STUDIES ON THE PHYTOPLANKTON OF THE WEST COAST OF INDIA

Part II. Physical and Chemical Factors Influencing the Production of Phytoplankton, with Remarks on the Cycle of Nutrients and on the Relationship of the Phosphate-Content to Fish Landings*

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I. INTRODUCTION

IN the first part of this series of studies, the biological investigations on phytoplankton and zooplankton crop, their interrelationships, the magnitude of the standing crop, an assessment of total phytoplankton production and its relationship to fish landings, etc., were reported. In the present account, the environmental factors, physical (such as temperature of the water, light intensity, ocean currents, wind force, etc.) as well as chemical (such as salinity of the water, nutrient salts—phosphates, nitrates, silicates—dissolved oxygen, etc.) are described and their bearing on the fertility of the waters, phytoplankton production, and to fish landings discussed.

The methods employed in the analyses of sea-water are the same as those described by Harvey (1928 *b*, 1945; *see* also Jayaraman, 1951, 1954). A hydrological register is being maintained at the Central Marine Fisheries Research Substation since October 1949, by the collaboration of the several members of the scientific personnel including the writer and the chemical data presented here are drawn from this register. During the period June 1955 to November 1956, the writer was in charge of all aspects of hydrological studies. The interpretations are the writer's own.

II. TEMPERATURE OF THE WATER AND LIGHT INTENSITY

(*a*) *Temperature*

The sea surface temperature data recorded relate to the stations from where plankton samples were actually collected, 5 to 6 miles from the shore. At Calicut, the sea surface temperature (Text-Figs. 1 and 7) is lowest in July being 25·3° C. and highest in April being 30° C. (average of 5 years). There is a tendency for the water temperature to fall slightly (a degree or so) in January from the value obtaining in December, after which it rises again.

The sea surface temperature also presents a double oscillation during the year as does the air temperature. The main maxima occur in April (1950, 1952–54) or May (1951) and the secondary one in October (1953), November (1949, 1950, 1951 and 1954) or December (1952) (Text-Fig. 1). The minimum values occur in July (1950), August (1951 and 1952) or Septem-

nd 1954). A similar bimodal or double oscillation of the sea
perature has been found to be common for several of the warmer
tigated in the regions around India (Weel, 1923; Sewell, 1929;
946; Chevy *et* Serene, 1948; Chidambaram, 1950; Kow, 1953;
56; Chacko *et al.*, 1954; *see* also Prasad, 1957). Observations
anapati and Murthy (1954) in the Bay of Bengal off the Vizaga-
ast show a triple oscillation of the surface temperature with a
of 4·4° C. between maximum and minimum. Lowest values
January and highest in October as at Madras. Ramamurthy
wever, could find no double oscillation in the temperature of the
he Madras coast; his values vary from 27·16° C. to 31·1° C. in
d October respectively.

be seen from the above that the nature of fluctuation in the sur-
ature of the water is not very different over a wide area in and
ian waters in the tropics.

not possible to record the temperature differences in relation to
of the water; a few observations made in the beginning of the
n showed that even at a little depth of about 15 metres, the bottom
slightly lower. Prasad (1952) and La Fond (1954) have made
vations in this regard in the Bay of Bengal while on short cruises.

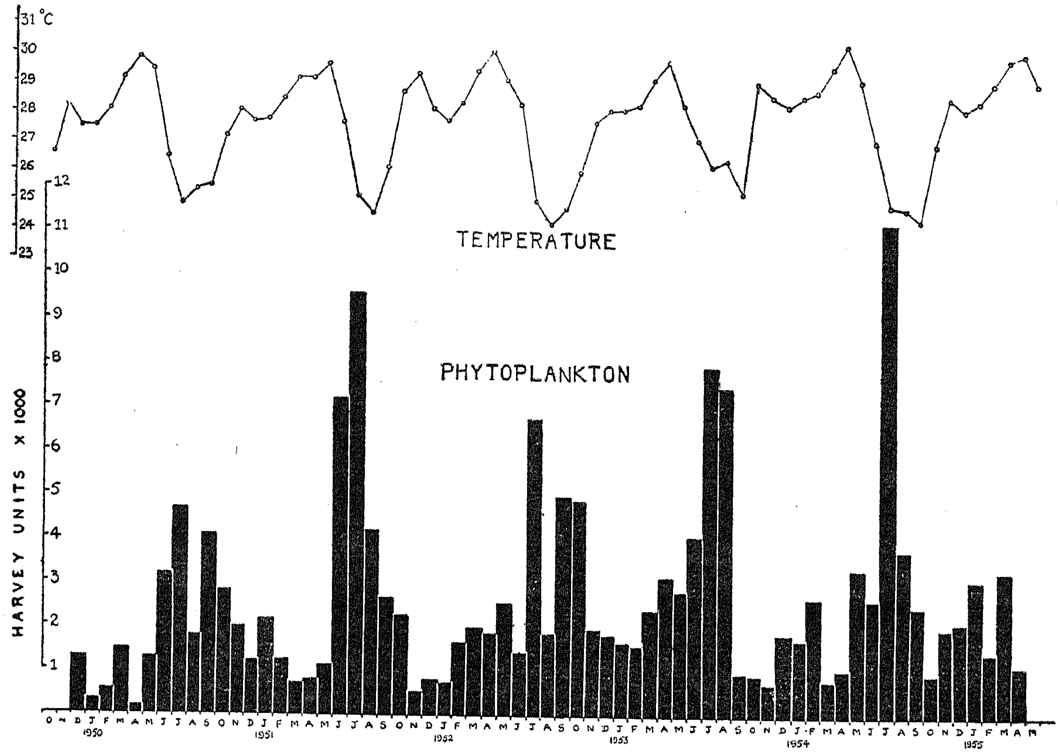
(1929, p. 212) who studied the Laccadive Sea has also recorded
asonal oscillation of the surface temperature as well as air tem-
The other points made by him are: In the Indian waters the
perature is normally higher than the air temperature at all times
; the sea temperature when it becomes lower than the air tem-
es so at or about midnight, and as the temperature of the air
lls more rapidly than that of the sea-water, it would further seem
at at this time of the night there is some phenomenon occurring
es the abnormal lowering of the surface temperature; the altera-
relationship of the two temperatures ultimately depends on the
the wind; the wind brings about a diurnal variation in the tem-
rise in wind force being accompanied by a fall in the temperature;
winter months, the temperature of the sea is colder at the surface
epth of 20–50 metres, particularly at night or early morning hours;
he wind force will tend to cool the surface, but increase the ampli-
waves and bring about admixture of surface and bottom waters
g the temperature relationship of the air and the sea surface and
the temperature difference; during the hot dry months of
pril and May, increase of wind force causes lowering of surface

temperature and gives rise to an admixture of surface water with water from some depth which is at a lower temperature, both facts thus decreasing the temperature difference between sea and air so that in these months the wind force and temperature difference vary in opposite directions; there is thus a double diurnal upwelling of water from some depth below towards or actually on to the surface. Obviously, in the present area, such diurnal changes must be constantly replenishing the surface layers with nutrients which also accounts for the high production of plankton seen here.

It may be mentioned that during these months concerned, October, April and May, but for the increase in the wind force (Text-Fig. 8), the surface temperature would still rise very much.

According to Carpenter (1887 in Sewell, 1925, pp. 47–48, Chart VI), the Cold Antarctic Flow, which makes up for the greater evaporation, is probably uniform in temperature and widely spread; it extends up to 10° N. and gradually surfaces. One arm of this current extends to the Arabian Sea. This current may have considerable influence on the temperature conditions also in the Arabian Sea besides on the salinity and nutrient salt content. Further, the waters of the Antarctic Intermediate Current which rise towards the surface from great depths as they move north along the East African Coast (Mohamed, 1940, p. 193) also enter into the current circulation of the Arabian Sea and thus the west coast of India and affect the chemical and physical properties of the water including the temperature.

An examination of Text-Fig. 1 shows that the main bloom of phytoplankton occurs when the water temperature is falling, though the lowest temperature attained is only about 24–25° C. But phytoplankton bloom also occurs even at higher temperatures of about 27–28° C. Generally, when the water temperature goes above 29° C., the phytoplankton content is either poor or unhealthy and the elements are found dead and degenerating. Marshall (1933, p. 104), however, states that a rise in temperature had no depressing effect on the Diatom population in the Great Barrier Reef. It is known that a linear relationship exists (between 15 and 25° C.) between the temperature and growth below the former's optimum value and this optimum varies with the species (Barker, 1935). Gran and Braarud (1935) found that in the Gulf of Maine, different species of Diatoms showed maximum growth at different temperatures which varied from 3–12° C.; even species within the same genus show different temperature preference. Spencer's (1954, p. 278) experiments showed that the mean generation time falls with increasing temperatures reaching a minimum at about 20° C.; further increase had no effect on growth though there was no inhibiting effect



TEXT-FIG. 1. Seasonal fluctuation of the temperature of sea-water (surface) and phytoplankton crop (Harvey Units). Explanation in text.

up to 25° C.; above 25° C., adverse effects came to be noticed. According to McCombie (1953), in freshwaters, the seasonal cycle is caused chiefly by the seasonal change in the water temperature resulting from the change in the solar radiation. Wallace (1955) states that the optimum and maximum temperature tolerated respectively by some freshwater Diatoms are 26–20° and 34° C. for *Nitzschia filiformis*, 22 and 30° C. for *Gomphonema parvulum*.

The range of temperature here in this tropical environment is not much. It has also been shown above that there is a constant mixing up of the layers which tends to bring an equilibrium in the temperature conditions and during the south-west monsoon season this is very pronounced owing to upwelling of the deeper waters. It is interesting to note that the peak of phytoplankton production occurs on the west coast of India when the water temperature is between 24° and 25° C. resembling the optimum temperature conditions noticed in the cultures by several workers cited above. Temperature here, most of the time, appears to be at about optimum levels for production of phytoplankton.

(*b*) *Light*

In a region such as the present one with the average hours of sunshine exceeding nine hours a day, light cannot, obviously, be a limiting factor for growth of phytoplankton, as it is so in the higher latitudes, the temperate and polar seas. The stations sampled are situated within an area where the depth does not exceed 40 metres. It is well known that photosynthesis can take place even at 100 metres depth (Clarke, 1936) though often this *compensation point* may vary according to the transparency of the water which depends on the amount of suspended matter present in it.

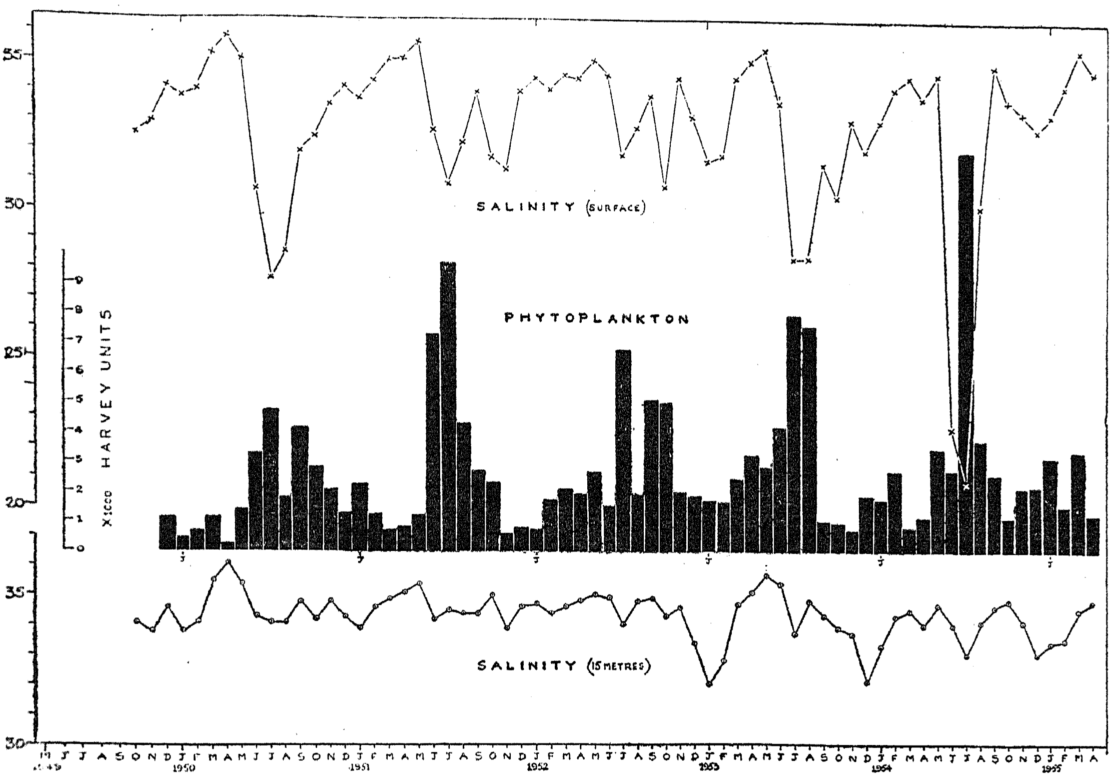
The influence of light on the growth of phytoplankton has been studied in detail in the higher latitudes (Stanbury, 1931; Gaarder and Gran, 1927; Gran and Braarud, 1935; Marshall and Orr, 1928; Jenkin, 1937; Petterson, 1936; Petterson, Höglund and Landberg, 1934) as also the quality of light utilized (Clarke and Oster, 1934; Oster and Clarke, 1935; Clarke and James, 1939; *see also* Harvey, 1955). Chidambaram and Menon (1945, p. 365) state that " lack of sunshine " and " unstable conditions " arrest the development of plankton organisms during the south-west monsoon season on the west coast of India. These authors have no data for the months of June and July, the peak of the monsoon period as no collections could be made then by them. The investigations covering a period of nearly 6 years by the writer shows that it is *during these very months* that the phytoplankton attains its zenith of development on the west coast of India.

III. SALINITY OF THE SEA-WATER

The values recorded for salinity of the sea-water are shown in Text-Fig. 2 on the basis of monthly averages. The salinity of the surface water fluctuates more sharply than that of water at a depth of 15 metres. At the surface, the maximum values occur in April or May and the lowest in July, during the south-west monsoon. The salinity rises after July and there is a second fall in October, November or December from when on there is a rise till the drop in the following year with the beginning of the south-west monsoon.

The variation in salinity in parts per *mille* was as follows: at the surface, 27·68–35·14; 30·93–35·65; 30·80–35·05; 28·35–35·47 and 20·74–35·54; at the bottom, 33·89–35·43; 33·93–35·43; 32·76–35·11; 32·08–35·72 and 33·02–34·69 during the years (May–April) 1950–51, 1951–52, 1952–53, 1953–54 and 1954–55 respectively.

Generally, salinity at 15 metres depth is higher than that at the surface but on some occasions (January and February 1950; March, April and May 1951; March 1952; and March, May and September 1954) the salinity of the bottom samples was slightly less than the surface value. This is very possibly due to the evaporation of the surface water on account of the higher



TEXT-FIG. 2. Seasonal fluctuation in the salinity of the surface and bottom water, and of phytoplankton (Harvey Units). Explanation in text.

temperature prevailing at those times, or incursion of low salinity water from below through currents.

The greatest variation between surface and bottom values occurs during June–July of the south-west monsoon period and the least during the north-east monsoon period, November to April or May.

It may be seen that there is more or less a triple oscillation in the fluctuation of the salinity during a year in these waters, two of which are clearly marked.

At 15 metres depth, the salinity changes are more gradual and the lowest average value recorded is 32‰ (January and December 1953) unlike the surface layer where the lowest value occurs in June–July. While the surface salinity shows a very appreciable fall, sometimes to even as low as 21‰, during June–July, the height of the south-west monsoon, the bottom values are as high as 33–34‰ at the same period. The rainfall at sea beyond 20 miles from the Malabar coast is very much less (Subrahmanyan, Part I) hence salinity would appear to attain an equilibrium soon and the overall fall in salinity during the period of maximum rainfall does not exceed 3% of the high values obtaining before the onset of the south-west monsoon.

The higher values for salinity are recorded during periods when the air and water temperatures are high, wind force greater and humidity low, factors which permit evaporation. It is during such periods that the range of salinity between the surface and bottom layers is least, probably because of the higher wind force obtaining at the time which leads to the mixing up of the water layers. Sometimes the surface values for salinity exceed those of the bottom slightly, as indicated already, due to the heating up of the water and consequent evaporation and lack of mixing up of the layers by wind. Very often, during the summer, when wind force also is high, the surface and bottom values are the same.

The lower values for surface salinity occur with the fall of temperature, occurrence of rainfall, increased humidity and fall in the strength of the wind force which does not allow of the mixing up of the water layers. During this time, the difference in the salinity of the surface and the bottom is greater.

Like temperature, salinity also shows a well emphasized double oscillation and a third minor one. When dealing with the temperature changes of sea-water, it was mentioned that, according to Sewell (1929) there is a diurnal change of temperature depending on wind force and this leads to an upwelling of the water from the lower layers towards the surface bringing about changes in the temperature of the water. Sewell (1929, pp. 274–75) has shown that salinity also is affected by the same forces. According to him, in the Indian seas, there is a distinct double oscillation during the course of the day in the salinity of the surface waters; this is correlated with the double oscillation of the wind force during the twenty-four hours of the day. This double oscillation of the salinity exhibits two phases at different periods of the year; at one period, salinity rises and falls with the variation in the strength of the wind, while at another period, it oscillates against the wind force, the oscillation and phases depending on the relative salinity of the surface water and that at the bottom which wells upwards under the influence of the wind. During the wet monsoon months, the surface water becomes diluted and rendered less saline either directly by rainfall or indirectly by the increased outflow of river-water and the oscillation of the salinity is the positive phase, *i.e.*, an increase in the wind force tends to increase the salinity of surface water by bringing up water of higher salinity from below; whereas during the hot dry months, the surface water is more saline due to evaporation and an increase of the wind force brings about a diminution in the salinity owing to the mixing up of lower salinity bottom water with the highly saline surface water and this phase is the negative one.

Sewell's observations cover only the months, October to May. According to him, in the Laccadive Sea, the oscillation phase is positive in October and November indicating that the surface value of salinity is less than that at some depth owing to the effect of the south-west monsoon. In December, the phase is negative and remains so in February and March; in April and May, it is either positive or negative depending on local condition. In the present area in the Laccadive Sea, investigated by the writer, which has been covered throughout all the months for over 5 years, the oscillation phase is positive throughout the south-west monsoon period of May to September and up to December generally, the only exception being September 1954 (when the bottom values were lower than the surface values slightly); from January to May, the phase may be positive or negative.

The north-east monsoon, according to Sewell (1929, p. 338) seems to have no effect on the relationship of salinity of the surface water to that in the deeper layers. The effect of the north-east monsoon is felt more on the eastern side of the Peninsula than on the western side as evidenced by the range of temperature, increase of humidity, etc.

The oscillation of the salinity in the present area may be positive or negative from January onwards up to May. The change in the phase from positive to negative mentioned by Sewell (1929, p. 338) for the Laccadive Sea is not felt in the present area, perhaps due to the proximity of the station investigated to the shore. However, one point appears to need emphasis as far as salinity is concerned, *viz.*, that the north-east monsoon active on the east coast of the Peninsula appears to affect the salinity of the water on the west coast; for, the salinity values for both the surface and the bottom water record a fall in December or January, though there is no precipitation on the west coast at this time. This fall in the salinity appears to be due to the coastal current around the Peninsula at this time, which flows in a north-westerly direction, bringing in water of low salinity from the east coast and other areas where the north-east monsoon is active and heavy rainfall occurs.

George (1953 *a*) has tabulated the salinity values for three years, 1948–49 to 1950–51 for the area covered by this investigation including a part of the period and the values recorded are identical; but, beyond pointing out the effect of the heavy rainfall during south-west monsoon on the lowering of the salinity values, other aspects of the question have not been dealt with by him.

The salinity oscillations on the east coast of the Peninsula show some differences. At Madras (Jayaraman, 1951) salinity remains more or less constant, around 34·5‰ from about March to September, the amplitude of the oscillations being too small. The highest values are attained in April or May as at Calicut. From October to December, low values are recorded down to nearly 24‰ during periods of rainfall. The very low salinity recorded is not only due to the local rainfall at that time, but also to the effect of influx of freshwater discharge into the Bay of Bengal by the large river systems of India which are in floods owing to the south-west monsoon precipitation in the mountain ranges, their source. This flood water enters the coastal circulation thus lowering the salinity of the sea-water (Sewell, 1929, Text-Figs. 78 and 79). Ramamurthy's (1953 *b*) results for Madras are similar to those of Jayaraman; they vary between 23·23 to 34·94‰.

The salinity values recorded by Jayaraman (1954) for three years in the Gulf of Mannar and two years in the Palk Bay show that, high values occur during May to October, south-west monsoon season, and the lower values between November and April, the north-east monsoon season. In the Gulf of Mannar, the values range between 28·85 and 36·47‰, the lower value occurring in January and the higher in September; in the Palk Bay also, the lower values obtain in January and the highest in October, the values varying between 25·52 and 36·39‰ respectively.

Some data relating to salinity estimations in Indian waters is given in Table I for comparison. It may be seen that the variation in values at Calicut is least compared with the other areas which is indicative of oceanic conditions.

Since the main peak of production of phytoplankton (Subrahmanyan, Part I) occurs during or immediately following a drop in salinity values, owing to the monsoon precipitation, the bearing of salinity on the biological content of the water, particularly as it affects the phytoplankton may be examined now.

Salinity, as is well known, is important in maintaining the proper osmotic relationship of an organism. Species of phytoplankton have their own range of toleration to salinity changes (Braarud, 1951). However, not much is known about the osmotic relationship of Diatoms, the main constituents of the phytoplankton; but, Gross (1940) found that the Diatom *Ditylum Brightwelli* does not fit into the normal concept of an osmotic system and the plasmatic membrane of *Ditylum* cannot be regarded as a semi-permeable membrane as transfer of water between the cell and the medium is to a large extent independent of the differences in the osmotic pressure between cell content and the medium. Changes in the volume of *Ditylum*

TABLE I

Salinity in parts per mille in the Indian Waters

	Region	Minimum	Maximum	Remarks	References
1.	Madras ..	24·00	34·50	Lower value effect of North-East Monsoon	Jayaraman, 1951
2.	Madras ..	23·23	34·94	do.	Ramamurthy, 1953*b*
3.	Gulf of Mannar ..	28·85	36·47	do.	Jayaraman, 1954
4.	Palk Bay ..	25·52	36·39	do.	Jayaraman, 1954
5.	Vizagapatnam ..	25·00	34·00	Lower value effect of both monsoons mainly South-West Monsoon	Ganapati and Murthy, 1954
6.	Bombay Harbour	23·56	38·40	Lower value effect of South-West Monsoon	Bal *et al.*, 1946
7.	Calicut ..	31·00	35·00	do.	Present investigation—Figures average (of 5 years' data) for water column

protoplasts cannot be brought about by changes in the concentration and composition of the surrounding medium and these changes are not governed by the laws of osmotic equilibrium. It would appear that the Diatom cell has a peculiar reaction to changes in the salinity depending on its own physiological state.

One reaction of the Diatoms to changes in the salinity has great significance to the life-history of the organism, *viz.*, a fall in the salinity under certain conditions. A few instances from experiments will be found useful to clarify this point.

Iyengar and Subrahmanyan (1944, pp. 132–33) and Subrahmanyan (1947, p. 245) found in the cultures of Diatoms that the Diatom cells show a period of rapid multiplication by vegetative division and frequent transference of them to fresh culture media helps to keep up the multiplication of the Diatoms concerned; but, there comes a stage when the Diatom cells do not respond to further changes of culture media and no increase by division could be noticed. The cells by this time had considerably diminished in size owing to repeated divisions, a characteristic feature of the Diatoms. If left in the medium now for long, they begin to degenerate and die. But, if at this stage they are transferred to sterilized water slightly diluted (10–20%) with distilled water, the cells continue to live healthily but do not divide further. However, after some time, they begin to show auxospore-formation, which is a mode of rejuvenation and the process is often sexual; after this, the zygotes germinate and give rise to large cells which in their turn divide vegetatively and continue the cycle. The rate of division in the early stages is very rapid. The authors also found that dilution beyond 20% tends to kill the Diatoms. It has also been found that cells forming auxospores were within a certain range of size, characteristic for each species; cells either larger or smaller do not form auxospores, but ultimately they died in the medium. Somewhat similar observations have also been made by several workers on marine and freshwater Diatoms (*see* Iyengar and Subrahmanyan, 1944, for literature on this aspect; Subrahmanyan, 1947; Wimpenny, 1956; and Harvey, 1945, pp. 129–30). Such occurrences are considered possible by Lucas and Stubbings also (1948, p. 164).

It may be interesting to recall here that according to Gran (1929 *b*) the melting of snows and the inflow of freshwater from land (comparable to rainfall on the west coast of India) is an essential factor for the initiation of the vernal bloom of phytoplankton in the Norwegian waters. For the Gulf of Maine, Bigelow (1926) has made the same suggestion. Gaarder and Gran (1927) found in the Oslo Fjord that abundant phytoplankton is restricted to a surface layer with a relatively low salinity. Between Yorkshire coast and Dogger Bank, the peaks of plankton production (as seen from the Text-Fig. 1 in Wimpenny, 1944) coincide with periods of lower salinities.

Coming to the conditions in the sea off the west coast of India, it is found that during the south-west monsoon months, owing to the abundant rainfall, there is a fall in the salinity of the water which is very considerable at times in the surface layers. Such a steep fall is not noticed in the bottom layers of the water and, moreover, an equilibrium is attained soon, bringing the overall average value to 30‰, *i.e.*, a lowering of 12–15% from the high values obtaining (34–35‰) during the previous months. It is believed (Admiralty, 1950) that beyond 20 miles from the shore, over the sea, the rainfall is considerably less; hence, restoration of an equilibrium in the salinity of the water is facilitated. Further, it is possible that there is a reflux of offshore water following the influx into the sea of river-water as pointed out by Huntsman (1955) which also helps in raising the abnormally low salinity of the surface waters. On occasions when salinity is very low (*circa* 25‰) it is found that the plankton in the water is no longer healthy.

During this period of lower salinity, cells of those species which have attained their minimum characteristic size form auxospores as conditions are favourable. Auxospores of several species as also large cells of many others indicating the occurrence of such a process in the recent past, have been met with in the plankton collections at this period, which confirms the view that conditions are very favourable for this process of rejuvenation of the protoplast of the Diatom cells. Further, there is a plentiful supply of nutrients in the water during this period, phosphates, nitrates, silicates, etc., (refer later below) so that the sea-water at this time of the year, so to say, is an ideal culture medium from which phytoplankton draws its requirements and rapidly multiplies leading to the main bloom of the same. It should be mentioned that not all species react in this manner. That each species may have its own optimum conditions of salinity is shown by the recent study of Braarud (1951) on a number of phytoplankton species.

During the north-east monsoon season also, though the west coast of India has practically no rainfall, salinity values register a fall owing to the water of low salinity from the Bay of Bengal entering the Arabian Sea. Then also, there is a bloom of phytoplankton, a smaller secondary peak, in which the species concerned are different.

The reaction of different species to variation in the salinity values may probably determine the floral composition of the plankton which is never alike for a long time and the species responsible for the peak blooms also change from season to season and from year to year.

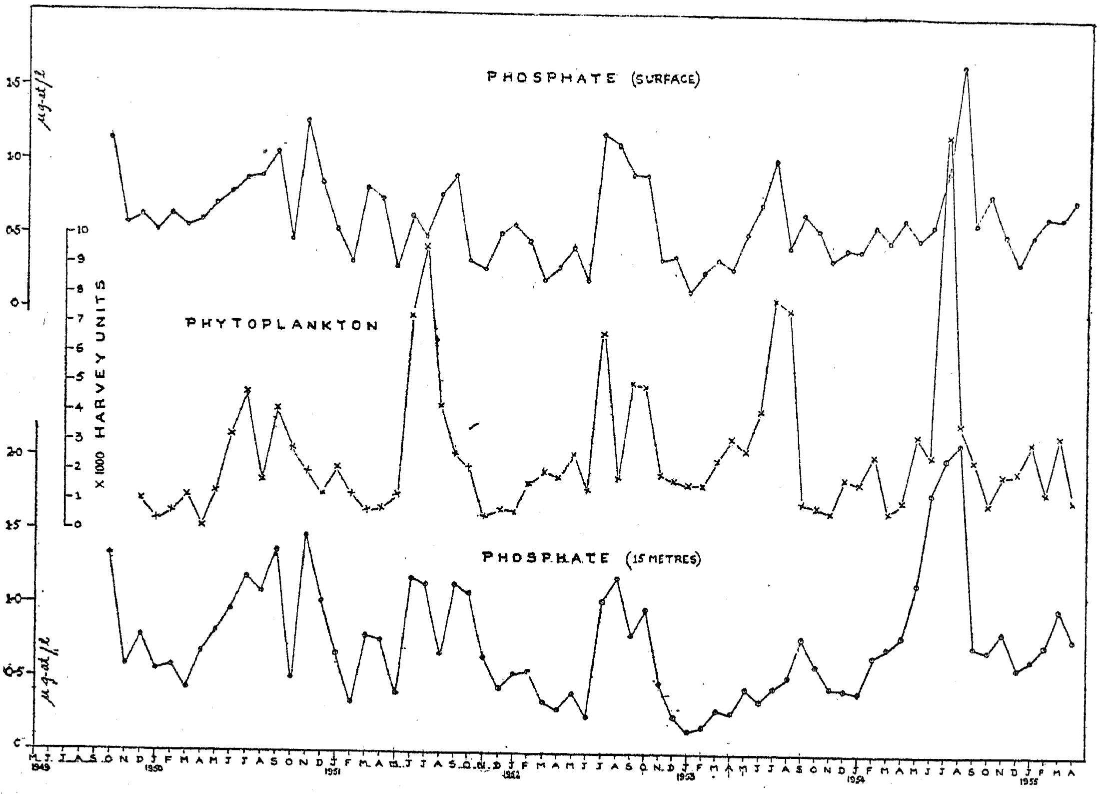
Further, it is possible that salinity changes may determine the nature of reproduction of a species to some extent. It has been found that, sometimes, a bloom of phytoplankton occurs even when the salinity is as high as 34 or 35‰. This does not, however, appear to be a result of sexual reproduction and auxospore-formation of the Diatom elements as it appears to be the case during instances when the salinity values are lower. Here it appears to be due to the vegetative multiplication, chiefly of the Diatoms. Such blooms occur during or after a period of strong winds which appear to mix up the water layers and make available certain growth-promoting substances from the lower layers or the bottom sediment; for, there is always a good quantity of the well-known inorganic nutrients like phosphates, nitrates and silicates, present in the water (refer later below), such a change leading to the multiplication resembling renewal of media in the cultures referred to earlier.

IV. NUTRIENT SALTS AND THEIR CYCLE

It is well known now that sea-water is an aqueous solution containing a variety of dissolved salts and gases. Some are present in high concentrations while others only in very minute quantities. Of these, from the biological aspect, the most important are phosphates, nitrates and silicates; these are the most essential nutrients for plankton growth in the sea.

(*a*) *Phosphate-Phosphorus**

The fluctuation in the phosphate content of the water is shown in Text-Fig. 3 on the basis of monthly averages. The trend of fluctuation at the surface and at 15 metres depth is more or less similar, except that the bottom values tend to be somewhat higher generally; but on some occasions, the latter fall below those at the surface, *e.g.*, February–March, 1950; March and December 1951; June, July, September and December 1959; February, March, May, June, July 1953; and October, 1954. Both at the surface and bottom, the lowest values occur in December or January, February or March, and the highest values between June and November. The values fluctuated between 0·46–1·26, 0·31–0·85, 0·20–1·19, 0·13–1·02 and 0·41–1·68 μg. at/L. respectively during the years 1950–54 at the surface; and



TEXT-FIG. 3. Seasonal fluctuation in the phosphate content of the water, surface and bottom, and of phytoplankton (Harvey Units). Explanation in text.

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* Values not corrected for salt error.

at the bottom, during the same period, 0·42–1·46, 0·34–1·18, 0·30–1·19, 0·16–0·79 and 0·42–2·11 μg. at/L. respectively.

At the surface, the lowest value recorded in any one year was 0·13 μg. at./L. in January 1953, and the highest was 1·68 μg. at./L. in August 1954; similarly, at the bottom, the lowest value of 0·16 μg. at./L. occurred in January 1953 and the highest of 2·11 μg. at./L. in August 1954.

It is seen from the data recorded that there is a well-defined oscillation in the concentration of phosphate in the sea here; the peak occurs generally in the latter half of the south-west monsoon and the minima occur in the north-east monsoon months. There is no complete depletion of this nutrient in the water at any time during the year.

In view of the generally held opinion that the warmer waters are not so productive as the colder seas, the concentration of phosphate in some of the regions where this has been estimated are shown in Table II for comparison, in order that a reliable understanding of the relative fertility of the waters may be obtained.*

The observations at Calicut, reported in this account, show that the values recorded here are fairly high; the lowest monthly average value recorded during the 5 years was 0·13 and the highest 2·11 μg.at./L. The variation of the phosphate content in the *water column* as seen by the average of five years' data is 0·474–1·044 μg. at./L. (Text-Fig. 7). Further, it may be seen that there is a seasonal fluctuation in the phosphate content; from a minimum in January, the value increases gradually and reaches the maximum in July; it remains high till September and thereafter falls. This fact does not appear to have been recognised by the earlier workers on the west coast. In the temperate regions, the oscillation of the phosphate content is a double one; there is a pronounced winter maximum and a subsidiary one in summer. The values oscillate much, sometimes over a wide amplitude when short periods are reckoned with; but, when considered over several years, the mode of fluctuation in the present area distinctly stands out as described above.

In the temperate and polar waters, generally an inverse relationship is found between the phosphate and phytoplankton content of the water; a fall in the former being followed by a bloom of the latter (*vide* Papers of Atkins, Harvey, Cooper, Gran, Braarud, Phifer and Thompson, Riley, Hart and so on under references). Here such an overall inverse relationship is

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* The writer has converted to μg. at/L. all values expressed in other terms in the sources quoted in this paper.

TABLE II

Region	Depth in metres	Conc. PO_4—P in µg. at./L		Reference and remarks
		Lowest	Highest	
1. Indian Ocean ..	700–1000		3	Sverdrup *et al.*, 1942 (value assessed from figure)
2. Red Sea ..		0·142	1·126	Thompson, 1939
3. Java Sea ..		0·03515	0·141	Delsman, 1939
4. Singapore waters		0·1128	1·28	Kow, 1953
5. Bombay Harbour		0·1837	0·5324	Bal *et al.*, 1946
6. Bay of Bengal ..		about 0·2	1·50	Jayaraman, 1951. Once 3·0
7. Bay of Bengal ..		0·3384	1·198	Ramamoorthy, 1953 *b*
8. Gulf of Mannar ..		0·15	0·30	Jayaraman, 1954
9. Palk Bay ..		0·12	0·25	Jayaraman, 1954
10. Calicut—West Coast of India	Surface 15	0·13 0·30	1·68 2·11	Present investigation
11. Atlantic Ocean ..	Intermediate layer—1000		2·00	Sverdrup *et al.*, 1942
12. Caribbean Sea ..	Surface Depths	0·1	2·00	Rakestraw and Smith, 1937
13. English Channel and Mill Port		0	1·05	Atkins, 1923; 1925, 1926 *b*, 1928, 1930, 1953; Armstrong, 1954, 1955; Cooper, 1933 *a*, 1933 *c*; Harvey, 1928 *b*, 1934 *b*, 1945, 1955; Harvey *et al.*, 1935; Marshall and Orr, 1927
14. Gulf of Maine ..		0·6	1·61	Redfield, Smith and Ketchum, 1937
15. Gulf of Maine ..		0·0	0·84	Gran and Braarud, 1935
16. Gulf of Maine ..			1·5	Bigelow *et al.*, 1940
17. Block Island Sound	0–30	0·43	2·29	Riley, 1952
18. Mediterranean ..	Surface 90	0·00282 0·0141	0·04 0·0451	Ercegović, 1934
19. Pacific Ocean ..			3·5	Sverdrup *et al.*, 1942
20. Equatorial Pacific		0·0423	1·39	Graham, 1941 *a*
21. Transequatorial waters 9° N to 7° S at 140° W		0·8	2·4	Austin, 1954; Stroup, 1954; Cromwell and Austin, 1954
22. Hawaiian waters ..	1000 100		3·0 1·0	McGary, 1955; Seckel, 1955
23. Eastern Tropical Pacific		0·29	0·81	Wooster and Jennings, 1955
24. Friday Harbour ..		1·20	2·4	Phifer and Thompson, 1937
25. Great Barrier Reef			0·161	Orr, 1933
26. New South Wales		0·2115	0·282	Dakin and Colefax, 1935 *a*, 1935 *b* and 1940
27. Sub-Tropical Zone of Southern Ocean		0·0705	0·432	Clowes, 1938
28. Antarctic waters			2·256	Ruud, 1930, Clowes, 1938

not obvious though on a few occasions an inverse relationship was seen on a sample-to-sample basis (*see* also George, 1953 *a*; Prasad, 1956). As in this warmer environment there are no sharp climatic distinctions to retard production, development of phytoplankton is possible throughout the year though with differing intensities, and a fairly high standing crop is present in the water always. The relationship, therefore, between phosphate content and phytoplankton is somewhat different from that generally known and a knowledge of the source of this phosphate appears to be necessary for understanding their relationship and the cycle of phosphorus in the sea on the west coast of India.

Various suggestions have been put forward as to the source of phosphate in the sea. Pearsall (1923) suggested that the heavy rainfall of spring and autumn increased the amount of nutritive salts brought down to the sea, indicating that there is considerable contribution of these salts from the land to the sea. Gran (1931) states that the quantities of phosphate and nitrate which are washed out every year from the land are quite insignificant compared with the great regeneration in the depths of the sea. In the Great Barrier Reef region, there is no evidence of enrichment of the sea with phosphate by river outflow though the latter was rich in silicate (Orr and Moorhouse, 1933). According to Riley (1937–38) the Mississippi river brings in large quantities of phosphate into the Gulf of Mexico and the concentration of this salt in the latter is nearly four times that found in the surrounding region. In the south-western area of the English Channel, Hickling (1938) believes that drainage from land contributes to the phosphate content of the North Sea and the Channel. Delsman (1939) believed that there is not much addition of nutrients to the sea from land drainage. Seshappa (1953) states that some phosphate is also brought to the sea by the rivers on the west coast of India which flow over laterite soil as the laterite on analysis was found to contain phosphate.

In this connexion, some observations in estuaries are of interest. High phosphate content has been reported in marine estuaries by MacGinitie (1935) and Howes (1939); the latter author also gives some reasons for the relative richness of phosphate in the estuaries. Stephenson (1949 *a*, *b*) observed an increase in the phosphate content of the water in which estuarine muds had been shaken. Rochford (1951 *a*, *b*) has indicated an exchange of phosphate between the mud and overlying water in the Australian estuaries. He further states, however, that the assumption of persistent discharge of nutrients by rivers and estuaries into the adjoining neritic waters is not generally true for most of the Australian coast-line so far investigated. The importance of the bottom muds in the phosphate cycle has also been stressed, particularly in the freshwaters, by Mortimer (1941, 1942), Hayes *et al.* (1952) and Hayes (1955).

In the area of the present investigation analyses of the water of the Korapuzha estuary (a few miles north of Calicut) showed (George, 1953 *b*; Mr. S. V. S. Rao, oral communication) that the phosphate content of the water was generally of a low order during the south-west monsoon floods; hence, it would appear that there is not any significant addition of this nutrient to the sea from the land drainage here on the west coast (*cf.*, however, p. 236, below). The causes for the considerable increase of phosphate in the sea during the south-west monsoon season have to be sought elsewhere; and, as in the case of estuaries, the bottom muds are of interest.

Moore (1930, 1931) who investigated the muds of the Clyde Sea area found phosphate and nitrate in the mud; the phosphate values fell off with increasing depth in the mud, but usually showed a rise at the 10–15 cm. level; and nitrogen values usually fell with increasing depth. In the English Channel, Armstrong and Harvey (1950) attribute the changes in the integral mean concentration of phosphate to different water masses of different total phosphorus concentration passing through the area, rather than to a seasonal change in the total phosphorus content of a water mass. No marked deposition of phosphorus containing detritus was found by them; however, they noticed that deposits well offshore were not devoid of phosphate, some of which may dissolve in the water in the course of years. Hendey (1951, p. 14) reports that water expressed from the mud banks gives high figures for phosphate and silicate and that these nutrients show a rise in the concentration with falling tide due possibly to turbulence set up by the ebb tide bringing the nutrients out of the sand and mud banks. Miller (1952) who analysed phosphorus in the water and bottom sediment in the Biscayne Bay, Florida, found that a *decrease* of phosphorus in the water was associated with an *increase* in the sediment and *vice versa*. Ingle, Ceurvels *et al.* (1955) have shown that the muds of Mobile Bay are rich in phosphorus and also contain nitrogen in a form that can be used directly or indirectly by plant life.

Seshappa (1953) and Seshappa and Jayaraman (1956) investigated the bottom muds of the inshore area very near the sampling stations of the present investigation. They found that the values for interstitial phosphate were higher than corresponding values for inorganic phosphate in the overlying water during the pre-monsoon months; that the mud here retains relatively large quantities of phosphate and perhaps other nutrients. It is further stated that the mud is of laterite origin and an analysis of the sample of laterite has revealed high " adsorbed " phosphate. Another cause for the increase of phosphate during the south-west monsoon months is attributed by them to the death and decay of bottom fauna at the commencement of the season. Observations by the writer during the past seven years, however, have shown that large-scale mortality is not a regular feature every year on this coast to be construed as a source for phosphates in the enrichment of the waters. It may be mentioned here that Du Cane *et al.* (1938, pp. 42–43) mention phosphoric anhydride in their analysis of laterite and mud from the west coast of India (*see* p. 231 of this paper).

It would, therefore, appear that in the present area, considerable quantity of phosphate is locked up in the sea bottom mud and this goes into solution during the stormy weather such as during the south-west monsoon season or during periods of high wind velocity (as observed by Moore, *l.c.*, phosphate content in the bottom mud in the present area also may be higher slightly beneath the surface of the mud than at its surface and only a strong agitation of the water affecting the mud as well will bring the phosphate into solution) and become available in plenty for phytoplankton growth; and, the concentration of the same remaining high till about September is very probably due to the quick regeneration as well of the phosphate into the water as suggested by Cooper (1935 *c*), Seiwell and Seiwell (1938), Renn (1937), Gardiner (1937) and Waksman, Hotchkiss, Carey and Hardman (1938). Seiwell and Seiwell state that the rate of liberation of phosphate both from sea-water and from decomposing plankton by the growth of the organisms associated with the decomposition exceeds the rate of consumption. There may also be considerable addition by the upwelling of deeper waters during this season. These may explain the high concentration of phosphate in the waters of the west coast during the bloom of phytoplankton and, obviously, there is more phosphate in the water than is required for the growth of the floral elements; hence, the high standing values. Later on, when calmer weather prevails, the dying and dead elements of plankton would sink and decomposition of them takes place *at the bottom* and the phosphate thus liberated remains " stored up " in the bottom sediment while the concentration of the same in the water diminishes. The stored up phosphate would go into solution and become available for phytoplankton growth again when stormy weather conditions occur next, particularly during the south-west monsoon. Thus, on the west coast of India, as shown by Miller (1952) elsewhere, a cyclical seasonal exchange of phosphorus between the sediment and water seems to occur, a decrease of phosphate in the water meaning an increase of same in the sediment and *vice versa*; and, this is confirmed for the west coast by Seshappa (1953) and Seshappa and Jayaraman (1956).

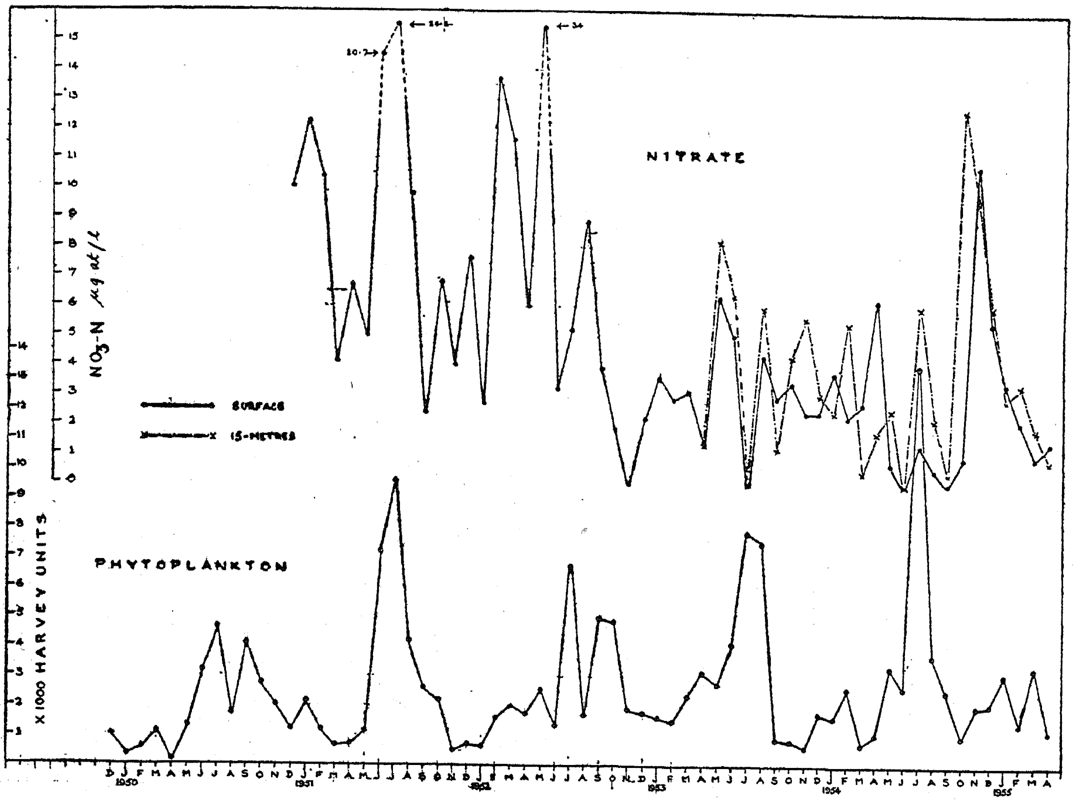
It was pointed out in the beginning of this section that, on some occasions, the concentration of phosphate is greater at the surface than in the bottom water. This is perhaps due to the greater regeneration in the surface layers by a shortened cycle also, through the fæcal pellets of zooplankton resulting from their feeding profusely on the phytoplankton and lack of mixing up of the water layers.

Finally, it may be stated that the phosphate content recorded indicates a high fertility rate for the waters on this coast.

(*b*) *Nitrate-Nitrogen*

Investigations on nitrate content of surface waters cover a period of just over four years during two years of which the bottom samples were also studied. The results are shown in Text-Figs. 4 and 7.

The concentration of nitrate is characterised by frequent rise and fall. Generally, the bottom values are slightly higher than surface values but on some occasions the latter exceeded the former. Higher concentrations of nitrate in the water are recorded during the pre-monsoon months of April



TEXT-FIG. 4. Seasonal fluctuation in the nitrate content of the water, surface and bottom and of phytoplankton (Harvey Units). Explanation in text.

or May and the main peak also occurs during this period or in the early part of the south-west monsoon. In 1954, however, the main peak occurred in October. In addition to the major peaks occurring during April, May, June or July, peaks of the second order occur during November or in some years in February (Text-Fig. 7).

The nitrate content of the water goes up to even 34 μg. at./L.; but, generally, the values do not exceed 13 μg. at./L. The values fluctuated between 2·37–26·2 μg. at./L. in 1951–52; 1·40–34 μg. at./L. in 1952–53; 2·25–6·27 μg. at./L. in 1953–54; and 0·47–10·75 μg. at./L in 1954–55 at the surface. At the bottom, the values were 0·43–8·20 μg. at./L. in 1953–54 and 0·36–12·71 μg. at./L. in 1954–55. The overall average for the water column ranged between 2·146 and 9·67 μg. at./L. On the whole, the concentration of nitrate in the water in 1951 and 1952 was of a higher order than in the succeeding years till October 1954. There appears to be an abundant supply of this nutrient as at no period depletion was recorded though occasionally in a few individual samples no nitrate could be detected.

No separate estimation of nitrite was made but the values for nitrate include that for nitrite as well, as both give the same colour reaction with reduced strichnine (Harvey, 1945). A few analyses made since June 1955, by the writer, however, show that nitrite is absent most of the time in the surface water, but present in small quantities in the bottom samples. Its concentration varied from 0–0·025 μg. at./L. at the surface and 0–1·25 μg. at./L. at the bottom (*see* also Bal *et al.*, 1946; Jayaraman, 1951; Ramamurthy, 1953 *b*).

There are not as many accounts of nitrate estimations as there are for phosphate. Some of the accounts available are shown in Table III for comparison.

Compared with the nitrate values of certain rich phytoplankton-producing areas in the temperate regions, the sea off Calicut, as in the case of the phosphate, has fairly abundant quantity of nitrate and hence nitrate could not possibly be a limiting factor in the production of phytoplankton here.

The nitrate content attains its maximum during the south-west monsoon season; in fact, high values (Text-Figs. 4 and 7) are recorded even prior to the onset of the monsoon which remains more or less stationary even when enormous production of phytoplankton is taking place showing thereby that there is a continuous supply of this nutrient to the water and the recorded value is the "standing" nitrate content of the season. Peaks of lesser intensity follow in November and February.

TABLE III

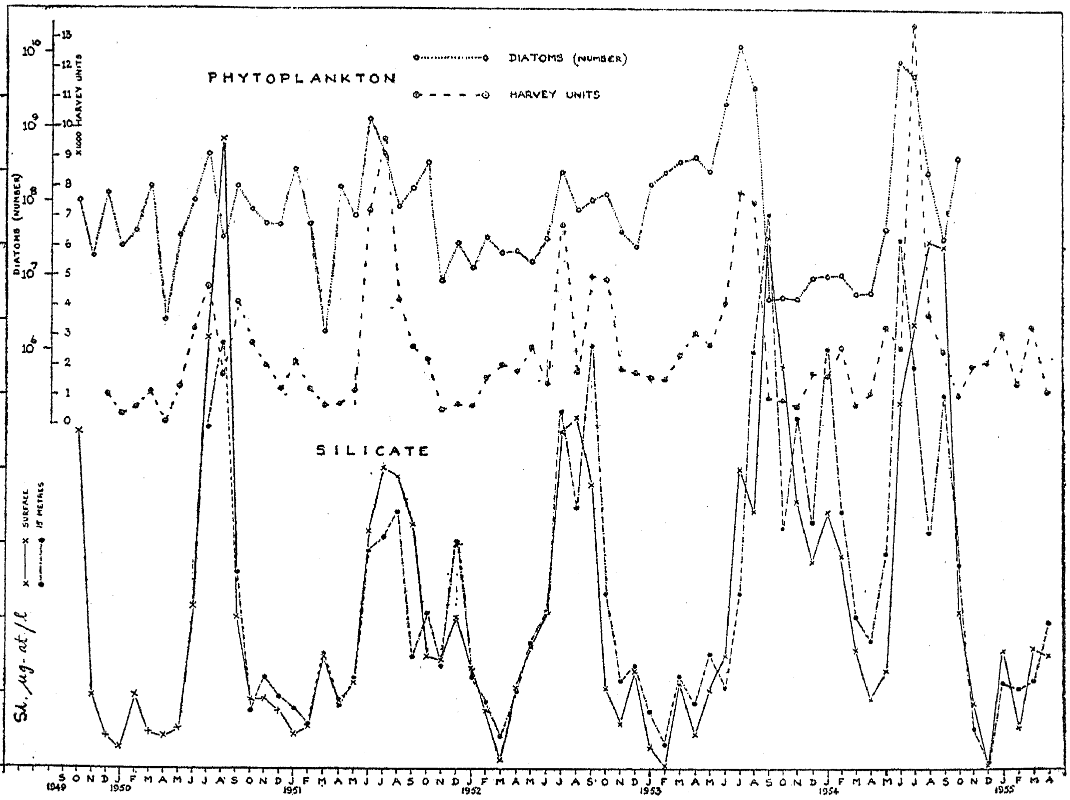
	Region	Depth in metres	Conc. NO_3—N in μg. at./L		Reference and remarks
			Lowest	Highest	
1.	Indian Ocean ..	1000		Circa 38·0	Sverdrup *et al.*, 1942 (value from figure)
2.	Arabian Sea ..		20·0	35·0	Gilson, 1937
3.	Bay of Bengal ..		8·0	16·0	Jayaraman, 1951
4.	Gulf of Mannar ..		0·0	5·0	Jayaraman, 1954
5.	Calicut—West Coast of India	Surface	0·47	34·0 (rare; Circa 20 common)	Present investigation
6.	Calicut—West Coast of India	15	0·77	12·71	do.
7.	Atlantic Ocean ..			Circa 30	Sverdrup, *et al.*, 1942
8.	English Channel			8·0	Cooper, 1937 *b*
9.	Pacific ..			Circa 35	Sverdrup *et al.*, 1942
10.	Friday Harbour ..			25	Phifer and Thompson, 1937
11.	New South Wales Coast	Surface		3·5	Dakin and Colefax, 1940
		45·7 metres		9·5	
		160 metres		10·7	
12.	Barents Sea ..		14	22	Kreps and Verjbinskaya, 1930
13.	Antarctic ..		28	43	Ruud, 1930

Moore (1930, 1931), Rakestraw (1933) and Ingle *et al.* (1955) have given evidences for the presence of higher concentration of nitrates in the bottom mud and water layer immediately overlying it. While one does not know the contribution made by river influx to the nitrate content of the sea around Calicut, it is possible that the bottom sediments here may similarly have considerable quantity of nitrogen compounds which are liberated into the overlying water in an assimilable form (*see* also Gilson, 1937, pp. 59–69) during the monsoon season in addition to contribution by upwelling in much the same way as the phosphates are replenished.

(*c*) *Silicate-Silicon*

The bulk of the phytoplankton in the sea is contributed by the Diatoms. Silica is essential for their growth and a lack of it acts as a limiting factor (Richter, 1904, 1906; King and Davidson, 1933; Meloche *et al.*, 1938; Gardiner, 1941; Denffer, 1949; Lund, 1950; Goldberg *et al.*, 1951; Jørgensen, 1952, 1953; Wawrik, 1952; Komarowsky, 1953). A shortage of silica is known to slow down Diatom growth in the Antarctic (Hart, 1934, 1942; Clowes, 1938). Individual Diatom species too have shown a similar behaviour in varying concentration of silica (Hart, 1934; Braarud, 1948; Lewin, 1955 *a*).

The results of silicate estimations are presented in Text-Figs. 5 and 7. It will be seen that most of the time the bottom values for silicates are slightly higher than those for the surface, but on some occasions, the south-west monsoon period, the surface value often exceeds that of the bottom layers. The silicate content is at its maximum during the south-west monsoon period, July to September. Peaks of diminishing intensity occur during the following months. The lowest values are recorded between January and April. The silicate content never goes below 5 μg. at./L.; usually, it oscillates between 8 and 15μg. at./L. during the north-east monsoon months, and during the south-west monsoon months, the values commonly vary from 20–27 μg. at./L. (occasionally up to 47·22 μg. at./L.).



TEXT-FIG. 5. Seasonal fluctuation in the silicate content of the water, surface and bottom and of phytoplankton (Harvey Units) and Diatomaceæ (numbers), the silica consumers. Explanation in text.

The annual variation in the concentration of silicate-silicon in μg. at./L. was respectively as follows in the years 1950–51 to 1954–55 (May–April): 7·34–47·22; 5·60–25·08; 5·18–28·53; 9·64–40·58; 5·17–40·43, at the surface; and 8·33–54; 7·17–22·22; 6·167–33·33; 10·42–42·24; 5·30–40·47, at the bottom.

Silicate concentrations noted here are generally considerably higher when compared with similar records from other areas. Silicate values range, in terms of μg. at./L., 0·167–7 in the English Channel (Atkins, 1926 *a*; 1928, 1930, 1953; Cooper, 1933 *a*, *b*, *c*; Armstrong, 1954, 1955); from 0·0668–1·67 in the Great Barrier Reef region (Orr, 1933); 5·25–32·55 in the Bombay Harbour (Bal *et al.*, 1946); from 2–22 in the Bay of Bengal (Jayaraman, 1951; Ramamurthy, 1953 *b*); and 3–30 in the Gulf of Mannar and Palk Bay (Jayaraman, 1954). In the Bay of Biscay, even at a depth of 3,000 metres, a silicate value of 23 μg. at./L. only is reported (Atkins and Harvey, 1926). In the Antarctic (Clowes, 1938) and Pacific (Barnes and Thompson, 1938; Thompson *et al.*, 1934) the silicate values are very much greater, 117–170 μg. at./L. respectively. The values recorded in the present investigation are quite comparable with most of those mentioned above. There is always an abundance of silicate for Diatom growth in the waters of the west coast, the minimum value recorded here being comparable with the maximum in the English Channel.

There is an inverse relationship between the Diatom content in the water and silicate concentration, particularly during the period October to April following, on a sample-to-sample basis (*see* also Lund, 1950; Iyengar and Venkataraman, 1951); but owing to a continuous replenishment or addition of silicates during the south-west monsoon months, such a relationship between the Diatom population and silicates is obscured. It is to be noted here, however, that silicate concentration attains its maximum only after the Diatom bloom has started to wane (Text-Figs. 5 and 7).

The exact source and mode of this continuous replenishment of silicate is not known. However, it may be mentioned here that various views have been expressed on the silicate source. A terrigenous origin of the silicates is suggested by Atkins (1927). According to him, soils and disintegrating rocks part with silicate to the water readily and the silicate content of the water is most likely derived from dispersed clay than from Diatom skeletons whose rate of solution is too slow to matter. Hart (1934), Cooper (1933 *b*) and Harvey (1955) have shown evidences of a certain amount of solubility of the siliceous Diatom frustules, while a major portion is generally insoluble (Coupin, 1922; Conger, 1941; Rogall, 1939; Atkins, 1945).

A great deal has to be said towards the locking up of a considerable quantity of the silicate in an insoluble form in the Diatom frustules leading to the formation of large fossil deposits at the bottom. Still one has to mention that there are many Diatom genera which have weakly silicified frustules (or walls). These are not represented at all or very scarcely represented in the deposits (*vide* Karsten, 1928; Small, 1945; Kolbe, 1954, 1955, 1957). Some of these weakly silicified Diatom genera are known to form extensive blooms. It is probable that the weak nature of the silicified wall might be responsible in the same way to bringing back a part of the silicate from the Diatom detritus.

Apart from the above factors, there is a lot of available silicate in the bottom mud in the sea on the west coast of India which goes into solution into the water layers above when the sea bottom is agitated by wind action. It is also probable that some quantity is derived from the influx of river-water into the sea during the south-west monsoon season as many estuarine areas are known to have high silicate values (MacGinitie, 1935; Orr and Moorehouse, 1933; George, 1953 *b*; Iyengar and Venkataraman, 1951). Cooper (1952 *b*, p. 579) states that the drainage from the Tundras of the Northern Hemisphere should yield very large quantities of silicate to the North Polar Sea. Hendey (1951) has stated that water expressed from mud banks gave high values for silicate and also for phosphate. These investigations show the importance of bottom sediment in the silicate cycle.

In connexion with the silicate cycle, it may be mentioned here that, at the time of the occurrence of intense blooms of *Noctiluca* with *Protoeuglena noctilucæ* Subrahmanyan as a symbiont (referred to below as *green-Noctiluca*), Subrahmanyan (1954 *a*) found that Diatoms were almost absent in the water and silicate content of the water had gone up considerably even comparable with the high values obtaining during the south-west monsoon months. The salinity during the occurrence of this *Noctiluca* varied from 33–35·4‰, contrary to Delsman's (1939) observation in the Java Sea. Prasad and Jayaraman (1954) also found during the swarming of *green-Noctiluca* in the Palk Bay and Gulf of Mannar, high silicate concentration compared with the usual concentration and at that time the salinity also was high owing to the influence of the waters of the Indian Ocean and Arabian Sea. Usually, an occurrence of high silicate is associated with a fall in the salinity caused by admixture of river-water. They, therefore, attribute the high concentration of silicate to the active regeneration *in situ* of silicate from the frustules of Diatom by " comminution " as suggested by Cooper (1952 *b*) and, that such a change may be taking place during the active feeding of Diatoms by the *Noctiluca*.

The rôle of biological flora in the replenishment of the silicates has been stressed recently in some papers. Cooper (1952 *b*) has suggested that breaking up of the Diatom frustules in the guts of animals help to a certain extent in exposing fresh surfaces for action of water in dissolving silicates. The rôle of enzymes in this silicate regeneration has been earlier stressed by King and Davidson (1933). Recently Prasad and Jayaraman (1954) suggested that silicates from Diatoms are made available (soluble) by *Noctiluca* eating them, in much the same way as was suggested by Cooper and it is to this process that these authors attribute the high silicate value that accompany these blooms of *Noctiluca*. While Cooper suggested fracturing of Diatoms in organisms as enabling such a regeneration, the process by which these Diatoms are rendered soluble by *Noctiluca* is yet to be known, whether enzymes of *Noctiluca* have any rôle in this is yet to be worked out.*

Copepods have been known to occur in plenty simultaneously with *Noctiluca* though not in the same swarm or patch. The fæcal pellets of these Copepods have in them broken frustules of Diatoms (*see* Part I for relationship with types of Diatoms). Similar fractured frustules have also been found to occur in many instances of feeding on Diatoms. Thus the rôle of biological replenishment of silica may involve many more feeders than any single organism.

In fact, the silicate concentration shows little or no relationship to the bloom organism (refer Table IV). Notwithstanding the specific nature of the bloom, there is generally a complete eclipse or elimination of the Diatoms in that water mass (*see* p. 213 and below ; Prasad and Jayaraman, 1954) and in the neighbouring water mass too the Diatom population is minimal. Thereby, one is prone to conclude that the appearance of a monospecific bloom of an organism more or less affects the environmental conditions for the growth of Diatoms and probably causes its disappearance. Thus, there seems to be a greater degree of inverse correlation between silica content and silica consumers, the Diatoms.

A somewhat inverse relationship obtains between the silicate content and salinity (Text-Figs. 2 and 5; *see* also Jayaraman, 1954). But, this relationship is upset during monospecific blooms of organisms discolouring the water, such as *green-Noctiluca*, *Hornellia marina* (Subrahmanyan, 1954 *a*, *b*) and a palmelloid Chrysophyceæ (Subrahmanyan, unpublished), when high

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* *See* also Prasad (1958). The majority of the genera reported within *Noctiluca* are strongly silicified representatives which are known to occur in fossils and oozes; only three out of ten genera, *viz.*, *Rhizosolenia*, *Bacteriastrum* and *Chætoceros* are absent or scarce in deposits. *See* also p. 213.

TABLE IV

Year, Month, Date	Salinity ‰		Silicates μg. at./L.		Tempe-rature ° C.	O_2 Percentage saturation	Diatomaceæ No. of cells in each vertical haul	Remarks
	Surface	15 metres	Surface	15 metres				
1949 Oct. 14								*Hornellia marina* occurred
31	31·20	33·40	25·00	..	..	91·40	189 120 960	
Nov. 1								*Hornellia marina* present
3								
7	28·60	31·50	12·00	..	..	95·00	12 960	
14	34·40	34·30	11·67	..	27·5	63·80	227 500	
21	34·20	34·50	7·83,	..	28·5	97·0	5 734 800	
28	34·80	34·90	8·17	..	28·4	114·7	64 909 440	
Dec. 5	35·20	35·40	7·67	..	28·0	96·0	14 060 880	*H. marina* occurred
7								*H. marina*
12	34·20	34·20	6·00	..	27·5	89·0	257 598 720	
1950 Aug. 7	26·50	34·60	41·67	37·00	25·1	151·0	15 878 400	
14	25·00	34·30	66·67	30·30	25·9	89·1	22 492 800	
21	31·90	34·30	33·33	33·33	23·7	46·6	6 662 400	*H. marina* present
28	31·30	33·60	..	..	27·0	105·9	69 480 000	
Sept. 4	32·10	34·20	14·17	16·67	26·3	74·8	29 068 800	*H. marina* in enormous numbers
11	30·30	34·60	..	16·67	23·9	97·1	136 968 000	
18	30·50	35·20	14·50	..	26·1	140·2	423 456 000	
25	35·00	35·20	16·67	20·83	25·7	92·3	39 321 600	*H. marina* present
Oct. 16	33·60	34·80	8·17	7·50	27·1	79·7	166 560 000	
23	32·10	32·20	11·17	12·50	28·4	116·4	46 402 560	*H. marina* present
30	33·20	34·90	7·50	10·00	27·8	103·0	116 966 400	*H. marina* present

TABLE IV (*Contd.*)

Year, Month, Date		Salinity ‰		Silicates μg. at./L.		Tempe-rature ° C.	O_2 Percentage saturation	Diatomaceæ No. of cells in each vertical haul	Remarks
		Surface	15 metres	Surface	15 metres				
Nov.	6	33·20	35·60	12·50	15·83	27·6	110·3	147 363 840	*H. marina* present
	13	32·00	34·30	7·50	9·00	28·2	128·4	15 605 760	*H. marina* present in good numbers
	20	34·20	34·00	9·50	10·00	28·5	161·8	13 017 600	*H. marina* present in considerable numbers
	27	35·00	35·20	8·83	9·50	28·2	114·1	20 044 800	*H. marina* present in considerable numbers
April	2	35·00	35·00	11·67	10·83	29·3	79·8	51 600	
	9	35·80	35·60	14·17	13·33	29·3	88·3	326 400	
	14								*H. marina present*
	16	34·50	34·90	6·67	6·00	29·0	108·0	694 517 760	
	18							182 928 000	*H. marina* present
1951 Aug.	20	32·30	34·80	22·21	22·21	26·0	114·4	60 160 000	*H. marina* present
	27	30·40	33·80	23·80	27·67	23·0	47·8	95 942 000	*H. marina* present
Sept.	3	34·40	34·60	16·67	. .	25·2	29·9	23 592 000	
	10	33·90	34·00	37·03	16·67	26·0	98·8	388 224 400	*H. marina* appeared in good numbers
	17	34·20	34·70	22·21	. .	25·1	45·9	53 742 000	*H. marina* appeared in good numbers
	24	33·60	34·20	9·17	8·33	28·6	87·6	125 964 000	*H. marina* present
Oct.	3	30·80	35·10	12·50	16·67	28·1	95·6	1585 440 000	
	10	34·60	34·90	. .	. .	28·0	111·5	23 184 000	*H. marina* in large numbers
	15	26·80	35·20	16·67	. .	28·9	106·2	40 137 600	*H. marina* in large numbers

		22	34·60	35·00	8·33	14·20	28·7	114·8	7 440 000	*H. marina* in large numbers
		29	32·20	34·00	..	..	30·0	114·2	1 593 600	*H. marina* in large numbers
	Dec.	3	31·50	34·00	10·83	10·83	28·5	111·0	129 561 600	
		10	34·50	35·00	13·33	16·67	28·6	64·4	739 200	*H. marina* present
		17	34·00	34·40	23·80	47·62	28·4	84·9	16 014 000	
		24	34·80	35·10	13·33	13·33	27·8	90·0	3 074 400	
		31	35·20	34·60	14·17	12·50	27·9	85·3	148 800	*H. marina* few present
1952	Aug.	18	32·20	34·00	7·50	12·00	24·8	95·7	249 062 400	
		25	31·20	34·90	20·83	22·17	24·1	90·8	2 313 600	
	Sept.	1	34·40	34·80	16·67	..	25·0	87·9	67 929 000	
		6								*Hornellia marina* made its appearance
		8	34·00	..	23·67	33·33	24·2	60·8	32 025 600	*H. marina* in abundance
		15	33·40	33·80	22·17	33·33	24·8	47·4	61 344 000	*H. marina* some dying
		22	34·00	35·00	33·33	33·33	24·3	52·7	282 816 000	*H. marina* some dying
		29	34·20	34·80	..	..	25·9	50·8	72 307 200	
	Oct.	6	32·60	34·20	9·17	16·67	27·2	78·7	106 629 120	
		13	21·80	33·40	..	..	27·8	86·8	1 502 000	
1953	Sept.	2	..	..	..	..	26·3	55·2	2 995 000	
		7	30·20	34·40	41·67	36·67	24·9	83·7	249 600	*H. marina* present
		14	25·80	34·20	59·60	60·60	..	..	1 670 400	*H. marina* increased a little
		21	34·20	34·20	6·06	16·67	25·2	..	15 494 400	
		26								*H. marina* reappears in large numbers
		28	34·60	34·00	55·00	55·00	25·2	..	4 915 200	*H. marina* blooms discolouring water. Bloom *continued* till Oct. 5, 1953. Later part of the period of bloom with dead and decaying elements in the
	Oct.	5	28·20	35·00	41·67	16·67	..	..	9 100 000	
		12	32·40	34·20	16·67	16·67	..	..	806 400	
		19	30·80	33·20	50·00	41·67	..	..	3 110 406	
		26	30·00	33·20	19·50	19·50	..	94·5	8 928 000	
	Nov.	2	32·60	34·60	20·33	30·33	28·7	77·2	283 000	
		9	34·60	34·80	30·33	41·67	28·4	93·6	7 641 000	

TABLE IV (*Contd.*)

Year, Month, Date	Salinity ‰		Silicates μg. at./L.		Temperature ° C.	O_2 Percentage saturation	Diatomaceæ No. of cells in each vertical haul	Remarks
	Surface	15 metres	Surface	15 metres				
16	34·00	34·20	20·83	19·50	29·0	105·5	11 040 000	water. Data for O_2 not available (lost); however it may be mentioned that O_2 content was at or above saturation level most of the period except towards the end when values fell with increase in dead organic matter in the water. Note high silicate values. After Oct. 10, the alga waned.
23	32·60	32·60	22·16	30·16	29·0	94·3	..	
30	31·80	32·00	20·83	20·83	28·6	..	633 600	
Dec. 7	32·20	32·20	20·83	25·00	28·5	88·9	8 486 000	
14	32·60	32·60	16·67	23·66	28·5	83·7	11 788 000	
21	31·20	31·20	16·67	16·67	28·1	..	3 590 000	
28	32·00	32·00	20·83	20·83	28·4	90·5	14 899 000	
1952 Nov. 3	34·80	34·80	9·33	9·83	28·0	72·1	64 944 000	
10	34·00	34·20	8·33	13·33	27·8	116·9	57 216 000	
17	34·80	34·80	5·83	5·83	27·2	119·5	21 120 000	
24	34·40	34·60	8·33	14·70	28·5	107·6	998 400	
Dec. 1	34·20	34·20	12·50	9·17	27·9	75·7	34 368 000	
8	34·40	34·70	20·83	22·17	28·2	93·6	82 252 000	*Green Noctiluca* began to appear and occurred in plenty from 10–13, Dec. 1952
15	33·70	33·70	8·33	12·50	28·7	97·6	10 732 800	
22	32·20	32·50	7·50	7·50	28·1	97·7	2 323 200	
29	31·30	32·00	8·33	8·33	28·3	90·4	2 899 200	

1953 Mar.	2	34·60	34·60	4·17	4·17	29·0	85·9	1467 360 000	and continued till end of the month.
	9	34·40	34·60	..	8·33	29·8	91·4	223 296 000	
	16	34·60	34·70	14·17	16·67	29·0	67·6	7 220 000	
	23	34·60	34·80	14·17	16·67	29·0	67·6	7 220 000	
	30	34·10	34·60	10·00	10·00	29·6	87·0	1 560 000	*Green Noctiluca** re-appeared and began to increase quickly and discoloured the water. Note sharp fall in number of Diatoms and increase of silicate value.
1953 April	6	34·80	34·90	9·17	9·17	29·7	92·5	121 800 000*	Bloom continues
	14	35·00	35·00	6·67	10·00	31·4	94·8	1032 480 000*	Fewer numbers
	27	35·20	35·40	6·67	10·00	28·5	74·4	6 288 000*	In abundance
May	4	35·50	35·60	12·50	16·67	28·5	69·6	2 856 000*	In abundance
	11	35·60	35·60	16·67	16·67	28·8	73·6	1 128 000*	In abundance
	18	35·40	36·00	8·33	12·50	27·8	65·2	12 192 000*	Diminishes in number
	25	35·40	35·80	3·33	5·00	28·4	97·7	1027 008 000*	Nil
June	2	35·20	35·80	12·50	12·50	27·4	52·13	686 496 000*	Few numbers
1955 Mar.	7	34·20	34·30	17·40	13·50	30·0	81·9		Palmelloid chrysophyceæ appears. Most abundant bloom on 14th and 15th March, discolouring the water. Diatoms practically nil in that water.
	14	34·40	34·40	6·00	7·50	29·5	106·6		
	21	34·60	34·60	13·50	13·50	30·0	82·8		
	28	34·90	34·70	15·00	9·00	30·5	83·2		

silicate values were recorded coincident with higher salinity values (refer Table IV). This is to be attributed, again, to the scarcity or absence of the Diatoms from the water mass owing possibly to the deleterious effect caused by the organism concerned as suggested by the work of Lucas (1947, 1949, 1955), Rice (1954) and Provasoli and Pinter (1953 *b*).

(*d*) *The Phosphate-Nitrate-Silicate Ratio*

The fluctuation in the nitrate content is so erratic that the ratio of P to N in the sea-water on the west coast of India, at any given time, varies very much as in other regions (Harvey, 1945, 1955; Phifer and Thompson, 1937; Redfield, 1934, Cooper, 1938 *b*). Nevertheless, over long periods, there is a constancy in the ratio of these elements in the water in the seas. When the overall average obtained here over some years is worked out, the ratio in terms of μg. at./L. (with P-value corrected for salt error by × 1·12*) (Cooper, 1938 *b*) was found to be P : N : : 1 : 15, the same as has been found in the temperate regions (Cooper, 1937 *a*, 1938 *a, b*; Redfield, 1934; Sverdrup *et al.*, 1942, pp. 236–37).

Fluctuations do occur in the ratio of silicate-Si to phosphate-P, though not to the same extent as in the case of phosphate-P and nitrate-N. The ratio of silicate-Si to phosphate-P in terms of μg. at./L. was found to be 20 : 1, when based on an overall average of five years' observations. The same ratio is indicated in the temperate region also (Sverdrup *et al.*, 1942, p. 261).

Therefore, the ratio between these elements Si, N and P is 20 : 15 : 1 which is the same found in other regions where intense work had been done. This resemblance to the temperate regions is interesting and is possibly an indication of the uniformity and equilibrium in the content of these elements in most marine environments.

As observed by Armstrong and Harvey (1950, p. 145) the water mass sampled on each occasion is not the same, but a series of observations taken at one position for a number of years will iron out differences arising from changing water masses. Thus it is evident that the differential requirements of these elements by the individual biological components in the water might bring about temporary anomalies as seen in the fluctuation of the ratios (*see* Redfield, 1934). One has only to support Armstrong and Harvey on the need for studies ranging over long periods as such studies alone can iron out differences arising from studies of individual water samples and bring out ultimately a general pattern characteristic of each water mass and region.

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* 1·15 according to Robinson and Thompson (1948).

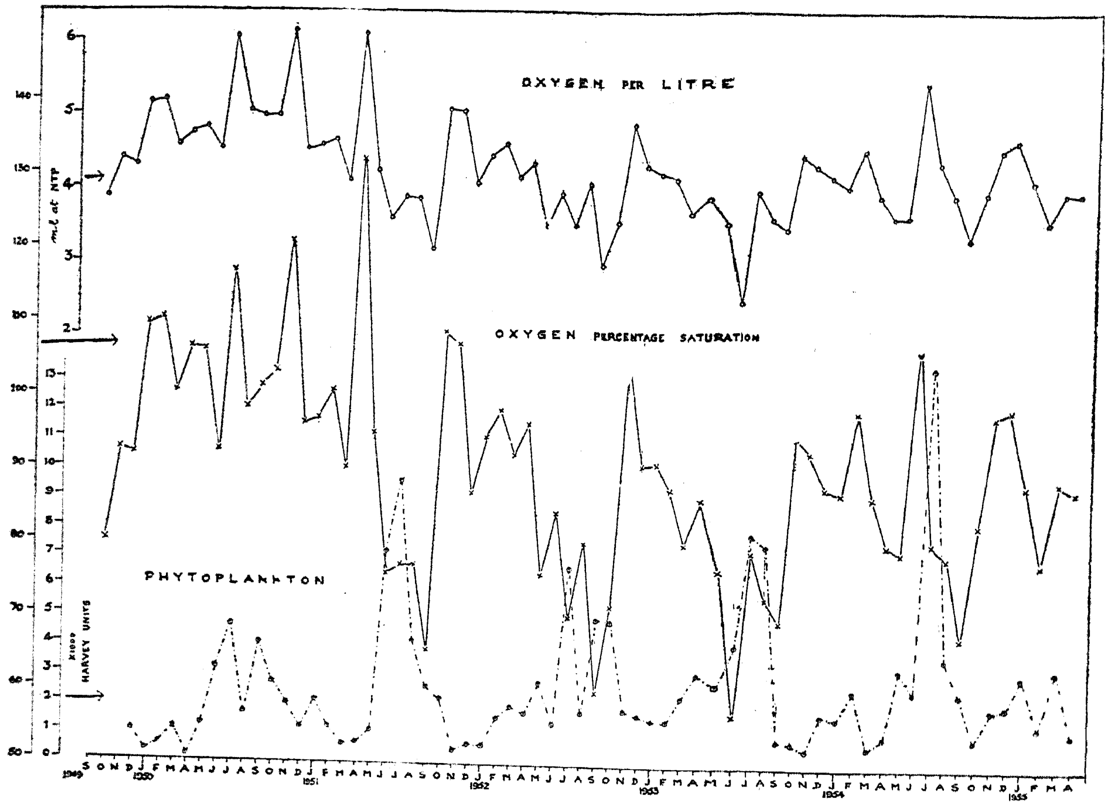
In this connexion, the remarks of Redfield (1934, pp. 189–91) made with particular reference to phosphate and nitrate may be quoted here: "It appears to mean that the relative quantities of nitrate and phosphate occurring in the oceans of the world are just those which are required for the composition of the animals and plants which live in the sea. That two compounds of such great importance in the synthesis of living matter are so exactly balanced in the marine environment is a unique fact and one which calls for some explanation, if it is not to be regarded as a mere coincidence. It is as though the seas had been created and populated with animals and plants and all of the nitrate and phosphate which the water contains had been derived from the decomposition of this original population.... Whatever its explanation, the correspondence between quantity of biologically available nitrogen and phosphate in the sea and the proportions in which they are utilised by the plankton is a phenomenon of the greatest interest." Further, "the general agreement indicates that the amounts of nitrate and phosphate present in the sea are controlled in the main by the same agency—the consumption by the phytoplankton and regeneration from its remains" (*see* also Harvey, 1928 *a*, 1955, p. 28). This constancy has been used elsewhere (Part I) as a basis for the assessment of the standing crop for comparison with other areas as the ratio of these factors in plankton organisms show a constancy by weight (Fleming, 1940).

V. DISSOLVED OXYGEN

The results of oxygen estimations are shown as monthly averages in Text-Fig. 6. Only surface values were being determined but some data for bottom samples are available for a short period since July 1954, estimated by the writer.

The monthly averages for dissolved oxygen per litre of sea-water varied from 4·10–6·11 c.c. in 1950–51; 3·18–5·06 c.c. in 1951–52; 2·97–4·88 c.c. in 1952–53; 2·48–4·55 c.c. in 1953–54; and 3·34–5·43 c.c. in 1954–55. There were more instances of supersaturation of the water in 1950 than during the following years. The oxygen content, generally, keeps fluctuating between 3·5 and 5 c.c. per litre.

The values for bottom samples, on most occasions, are lower than those for the surface water; but, in a few rare instances, the bottom samples showed more dissolved oxygen, particularly when sampling was done in the day, at about 10–11 a.m. as on offshore collection days. This may be due to the rise in the temperature of the surface water later in the day. Normally, the lower oxygen content of the water near the bottom is, perhaps, due to the very rapid oxidation of the sediment and the slow diffusion of the dissolved gases as suggested by Brouardel and Fage (1955; also refer pp. 224–25 below).



TEXT-FIG. 6. Seasonal fluctuation in the oxygen content of the water ml./L. and its percentage saturation, and of phytoplankton (Harvey Units). Explanation in text.

The distribution of dissolved oxygen has been studied intensively in several geographical regions (*cf.* Sverdrup *et al.*, 1942; Harvey, 1928 *b*, 1945 and 1955). For comparison, the values recorded in some select regions may be cited here as it is not possible to refer to all the accounts from various regions.

In the English Channel, Cooper (1933 *b*) found the oxygen content increasing rapidly, reaching 8% supersaturation during the phytoplankton outburst. With rising temperature, degree of supersaturation fell. In the Great Barrier Reef region, Orr (1933) found the water 90–100% saturated and only once supersaturated. Only for a short period was saturation below 90%. At one station the range of saturation was 55–120%. Near Triumph Reef, Riley (1939) reports 99% saturation. At 15° S. in the Atlantic, Wattenberg (1929) found high oxygen content at the surface which extended to some depth below also. Smith *et al.* (1950) found that the oxygen content of the water, at a sub-tropical inshore region adjacent to Miami, to be near saturation at all the stations away from pollution. McClenden (1918) reported that the sea-water in the shallow areas of Dry Tortugas was generally slightly supersaturated with oxygen during day and undersaturated by night.

In the Bay of Bengal, off Madras, the concentration of oxygen, according to Jayaraman (1951) and Ramamurthy (1953 *a*), varied from about 2·5–5 c.c. per litre; the latter found that the percentage saturation remained about 83–90%. In the Gulf of Mannar and Palk Bay (Jayaraman, 1954) there was no marked variation in the seasonal distribution and rarely did the water attain saturation with oxygen. The values ranged between 3·5 and 4·5 c.c. per litre. There was little difference between the surface and bottom values as the region concerned is shallow and vertical mixing takes place easily.

According to Harvey (1945, p. 46), the concentration of oxygen varies from 8 c.c. per litre in the Arctics to 4·5 c.c. in the tropical surface waters.

The *overall monthly average* of five years' data at Calicut shows an oxygen content variation of 3·88 c.c. per litre in March to 4·88 c.c. per litre in November; the percentage saturation varied from 72·68 in September to 105·91 in November. The values recorded here are very well comparable with those of other geographical areas cited above.

The seasonal fluctuation in the oxygen content of the sea-water at Calicut shows some interesting features. It is well known (Sverdrup *et al.*, 1942, p. 190) that solubilities of gases like oxygen and nitrogen which do not react chemically with the water or its dissolved salts decrease with increasing temperature and salinity. It is also well known that during the phytoplankton outburst oxygen concentration increases and even exceeds saturation point. Further, agitation of the water tends to increase the solubility of oxygen in it.

A study of Text-Figs. 1, 2 and 6 will indicate certain results, apparently, in contradiction of the points mentioned above. To begin with, high oxygen concentrations are met with in April, May or June, prior to or in the early stages of the bloom of phytoplankton. At this period, before the onset of the rains, temperature and salinity are both high; however, the effect of this is offset by the high wind force prevailing at this time which brings about agitation of the water leading to increased dissolution of atmospheric oxygen. There may, perhaps, be also water rich in oxygen brought in by the currents. It was mentioned earlier that there is an arm of the Antarctic flow surfacing in the Arabian Sea, and Antarctic waters are generally rich in oxygen content.

The south-west monsoon winds bring about an upwelling of these waters to the surface.

During the intense phytoplankton bloom in June–July, one would expect a further increase in the content of dissolved oxygen. In fact, there is slight increase compared with the earlier month. The concentration of oxygen at this time was between 3 and 4 c.c./L. only and the percentage saturation value was between 75 and 85%; In June 1954, however, the dissolved oxygen showed a supersaturation of about 6%. Similarly in 1950 a supersaturation of the waters was recorded. Salinity and temperature also at these times were in favour of a high dissolved oxygen content; but, curiously enough, there is a fall in the oxygen content after July even when the phytoplankton bloom is at its peak period. From September onwards, the oxygen content increases again.

Many factors have been held responsible for a lowering of the oxygen concentration. It is well known that while oxygen is liberated by plants during carbon assimilation during day, it is also consumed throughout day and night by both plants and animals in respiration. The phytoplankton bloom on this coast during June–July is very intense, and during this period, the number of zooplankters, particularly the smaller species, are also on the increase including reproductive stages of them with a greater demand on oxygen. Further, development of phytoplankton is accompanied closely by bacterial development (Waksman, Reuzer, Carey, Hotchkiss and Renn, 1933) and, obviously, during the phytoplankton bloom, bacterial population increases and oxygen is also increasingly consumed by the bacteria (*see* also Nash, 1947, p. 169). So, it would appear that the demand on oxygen liberated during photosynthesis is so high as to leave back little to raise the overall level of the concentration considerably towards the saturation or supersaturation level. Moreover, at this period, plankton detritus considerably increases in the water. The dead and decomposing organic matter in the upper layers consume considerable quantities of oxygen (Seiwell and Seiwell, 1938) and tend to lower the oxygen content of the water. According to Stephenson (1949 *b*) there is a close correlation between the reduction in oxygen concentration of the supernatant sea-water and the rate of release of phosphate during regeneration from mud surface. According to Richards and Redfield (1954, p. 281) high organic content is equivalent to high oxygen demand and so contact with organic-rich bottom sediment might be held responsible for the oxygen minimum (*see also* Thompson, Thomas and Barnes, 1934). The bottom sediment on this coast contains considerable quantities of organic matter, " marine humus " as will be indicated later in the next section. It has been shown earlier that blooms develop following similar regeneration of phosphate, etc., from the bottom and this regeneration has similar demand on oxygen.

Yet another possible reason for the apparent low concentration of oxygen is indicated by the recent contribution of Lewin (1955 *b*). Lewin found that the uptake of silicate by Diatom cells is an aerobic process and addition of silicate stimulates *respiration* of silicon deficient cells. The bloom period on the west coast is one of a rapid increase of Diatoms and it is very likely that more oxygen is consumed by the rapidly dividing Diatoms with more and more utilization of silica. When organisms concerned are not Diatoms, but other algæ, green algæ, the increase of oxygen has been far more than that recorded at the Diatom bloom period (Table IV). Instances are known from freshwater environments where high supersaturation of the water due to photosynthetic activities of the algæ have led to injurious effect on the faunal elements; perhaps, if a fair quantity of Diatoms were present it would act as a check on supersaturation as the Diatoms consume oxygen during silica assimilation also. Suffice it to say here, that the oxygen content recorded in the sea-water here is that which is in equilibrium after the interaction of all these factors, and the quantity recorded, 3–4 c.c./L. during the season of the phytoplankton bloom is not inconsiderable at all.

After the period of the main bloom, the standing crop still holds relatively a considerable quantity of phytoplankton and fewer number of zooplankters and less of decaying organic matter; further, the rate of multiplication of the Diatoms also appear to fall off. So, the oxygen content shows an upward trend and saturation levels are reached in November or so, very probably also due to the fall in the quantity of oxygen-consuming plankters, for, generally, in November, the plankton content is poor in the water. During this time, however, the effect of the reversal of the coastal current in the Arabian Sea—from a clockwise to an anticlockwise direction—the influx of water from the Bay of Bengal and the higher wind velocity also should not be overlooked. Thus, it is seen that the seasonal fluctuation of the oxygen content on this coast is peculiar and interesting, influenced by meteorological, chemical and physical factors and the biological content of the water.

Addendum.—Since this paper was completed (1956) for publication, an account by Kasturirangan (1957) on the seasonal fluctuation in the dissolved oxygen content of the surface waters of the sea in the same area as that of the present investigation has appeared based on four years' data which are more or less common to his as well as the present account for the years concerned. This author, while discussing the fluctuation in the oxygen content, remarks about the peculiarities noticed (*l.c.*, p. 145): " positive correlation with temperature and salinity from September to November " and the puzzling feature in the " great diversity of behaviour exhibited by the oxygen-curve in the period May to September". According to him, while the low values for September could be accounted for by the fall in the phytoplankton production and increase of zooplankton, " the reasons for the subsequent rise in the values and occurrence of a peak in November are not altogether clear". One explanation sought out for the period May to September concerns the mud banks which are supposed to exercise an effect in the direction of reduced oxygen. (It must be noted here that mud bank formation is not a very regular feature every year—writer.) The author himself has pointed out that the investigations of the present writer on phytoplankton production might throw some light on a number of puzzling features noticed. The discussion on these aspects in this section of the present paper provides answers for several apparent contradictions noticed in the fluctuations of the oxygen content of the waters on the west coast of India.

VI. OCEAN CURRENTS*

No direct work has been done on this aspect; however, some points of interest may be mentioned here. The currents move the water masses; and, sometimes, within the same water mass, some small changes in the direction may occur over small areas, probably owing to the contour of the coast and/or of the ocean floor, often indicated by the drifting of the nets cast. Be that as it may, the information gathered through fishermen fully confirms the picture of the course of circulation described based on the Admiralty records (Subramanyam, Part I). It may be mentioned here that the coastal currents are likely to have the waters of the Cold Antarctic Flow (Carpenter, 1887) and of the Antarctic Intermediate Current (Mohamed, 1940), already referred to elsewhere. These are bound to be rich in nutrients as the latter especially (Mohamed, *l.c.*, p. 193) on the east coast of Africa is found to favour the production of phytoplankton.

From the constancy of the main pulses of the plankton over five years, it is fairly certain that the movement of water may have a seasonal rhythm and conditions over a large extent of the west coast of India are similar though the intensity of production of plankton and its time may show some slight variations. The water mass sampled on each occasion is not the same,

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* More details relating to this aspect will be presented in another account (Subrahmanyan, 1959).

nor is it so in chemical composition or biological content; the seasonal meteorological changes control the nature and movement of the water masses; but, still the overall picture of the seasonal fluctuation of the biological elements in the water remain almost identical year after year, though there may be differences in the intensity of production.

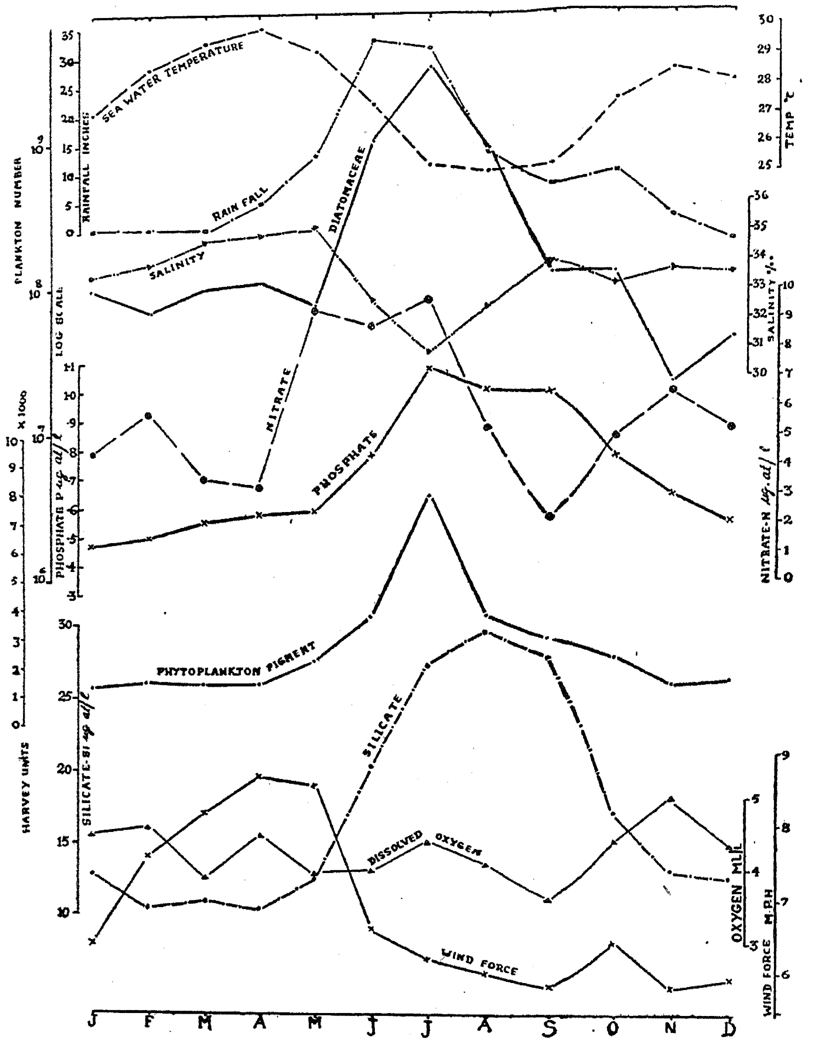
VII. General Observations on the Environmental Factors Affecting the Production of Phytoplankton with Remarks on Possible Limiting Factors

To help understand the rôle of the environmental factors in the production of phytoplankton, the results of the investigation described in the foregoing pages may be briefly reviewed here and discussed. It may be borne in mind that the water occupying the area of investigation does not remain there stationary but is replaced by other water masses at intervals by currents, upwelling and other physical factors responsible for such changes; and, as such, the seasonal changes in a particular water mass cannot be determined directly. In the words of Armstrong and Harvey (1950, p. 145), " From observations at one position small seasonal changes may not be apparent and could be demonstrated only by a series of observations taken at one position throughout many years, sufficient for fluctuations due to changing water masses to iron themselves out. On the other hand, the considerable seasonal changes which occur in phosphate, nitrate, phyto- and zooplankton are quite apparent. They outweigh fluctuations arising from a succession of water masses passing through the area." These remarks appear to be equally applicable to the present area.

In Text-Fig. 7, the overall picture of the results presented in the earlier pages is shown based on the average of five years' data. This gives a clearer idea of the factors concerned in phytoplankton production dealt with in this account.

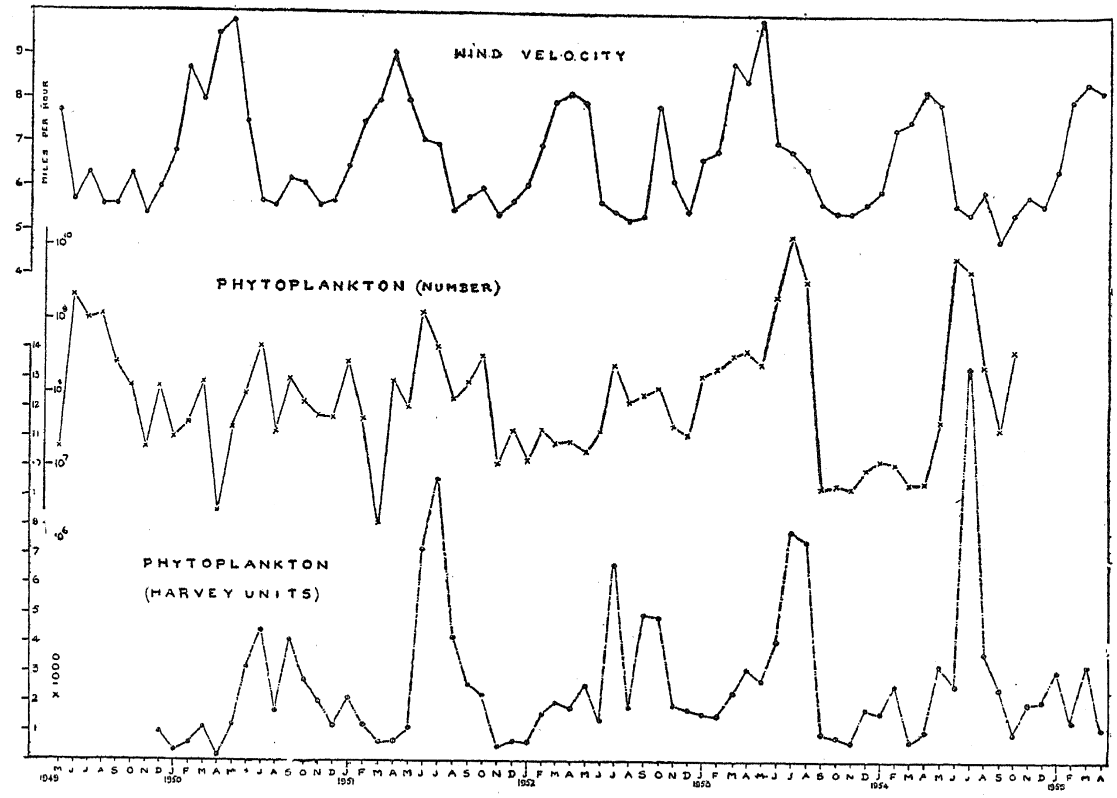
It has already been pointed out earlier that there is no lack of nutrient salts, such as phosphates, nitrates and silicates in the waters on the west coast of India, to act as a limiting factor; and that a fall in temperature to optimum levels (*circa* 25° C.) and that of salinity by 3–4‰ (to *circa* 30‰) during the south-west monsoon season brings about a bloom of phytoplankton (*see* pp. 193 & 200). This bloom is not sustained for long. However, phytoplankton crop again increases, irrespective of temperature and salinity values (*see* pp. 192 & 201) every time there has been a period of high winds.

A reference to Text-Fig. 8 will show that phytoplankton peaks *follow* immediately the peaks of wind force. In the area of the present investiga-



TEXT-FIG. 7. Seasonal fluctuation, based on overall average data of five years, of wind force, rainfall, dissolved oxygen, phosphate-P, nitrate-N, silicate-Si, salinity, temperature of the water, total phytoplankton (Harvey Units) and Diatomaceæ (numbers). Explanation in text.

tion, bottom-living forms like *Melosira sulcata*, *Navicula* spp., *Pleurosigma* spp. and several other pennate Diatoms were found to be common in the plankton samples, brought up to the upper layers, in addition to the increased development of the plankton forms, following periods of high wind velocity. In the Great Barrier Reef region, Marshall (1933, pp. 122–23) has found that wind force affects the depth distribution of the Diatoms and their total number also; there was a sharp rise of Diatom numbers on or just after the days of strong wind. Further, the general and lasting rise in Diatom numbers coincided exactly with the beginning of the South-West Trades. Not only the bottom-living pennate forms increased in number (also being brought n from lower levels to the surface) but non-pennate forms also increased



TEXT-FIG. 8. Seasonal fluctuation of wind velocity and of phytoplankton (numbers and Harvey Units). Explanation in text.

owing to greater growth consequent on the enrichment of the upper layers by the action of the wind (*see* also Cooper, 1952 *a*). Conversely, the Diatom numbers decreased when the South-East Trades began to slacken. Similarly, with fall in wind force the phytoplankton population diminished on the west coast of India also.

The effect of wind is not direct; obviously, the action of wind increases the supply of nutrients to the surface layers from the bottom layers, which acts as a stimulant to the growth of phytoplankton. In the present area, it has already been stressed that none of the usual inorganic nutrients, taking even the surface values alone, are deficient at any time in the water. Therefore, very probably, certain essential growth-promoting substances also seem to be liberated into the water from the bottom in addition to the phosphates, nitrates, silicates and so on. That there is an exchange of substances between the mud and the overlying water has been proved earlier. It appears that there is also some other (undetermined) substance, organic or inorganic, present in the mud which also is set free into the water, thus providing the stimulation for the growth of the standing crop of phytoplankton.

No investigation could be undertaken to determine the nature of this substance. Nevertheless, it may be mentioned that in cultures addition of soil extract, weed extract or organic substances such as thiamine, biotin, glutathinine, cystine, cobalamin (vitamin B_{12}), presence of trihydrol, or supply of certain elements like Fe, Zn, Mn, Mo, Co, etc., have an important rôle in the metabolism of algæ including the Bacillariophyceæ, the dominant element in the flora of the sea (Allen, 1914; Allen and Nelson, 1910; Barnes, 1932; Chu, 1943; Cooper, 1935 *a*, *b*; de Valera, 1940; Droop, 1954, 1955 *a*, *b*; Fogg, 1953; Gaarder and Gran, 1927; Goldberg, 1952; Gran, 1931, 1933; Gran and Ruud, 1926; Harvey, 1933, 1937 *b*, *c*, 1939, 1942, 1945, 1947, 1949, 1950, 1955; Hutner and Provasoli, 1953; Hutner, Provasoli and Filfus, 1953; Imamura, 1952; Iyengar and Subrahmanyan, 1944; Kylin, A., 1945; Kylin, H., 1942, 1943, 1945; Levring, 1945, 1946; Lewin, 1954; Marshall, 1933, Noack and Pirson, 1939, Pirson, 1937; Pirson and Bergmann, 1955; Pringsheim, 1946; Provasoli and Howell, 1952; Provasoli, McLaughlin and Pinter, 1954; Provasoli and Pinter, 1953 *a*, *b*; Robbins *et al.*, 1950 *a*, *b*; Rodhe, 1948; Schreiber, 1931; Subrahmanyan, 1947; Suneson, 1942, 1943; Sweeny, 1954). According to Iyengar and Venkataraman (1951) a high value for oxidizable organic matter favoured profuse growth of the Diatoms, *Nitzschia palea* and *Thalassiosira marginata.* In nature these substances occur in solution in the water and become available by various means, from bottom sediments, land drainage, melting ice or synthesis by bacteria (Ingle *et al.*, 1955; Johnston, 1955; Gran, 1929 *a*, *b*; 1930; Hart, 1934, 1942; Clarke, 1940; Nelson, 1947; Gilson, 1937; Grøntved and Seidenfaden, 1938; Føyn, 1929; Marshall, 1933). There is every reason to suppose that here also such substances occur in the bottom sediments in which decaying organic matter, the marine *humus* (Waksman, 1933) is present in abundance (*vide* also Anderson, 1939; Pillai, 1956) or are brought in by river influx during the season. According to Sewell (1952, p. 716) the bottom deposits in the Arabian Sea contain a high percentage of organic matter and this as well as other nutrients are brought up during the upwelling in the south-west monsoon season.

While considering the possible rôle of the bottom mud on the chemistry and biology of the waters on this coast, it may be interesting to know its composition in order to find out whether there is any evidence in it in support of the views given above. The mud of the mud banks on the west coast of India is believed to have been brought down by the present and past rivers and is mainly of a lateritic and alluvial formation and through them traceable to the decomposing gneissic rocks of the interior (Du Cane *et al.*, 1938). Laterite, from a chemical point of view, is a ferruginous clay, a lithomarge containing variable quantities of ferric hydrate (Du Cane *et al.*, *l.c.*, pp. 43–44). The analysis of laterite as given by Du Cane *et al.* is given below:—

		Laterite*	Mud†
Volatile matter	..	12·41	14·40
Silica	..	46·84	44·05
Alumina	..	24·24	19·14
Ferric Oxide	..	13·53	4·45
Ferrous Oxide	..	1·27	3·64
Lime	..	0·42	6·18
Titania	..	1·38	Nil
Magnesia	..	Nil	5·34
Sulphuric Anhydride	..	Nil	2·26
Phosphoric Anhydride	..	0·02	0·38
TOTAL	..	100·11	99·84

* Laterite from the beach at Tellicherry, some miles north of Calicut.

† Mud from the mud banks of Narakkal, Calicut and Alleppey.

It is thus clear that the mud of the mud banks could be derived from the lateritic deposits. The data further show that the land drainage could be a good source of Fe, found so essential for the growth of phytoplankton, and of silica for the Diatoms in particular. Fe is important for the building up of chlorophyll and it is known that lack of it can be a limiting factor (Harvey, 1937 *b*). It is also evident that the mud is a storehouse of several other compounds and the presence of sulphur is interesting in that this element has been found to have a rôle in the silicon metabolism of Diatoms (Lewin, J. C., 1954; Harvey, 1939; Matsudaira, 1942). It may also be mentioned here, that waters rich in phosphate have also been found richer in iron (Cooper, 1948 *a*, p. 302, *b*; Armstrong and Harvey, 1950, p. 151). The rich phosphate content noted in the waters here may bear a relation to this fact.

The monsoon bloom of phytoplankton, in the absence of any other factor recognizable as a *trigger*, therefore, could be due to the stimulus provided by elements such as Fe, Mn and/or organic substances such as vitamin B_{12}. A study of the Fe-cycle here would be interesting, as also a detailed investigation of the bottom muds of this coast from all aspects, particularly, chemical and bacteriological. This would throw light on many problems including the fertility and production of organic matter in the sea on the west coast.

So far, the external factors, mainly the physical and chemical, influencing phytoplankton production were considered. The most important factor, however, is the physiological state of the organism concerned. Though this has long since been recognized, the *how* of it does not appear to have been dealt with.

Morphological and life-history studies (*e.g. see* Hustedt, 1930; Geitler, 1932; Fritsch, 1935; Iyengar and Subrahmanyan, 1944; Subrahmanyan, 1947) have shown that the Diatoms (they form the bulk of the phytoplankton in all seas) generally multiply by vegetative division, and after each division there is a diminution in the size of the cells and when the cell finally reaches a minimum size characteristic for the species, a process of sexual reproduction and auxospore-formation takes place and a new rejuvenated generation of actively dividing cells is produced which repeats the cycle. Experimental studies have proved that this process of sexual reproduction could be induced by a lowering (dilution of the culture medium) of the salinity of the medium within certain limits, provided the cells are of the right size. Studies of plankton samples reveal that auxospore-formation is mostly met with during the south-west monsoon period, the drop in the salinity also at that time favouring those species concerned to undergo sexual reproduction leading to the rapid increase in the population soon after. Experience in culturing Diatoms have shown that a fresh change of the culture medium with addition of soil extract or sea-weed extract promotes rapid growth. A comparable favourable change appears to take place in the sea also on the west coast of India during this season, when owing to strong wind action, the water and sea bottom are well agitated thus bringing about dissolution into the water of the locked-up nutrients and other essential growth-promoting substances. The sea-water at this time is more or less an ideal culture medium. This state obtains for some time. Later, the intensity of the phytoplankton bloom subsides though apparently there is no deficiency of any of the obvious nutrients. It seems very probable that some substance, organic or inorganic, having got exhausted, acts as a limiting factor. That this is present in the bottom sediment is indicated by the fact that there is a blooming of the phytoplankton more or less invariably following a period of strong winds which help mixing up of the water layers and bottom sediment.

The decline in the standing crop in the following season, north-east monsoon, could also be due to the *senescense* of some of the elements following a period of rapid multiplication, for, such a state has been observed in cultures of Diatoms even when the medium contained all nutrients; reference to this state has also been made by some authors (Marshall and Orr, 1930; Harvey *et al.*, 1935; Riley, 1943; Gross and Koczy, 1946; Iyengar and Subrahmanyan, 1944; and Subrahmanyan, 1947). Riley (1952, p. 63) states: " It is apparent from the experiments that the seasonal cycle is partly controlled by biological or chemical factors. Growth rates were high during the time when the spring flowering was developing; later they became much lower. The change cannot be accounted for by any of the observed environmental factors. However, the existence of reduced growth rates in the experiments subequent to the flowering is sufficient evidence that the population was kept at a low level by physiological limitation as well as by physical dispersal."

Therefore, it would appear that a phytoplankton bloom could occur only if the organisms concerned are also in their proper physiological state and the medium at that time is in a suitable composition. Such a condition appears to be fulfilled, ideally, during the south-west monsoon season on the west coast.

The magnitude of the standing crop is also affected by the zooplankton and nekton organisms present in the water which graze on the plant crop and are dependent on it for their existence. During the south-west monsoon season, the standing crop of phytoplankton is at its peak and though the grazers, zooplankton, also are on the increase and even attain a peak in numbers during the same season, the rate of production of phytoplankton appears to be so high as to maintain a high bulk in the water and exceed that of the animal population. During the following season, the standing crop is of a lower magnitude. During this season, herbivores in the form of Copepods and other zooplankters also occur in abundance as also plankton feeding fishes so much so the crop appears to be heavily grazed down. It is also possible that the rate of production of phytoplankton also slows down for reasons indicated earlier thus leading to a lower order in the magnitude of the crop as compared with the earlier period. Details of the relationship between phyto- and zooplankton and nekton have been discussed elsewhere (Subrahmanyan, Part I).

VIII. PHOSPHATE CONTENT OF THE WATER AND FISHERIES

In the English Channel, Russel (1935 *b*, 1936 *b*) has observed a parallel relationship between the quantity of phosphate in the water at the beginning of the year and the abundance of young fish. " This winter maximum is a measure of the amount of phosphate available for the following season's crop of phytoplankton and indirectly may control the survival of the larval planktonic stages of many marine animals " (Cooper, 1938 *c*, p. 183). An impoverishment of the phosphate in the water, coincident with a change in the type of plankton—which also distinguishes a different water mass—(Russel, 1936 *a*, *b*, *c*, *d*; Wilson, 1951; Wilson and Armstrong, 1952, 1954) is reflected in the fall in the abundance of fish. Thus, it was noticed that the thirties were poor years compared with the twenties when the phosphate content was higher (Cooper, 1938 *c*; Russel, 1935 *b*, 1936 *b*). To quote Harvey (1945, pp. 152–53), the changes in the phosphate content " indicates the water's biological future.... The relation, found by Russel between the fertility of the area and the winter store of phosphorus in the water, is a definite step" towards gauging "the extent of fishing which would give maximum return for human effort without unduly depleting the stock". Cooper's (1948 *c*) study of the relationship between phosphate content of the water and fisheries show that the commercial landings of some fishes follow major changes in the nutrient content of the overlying water with a time-lag of some years. The dependence of the bottom in-fauna upon the fertility of the overlying water is also indicated.

Naturally, the above cited accounts led to an examination of the phosphate content of the water recorded here on the west coast of India and the fish landings. Though the period of investigation has not been of sufficiently long duration as in the English Channel, the data relating to the fish landings for about 5 years appear to indicate a parallel relationship between the phosphate maximum recorded during the year and also the integral mean phosphate content of the water of the years. The time lag is bound to be shorter in this peculiar tropical environment where the nutrient cycles and metabolism of the organisms are different. The data are shown in Table V. While the parallel relationship is seen reflected in the fluctuation of the total fish landed, the mackerel and residual landings, the oil-sardine shows a somewhat opposite relationship; the quantity tends to increase with a fall in the phosphate content, probably because the fish is predominantly a phytoplankton feeder and as an inverse ratio obtains between phytoplankton production and phosphate content of the water. However, the clear-cut inverse relationship between phytoplankton and phosphate noticed in the temperate regions is

TABLE V

Phosphate and fisheries

Years May–April	Phosphate Mean integral value µg. at./L	Phosphate Maximum µg. at./L	Total landings Metric tons	Mackerel Metric tons	Oil-sardine Metric tons	Remaining fish Metric tons	Rainfall Inches
1949–50	0·798	1·235	..	..	..	..	130·94
1950–51	0·840	1·382	156,810	57,335	12,779	85,696	131·78
1951–52	0·589	0·905	144,833	76,930	18,548	49,345	102·66
1952–53	0·537	1·110	62,302	16,725	22,218	23,359	95·56
1953–54	0·559	0·735	50,754	5,934	30,397	14,423	97·30
1954–55	0·908	1·895	..	..	..	..	143·80

not emphasized on the west coast of India, though on some occasions such a one is seen on a sample-to-sample basis. In the present instance, the overall relationship is parallel; the phosphate attains the maximum during or immediately following the phytoplankton maxima and this complicates the picture of relationship between different groups of organisms. Nevertheless, it is felt that data gathered over several years, as for the English Channel, might reveal a relationship on a time-lag basis in our waters also, and when more knowledge accrues on the biology of the fishes constituting the fishery, it should become possible to predict much ahead the prospects of fish landings. For the present, the relationship observed on the west coast of India to those recorded in the English Channel is worth noting.

Again, another relationship becomes evident which is interesting. It was mentioned earlier that the freshwater influx into the sea during the south-west monsoon months might contribute a little phosphate to the nutrient content of the water, though not in significant quantities. Some evidence for this could be inferred in the somewhat parallel relationship seen between the integral mean value of the phosphate content and the total amount of rainfall during the years (Table V). The intensity of rainfall will depend on certain weather conditions and the same conditions might lead to a mixing up of the sea-water layers and the bottom sediment bringing about an increase in the phosphate content. It is also possible that the increased strength of the monsoon as indexed by rainfall might affect the conditions in the water in such manner as to lead to an increase in the dissolution of the bottom phosphate. Be that as it may, we are here concerned with the whole phosphate content in the water. The relationship pointed out between phosphate content and fisheries would, therefore, indicate indirectly a relationship with the rainfall, it being the same as with phosphate, a direct one. It may be interesting to mention in this connexion that Kalle (1949) has demonstrated a parallel relationship between precipitation and herring catches in the northern waters.

IX. SUMMARY

1. In this account, particulars relating to the environmental factors influencing phytoplankton production, such as temperature, salinity, phosphate, nitrate, silicate, and oxygen content of the sea-water are dealt with and compared with data from other regions in India and elsewhere, and their cycles and rôle are discussed.

2. There is a bimodal oscillation in the temperature of the water. The fall in temperature during the south-west monsoon season reaches optimum levels favourable for the growth of phytoplankton.

3. Salinity also shows a bimodal oscillation during the year, the lowest values being recorded during the south-west monsoon months, which, however, does not go beyond 4‰ of the highest values recorded. Changes in the salinity are found to have an important rôle in the metabolism of the Diatom cells when they are in a particular physiological state. A fall in salinity within limits acts as a stimulus to sexual reproduction of several species and their subsequent rapid vegetative multiplication leading to the peak bloom of the year. This aspect is discussed with reference to culture work on the Diatoms.

4. The nutrient salts, phosphates, nitrates and silicates show a seasonal fluctuation, the peaks in their concentration being attained during the south-west monsoon months, at the same time as or immediately following that of the peak phytoplankton bloom. It was found that there is always an abundant supply of these nutrients in the water for the growth of phytoplankton. The results are compared with earlier records from elsewhere and the source and cycle of the nutrients are discussed.

5. The dissolved oxygen content is never steady and oscillates very much. The peak in the oxygen-content is reached after the wane of the phytoplankton bloom. The relationships between oxygen-content, silicate metabolism and phytoplankton production are pointed out and discussed.

6. It was found that here also, as in the temperate waters, the ratio of 1:15:20 obtains between phosphate-P, nitrate-N and silicate-Si respectively in the waters which is very significant. Previous workers in this country were unable to establish any such relationship.

7. It is shown that the bottom mud on this coast is a rich storehouse of nutrients which are released into the waters during the south-west monsoon season generally and during periods of high winds in particular, when a mixing up of the layers occurs as also the bottom sediment. It is indicated that the mud also contains, besides inorganic nutrients, important organic substances and growth-promoters which are essential for the growth of phytoplankton, and the absence of which could act as a limiting factor.

8. Aspects of river influx contributing to the fertility of the inshore waters are discussed.

9. Besides the influence of external factors, the nature of the internal factors responsible for the multiplication of the Diatoms, the predominant element in the flora, is pointed out and its relationship with the environment is discussed.

10. It was found that a parallel relationship exists between both the phosphate maximum recorded during the year and the integral mean phosphate value of the years on the one hand and total fish landed on the other.

11. A somewhat parallel relationship also exists between the integral mean phosphate values and the total annual rainfall during the years; therefore, fish landings show indirectly a parallel relationship, similar to phosphate, with the annual rainfall.

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