and photosynthesis at higher light intensities are thus also dependent on temperature. If algae are transferred to a higher temperature the rates of both processes automatically increase. It is thus easy to understand that several scientists have got the idea that the rate of metabolism is much higher in tropical than in colder waters. This very idea was presented by the present writer concerning the bacteria active in the regeneration of the nutrient salts.

However, we shall try to show that the bacteria represent a special case. Ordinarily—and thus in the case of plankton algae—the metabolism seems by no means to be higher in tropical than in temperate and arctic waters (*cf.* Steemann Nielsen and Hansen, 1959, for details). The rate of an enzymatic process is a combined result of enzyme concentration and temperature. If the temperature is low, the effect may be completely counteracted if the enzyme concentration is high. In Nature most kinds of organisms able to live in a certain habitat seem to be capable of adjusting their enzyme concentration at a level most appropriate to the prevailing ecological conditions in that habitat.

In organisms like the autotrophic plankton algae containing for example relatively big chloroplasts, the enzymes constitute only a minor part of the organic matter found. Thus a considerable augmentation of the concentration of enzymes does not cause a considerable increase in the amount of total organic matter per cell. In bacteria, on the other hand, a major part of the dry substances ordinarily consists of protoplasmic proteins, most of which must be considered to be enzymes in the widest sense. If the content of enzymes, in order to counteract a decrease in temperature, has to increase by a factor of say 2, the content of total organic matter will also increase considerably. Although the rate of the different metabolic processes increases per cell when the contents of the enzymes are augmented, relatively much more organic matter must now be produced in order to reproduce the bacteria. It is thus not possible to keep the reproduction time constant in bacteria at a low temperature by simply increasing the concentration of the enzymes.

As shown in the preceding section, the bacterial regeneration rate of the nutrient salts is the main factor governing primary production in coastal waters. The apparently astonishing fact is therefore found, that production here is strongly dependent on temperature, although the direct influence of this factor on phytoplankton growth is rather insignificant. We obtain thus the background for understanding why temperature is an important factor for the size of the production in coastal waters but not in the open ocean, where the replenishment of the nutrient salts is not primarily due to the regeneration *in situ* of these salts.

SUMMARY

An outline of the primary production in tropical waters is presented. It is shown that the replenishment of the nutrient salts ordinarily governs the size of the production both in the open sea and in coastal waters. Whereas in the open sea this replenishment is provided primarily by water circulation, in shallow coastal waters it is provided by decomposition taking place primarily in the upper layers of the bottom sediments. Because the decomposition is due to microbiological processes it is dependent on temperature. The water circulation in the open sea, on the other hand, is not dependent on temperature. Hence this factor is of quite different importance in the two habitats.

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