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Seasonal Primary Production in Antarctic Sea Ice at McMurdo Sound in 1967[1]

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ABSTRACT

Between late June and early December 1967, observations were made at numerous stations in McMurdo Sound in the Antarctic. This paper, dealing primarily with Sts. A and H in the Hut Point region, provides some new physico-chemical data on the ice habitat as well as information on the development of microalgal populations in the sea ice, data on levels of chlorophyll *a* and particulate carbon, and results of periodic laboratory measurements of C^{14} fixation. Although heavy algal growth occurs within the ice, and notwithstanding marked adaptation to shade created mainly by snow, it appears that production is commonly limited by the amount of light available at the prevailing temperatures. Primary production in sea ice is unusual in that the algal material accumulates during the season of growth with little or no loss. Laboratory productivity data are compared with yields of plant material recovered from the brash ice layer.

Introduction. Interest in the microalgae of sea ice has had a long, if sporadic, history. In 1904, Gran described diatoms recovered from Arctic ice floes, and many years later his work was continued and extended by Usachev (1949), Appollonio (1961), and Meguro et al. (1966). English (1961) collected samples beneath the Arctic ice in 1958.

In the Antarctic, studies on microalgae in the lower layers of the sea ice or in the layer between the snow and sea ice have been performed by Meguro (1962), Hoshiai and Kato (1962), Bunt (1963, 1964a, 1964b, 1965, 1968a, 1968b), Bunt et al. (1966), Bunt and Wood (1963), Burkholder and Mandelli (1965a, 1965b), Buinitskii (1965), and Iizuka et al. (1966). Direct sampling of the Antarctic ice layer by SCUBA divers appears to have been reported only by Bunt (1963) and Andriashev (1968). Most of these studies have been isolated in time and space. Without exception, all of the above Antarctic investigations have been carried out in the middle to late summer.
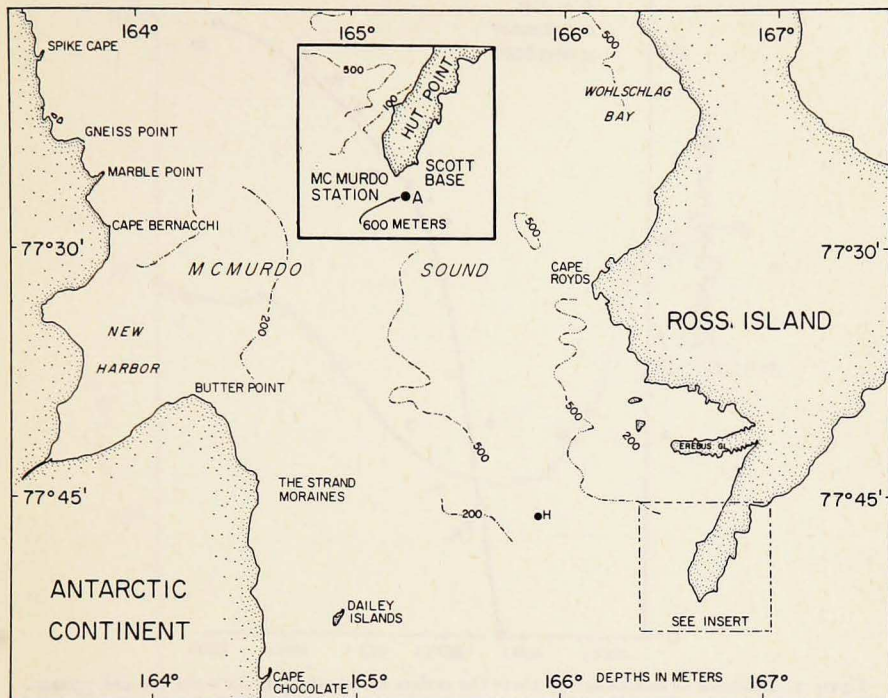
Figure 1. Station locations in McMurdo Sound.

This paper reports the appearance and growth of microalgae in the sea ice at selected stations in McMurdo Sound (Fig. 1) between late June and early December 1967; it also gives an account of the primary environmental influences to which the microalgae were exposed. Predictions of development, based on laboratory measurements of C^{14} fixation, have been compared with the observed increases in the standing stock at McMurdo Sound.

Methods. Access to the ice and its undersurface was achieved by means of ice houses (Tressler and Ommundsen 1962) and through open seal holes. In and beneath the ice, we carried out observations on the light penetration, temperature, salinity, pH, reactive phosphate, nitrate, nitrite, particulate carbon and nitrogen, algal population densities, photosynthetic pigments, and carbon fixation under standard conditions. The station locations are indicated in Fig. 1. The field and laboratory procedures and the raw data have been published (Bunt and Lee 1969). Technical information will be provided in this account only where it seems pertinent.

Plant production was measured in the laboratory using the C^{14} technique described by Strickland and Parsons (1965) and modifications to suit local con-
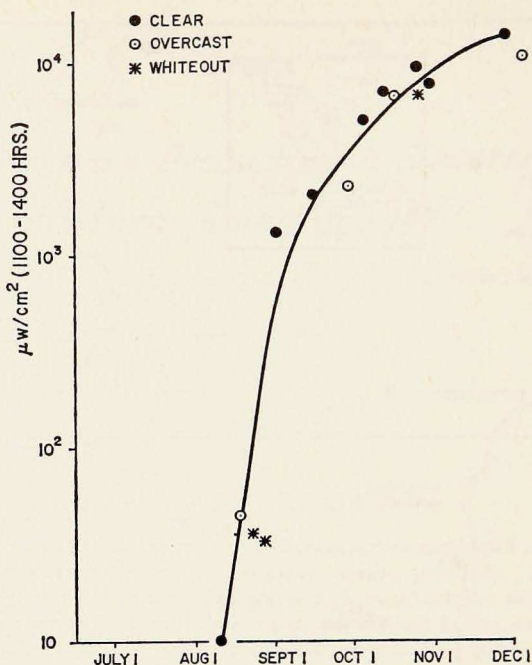
Figure 2. Incidence of radiant energy above the surface for wavelengths between 380 and 750 nm.

ditions. Reactive phosphates and carbons were also determined according to Strickland and Parsons (1965). Nitrates were estimated by the procedure of Grasshoff (1964), with additions recommended by E. F. Corcoran (personal communication). The technique of Holm-Hansen (1968) was used to determine particulate nitrogen. Material preserved during the study period has been forwarded to G. R. Hasle for taxonomic analysis.

The McMurdo Sound Sea Ice. In McMurdo Sound, the thickness of the sea ice varies considerably from year to year. In 1967, the ice was relatively thin. Because several ice breakouts occurred during the austral winter, one of which extended as far south as Hut Point, the thickness of the hard ice never exceeded 2.0 to 2.5 m, even at St. A (Fig. 1). The mean thickness from Cape Royds south to Hut Point was about 1.5 m. At St. A, along the shore and south of the line between the Dailey Islands and Hut Point, the snow cover was continuous throughout the season and was especially heavy in the vicinity of the ice houses. Toward the middle of McMurdo Sound, the snow cover was thin and, through November at least, much of the ice surface was bare. Beneath the hard ice, the thickness of the brash zone, where algae develop (Bunt 1963, Bunt and Lee 1969), varied from station to station and during the observation period.
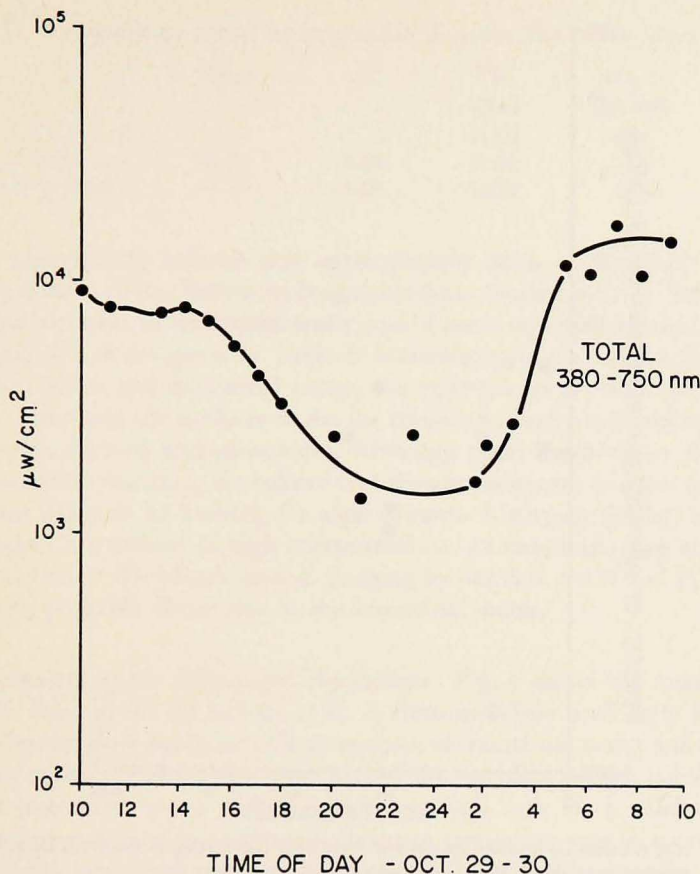
Figure 3. Diurnal variation in above-surface light intensity, October 29–30, 1967.

The brash zone consists of a layer of unconsolidated crystals and a labyrinth of interconnected small water pockets that are continuous with the brine of the hard ice above and the water column below; the brash zone is created by an accumulation of large ice crystals that separate from the super-cooled water column. Normally the crystals are held in loose aggregation only by their positive buoyancy. However, compression and fusion appear to take place at the interface of the brash and hard ice; and sometimes a partial fusion with the formation of a crust takes place between the brash ice and the water column. On a microscale, the physical and hydrological conditions within the brash layer must be complex, and practical considerations require simplification.

During the first dive on June 26, no brash crystals were seen at St. A, but during July the brash layer at St. A developed to a depth of 30 or 40 cm, and by approximately mid-October its maximum thickness was 2 m. At St. H, the
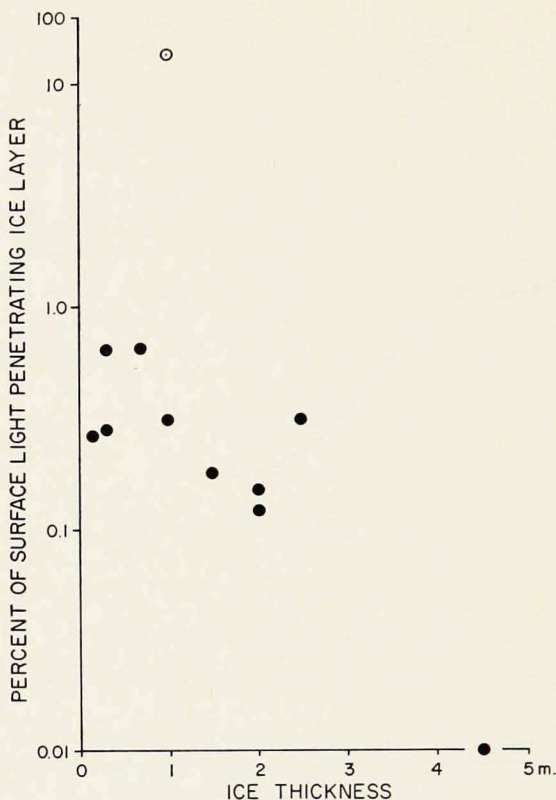
Figure 4. The relationship between ice thickness and light penetrating to the brash layer. Solid dots indicate snow cover. Open circle indicates no snow cover.

brash layer on November 4 was almost 1 m thick, but by November 20 it had been reduced to about 5 cm. Observations by divers suggest that, in some areas, the brash layer probably never became very thick during 1967. Measurements of incident light at the surface by spectroradiometer (ISCO, Inc., Lincoln, Nebraska; see Bunt and Lee 1969) first became feasible around August 10. Thereafter, the levels of incident light increased rapidly to peak values of almost $1.5 \times 10^4 \, \mu W/cm^2$ for wavelengths of 380 to 750 nm, as shown in Fig. 2. One set of readings, obtained on October 29–30 at hourly intervals for 24 hours, is shown in Fig. 3. The results of a limited number of measurements on light penetration into the brash layer, including several obtained early in 1968 in the Weddell Sea, are summarized in Fig. 4. Only one set of data, at St. H., was obtained from beneath ice that was free of snow. Wherever snow was present, less than 1 % of light incident at the surface penetrated to the brash layer.

Table I. Summary of mean hydrographic data for the brash layer at St. A.

	Temp.	pH	S (°/oo)	NO$_3$·N (μg at/l)	PO$_4$·P (μg at/l)
Ice.................	–	–	11.63	4.34	0.75
Interstitial water......	–1.75	8.03	31.89	7.07	2.16
Water at 5-m depth ..	–1.75	8.00	34.26	7.70	2.16

Our observations indicate that approximately 20% of the brash layer, by volume, consists of ice. Salient hydrographic data obtained at St. A from samples of melted brash ice, of interstitial water, and of water taken below the brash layer at a depth of 5 m are given in Table I. Notwithstanding an unavoidably crude separation of ice and interstitial water, the existence of gradients between the water column and the surfaces of the ice crystals is clearly reflected in the data for salinity, nitrates, and phosphates. Although these mean values do not disclose a seasonal variation, we believe that they are adequate to show that N and P are not likely to be limiting for algal growth. Littlepage (1965) has shown that silicates are present in high concentrations—in excess of 40 μg at/l—in the water column at McMurdo Sound. Judging by our data for N and P, high silicate levels probably occur also in the interstitial water.

Development of the Microalgal Populations. Fig. 5 shows the numerical increase in algae in the ice habitat at St. A from mid-July until early December 1967. Counts were made on cells in samples of interstitial water and of melted brash ice crystals. During the early part of the sampling period, 9-l aliquots of ice and interstitial water yielded scarcely enough cells for a valid count. In August, however, and in continuous darkness, the counts rose to approximately 10^5/l for the interstitial water and to 5×10^4/l for melted ice crystals. From the end of August through October, the populations remained more or less constant, but in November they increased sharply to $> 10^6$/l by early December. Regarding the increases observed between July and September in the interstitial water and melted ice, these may have been caused by algal cells in free suspension being carried upward on ice crystals formed following supercooling of part of the water column. Although we lack conclusive evidence of such a mechanism, we have observed debris being carried upward in the water column on fragments of anchor ice (Dayton et al. 1969) dislodged from the sea floor.

The Antarctic summer increase probably resulted from normal growth and cell division. Although the summer rise appears steep, growth constants (k) indicate a value between 1.5×10^{-3} and 3.8×10^{-3}; the calculations were made with the formula

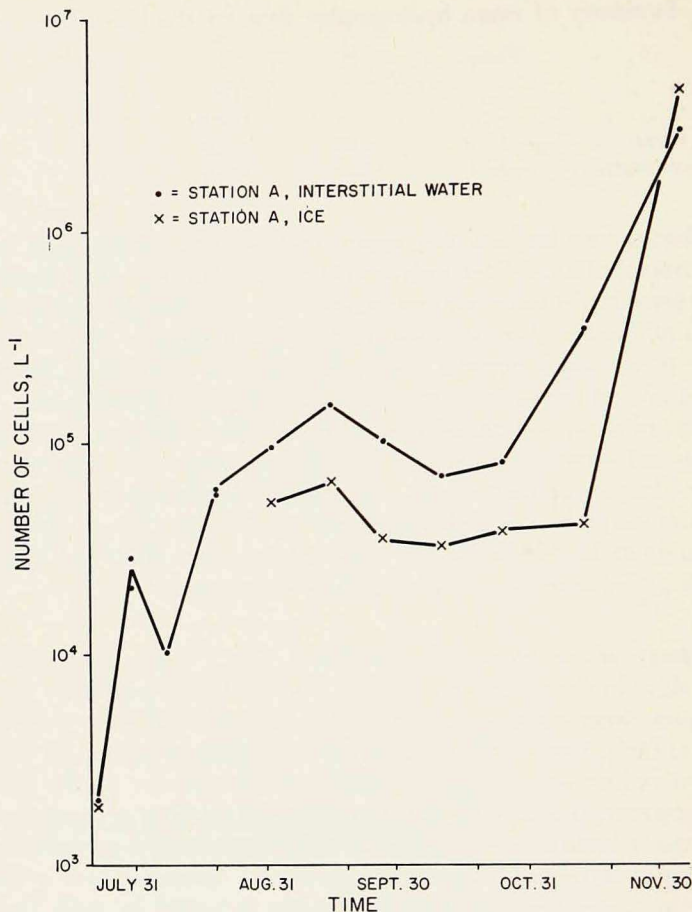$$k = \frac{\log_{10} n_2 - \log_{10} n_1}{t},$$

Figure 5. Changes in algal cell numbers with time in samples of interstitial water and melted brash ice at St. A.

where k = a growth constant, $\log_{10} n_2$ = the concentration of cells on December 4, $\log_{10} n_1$ the number on November 13, and t = the duration of the intervening period in hours. The above values are comparable to those obtained by Bunt (1968a) with pure cultures obtained previously from the same habitat and grown under conditions intended to simulate the temperature of the environment and the intensity of light, but not the quality of light. With pure cultures, however, k values as high as 21×10^{-3} can be obtained by culturing around 7.0°C, following adaptation to high light intensities.

Regular sampling at some stations during the Antarctic winter was not feasible. Data from survey dives made in November and December 1967 indicate that local variations in light intensity alone produce striking patchiness in
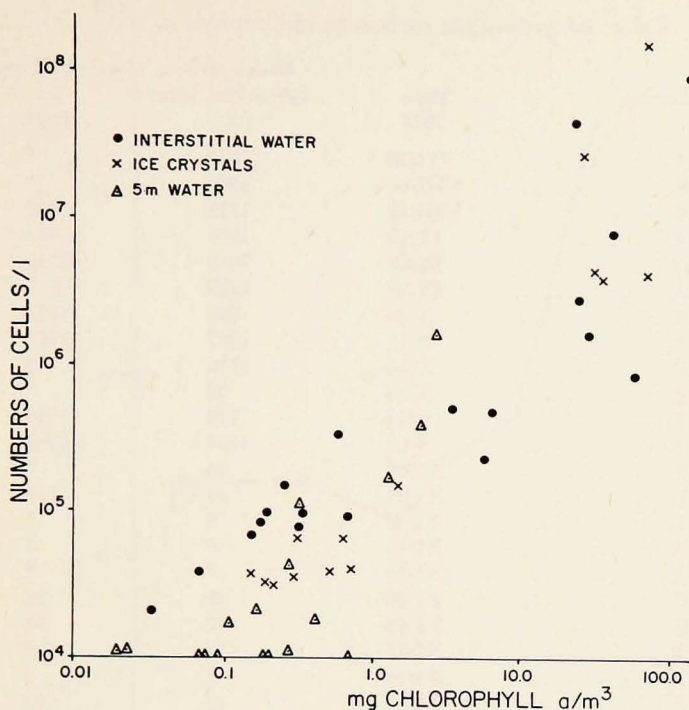
Figure 6. The relationship between algal cell numbers and concentrations of chlorophyll *a* in 5-m water, melted brash ice, and interstitial water.

growth. From below, the ice appeared yellow to dark brown in well-lit areas and blue in the poorly lit areas. At St. H on November 20, 1967, where the sea ice was bare of snow, algal cell densities were found to have reached $10^9/l$ in the brash ice.

Fig. 6 shows the relationship between cell numbers and chlorophyll *a* concentration. At algal concentrations between 10^4 and 10^5 cells/l, generally higher pigment concentrations per unit cell number were found in the 5-m populations of the water column and in algae closely associated with brash ice than in populations recovered from the interstitial water. We do not ascribe these differences to chance but cannot offer a satisfactory explanation.

Standing stocks of cell carbon in algal populations are commonly predicted from pigment determinations. Unfortunately, assumptions that must be based on the likely ratio of carbon:chlorophyll *a* have serious limitations. Bunt (1968a) reported that this ratio varied between 20 and 60 in the ice-diatom *Fragilaria sublinearis*, grown in the laboratory at − 2.0°C with light intensities up to 300 ft. cdles. Table II lists the ratio values based on samples collected in the field.

Table II. Ratios of particulate carbon to chlorophyll *a*.

Station	Date 1967	Ratios carbon: chlorophyll *a*/m3 Interstitial water (mg)	Ice (mg)
A..............	VII/30	13591	*
B..............	VIII/06	3500	*
B..............	VIII/12	1715	682
A..............	IX/15	988	927
B..............	IX/22	7019	3234
A..............	IX/27	1289	878
B..............	X/04	889	2703
A..............	X/11	1287	1321
C..............	X/16	1716	*
E..............	X/19	52	*
F..............	X/24	738	1146
A..............	X/25	1101	1266
E..............	XI/02	24	*
H..............	XI/04	29	116
I..............	XI/06	*	*
A..............	XI/13	*	*
A..............	XI/14	*	*
C..............	XI/18	45	52
K..............	XI/22	42	44
E..............	XI/27	59	*
H..............	XI/29	*	*
F..............	XI/30	45	43
A..............	XII/04	24	12

*Data not collected.

Many of these data might be suspect were it not for the fact that large and variable amounts of organic debris, especially in the Antarctic winter samples, were detected in microscopic examination. Even so, data for the period of major algal growth, from early November to early December, when there was relatively little debris, indicate considerable variation in the ratio; values over that period ranged from 24 to 59 in material recovered from interstitial water; these values are within the limits obtained for *Fragilaria sublinearis* (Bunt 1968a). Strickland and Parsons (1965) have indicated that values for the ratio in phytoplankton range generally between 20 and 70. Any estimation of the standing stocks of plant-cell carbon based on pigment data in ice-covered waters should be accepted with caution unless the estimates are based on good local values of the carbon-pigment ratio.

At or close to the peak of the growing season in November and December (allowing for a 4:1 ratio of interstitial water to ice), the total levels of organic carbon in the ice habitat ranged from 538 μg/l at the heavily shaded St. A to 10,415 μg/l at the well-illuminated St. H. With the brash ice layer approximately 2 m thick at St. A and 0.005 m thick at St. H, the 538 μg/l converts
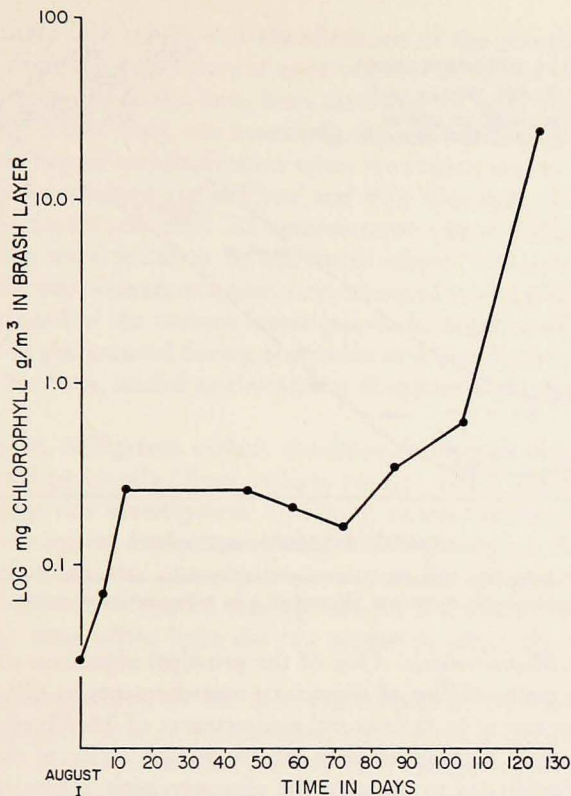
Figure 7. Changes in chlorophyll *a* concentrations in samples of interstitial water and melted ice from St. A.

to 1076 mg organic carbon/m², the 10,415 μg/l to 520 mg organic carbon/m². Since there was little detrital material in these samples and since losses from grazing were of little or no significance,[2] these values indicate the net annual 1967 production. Development of the stock at St. A, in terms of chlorophyll a/m³, is shown in Fig. 7. The standing stocks of the water column, perhaps with the exception of those in the upper few meters, may be discounted in the present discussion of production. Bunt (1964b, 1968b) has shown that this material is unlikely to be produced *in situ*. Where there was little evidence of nonliving organic material, the C/N ratios, with few exceptions, were narrow; 70% of the values that were < 4.0 during November and early December suggest that there is a high protein content in the ice flora.

2. Actually, some grazing may occur. While we did not recover zooplankters from the interior of the ice habitats, pteropods were observed swimming immediately beneath the ice during the winter. During November, we observed small fish with their heads up into the ice layer, apparently feeding. Amphipods were also seen at some locations. In the light of these observations, the biomass estimates should be taken as conservative.
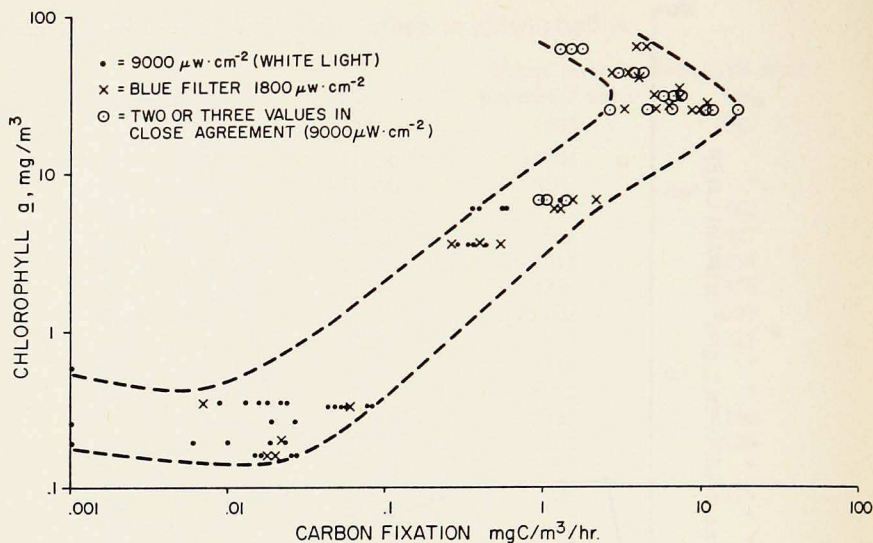
Figure 8. The relationship between laboratory measurements of carbon fixation in milligrams carbon/hour/cubic meter and chlorophyll *a* in milligrams/cubic meter.

Productivity Measuremeuts. One of the principal objectives of these studies was to test the compatibility of laboratory measurements of C¹⁴ fixation with algal growth occurring in the natural environment of McMurdo Sound. The following discussion pertains to only the interstitial water of the ice habitat. Although we had hoped to measure the photosynthetic activities of cells that are closely associated with ice crystals, an acceptable experimental method could not be devised. Therefore, it has been necessary to assume that the physiological responses of the flora retained with the ice crystals are similar to the responses of cells in the interstitial water. There is no reason to suppose that this assumption is seriously in error.

Fig. 8 shows the relationship obtained by plotting, on a log/log basis, milligrams carbon/hour/cubic meter against corresponding concentrations of chlorophyll *a*. Largely because of a superior light-bath and incubation-bottle design, the results have been more coherent than those already reported (Bunt 1964b). Nonetheless, scatter was still appreciable; this is attributed primarily to cell clumping and to a conscious effort by us to reveal the variability by running dark bottles in triplicate and then subtracting each "dark count" separately from counts of radioactivity in cells filtered from triplicate light bottles. Low population densities and low activities in September and October led to wide variations in data during that period. At the peak of the growth season, in November and December, mutual shading in the dense populations was suspected. An attempt was made on several occasions to avoid this difficulty by diluting the cell suspensions in Millipore-filtered interstitial water, but this practice led to

disproportionately low results and abandonment of the procedure. Complications arising from the suspension of pure cultures at altered densities in fresh or previously occupied media have been described by Bunt (1968a).

Note in Fig. 8 that there was essentially the same relationship between pigment level and rate of carbon fixation when incubation was carried out with a light intensity approaching 10^4 μW/cm² and with blue light (Corning 4303) at approximately 2×10^3 μW/cm². As demonstrated (Bunt 1964b), the populations in the ice were found to be extremely adapted to shade; their carbon-fixing activities were almost, or completely, saturated at 350 μW/cm², the lowest intensity employed in the current investigation. Retardation of activity, which was found to be pronounced during September and October at the highest light intensities in the bath, tended to diminish or disappear as the Antarctic summer advanced.

The quotient, milligrams carbon fixed/hour/milligram chlorophyll *a*, was low, as reported previously (Bunt 1964b, 1968a), and it did not remain constant throughout this investigation. In Fig. 9, values for the assimilation quotient are plotted against days, commencing with September 1. At 350 μW/cm², roughly 200 ft. cdles, the intensity was adequate for full saturation of photosynthetic activity where mutual shading was not a source of interference. Use of blue rather than white light did not appear to affect the rates of carbon fixation.

Notwithstanding scatter in the data, due in part to replication of the light and dark bottles, the rates of fixation/unit chlorophyll *a* increased from negligible levels to a maximum around 0.4 and then declined subsequently. Reduction of the data for the season indicates a mean maximum of 0.24 for the assimilation quotient and a mean minimum of 0.056 at light intensities adequate to saturate photosynthesis; in previous studies in McMurdo Sound, Bunt (1964) obtained a mean value of 0.07 for the assimilation quotient, and with light-adapted pure cultures, values as high as 1.2 (Bunt 1968a).

Discussion. The microalgal flora of the sea ice is likely to be of considerable importance in determining the magnitude of marine primary production in Antarctic waters (Bunt 1968b). There is a broader interest, however, in that this phenomenon offers what may be a unique opportunity to check the credibility of carbon fixation measurements against direct estimates of yield under natural conditions where grazing, sinking, and other losses may be almost negligible (at least in McMurdo Sound). Although we still lack sufficient data for a rigorous analysis, it is possible to make a projection based on a limited set of reasonable assumptions.

The final concentrations of plant-cell carbon at Sts. A and H were about 540 and 10,000 mg/m³, respectively. At St. A, the introduced standing stock of carbon in algal cells prior to the beginning of the photic period was 6.5 to 16.0 mg/m³; these figures are based on the most likely upper and lower limits
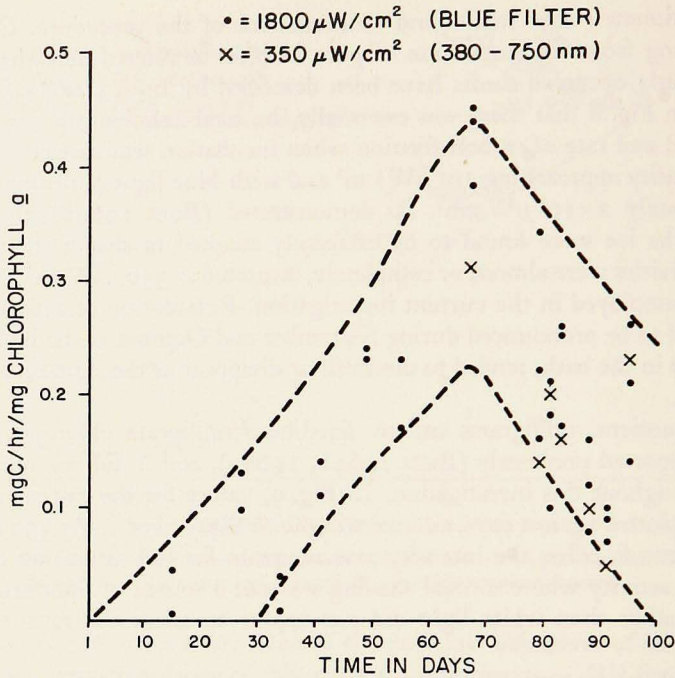
Figure 9. Variation and seasonal changes in the assimilation quotient, milligrams carbon/hour/milligram chlorophyll *a*.

for the ratio of carbon:chlorophyll *a*. Since the amount of plant-cell carbon present during the Antarctic winter could not be determined directly because of the presence of nonliving organic materials, it seems reasonable to assume limits for St. H. that are similar to those for St. A. Using the limits for cell carbon:chlorophyll *a* and for the mean seasonal assimilation quotient, from

$$k = \frac{2.303}{t_2 - t_1} \log \frac{C}{C_0}$$

we can calculate four possible values for the net specific growth rate of the crop, k, expressed in milligrams carbon/hour; in this equation, $t_2 - t_1 =$ the length of any growing period in hours, $C =$ the standing stock of cell carbon at t_2, and $C_0 =$ the standing stock of cell carbon at the start of the growth period, t_1. It is possible, then, to calculate the number of days required to produce, by exponential growth, the measured final yields of plant carbon; thus we obtain a range of values for k with the upper and lower limits set for C_0. Data so estimated are presented as a family of curves in Fig. 10.

Judging by our knowledge of the state of the ice surface and of the light incident at the surface and having some indication of the extent of light pene-

tration into the ice habitat, it is reasonable to believe that the photosynthetic capacity at St. H could have been fully saturated for at least 80 days. The appropriate curves in Fig. 10 indicate that, with $k = 0.0034–0.0040$, the observed yield could have been produced in 80 days. A value of $k = 0.0034$ corresponds to assimilation quotients (according to limits for the ratio of carbon:chlorophyll a) of 0.08 to 0.20; this is within the range obtained in the laboratory. We conclude that, at least under these conditions, the measurements of radiocarbon uptake in the laboratory are generally compatible with activity in the field.

For St. A the situation is complicated by the fact that the light intensities were not adequate to saturate photosynthesis. The mean light intensity within the ice layer was probably no higher than 6 to 10 $\mu W/cm^2$.

Figure 10. Relationship in September 1967 between the production constant, k, and the time in days required to obtain several stated levels of plant-carbon production. See text for details.

However, it is known from the chlorophyll data that growth to the level finally recorded on December 4 could not have occupied appreciably more than 60 days. Fig. 10 indicates that values of $k = 0.0026$ to 0.0030 would be required to achieve the observed development; $k = 0.0026$ is equivalent to assimilation quotients lying between 0.06 and 0.15. The lower value, 0.06, represents a 25% saturation of photosynthesis compared with a mean maximum assimilation quotient of 0.24. Judging by previous experience (Bunt 1964b, 1968a), this degree of shade adaptation is possible. However, in order to predict the yield for heavily shaded areas, the carbon uptake should be measured routinely at light levels that are low enough to establish the slope of the linear portion of the response curve of photosynthesis relative to light intensity. The lower limit, 350 $\mu W/cm^2$, in the current investigation is too high.

If a reliable prediction of the final yields of plant carbon in the ice habitat is to be achieved from laboratory measurements of carbon fixation, serious error must obviously be eliminated. It is essential, therefore, to obtain sound data on the ratio of cell carbon to chlorophyll a and its range of variation, to carry out adequate replication in both illuminated and dark-bottle controls, to check seasonal variations in the photosynthetic quotient, and to establish the rates of carbon fixation at low light intensities without extrapolation. Because of the sensitivity of the ice algae to temperature and light intensity at low levels, refined control of these parameters is critical.
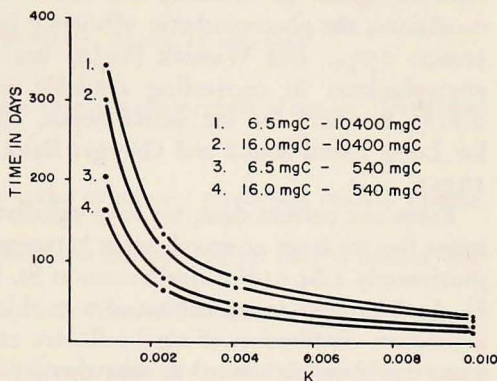
Over the years, there has been considerable interest in determining the efficiency of photosynthesis and the variations in efficiency relative to a given environment. Wassink (1959) has given values for agricultural crops, with efficiencies ranging between 0.5% and 2%. For sugarcane, Westlake (1963) has reported figures for efficiency that were as high as 3%. Under ideal laboratory conditions, the photosynthetic efficiency in algal cultures can be made to approach 25%. But Wassink (1959) has concluded that the efficiency of phytoplankton in converting available energy is probably no more than 0.11% annually for the world ocean. Riley has obtained efficiency values for Long Island Sound and Georges Bank that are close to 0.3% (Ketchum 1951).

From our current data, we have calculated that the total energy that penetrates the ice layer at wavelengths between 380 and 750 mm amounts to approximately 1.64×10^7 cal/m²/season at St. H and 0.012×10^7 cal/m²/season at St. A. Assuming an ice habitat of 2-m thickness at St. A on December 4 and a uniform distribution of algal cells, we estimate that there would be almost 1100 mg plant carbon/m² at that time; and assuming an ice habitat of 1-m thickness at St. H on November 4, there would be 4760 mg plant carbon/m². Westlake (1963) has indicated that there is at least 5000 cal/g organic matter in the microalgae, of which 50% is carbon. Using his figures, we calculated that the field efficiency of photosynthesis at St. A is approximately 9%, at St. H, approximately 0.3%.

The 9% value is remarkably high and deserves closer examination. It is widely held that, under ideal conditions, approximately 10 quanta must be absorbed by the photosynthetic apparatus to produce 1 molecule of oxygen. With this assumption and a photosynthetic quotient of 1.4, we estimate that, at St. A, approximately 1 molecule of oxygen evolved for every 30 incident quanta. Therefore, since the efficiency in utilizing absorbed quanta must have approached the ideal, it seems reasonable to conclude that light, not temperature, limited production at St. A. In areas typified by St. H, however, temperature must have been the limiting factor.

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