Primary Productivity and Fertility at Station "P" in the North-East Pacific Ocean

By

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I. Introduction

The weathership "St. Catharines" of the Canadian Department of Transport patrols at a position 50°N, 145°W in the north-eastern Pacific Ocean (Ocean Station "P") for alternate six weeks periods. There is a sizable and well equipped laboratory built into the ship and full facilities for overside oceanographic operations are available. Regular meteorological observations are made and for the past four years programmes of physical and biological oceanography have been undertaken during each patrol.

Ocean Station "P" lies within the subarctic water mass of the north-east Pacific Ocean (Fig. 1). This subarctic water mass is characterized by its vertical distribution of salinity which consists of three layers; 0–100 m, an almost homogeneous zone of relatively low salinity; 100–200 m, a halocline in which salinities increase by about $1^0/_{00}$ and which marks the limit of seasonal mixing; and, at greater than 200 m, a deep zone in which salinities gradually increase with depth. Temperature-salinity relationships observed during the present study (Figs. 2 and 3) are typical of the subarctic water mass.

A current enters the area surrounding Station "P" from a westerly direction and divides east of the station to form the south-flowing California Current and the counter-clockwise Alaska Gyral. The centre of the Alaska Gyral, where there is slow upwelling, lies about 300 miles north-west of Station "P". To the south, gradients of salinity and temperature increase to form the Polar Front, between 38° and 46° north latitude.

The location of Ocean Station "P" is truly oceanic, being about 500 miles from the nearest part of the continental shelf. It is reasonable to suppose that, for biotic considerations, the position is typical of much of the eastern subarctic Pacific Ocean.

The work described here was undertaken during a six-week period between 10. July and 21. August 1959, with the purpose of monitoring the summer productivity at a fixed point in the open ocean. To the best of our knowledge

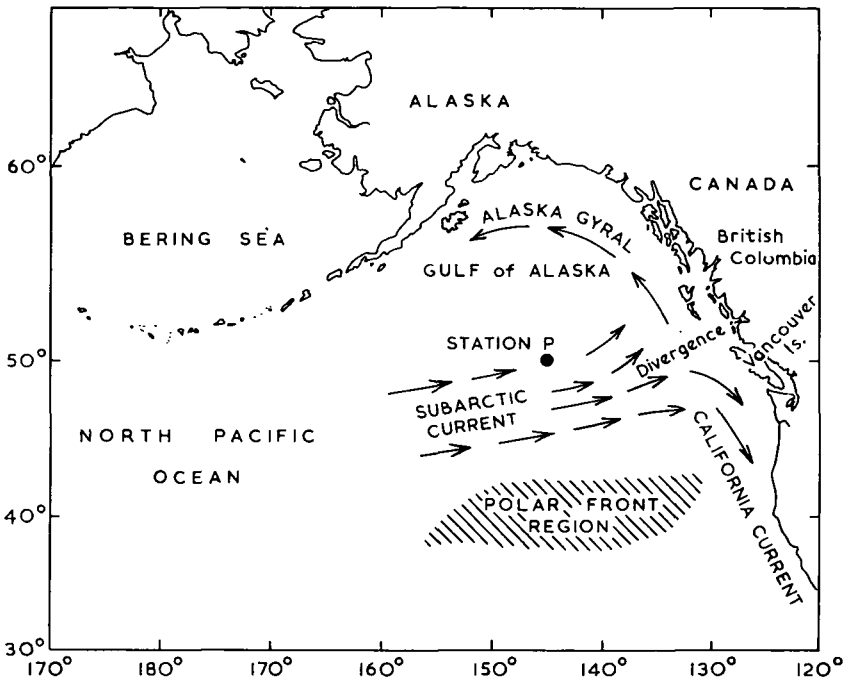

Figure 1. Location of Ocean Station "P".

the primary productivity and fertility of a temperate ocean has not before been continuously measured *in one place* over such a protracted period.

The programme was also the most diverse study of its kind so far reported. The basic programme consisted of the weekly measurement of a wide variety of nutrients, of the standing crop of (microscopic) organic material, and of photosynthetic production in the euphotic zone. The variation of organic matter with depth and location (over traverses of a few miles) was determined and, in order to decide upon the significance of certain observations, a culture experiment was attempted using some 200 l of surface water with its endemic plant cells.

II. Methods

Full working details of the methods used are to be issued in a forthcoming Bulletin of the Fisheries Research Board of Canada. The following notes indicate the general type of approach. A statistical estimate of the precision of each technique has been determined under realistic working conditions.

1. Light

A continuous recording of solar radiation was obtained by an Epply pyrheliometer. The unit used in this paper, the "langley", is equal to one calory of radiant energy per square centimetre of surface. The light attenuation properties of the

sea water were measured from a seven-metre boom at the stern of the ship by matched underwater and deck Weston cells covered by 2 mm of Schott BG 12 glass. The wavelength of peak response of this assembly was about 4300 Å. Vertical extinction coefficients were measured whenever practicable and were generally constant throughout the euphotic zone. The extinction coefficient at 4300 Å was used to characterize the water mass using JERLOV's data (JERLOV, 1951) and hence the total intensity at any chosen depth could be calculated with sufficient precision for biological purposes.

2. Nutrients

Salinity was measured by an electrical conductivity salinometer, *oxygen* by the Winkler method, *pH* using a glass electrode standardized by standard phosphate buffer at pH 6·87, *alkalinity* by the Anderson-Robinson method (ANDERSON and ROBINSON, 1946), *silicate* by the method of MULLIN and RILEY (1955 a), *nitrite* by the method of BENDSCHNEIDER and ROBINSON (1952), *nitrate* by a modification of the procedure described by MULLIN and RILEY (1955 b), and *phosphate-phosphorus* by a modification of the method of ROBINSON and THOMPSON (1948). *Soluble organic phosphorus* and *particulate phosphorus* were determined as phosphate after a wet oxidation with perchloric acid (cf. HANSEN and ROBINSON, 1953). The particulate phosphorus is defined as that retained on a Millipore HA filter. The soluble organic phosphorus was measured as the difference between the total phosphate in a sample passed through a Millipore HA filter and the inorganic phosphate in the same sample. *Particulate reactive iron* and *ammonia* were estimated as described by STRICKLAND and AUSTIN (1959). The method used for *manganese* was based on the catalyzed oxidation of the leucobase of malachite green by periodate, as developed by one of the present authors (see also YUEN, 1958).

The levels of iron, manganese, and soluble organic phosphorus in the euphotic zone were estimated from pumped samples (see later). The remainder of the analyses were made on samples taken in 5 l capacity, all plastic, Van Dorn bottles with stainless-steel fittings.

3. Particulate organic material

Sampling and concentration

Weekly samples for the measurement of the amount of particulate matter in sea water were obtained by pumping sea water integrated from a depth of 0 to 50 m. This was accomplished by raising and lowering a hose and intake valve by means of an electrical winch. The hose and pump were constructed of neoprene and the unit had a delivery rate of 20 l per minute. Water was collected in a 200 l polyethylene container and sub-sampled into 8 litre sized polyethylene bottles. Large zooplankters and detritus were removed from the water by first straining it through a nylon net with a mesh size of about 150 microns. The concentration of the particulate matter in the resulting samples was accomplished by filtering the water through a Millipore type AA filter, previously treated with magnesium carbonate (PARSONS and STRICKLAND, 1959). When sufficient sea water had been filtered the Millipore filter was removed and the concentrated particulate material was washed from the surface with a small quantity of 3·5% saline. The suspended particulate matter and magnesium carbonate were then further concentrated by centrifugation and the supernatant

liquid was discarded. The resulting residue was used for the determination of carbon, carbohydrate, protein, and fat.

All apparatus involved in the determination of particulate matter was cleaned in acid dichromate or detergent and well rinsed prior to use. There was no evidence of contamination from external sources during the course of these experiments.

Plant pigments

Chlorophyll *a*, *b*, *c*, plant carotenoids and animal carotenoids were measured as described by RICHARDS with THOMPSON (1952) using the Millipore filter technique of concentrating the phytoplankton cells as described by CREITZ and RICHARDS (1955). Extinctions were measured in 10 cm cuvettes and a correction for turbidity was made using the extinction at a wavelength of 7500 Å, multiplied by a predetermined factor to allow for increased light scatter at decreasing wavelengths. Chlorophyll *c* and carotenoids are reported in the somewhat arbitrary units suggested by RICHARDS, the SPU, or better SPPU, specific plant pigment unit.

Carbon

Particulate carbon was determined by wet oxidation with potassium dichromate in concentrated sulphuric acid by a modification of the procedure described by JOHNSON (1949). The decrease in the extinction of dichromate solutions at a wavelength of 4400 Å acted as a measure of the amount of oxidizable carbon.

Protein

Particulate protein was determined using the phenol reagent of FOLIN and COICALTEU (1927). Protein was solubilized by treatment with 1 N sodium hydroxide for 1 hour at 100°C and the colour developed after the addition of the phenol reagent was measured at a wavelength of 7500 Å. The method was standardized on egg-albumin.

Carbohydrate

Particulate carbohydrate was determined by the anthrone reaction using the reagents employed by HEWITT (1958) and measuring the absorption of the colour developed at a wavelength of 6200 Å. Additional absorptions were measured at wavelengths of 5500 Å and 6500 Å in order to determine, qualitatively, the presence of hexuronic acids and pentoses. The method was standardized on glucose.

Fat

The amount of fat present in the particulate matter was determined by a modification of the method described by MUKERJEE (1956). The method specifically measures fatty acids and results obtained by the use of this method may be lower than values obtained by an ether extraction technique. The method was standardized on stearic acid.

4. Photosynthetic rate measurements

Rates of photosynthesis were measured using a modification of the technique described by NIELSEN (1952).

Sampling was always done between 0630 and 0700 hours local time (Zone

+ 10) using Van Dorn plastic samplers at depths of 0, 5, 10, 15, 20, 30, and 50 m. Aliquots for measurements were drawn into 300 ml BOD (Biological Oxidation Demand) bottles. (It was found that wire clamps on the stoppers of these bottles were necessary to prevent leakage.)

Aliquots were taken from each depth for measurement both in a shipboard incubator and suspended at their original depths from a free floating buoy. In addition, aliquots of a composite sample, prepared from equal parts of water from each depth, were both illuminated in the incubator and suspended in the sea. The buoy was released from the side of the ship, left in the sea between 0930 and 1530 hrs., a period of relatively uniform illumination, and was tracked by radar, thus freeing the ship for other duties.

Samples measured aboard ship lay horizontally in running sea water and were illuminated from above by blue and green fluorescent lamps in the lid of the incubator. By controlling the voltage, light intensity was kept constant at about 0·08 langlies per minute of photosynthetic radiation. The spectral energy distribution of the illumination approximated to that found at the depth of maximum photosynthesis in oceanic waters.

Samples were filtered through Millipore HA membranes of 0·5 micron pore diameter. It was found that a rinse with 0·002 N hydrochloric acid decreased sample activity by an amount proportional to the volume of acid used and an acid wash was therefore omitted. Sample activities were measured aboard ship within 24 hours of filtration, using a windowless flow counter, and counting rates were corrected for dark uptake and variations in counter sensitivity.

When bad weather prevented buoy releases, the *in situ* production of the ocean was estimated from a knowledge of the rates measured in the ship's incubator, the estimated *in situ* light intensities in the sea and a curve showing the relative rate of photosynthesis versus light intensity. The latter was constructed from the mean of several determinations made during the cruise.

5. Culturing experiment

Water from about 10 m depth was collected in Van Dorn bottles and used to fill a large polyethylene vat holding 185 litres. The vat was fastened to the rail on an upper forward deck, clear of any shadow from superstructure. The water was strained through nylon net of mesh size 70–100 microns to remove all but the smallest zooplankton. No significant quantity of phytoplankton was removed by the net. The top of the tub was covered by two thicknesses of 0·1 mm polyethylene sheet and the sides surrounded by sacking. Surface sea water was played on to the sides of the vat from a hose, so that the mean temperature of the culture was only about 2–3°C greater than that of the upper euphotic zone. The level of illumination in the vat, as measured by a photocell, was about 20% of the incident daylight, corresponding to the light level at about 20 m depth in the sea.

The contents of the tub were stirred three times a day and samples taken for analysis about noon. The carbon uptake was measured by sampling the water into a light and dark BOD bottle first thing in the morning, inoculating these bottles with radioactive carbon, and suspending them in the centre of the tub all day. In the evening the carbon uptake in both bottles was measured and equated to the increase of plant carbon. Allowance was made for night-time respiration by assuming that its hourly rate was about one-tenth of the mean hourly rate of photosynthesis. The results were recorded as daily means at each

noon, a day being taken as the period from midnight to midnight. In view of the nature of the measurement and the various assumptions made, the estimated uptake of carbon is probably low rather than high.

On alternate days the photosynthetic potential of the water was measured (using radioactive carbon) by illuminating a BOD bottle of water in a constant light incubator, to give a value for hourly photosynthesis that was independent of variable sunlight conditions. The content of the tub was analysed periodically for silicate, nitrate, and phosphate and the particulate material was analysed for carbon, carbohydrate, protein, and lipid. The pigment content was measured daily.

III. Results

A complete tabulation of all the results obtained on this cruise has been published as a Data Record by the Fisheries Research Board of Canada (McALLISTER, *et al.*, 1959). A limited supply of these reports are available and can be obtained from the Pacific Oceanographic Group, Nanaimo, B.C., Canada. In the present paper we are presenting only those data which seem to us to be of major importance or which serve to illustrate general trends and magnitudes.

1. Light

The vertical extinction coefficient (metre^{-1}, base 10 logarithms) at 4300 Å was roughly constant in the first 50 m and had a value of about 0·035 for much of the cruise. At some time in the second or third week of August the water cleared substantially, the vertical extinction coefficient decreasing to about 0·025.

2. Nutrients

A typical set of nutrient profiles is shown by Table 1, the data being obtained about halfway through the cruise. Such analyses were carried out once a week, giving seven profiles in all, and were restricted to the surface waters down to

Table 1

Nutrient profiles Station N 3 (24. July 1959)

Depth m	Temp.*) °C	S*) ‰	O_2 mg at/l	pH (*in situ*)	Total alk.	SiO_3 µg at/l	Nitrogen µg at/l			PO_4 µg at/l	N/P
							NO_3	NO_2	NH_3		
0	11·2	33·12	0·585	8·20	–	23·7	9·5	0·09	0·3	1·24	7·7
10	11·2	32·78	0·588	8·22	2·31	24·4	9·4	0·11	–	1·29	7·3
20	11·2	32·79	0·584	–	–	23·5	9·5	0·12	–	1·26	7·5
29	10·8	32·76	0·586	8·23	–	21·7	10·5	0·15	0·4	1·40	7·5
48	7·3	32·87	0·627	–	–	32·4	14·1	0·17	–	1·69	8·3
73	4·6	32·98	0·634	–	–	34·9	16·4	0·94	<0·2	1·83	9·0
97	4·5	32·98	0·632	8·02	–	32·9	17·3	0·64	–	1·87	9·2
121	4·7	33·55	0·500	–	–	48·7	25·6	<0.01	–	2·27	11·3
145	4·9	33·83	0·380	–	–	57·8	26·4	<0·01	–	2·37	11·1
280	3·8	33·94	0·190	7·78	–	76·9	33·0	0·01	<0·2	2·83	11·7
950	2·8	34·4	0·060	7·67	2·40	121	37·8	0·05	0·6	3·23	11·7

Specific alkalinity 0·124 at 10 m, 0·123 at 950 m.

*) Values measured about one hour earlier on separate cast. Approximate data for reference.

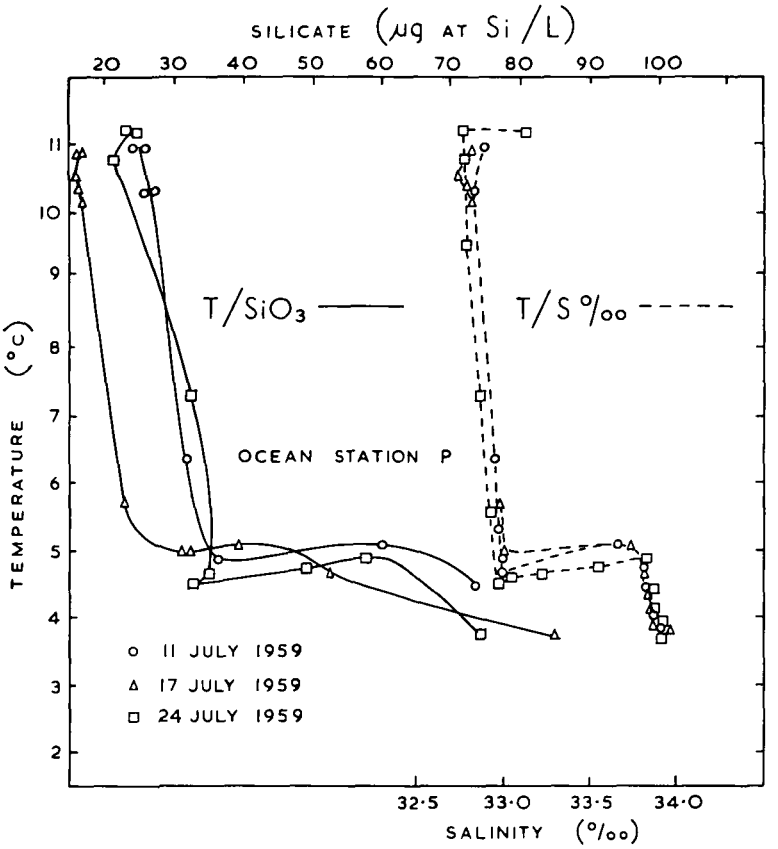

Figure 2. Comparison of temperature-silicate and temperature-salinity curves.

300 m, with a sample from near to 1000 m to establish the concentration levels in deeper layers. The figures for temperature and salinity were obtained from a cast of Nansen bottles "fired" about one hour earlier.

The oxygen content of the top 30 m was in the range 0·57 to 0·59 mg at/l for the entire cruise and pH values (corrected for *in situ* temperature) were between 8·16 and 8·22. The specific alkalinity at all depths was constant at 0·124, within the precision of the method used. Nitrite nitrogen was always present in the top 50 m to about the same extent (0·1–0·15 μg at/l) and always showed a peak around 75 m, where the concentration could be as high as 1 μg at/l. Ammonia concentrations were variable and had no obvious pattern.

Particulate reactive iron (0·03–0·13 μg at/l) and manganese (0·005–0·017 μg at/l) were present in appreciable concentrations in pumped samples. The soluble organic phosphorus ranged between 30 and 65 percent of the inorganic phosphate found in the same water which was of the same order as that found previously by one of us in north-eastern Pacific coastal and oceanic samples (STRICKLAND and AUSTIN, 1960).

The most marked feature of the nutrient picture was the variation, in the

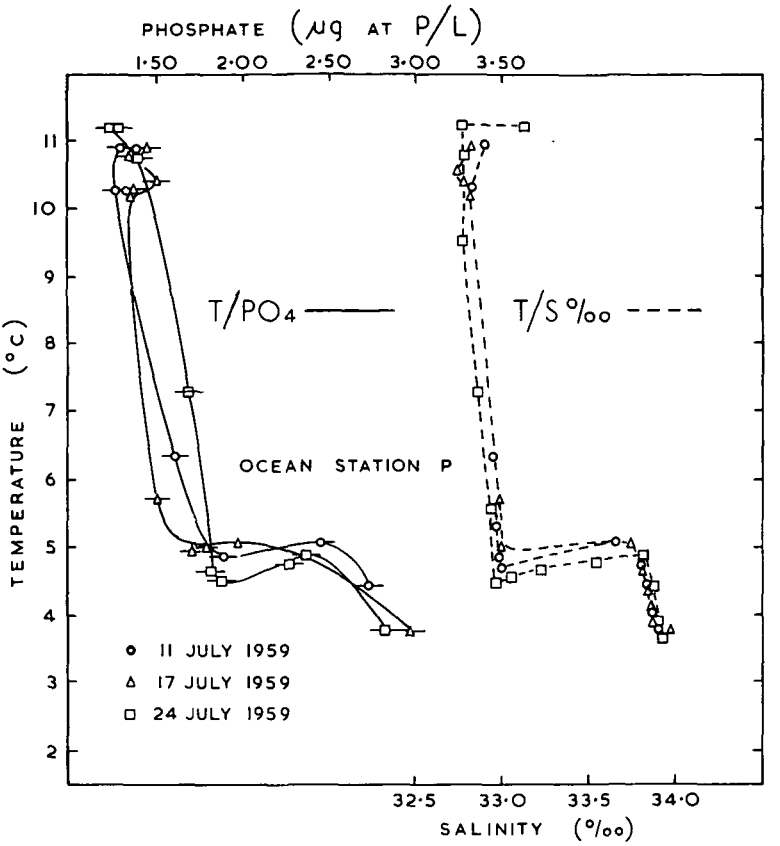

Figure 3. Comparison of temperature-phosphate and temperature-salinity curves.

top 50 m, of the silicate and nitrate concentrations. A similar variation in phosphate concentration may have occurred but was much less. We have illustrated this in Figure 2 where the silicate and salinity are plotted against temperature for three successive weeks. A similar plot for phosphorus and salinity is given in Figure 3. The size of the circles, squares, or triangles in Figure 2 represents, approximately, the uncertainty of the silicate analysis ($\pm 2\sigma$). In Figure 3, a horizontal line shows the $\pm 2\sigma$ uncertainty limits of the phosphate results. At 25 m, about the middle of the euphotic zone, the silicate varied from week to week between 16 and 31 μg at/l, with no obvious pattern. The corresponding range for nitrate was 6 to 12·5 μg at/l. For phosphate, however, the variation was only between 1·23 and 1·33 μg at P/l.

The nutrient levels also changed on a single day as the ship steamed over a traverse of a few miles. In an east-to-west journey of eight miles the silicate at 20 m changed from 26·7 to 22·6 μg at/l. An even more striking change is seen in Table 3 with a north-to-south traverse. These variations are greater than ever noted between surface and 30 m values at a single fixed point and are well outside the range of any possible experimental error.

Table 2

Routine crop station

Plant carbon = 60 × chlorophyll *a* concentration. Crop in mg/m³ or m SPPU/m³ (chlorophyll *c* and carotenoids).
Plant carbohydrate = 47 × chlorophyll *a* concentration.
Plant protein = 35 × chlorophyll *a* concentration.

Station	Date (1959)	Carbon Total	Carbon Plant	Carbon Rem.	Carbohydrate Total	Carbohydrate Plant	Carbohydrate Rem.	Protein Total	Protein Plant	Protein Rem.	Lipid (Total)	Chlorophylls *a*	Chlorophylls *c*	Carotenoids
C 1	13. July	240	35	205	100	26	74	125	20	105	13	0·55	0·8	0·52
C 3	20. July	145	20	125	38	14	24	165	10	155	31	0·30	0·5	0·17
C 5	27. July	145	25	120	58	21	37	115	15	100	20	0·44	0·9	0·16
C 6	4. Aug.	130	15	115	72	13	59	150	10	140	22	0·27	0·4	0·08
C 9	10. Aug.	160	35	125	49	29	20	105	22	83	13	0·62	0·8	0·40
C12	17. Aug.	145	15	130	59	13	46	109	10	99	7	0·27	0·4	0·11

Table 3

Stations on traverse; samples from 5–10 m

Nutrients in μg at/l. Crop in mg/m³ or m SPPU/m³ (chlorophyll *c* and carotenoids)

Station C 11	Time GMT	Miles	Position	Inorganic $HSiO_3$	Inorganic P	Carbon	Chlorophyll *a*	Chlorophyll *c*	Carotenoids
13. Aug. 1959....	1840	0	50°15′N, 145°00′W	16·6 ± 0·3	1·35 ± 0·08	214 ± 30	0·85	1·2	0·7
North-south	2000	10	50°05′N, 145°00′W	20·9 ± 0·3	1·30 ± 0·08	129 ± 25	0·25 (± abt. 0·06)	0·8 (± abt. 0·1)	0·1 (± abt. 0·1)
Traverse.....	2140	20	49°55′N, 145°00′W	21·0 ± 0·3	1·58 ± 0·08	120 ± 25	0·30	0·2	0·2
At Station "P" ..	2245	30	49°45′N, 145°00′W	17·7 ± 0·3	1·28 ± 0·08	224 ± 30	0·76	1·1	0·5

3. Particulate organic material

The analysis of six composite phytoplankton crops, measured over a period of six weeks, is shown in Table 2. The amounts of carbon, protein, and carbohydrate that could be attributed to phytoplankton have been calculated from the amounts of chlorophyll *a* present, using conversion factors obtained from the culturing experiment (see later). These quantities have then been subtracted from the corresponding metabolite found by analysis and the difference is reported as "remainder" (Rem.), which is an approximate measure of detritus.

The detritus was characterized by a high protein to carbohydrate ratio. However, not all organic material is accounted for in terms of these two metabolites, as may be deduced from the disagreement between total carbon and the sum of the carbohydrate and protein carbon. The amount of fat is low and does not contribute significantly. The cause of the discrepancy may be in the method used for estimating total protein which took into account only the tyrosine and tryptophane contents of a hydrolysate. A more satisfactory procedure has since been developed.

Microscopic examination of the detritus showed that a considerable portion was composed of fibrous material of irregular dimensions which had the appearance and gave a positive stain for cellulose. With the exception of station C1 the amount of detritus was fairly constant at about 125 mg carbon/m^3 in the euphotic zone and was still present in about half this quantity at 1000 m, which was the deepest sample analysed.

Microscopic examination of settled sea-water samples showed that the predominant plant cells were coccolithophores. Further evidence that the crop was composed predominantly of ultra-plankters was obtained from the fact that 75% of the pigment in a water sample passed through a 10-micron filter. Net-phytoplankton (greater than 50 microns) accounted for only a very small fraction of the plant crop. The predominant species of net-phytoplankton were the dinoflagellates, *Ceratium fusus* and *Ceratium tripos* and the diatom, *Coscinodiscus marginatus*.

Maximum pigment concentrations were found at between 50 and 75 m while no pigment at all was detected below 200 m. Particulate phosphorus was less than 1 mg P/m^3 in all samples.

Table 3 shows the variation of phytoplankton crop and particulate carbon over a north-to-south traverse of 30 miles, together with variations in the silicate and inorganic phosphate concentrations over the same distance. It may be seen that at positions 0 and 30 miles the plant pigments are higher than at the two centre stations. At the same time there is a statistically significant difference in the amount of organic carbon at the stations at the beginning and end of the traverse, compared with those in the middle.

4. Photosynthetic rate measurements

Table 4 gives the full results of a typical productivity experiment.

Six determinations of productivity were carried out, at weekly intervals. Table 5 gives the production beneath a square metre per day in the upper 50 metres for each weekly station, together with the total incident solar radiation on the day concerned. The rate of photosynthesis per milligram of chlorophyll *a*, as measured in the ship's incubator (at about 0·08 langlies/min. of photosynthetic illumination) is shown in the fifth column. This relative rate

Table 4

Results from a typical photosynthetic rate determination (Station P 2)

Depth m	Incubator rates (mg C/m³/hr)	Mean *in situ* light (langlies/min. 3800–7200Å)	Rates measured on buoy: *In situ* mg C/m³/hr.	Rates measured on buoy: Composite sample from euphotic zone mg C/m³/hr.
0	1·35	0·45	0·82	0·29
5	0·64	0·19	0·48	0·37
10	0·55	0·11	0·32	0·51
15	0·74	0·07	0·46	0·47
20	0·70	0·04	0·29	0·46
30	0·57	0·01	–	0·29
50	0·51	0·005	0·22	0·05

Table 5

Collected productivity data

Station	Date (1959)	Approx. euphotic zone production (mg C/m³/day)	Total light (langlies)	Rate per unit of chlorophyll *a* (mg C/hr./mg)	Rate per unit of total pigments (mg C/hr./mg)*)
P-1	15. July	390	330	1·34	0·45
P-2	22. July	160	500	1·31	0·47
P-3	29. July	260	280	1·50	0·56
P-4	6. Aug.	310	270	1·83	0·51
P-5	13. Aug.	55	260	1·07	0·23
P-6	19. Aug.	55	260	0·63	0·24
Culture (at 7·5 days)		–	–	1·8	0·6
Diatoms and dinoflagellates held by 40-micron net		–	–	1·0	–

*) Pigment units for chlorophylls *a*, *c*, and plant carotenoids all added together to give a somewhat arbitrary mixed unit.

Mean daily production 205 mg C/m² for the entire cruise.

has also been calculated on the somewhat arbitrary basis of total pigment units (chlorophylls *a*, plus *c*, plus carotenoids). The pigments and rates used to compute these ratios were measured on composite samples taken from the whole euphotic zone.

Weather prevented buoy releases on two days (Stations P3 and P5) and the *in situ* production was then calculated from incubator results. The ratio of the *observed* to calculated euphotic zone production in the other four experiments ranged from 0·8 to 1·2 and averaged at 0·98. A vertical profile of production, measured using the buoy, is shown in Figure 4, with the corresponding curve calculated from incubator results.

It will be noted in Table 5 that although the total photosynthetic production beneath a square metre per day varied over six-fold, the corresponding rates per unit pigment concentration in an incubator varied by little more than two-fold.

5. Culturing experiment

The results of this work are summarized graphically. In Figure 5 the daily value for the plant carbon in the vat is plotted on a log-scale against the duration of the experiment. The initial value of plant carbon has been estimated

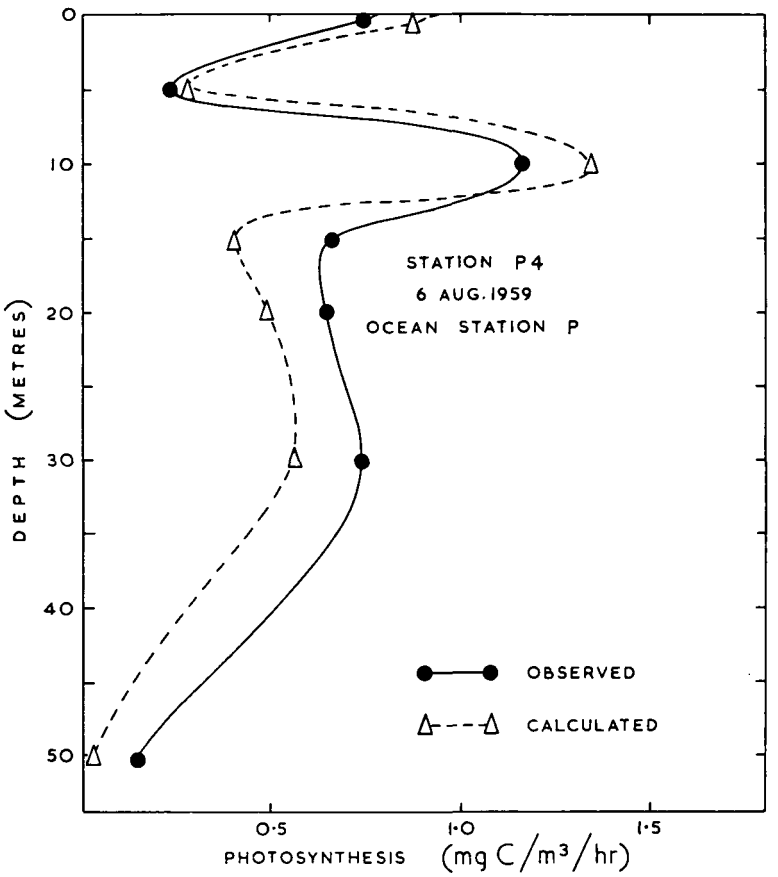

Figure 4. Typical productivity curve, observed and calculated values. Station P. 4. Sixth August 1959.

from the initial chlorophyll *a* concentration in the vat. The correct value could have been in the range 10 to 30 mg C/m^3 but we consider 20 mg C/m^3 the most likely figure. In Figure 6 the corresponding plot is given for the daily plant pigment data. In the top of both these figures there are histograms of the total *daily* radiation in langlies (cals/cm^2 of solar radiation between about 3000 Å and 50,000 Å) shown on a linear scale.

In Figure 7 A the variation of reactive silicon in the tub is plotted against time. The corresponding plots for phosphorus and nitrate (all as mg/m^3 of the element) are shown in Figure 7, B and C. The fourth section of Figure 7 (lettered D) shows the measured values of carbon, carbohydrate, protein, and lipid. The values for carbon were obtained from the oxidizable carbon results after correcting for the amount of lipid measured in the same sample. Analyses are only reported from the seventh day onwards as, initially, the detritus present masked the presence of living plant material. After a few days the detrital matter appeared to separate out by some form of clumping mechanism and could be separated by a fine nylon net. It was largely absent from the samples analysed after about five days.

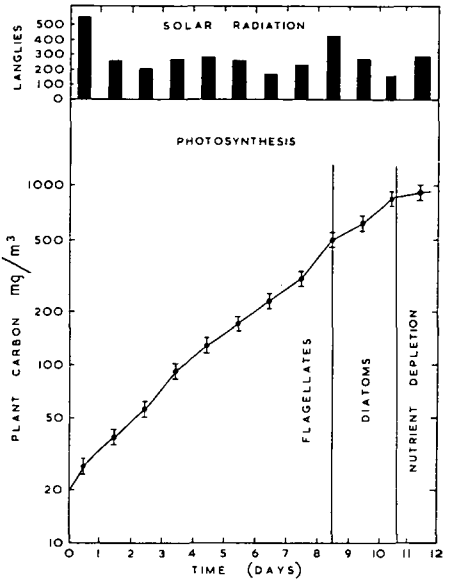

Figure 5. Production of photosynthetic carbon in the culturing experiment.

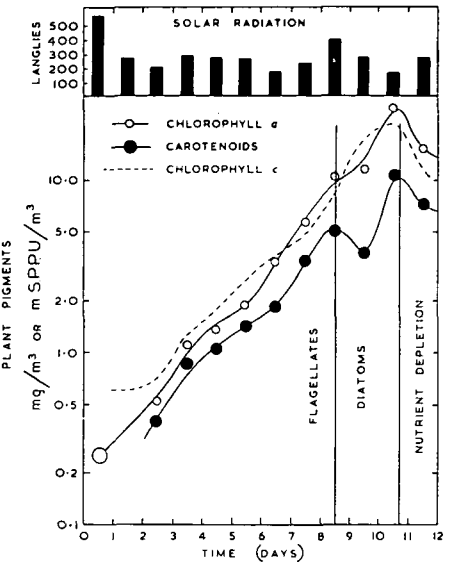

Figure 6. Production of plant pigments in the culturing experiment.

The predominant species in the culture for the first six to eight days was a small flagellate (tentatively *Pontosphaera huxleyi*). A consideration of elementary kinetics shows that this species must have comprised a substantial fraction of the initial plant crop. Between the seventh and ninth day the coccolithophore was rapidly replaced by a small pennate diatom and by the end of the eleventh day its growth was being severely limited by nutrient depletion. These major stages in the progress of the culture are shown in Figures 5, 6, and 7 by vertical lines.

IV. Discussion

It is clear that the level of concentration of the major plant nutrients at Station "P" is adequate for vigorous plant growth throughout the period studied. Occasional analyses, made during the past few years, have given no indication that the situation is ever otherwise. The presence of excess nutrient is confirmed by our culture experiment. Figures 5 and 7 show that plant growth is not seriously impeded by nutrient deficiency until after ten to eleven days of growth, when the nitrate concentration is reduced to less than 1 μg at/l. Phosphate is then still present at an appreciable concentration, about 0·35 μg at/l, as would be anticipated from the initial ratio of nitrogen to phosphorus (9·2:1 on an atomic basis). The N:P ratio in the euphotic zone was always found to be low during this patrol (between about 5 and 9) and even in the deeper waters it never reached 15:1 (see Table 1). If soluble organic phosphorus is included the ratios would be even smaller. When phytoplankters, containing combined nitrogen and phosphorus in a ratio of about 15:1, grow in such water nitrogen must be the first major nutrient to be used up (e.g., COOPER, 1937, 1938).

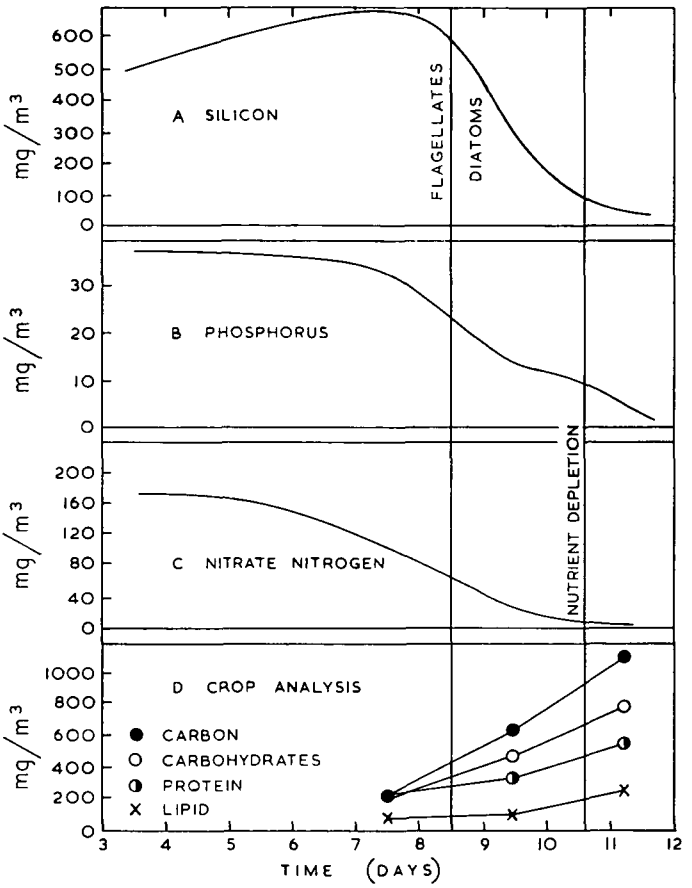

Figure 7. Depletion of silicon, phosphorus, and nitrogen and the formation of metabolites in the culturing experiment.

However, it must be stressed that a ratio of 15:1 for nitrogen to phosphorus in plants is a very rough average and will depend upon the availability of the two elements. Plant cells can adjust their levels of combined nitrogen and phosphorus over quite a wide range. Thus in our culturing experiment the average ratio of N to P abstracted from the sea water by the growing phytoplankters was 11:1 but the ratio was as high as 14:1 during the initial phase of growth, when nitrate was abundant, and as low as 8·5:1 during the final period of nitrogen deficiency, whilst the remaining phosphate was being used up. The complete removal of phosphate from sea waters where the N:P ratio is low can be explained on the basis of plant behaviour and one does not have to suppose a rapid regeneration of nitrate or the addition of atmospheric nitrate to explain the eventual loss of phosphate (cf. NIELSEN and JENSEN, 1957).

It is interesting to note the variability found week after week in nutrient-depth profiles, especially with silicate and nitrate. This is illustrated by Figure 2 in the case of silicate. Nitrate changes were similar but the variations of phosphate

were much less and, although probably significant, could scarcely be differentiated from analytical errors (Fig. 3). *In situ* plant growth cannot be responsible for the variations. At the observed rate of photosynthesis at Station "P" a month or more of phytoplankton growth, with no simultaneous remineralization, would be required to give the changes recorded from one week to another. The variation must be the result of the lateral changes of concentration that are encountered over a distance of only a few miles (see Table 3). The exact position of the ship could easily have differed by a mile or two from week to week. There would have been very little indication of different water masses from T/S curves or from oxygen and phosphate profiles, the three most commonly determined parameters on oceanographic stations, which draws attention to the desirability of using the silicate or nitrate content of surface waters to indicate their biotic origin.

The cause of the variations found near Station "P" is presumably in the past biotic history of two or more water-bodies situated near the ship. T/S variations were too small for these water-bodies to be considered as separate "water masses" in the currently accepted oceanographic sense and it seems necessary to use some such term as "biotic submass" to convey the necessary distinction. Such drastic changes in nutrient profiles over a few miles of sea, which we suspect characterizes much of the region and which cannot possibly have had a *recent* biotic cause, underline the dangers of applying the techniques of RILEY (e.g. RILEY, 1951) or STEELE (STEELE, 1956) for calculating primary production from nutrient and temperature profiles. In the vicinity of Ocean Weather Station "P" any results obtained by such an approach would have been completely misleading.

The amount of particulate organic material in the open ocean at 50°N, 145°W was unexpectedly large. The method of sampling removed all but a negligible quantity of whole zooplankters. The remaining organic matter, equivalent to some 100–200 mg C/m^3, was an appreciable fraction of the amount found for much of the year in Canadian coastal waters (unpublished results).

Nearly all the oceanic particulate matter was detrital (between 80 and 90%) and contained much protein, some carbohydrate and rather less lipid. A spot analysis showed very little chitin (about 2 mg/m^3). There were a considerable number of relatively long cellulose fibres present which could have accounted for much of the carbohydrate found in samples (see Table 2) and which were almost certainly of terrestrial origin. The total tonnage of disintegrated wood present in the Gulf of Alaska, if the amount of cellulose fibre at 50°N, 145°W is at all representative, would be truly enormous but it must be remembered that there are many thousands of miles of coastline surrounding the Gulf and the beaches are littered with dead wood to a degree which must be seen to be appreciated. The presence and stability of wood in ocean waters has been remarked upon by several authors (e.g. ATKINS, *et al.*, 1954; BRUUN, 1957; BARBER, *et al.*, 1959). A considerable amount of driftwood and kelp passed the ship during our patrol.

The detrital matter at Station "P"persisted to at least 1000 m and therefore constituted the bulk of potential food-stuff in this part of the ocean. It is unfortunate that we know so little about the availability of such particulate matter as a food for secondary producers.

The origin of the detritus (other than the cellulose) is open to some speculation. From its high protein content and appearance under a microscope one

may assume it to be largely of animal origin and some fragments of zooplankton could be recognized. Whether or not this detritus is endemic is not known, as we have no knowledge of the long-term stability of such material. Ocean currents in the top few hundred metres are such that coastal water could eventually reach the location of Station "P" from Asia or from the Canadian and Alaskan coasts but time factors are not known with any certainty.

In a north-to-south traverse (data shown in Table 3) the concentration of both detritus and plant cells change, both decreasing in the centre portion of the traverse where the water had a higher silicate content. This further underlines the presence of different water-bodies within a few miles of the ship's nominal position but the simultaneous decrease of both detritus and plants may have been fortuitous. In an east-to-west journey there was no such obvious relationship.

The maximum concentration of plant material, as indicated by pigments, occurred at around 75 m, at the very top of the halocline, and it is interesting to see that nitrite concentrations always had a marked maximum in the same region (cf. BRANDHORST, 1959), irrespective of the biotic submass of water as characterized by other nutrient profiles. It would appear as if nitrification processes are most active at a depth where there is an accumulation of relatively recent plant detritus; certainly the nitrite disappeared at depths where plant pigments were also absent.

The summer rate of primary productivity at Ocean Station "P", which in round numbers was 7 mg C/m^3/day near the surface or some 200 mg C/m^2/day for the entire euphotic zone, was of the order to be anticipated from the few other observations that have been made in the North Pacific. Values in the Pacific range from 1 mg C/m^3/day near the equator and in an area south of the Polar Front to some 50 mg C/m^3/day at a fertile area by the Aleutian Islands. The more productive parts of the subtropics and much of the northern ocean appear to have a productivity similar to that found during the present investigation (e.g. KING, *et al.*, 1957; NIELSEN and JENSEN, 1957; HOLMES, 1958).

Throughout our patrol the primary production was almost entirely from ultra-plankton that passed through the finest netting (cf. WOOD and DAVIS, 1956; NIELSEN and JENSEN, 1957) or even through a sintered-glass disc that filtered out cells larger than 10 microns. This provides yet further evidence, if further evidence were required, of the impracticability of plankton nets for quantitative work in oceanic waters, even in northern latitudes.

The productivity beneath unit area varied six-fold throughout the patrol but only about three-fold for most of the time. The variation was due mainly to differences in the concentration of plant cells in the euphotic zone and to differences in the distribution of these cells with depths. As with many other factors, major changes could best be attributed to the ship passing through various water bodies rather than to any great change within the same water mass. This is borne out by the observation that the rate of photosynthesis per unit concentration of chlorophyll *a* (at a standard light intensity) was fairly constant throughout the patrol (Table 5), especially when allowance is made for experimental errors in estimating chlorophyll. If the rate of photosynthesis were related to the sum of *all* plant pigments in an arbitrary mixed unit (CURRIE, 1958) the ratio was even less variable (Table 5).

In the culturing experiment the corresponding rate of photosynthesis per unit of pigment was a little higher than that found in nature. However this

difference is probably due to the population in the culture adjusting to a more uniform light intensity and a slightly higher temperature than that found in the euphotic zone.

After some seven to eight days the population in the polyethylene vat changed radically and a diatom began to predominate (this is shown very strikingly by the silicate curve in Figure 7 A) but for the first four to six days of growth the cells present were almost certainly major constituents of the initial population. There was no evidence of any sudden change of growth-rate during the initial period of culturing due to a "wall effect" and, in fact, there was a remarkably good approximation to steady exponential growth throughout the entire experiment if we allow for minor effects of solar radiation (Figure 5).

The amount of carbon in the culture doubled itself about once every 1·75 days although, as mentioned above, this rate would probably have been a little slower under more natural conditions. The doubling time found in nature, for the crop beneath a unit area of sea surface, was some four to five days (cf. the value of 4 days estimated by Nielsen and Jensen, 1957). This decrease of growth-rate is to be expected as the average illumination within the euphotic zone was much lower than that received by the culture. Even with a doubling rate of four to five days, however, the maximum variation of standing plant crop found throughout the entire six-week patrol could have occurred in one week of uninterrupted growth.

We thus have a situation of potentially "explosive" growth held in check by some mechanism that almost exactly balances the photosynthesis. Considering that much of the observed change of crop concentration during the patrol arose from the presence of different water-bodies, the constancy of standing crop is quite remarkable and "spot" analyses made before and since this patrol have indicated that the level throughout the year, even in December, is similar to that found in July and August. There is certainly no evidence of a phytoplankton "bloom"of the magnitude found in the culturing experiment which, in turn, was reminicent of the growth pattern observed in British Columbia coastal waters, where the nutrient and light levels are comparable to those at Station "P" and where the rate of photosynthesis per unit of plant pigment is also similar (cf. Currie, 1958).

If the population level is being held steady solely because plant cells are sinking from out of a 50–70 m euphotic zone, then a sinking rate of well over 10 m a day is required. No really satisfactory sinking rates have yet been determined in nature but a value of 10 m a day is at the upper limit of any suggested values and then only for tropical seas or for large phytoplankters (Allen, 1939; Riley, *et al.*, 1949; Steele, 1956; Nielsen with Andersen, 1957). A sinking rate of 10 m a day is most improbable for ultraplankters in cold northern waters (some of which we observed, experimentally to be positively phototactic) and it may be assumed with some confidence that sinking can only explain a small fraction of the inferred population loss.

The only other loss mechanism (ignoring natural mortality) is by grazing. This conclusion, namely that a low and relatively constant oceanic crop is the result of grazing, is not new and has been suggested by several workers (e. g. Nielsen and Jensen, 1957; Currie, 1958; Cushing, 1959). Most previous studies and theoretical treatments have been concerned with tropical oceans (in particular the Sargasso) where the nutrient levels are low and it has generally been assumed that some form of nutrient deficiency acts as the final control

preventing large population increases. Grazing has been thought of as the mechanism for levelling growth peaks and regenerating plant nutrients.

However, from the present work at Station "P" it appears that *grazing alone* must be largely responsible for keeping the population in check against a natural tendency to grow to some fifty times its observed concentration. Such a control is quite remarkable, even assuming a fairly constant population of herbivorous zooplankters with a lengthy reproductive cycle, and there is no obvious reasons why the standing crop of phytoplankton (and hence the whole biotic level) could not have been several times greater than was found.

Unless conditions at 50°N, 145°W are abnormal, and we have no reason to suppose this, it appears as if the low concentration of standing crop in this northern ocean is the result of constant overgrazing, whereas near the adjacent coasts, which have water of essentially the same fertility and illumination, the plant crop can increase to the maximum possible level by a "classical" cycle of blooming and grazing. If the explanation of this difference lies in the ecology of the grazing populations, the only obvious difference between the two environments lies in the water depth. In relatively shallow coastal areas creatures at higher biotic levels are dispersed in a depth of water which is comparable with the depth of the euphotic or the mixing layers. In the open ocean a complex vertical feeding pattern exists throughout a column which may be fifty or more times as deep as the euphotic layer.

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Summary

1. For a six-week period in July–August 1959, weekly measurements were made at Ocean Station "P" (50°N, 145°W) of all major nutrients, the standing crop of particulate organic matter and the *in situ* rate of phytoplankton photosynthesis. Two-hundred litres of water from the euphotic zone were freed from zooplankton and the endemic plant cells cultured under conditions comparable with those found at 10–20 m depth in the sea.

2. Particulate organic matter was present in surprisingly large amounts for an ocean area, equivalent to some 100–200 mg C/m^3 in the surface waters, and consisted mainly of detritus, persisting to a depth of many hundred of metres. The material was largely proteinaceous but about 40 mg/m^3 of carbohydrate (as glucose) were present, some of which is thought to be derived from disintegrated wood fibres of terrestrial origin. There was very little lipid (about 15 mg/m^3 as stearic acid) and only a trace (2 mg/m^3) of chitin.

3. Certain aspects of the nutrient analyses are discussed, in particular the N:P ratio. A distinct "patchiness" was found in the distribution of silicate, nitrate, and particulate matter in the euphotic zone over a lateral traverse of only a few miles. This presumably arises from the presence of "submasses" or fronts of waters of different biotic origin. The changes could not have resulted

from *in situ* productivity at the time of the patrol and they were not shown up very well by the more commonly measured profiles of phosphate, oxygen, or salinity.

4. The standing crop of phytoplankton was relatively constant throughout the six weeks (15–35 mg C/m^3) and the net photosynthetic productivity averaged at some 200 mg C/m^2/day, as measured by the radioactive carbon technique. Practically all the productivity was from organisms passing the finest plankton netting or even a coarse, sintered glass filter. Fair agreement was found between *in situ* productivity, measured in bottles suspended from a free-floating buoy, and the rates calculated from "incubator" results at a constant light intensity and a knowledge of the attenuation of light in the euphotic zone.

5. Neither nutrients, temperature, nor light were limiting growth factors. Left to itself the endemic crop from the ocean could bloom to fifty times its observed level before growth was arrested by nitrate depletion. The tight control of this "explosive" situation found in nature is considered to be the result of grazing and sinking, mainly the former. It is remarkable that such a stable condition is possible and that overgrazing should persist to such inefficient extremes whilst there is a large excess of nutrients still present.

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