Primary Production in Dumbell Bay in the Arctic Ocean*

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Abstract

Photosynthesis, chlorophyll, inorganic nutrients, and related factors were measured throughout a productive season in a small coastal inlet of the Arctic Ocean. Significant production was confined to 5 m for a very limited time period because of both light and nutrient limitations. Maximum chlorophyll was 8.2 mg Chl a m^{-3} and maximum "gross" and "net" photosynthesis rates were 830 and 550 mg C m^{-2} d^{-1}. Annual "gross" and "net" photosynthesis is estimated at about 12 and 9 g C m^{-2} respectively. The effect of light stimulation on assimilation is described, sources of coastal zone nutrient enrichment are considered, and discrepancies between "gross" and "net" photosynthesis are discussed with reference to the growth characteristics of the phytoplankton population.

Introduction

During the International Geophysical Year (IGY) primary productivity was measured in the offshore, deep waters of the Beaufort Gyre of the Arctic Ocean from 2 drifting stations by the author (1959) and by English (1961). Both reports indicate that annual production is probably less than 1 g C m^{-2}. For comparison with that work the author spent a summer — June 13 to September 10, 1959 — in an effort to measure primary production and related environmental factors in a shallow, coastal area of the Arctic Ocean. It was anticipated that the inshore, coastal environment would be sufficiently different from the deep waters of the Arctic Ocean to offer interesting comparisons in environmental parameters or in the patterns and rates of phytoplanktonic activity and thereby warrant additional and detailed study.

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The sampling location was Dumbell Bay, a small inlet on the north coast of Ellesmere Island, the northernmost of the Canadian arctic islands (Fig. 1A). Its latitude is 82° 30' north, and it is within 40 miles (64 km) of the latitude of Cape Columbia, the northernmost point of North America. The bay opens into the Lincoln Sea, an open embayment of the Arctic Ocean.

In spite of some melting and opening of the ice to be expected along the shore at the height of summer, ice cover in those regions, even at the height of summer, is generally thick and extensive. Ships have rarely navigated that coast because of the difficulties presented by the sea-ice in the approaches to and along the coast.

The land rises steeply around Dumbell Bay; the weather station Alert is at an altitude of 250 feet (76 m) over Parr Inlet which opens into Dumbell Bay. A small river runs into Parr Inlet during the summer, draining the land north of Mt. Pullen, a 1650-foot (504 m) hill about 9 miles (13 km) south of Alert. During the period of snow-melt there is continuous, unconfined drainage into the bays along the shore.

The shores and hills in the vicinity of Dumbell Bay are, according to Blackadar (1954) "...argillaceous limestone, shale, slate, greywacke, quartzite, limestone, chert and calcareous sandstone of middle Silurian or earlier age". Bruggemann and Calder (1953) noted that "...the strata vary greatly in hardness and only the softer shales appear to disintegrate readily into stiff, fast-drying clays and silts".

Those steep shores are susceptible to erosion during the summer runoff, with significant influence, as will be pointed out, on light penetration and the phytoplankton productivity in the coastal waters.

Materials and Methods

The sampling site was in the inner half of Dumbell Bay (Fig. 1B) about one quarter mile (400 m) offshore and in a depth of 30 m. Water samples were collected
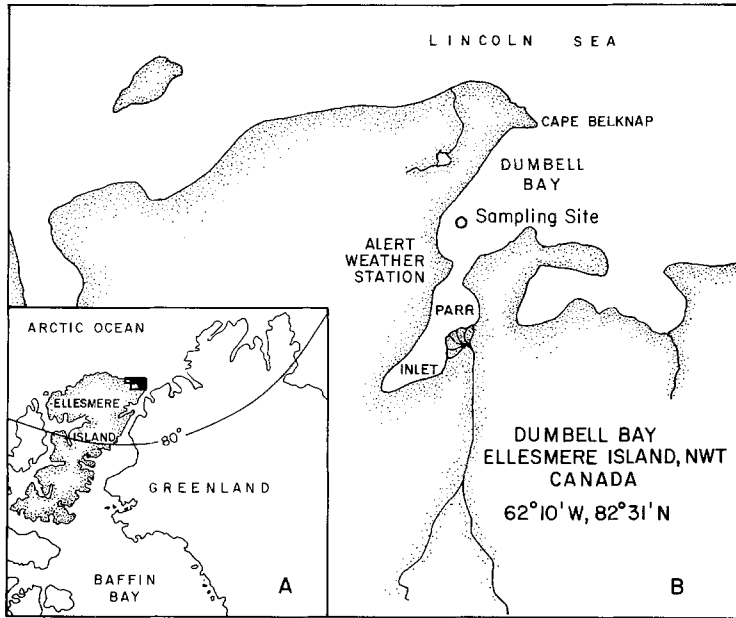
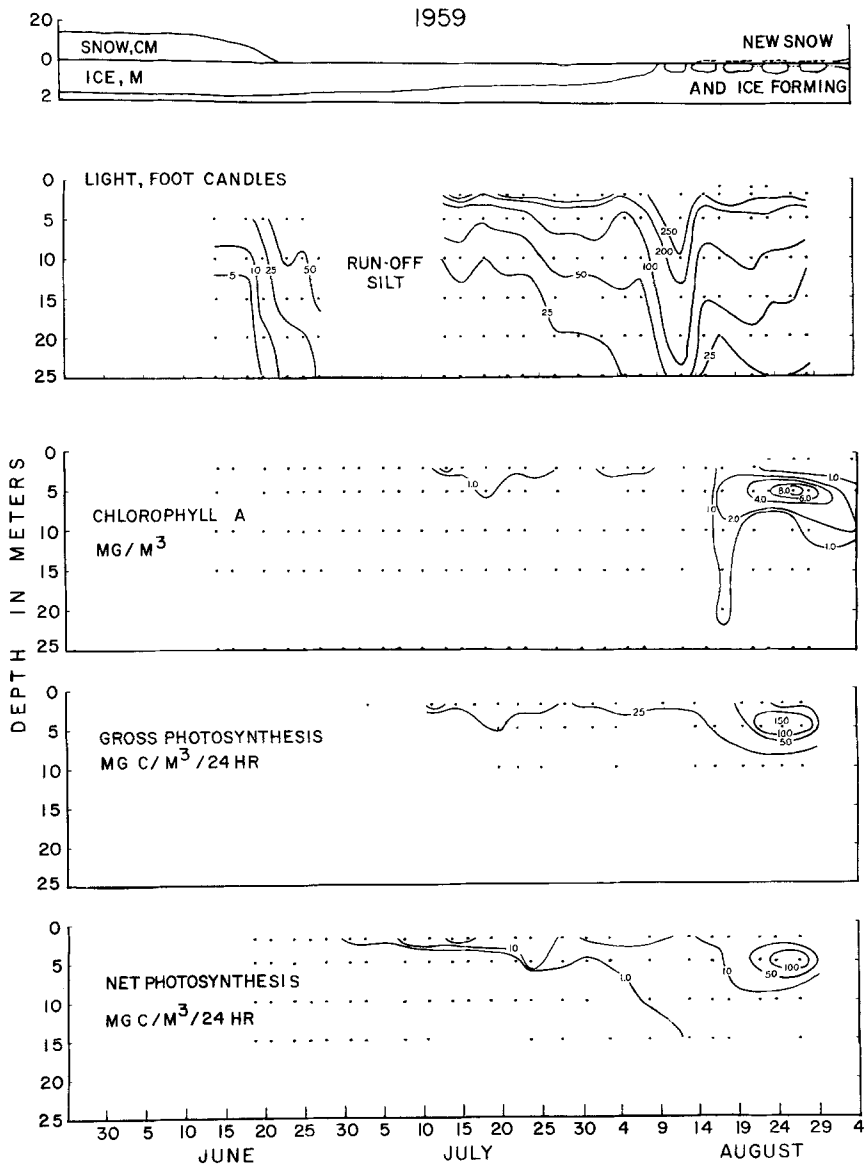Fig. 1. Map of Dumbell Bay, Ellesmere Island, NWT, Canada

Fig. 2. Seasonal and vertical changes in snow, ice, light, chlorophyll, photosynthesis, oxygen, and nutrients in Dumbell Bay
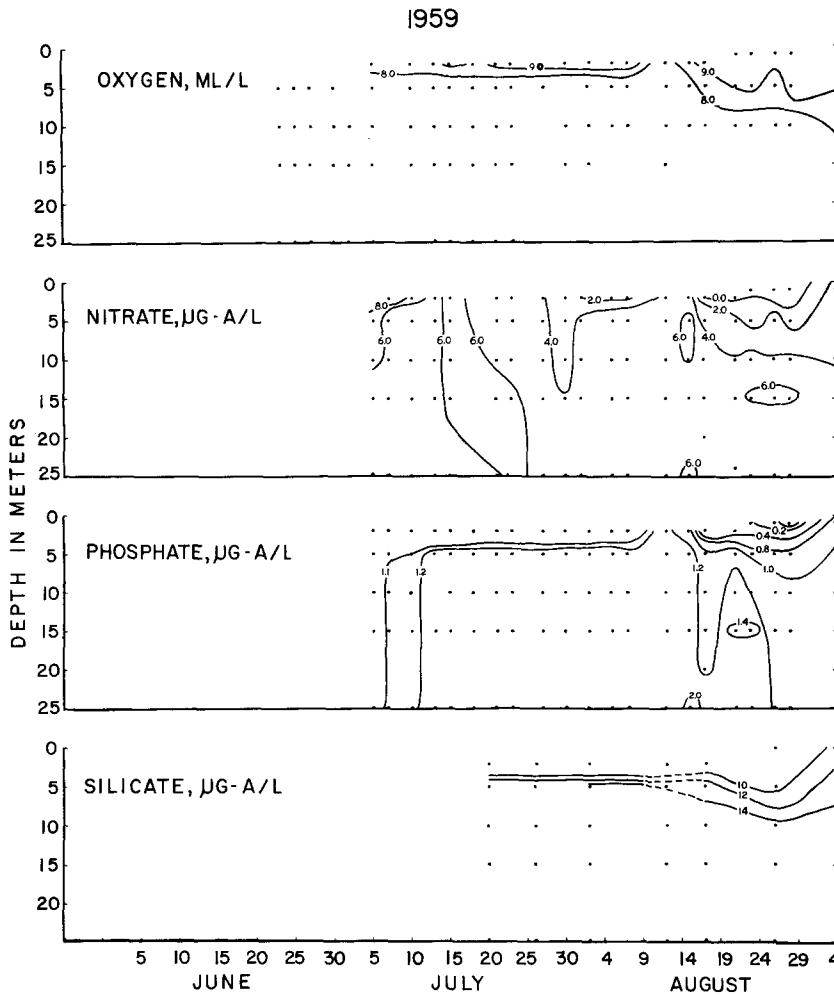
Fig. 2 (continued)

through a hole cut in the ice (covered when not actually in use) until August 7 when the ice became broken and partially dispersed. We then collected from a rowboat. Collections were made at 2 m just under the ice, or in late August at 1m, and at 5, 10, 15 and 25 m. Water samples were collected in a clear, all-plastic Van Dorn sampler and were carried to the laboratory in dark, brown, plastic bottles.

Chlorophyll was determined by the method of Richards with Thompson (1952), as modified by Creitz and Richards (1955), and the nomographs of Duxbury and Yentsch (1956).

Photosynthesis was measured by both the oxygen (gross photosynthesis) method, with Winkler titration, using a photoshynthetic quotient of 1.2 (Antia et al., 1963), and the C-14 (net photosynthesis) method (Steeman-Nielsen, 1952). The C-14 was prepared by, and the filter activities were counted at, the Woods Hole Oceanographic Institution. The C-14 had an activity of 5.4×10^6 CPM ml^{-1}. A "dark" bottle was suspended with each "light" bottle in the oxygen and C-14 measurements for corrections for respiration and for dark absorption of C-14. The oxygen bottles usually were suspended for 48 to 72 h, and the C-14 experiments ran for 24 h.

Nitrate was measured by the method of Mullin and Riley (1955), phosphate by the standard WHOI modification of the Harvey ammonium molybdate method, and silicate by that of Armstrong (1951). All optical densities were read with appropriate cells and filters on a Klett-Summerson colorimeter. Appropriate salt factors were applied to the data.

Light penetration was measured with a Whitney submarine photometer and a secchi disc, and temperatures were measured by direct thermometer readings in the water samples as soon as they reached the surface. Salinities were titrated at Alert.

Incident solar radiation was calculated, using the Alert meteorological records, from Mosby's equation (Sverdrup, 1953; Marshall, 1958) assuming a transparency factory (k) of 0.003.

A number of these analytical methods have been replaced, in the abundance of years since this endeavour, by more sensitive and more precise techniques. The general conclusions of this work are undoubtedly valid, nevertheless, because the magnitude of observed changes are large and consistent, and hardly subject to doubt nor dependent upon an analytical precision greater than that available at the time.
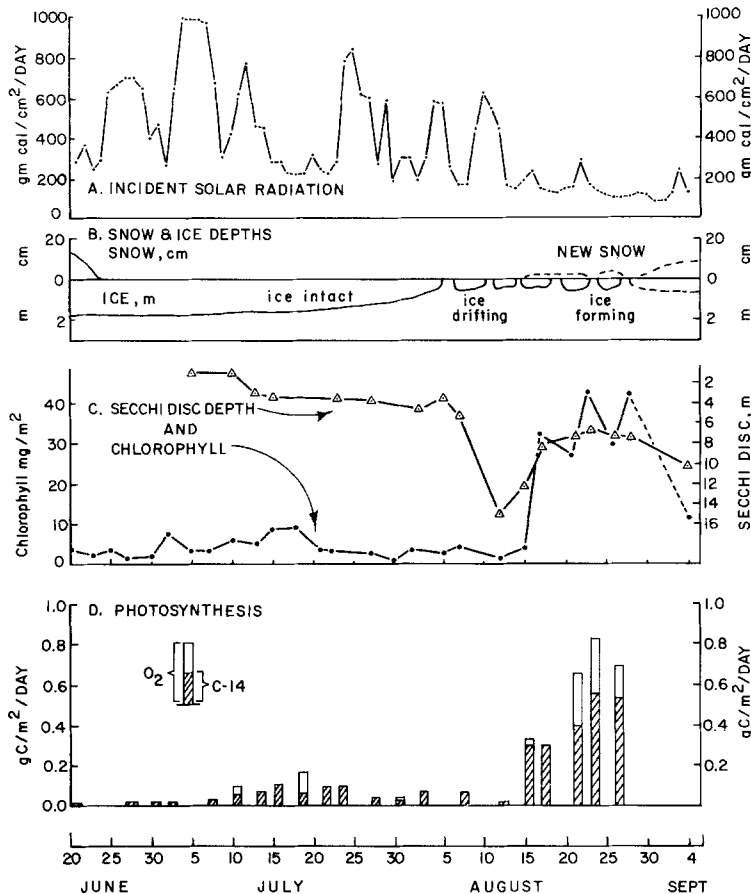
Fig. 3. Seasonal changes in solar radiation, snow and ice, secchi disc depths, chlorophyll, and photosynthesis in 1959 in Dumbell Bay. Chlorophyll and photosynthesis data represent integrated values from under the ice, or surface, to the bottom at 30 m (10 m on Sept. 4)

Climate

The climate of the area is severe. The mean temperatures for January through March are somewhat lower than $-25\,^{\circ}C$ and in the summer, June–August, the air temperature rarely exceeds $10\,^{\circ}C$. Continuous daylight prevails from March until the first sunset on September 5. Calculated incident solar radiation in 1959 is shown in Fig. 3. There are many foggy days in the summer, though the number is quite variable in different years. The summer is also the season of greatest cloud cover. July and August are the cloudiest months of the year, with 64 and 74% overcast skies ($\geqslant 8/10$ overcast). Annual precipitation does not usually exceed 12 cm and falls mostly as snow. Snow falls in all months and some rain may be expected in the summer. The summer is the windiest season but generally only light to fresh winds occur at that time. The summer of 1959 was relatively cold and calm, and this was reflected in the ice conditions which apparently were worse than usual.

Snow and Ice Conditions

The depths and the extent of snow and ice over Dumbell Bay in 1959 are summarized in Figs. 2 and 3.

No open water existed in the bay or beyond in mid-June, and about 15 cm of snow covered about 1.8 m of sea ice. Snow melt began in the third week of June, and from June 27 to July 5 the ice was covered by about 12 cm of slush and water. By mid-July the ice surface had drained but the ice was still about 1.2 to 1.5 m thick. A narrow, open lead appeared between the shore and the ice in late July.

Early in August the ice was broken, loose, and shifting with the tide, and an area of open water appeared in the middle of the bay. New ice formed frequently, but was broken up at the turn of the tide. Heavy polar sea ice lay scattered within the bay, and it was essentially continuous in the outer bay and in the Lincoln Sea beyond the bay. After August 12, new snow covered the land and ice, and after August 17 it was necessary to break 1 to 2 cm of ice each day to reach the sampling site. By September 1, new, soft, snowcovered ice, about 5 to 7 cm thick, covered the bay. This soft snow and ice cover, which effectively prohibited walking on the ice or boating over the water, prevented further sampling except close to shore on September 4 at a depth of 10 m. By that date the snow cover was more than 25 cm deep in some areas. The ice and snow would thereafter remain intact and increase in depth until the following summer.

Results

Temperature and salinity variations are briefly described below. The other data — chlorophyll, photosynthesis, light penetration, oxygen, nitrate, phosphate, and silicate — are summarized in Fig. 2. Only those sampling points that showed some measurable "oxygen" photosynthesis are included in the figure even though experiments with no detectable photosynthesis were made routinely at other standard depths. Incident solar radiation, snow and ice cover, secchi disc depths, and integrated chlorophyll and photosynthesis data are shown in Fig. 3.

Temperature and Salinity

Temperatures at 2 m just under the ice varied from +0.2 °C in late June to +1.9 °C in mid-July and 0.0 °C in late August. Salinities at 2 m varied from 14.9 °/$_{oo}$ S in late June to 1.8 °/$_{oo}$ S in mid-July and from 2.6 to 25.9 °/$_{oo}$ S through August. This layer was strongly and variably affected by run-off from the land and by melt of snow and sea ice.

Temperatures at 5 m and below varied between −1.7 °C in late June to −0.5 °C in mid-July and −1.5 °C in late August. Salinities at 5 m and below were between 31.2 and 32.5 °/$_{oo}$ S.

Oxygen

The chemical variations in the bay were quite simple. At 2 m oxygen concentrations were about 8.3 ml l^{-1}, increasing to 9.6 ml l^{-1} in mid and late August. At 5 to 25 m they were about 7.6 to 7.8 ml l^{-1} until mid and late August. The oxygen concentrations at 5 m then increased, reaching a maximum of 9.32 ml l^{-1} (110% saturation) on August 28. Decreases of oxygen were found at 1 and 5 m on September 4.

Nutrients

Nitrates were in the range of 5 to 6 µg A l^{-1} in late June through late July when there was a decline, briefly, to about 4 µg A l^{-1} in the upper 10 m. Substantial reductions in the upper 10 m and particularly in the upper 5 m were found after August 12, with exhaustion of nitrate near the surface (1 and 2 m) from August 17 through August 28 and depletion to 0.3 µg A l^{-1} at 5 m on August 28. Nitrate increased to 2.3 to 2.4 µg A l^{-1} at 1 and 5 m on September 4.

Phosphates were 1.1 to 1.3 µg A l^{-1} until mid-August when significant reductions were found at 5 m and particularly at 1 and 2 m. The minimum values were 0.0 µg A l^{-1} at 1 to 2 m and 0.9 µg A l^{-1} at 5 m, both on August 28. Phosphate increased to 0.9 and 1.1 µg A l^{-1} at 1 and 5 m on September 4.

Silicates, also, were quite uniform at 10 to 15 µg A l^{-1} from 2 to 25 m until late August when reductions were found in the upper 10 m and particularly the upper 5 m of the bay. The minimum values at 5 m were 7.4 and 9.8 µg A l^{-1} on August 12 and 26. Silicates increased on September 4 to 11.2 and 13.2 µgA l^{-1} at 1 and 5 m.

It is clear that these reductions of nutrients in the surface water (0-5 m) of Dumbell Bay in late August are not results of fresh water dilution by run-off from the land. At that late date new snow covered the area, new sea ice was forming, and run-off had ceased because of low air temperatures.

Chlorophyll

The nutrient changes coincide closely and inversely with the changes of chlorophyll at 1, 2 and 5 m through the summer. Some relatively low chlorophyll values of 1.1 to 1.3 mg m^{-3} were found at 2 m, just under the ice, in mid and late July and early August, but from August 15 through 26 chlorophyll increased dramatically (Figs. 3 and 6), at 5 m only, to 8.2 mg m^{-3}. By September 4, chlorophyll had decreased to 1.3 mg m^{-3} at 5 m.

Below 5 m, chlorophyll rarely reached or exceeded 0.5 mg m^{-3} throughout the sampling period, except on August 17 when 1.0 to 1.8 mg m^{-3} were found as deep as 25 m. Fig. 3 shows the near coincidence of that deeper development of chlorophyll with a brief period of deeper light penetration.

An estimate of the proportion of "net" plankton (i.e. those retained by No. 25 netting cloth, 0.064 mm aperture) in the total samples was attempted on 11 occasions during the season by measuring the chlorophyll content of water samples from 5 m after the water had been poured through netting. This estimate presumably measures the "nanno-plankton" of the sample. The difference between that and the whole sample estimates "net" plankton. The ratio of this estimate of netplankton to the whole-sample chlorophyll was measurable, because of sufficient quantities of chlorophyll, on 5 occasions and ranged from 48 to 100%, as follows: July 7, 71%; August 7, 100%; August 21, 55%; August 28, 70%; September 4, 48%. These estimates of "net" plankton average 69% of the whole sample.

Photosynthesis

At the time of this work published tables did not exist for the calculation of total CO_2 at temperatures below 0 °C or at the very low salinities observed at 2 m. Measurements of pH or alkalinity were not made for the calculation of total CO_2 for computation of C-14 data at 2 m. The C-14 data from 2 m shown in Figs. 3 and 4 therefore are over-estimates, calculated on the assumption of total CO_2 equivalent to that of normal sea water. The true values are likely to be less than these values. The overall estimates of productivity probably do not suffer greatly from these inaccuracies, however,

Table 1. Gross and net productivity at 2 m, and total daily production in Dumbell Bay, July 10 – August 12, 1959

Date	A		B	
	Photosynthesis at 2 m		Daily production	
	$mg\ C\ m^{-3}\ 24\ h^{-1}$		$mg\ C\ m^{-2}\ 24\ h^{-1}$	
	Gross	Net	Gross	Net
July 10	43	42.6	86	58
July 13	27	51.2	52	78
July 15	23	84.0	45	14
July 18	27	38.3	172	73
July 21	52	48.5	98	96
July 23	45	46.7	87	30
July 27	18	18.9	32	40
July 30	27	14.0	45	26
Aug. 2	37	48.6	64	70
Aug. 7	27	33.9	52	67
Aug. 12	23	4.2	40	21

Table 2. Estimates of production in Dumbell Bay and the Arctic Ocean

Method	Dumbell Bay $g\ C\ m^{-2}\ yr^{-1}$	Ice Island T3 $g\ C\ m^{-2}\ yr^{-1}$
O_2	12.3	–
C-14	9.6	< 1.0
NO_3-N	2.9	–
PO_4-P	5.8	–

for two reasons: 1) because in July and early August the oxygen photosynthesis estimates at 2 m (Table 1A) are quite comparable to the C-14 data, and 2) because in late August the large C-14 values, contributing most to total annual production, occurred in high salinity water at 5 m and therefore are probably accurate.

Low levels of photosynthesis (4–80 mg C m^{-3} d^{-1}) were detected by the oxygen (average 32 mg C m^{-3} d^{-1}) and C-14 (average 39 mg C m^{-3} d^{-1}) methods at 2 m from mid-July through mid-August (Table 1A). Photosynthesis was detectable at 5, 10 and 15 m by the C-14 method from late June to mid-August, but the values were usually in the very low range of 0.1 to 1.5 mg C m^{-3} d^{-1}.

Both methods showed increased photosynthesis at 5 m in late August, the oxygen and C-14 methods giving maxima of 158 and 110 mg C m^{-3} d^{-1}, respectively, at 5 m on August 23 and 24 (Fig. 2). Somewhat lesser amounts were found on August 27 and 28 at 5 m. Measurements of *in situ* photosynthesis could not be made after those dates because of gales, drifting ice, and slush ice covering the bay.

Because there were significant increases of nitrate, phosphate, and silicate at 1, 5 and 10 m on September 4, and significant decreases in solar radiation and in dissolved oxygen and chlorophyll, as well as assumed low light penetration through new snow and ice, it is reasonable to conclude that photosynthesis was very low or negligible after August 28.

Daily and Seasonal Production

The estimates of photosynthesis by the oxygen and C-14 methods were graphically integrated to obtain estimates of total daily production per m^2. The values of gross and net production (mg m^{-2} d^{-1}) from July 10 to August 12 are listed in Table 1B to point out the relative degree of correspondence between the 2 esti-

mates at low photosynthetic rates in Dumbell Bay. The maximum observed values were 830 and 550 mg C m^{-2}, respectively, on August 23 and 24. The daily total production estimates were then plotted as in Fig. 3, and the total seasonal production was estimated by graphic integration, assuming that production before June 25 and after August 28 was negligible. These estimates from the oxygen and C-14 methods were 12.3 and 9.6 g C m^{-2}, respectively.

The depletion of nitrate and phosphate in the upper 5 meters of the bay in the 12 d period, August 15–28, also may be used as independent estimates of net production. While it is recognized that nitrate is not the preferred form of nitrogen for many algae, in this high-arctic environment it may be the only readily-available form. Certainly, after the months-long, dark arctic winter, one would expect all nitrogen in the biological spring to be in the fully-oxidized form. Further, one would not expect rapid recycling and immediate availability of significant amounts of reduced nitrogen because of 1) the very low temperatures prevailing during the short period of phytoplankton activity, 2) the characteristic lag in these latitudes of zooplankton increase, grazing and metabolism after the phytoplankton production, and 3) because a large fraction of the phytoplankton is not re-cycled *in situ* at all, but instead sinks rapidly out of the near-surface waters (Fig. 6; see also Burkholder and Mandelli, 1965, for visual verification of rapid sinking of phytoplankton in Antarctic waters.) These are not circumstances that would be expected to contribute significantly to *in situ* re-cycling of nitrate to preferred forms of nitrogen. Therefore, under these special arctic conditions, the depletion of nitrate may roughly reflect the magnitude of primary productivity even though it could not be expected to do so in temperate waters.

The total depletions of nitrate and of phosphate per m^2 from August 15 to August 28 were calculated by graphic integration. These quantities were then converted to organically combined carbon using the ratios, by weight, of C:N:P::40:7:1 (Strickland, 1960). These estimates of carbon production were 2.9 and 5.8 g C m^{-2}, respectively. All estimates by the 4 methods (O_2, C-14, nitrate and phosphate depletions) for carbon production in Dumbell Bay and the offshore waters of the Arctic Ocean are summarized in Table 2.

It may be assumed that gross production in Dumbell Bay is about 11 g C m^{-2} yr^{-1}, and that net production is in the range of 6 to 9 g C m^{-2} yr^{-1}.

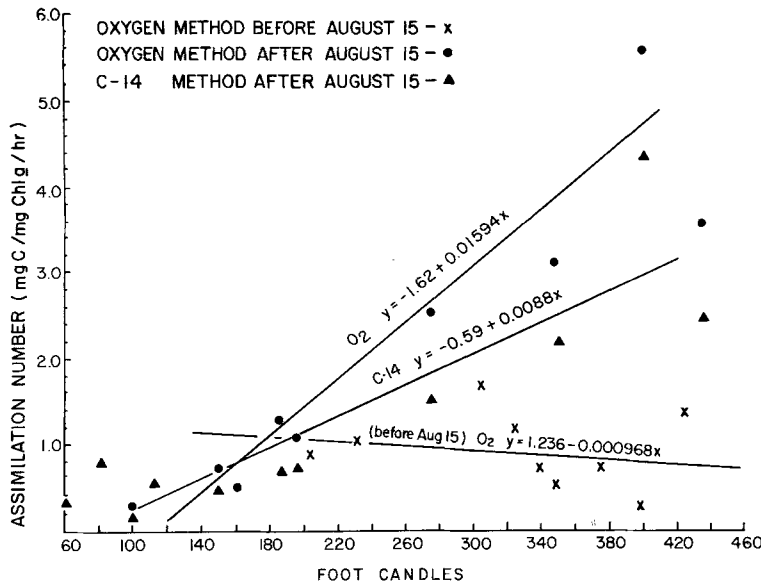Fig. 4. Assimilation numbers (mg C mg Chl a^{-1} h^{-1}) plotted against light intensity in Dumbell Bay prior to August 15 (oxygen method), and from August 15 to August 28 (oxygen and C-14 methods). C-14 and O_2 points on a particular intensity are paired values for a particular depth and time period

In the only comparable published study from arctic waters, McLaren (1969) found initial nutrient concentrations in meromictic Ogac Lake, Baffin Island, similar to those in Dumbell Bay. He estimated an annual net (C-14) production of 12 g C m^{-2} in the lake, concluding that production was limited by nitrate available at the beginning of the season. Similar nutrient-productivity relations exist in these two, small, high-arctic embayments.

Assimilation Numbers

Assimilation numbers (mg C mg Chl a^{-1} h^{-1}) for the "oxygen" and C-14 methods are plotted against light intensities in Fig. 4. For the period prior to August 15 only data from the "oxygen" method are shown because of the uncertainty of the C-14 data from the low salinities at 2 m where most measurable net photosynthesis occurred. The "oxygen" assimilation numbers prior to August 15 are distinguished in the figure from those of August 15 through 28. The first period was one of low chlorophyll and low photosynthesis, and the second period was one of maximum chlorophyll synthesis and photosynthetic production. The point of distinction follows the greater light penetration on and greater intensities after August 12-14 (Fig. 2).

Fig. 4 shows that in the first period assimilation numbers were generally $\leqslant$ regardless of light intensity. Following light simulation on August 12-14, however, both methods show higher assimilation numbers linearly related to light intensities. The slope for the "oxygen" method is greater than that for the C-14 method, as would be expected.

Discussion

The annual production of the Arctic Ocean, at least in the Beaufort Gyre on the Canadian - Alaskan side, is very low, probably less than 1 g C m^{-2} yr^{-1}. Both Apollonio (1959) and English (1961) attribute this low production to reduced light penetration by the heavy, thick, and nearly continuous ice cover. The nutrient concentrations in the surface waters of the Arctic Ocean in that area are not large, however. Kusunoki (1962, Fig. 2) summarized nutrient data from Ice Island T-3 (IGY Drifting Station Bravo) taken from 1957 to 1962. Kinney et al. (1970) presented more recent and more detailed data from T-3, which agree with those of Kusunoki. The values of nitrate, for example, reported by Kinney et al. from the upper 50 m were about 1 μg A l^{-1}. It seems clear that available nitrate would limit productivity to rather low levels even if low light intensities did not.

The observed chlorophyll and photosynthesis values in Dumbell Bay are high relative to those that might be expected on the basis of the available nitrate in the offshore surface waters of the Beaufort Gyre of the Arctic Ocean. In fact all the salinity and nutrient values in early summer, prior to biological utilization in Dumbell Bay, are substantially higher, and the oxygen concentrations are lower, than those summarized by Kusunoki (1962) and Kinney et al. (1970). The higher nutrient concentrations in Dumbell Bay support higher productivity than appears possible offshore in the Beaufort Gyre of the Arctic Ocean.

The higher salinities and nutrients and the lower oxygens in the spring in Dumbell Bay may be related to the source of Lincoln Sea water, of which Dumbell Bay is a part, and perhaps also to the local submarine topography as shown in Fig. 5. Arctic Ocean water moves south through Robeson Channel and Nares Strait (Bailey, 1956; Dunbar et al., 1967; Sadler 1976) within 25 miles (40 km) of Dumbell Bay (Fig. 5). In discussing the source of water in the Arctic Ocean that flows southward through Robeson Channel, Dunbar et al. (1967) "...found evidence of contributions of both Beaufort
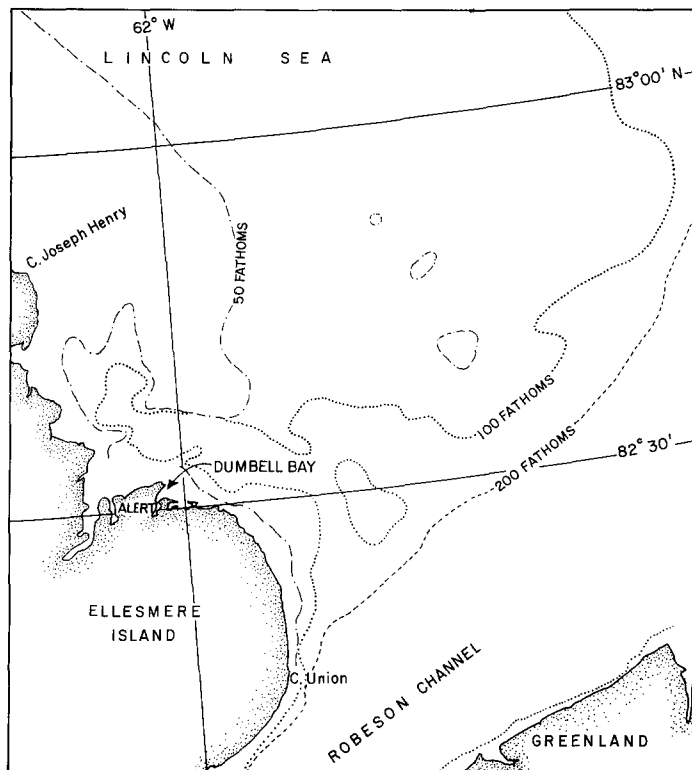
Fig. 5. The bathymetry of the Lincoln Sea and Robeson Channel, showing a deep trough in the vicinity of Dumbell Bay (from Chart No. 7072, "Kane Basin to Lincoln Sea", Canadian Hydrographic Service)

Gyre water and Eurasian surface water and this may be expected to extend into the Lincoln Sea source area north of Nares Strait". They noted also that the relative contributions of water from the Beaufort Gyre and of Eurasian surface water to the Lincoln Sea may be variable. Further analysis by Muench (1971) showed that Lincoln Sea water above 100 m appears to be derived from the near-surface layer of the Eurasian Basin.

It appears that the surface waters of the Eurasian side of the Arctic Ocean have nutrient concentrations higher than those observed in the Beaufort Gyre side. Published nutrient data from the Eurasian side are scarce, but Kawamura (1967) reported phosphate and silicate values at 10 m in the Eurasian Basin that are more comparable to those in Dumbell Bay than to those in the Arctic Ocean surface water in the Beaufort Gyre. Rusanov (1974) also described higher silicate concentrations at the surface on the Eurasian side.

Unpublished nutrient data taken from ice station "Arlis II", drifting in the Eurasian Basin from near the North Pole into the East Greenland Current, were obtained from the National Oceanographic Data Center. No nitrate data appear in those records, but the concentrations of phosphate and silicate appear significantly higher than those found from T-3 in the Beaufort Gyre, and they are comparable to those found in Dumbell Bay in the spring.

The nutrient content of the surface water of the Lincoln Sea (including Dumbell Bay), therefore, would appear to be higher than the normal nutrient levels of

the Beaufort Gyre of the Arctic Ocean because the Lincoln Sea is in large part derived from waters of higher nutrient content from the Eurasian side of the ocean.

In addition, because of geographic and bathymetric constrictions, surface waters off Dumbell Bay are further enriched by vertical mixing of subsurface waters of higher nutrient content, as follows:

Lincoln Sea water flows southward into the constriction of Robeson Channel. At depths greater than 100 m these waters are relatively rich in nutrients (Kinney et al., 1970). Some of this water, to depths of 400 m, would be diverted to, or tend to swing to the right of its flow, into the deep trough (not known to exist in 1959) that lies within 10 km of the sampling site in Dumbell Bay (Fig. 5). The trough terminates in rapidly-shoaling bottom about 20 km west of Dumbell Bay. One would therefore expect vertical movement of the westerly-flowing water as it encounters the shoal bottom at the end of the trough, resulting in the observed enrichment of nutrients in the surface waters off Dumbell Bay. Dunbar et al. (1967) noted that, "It may be expected that the water movement onto the continental shelf and into the bathymetric control of Nares Strait would result in some degree of turbulence with an attendant vertical mixing..."

The relative importance of vertical movements enriching surface water off Dumbell Bay is suggested by higher salinities in the surface and near-surface (0-50 m) waters found in this work in 1959 and by Seibert (1968), compared with those found from drifting stations offshore. Seibert's data are consistently higher than

$32.2\,^{\circ}/_{oo}$ S at depths of 10 to 50 m and most of his data are $>32.4\,^{\circ}/_{oo}$ S, compared to salinities from 30.9 to about $32.0\,^{\circ}/_{oo}$ S from comparable depths from "Arlis II". Further, Seibert's data show progressively increasing near-surface salinities in a series of stations running from the deep channel of the Lincoln Sea and Robeson Channel westerly into the "Dumbell" trough north of Dumbell Bay.

These facts suggest that the relatively high productivity observed in Dumbell Bay is due to special circumstances of nutrient enrichment associated with both the hydrography and bathymetry of the Lincoln Sea and Robeson Channel, and that productivity would perhaps be less on the Arctic Ocean coastal fringe of the Canadian Arctic Archipelago west of Cape Columbia, Ellesmere Island.

The timing of the main phytoplankton growth in Dumbell Bay is quite distinct from that observed in other arctic locations. This unique timing is emphasized by the sequential relation of the main bloom to the development of a small but sustained "halocline" concentration of chlorophyll, which is probably typical of other arctic locations, but reported only once previously. This timing and sequence is discussed, as follows.

From mid-July until mid-August in Dumbell Bay, prior to the main phytoplankton bloom, there was a persistent chlorophyll concentration of 1.1 to 2.3 mg m^{-3} located at 2 m just under the ice, at the depth of a halocline to be expected under those conditions. In meromictic Ogac Lake, in Frobisher Bay, Baffin Island, McLaren (1969) found a very similar, sustained, chlorophyll concentration (1.0 to 2.0 mg m^{-3}) in the halocline at 2 to 3 m, persisting from early July until mid or late August. This small chlorophyll concentration in Ogac Lake occurred for several weeks "after" the principle plankton bloom which developed in somewhat deeper water in late June.

Digby (1953) in East Greenland, and Bursa (1961) in the central Canadian Arctic, also found the main flowering of plankton to occur in late June or early July, as melting snow and wasting ice permitted increased light penetration.

Apollonio (1959), English (1961) and Kawamura (1967) found in the Arctic Ocean that phytoplankton production occurred in late June and early or mid July as surface snow melted and permitted greater light penetration through sea ice.

It is striking that in Dumbell Bay the abrupt and vigorous plankton bloom developed not in late June, as in other areas, but late in August, after incident radiation had declined to quite low levels, generally less than 200 g cal cm^{-2} 24 h^{-1}, and when new snow covered the freezing surface of the sea.

The relation between incident radiation, snow and ice cover, run-off, and light penetration (Figs. 2 and 3) is the probable cause of the unusual seasonal sequence of plankton production in Dumbell Bay. The melt and disappearance of snow from the sea ice occurred close to mid-summer's day, but the ice remained near its maximum thickness of 1.8 m until the second week of July.

Although maximum incident radiation occurred then, the amount penetrating through the ice and into the coastal water was low. Transparency was greatly reduced by run-off silt following the snow melt from the steep shores (Fig. 2). Much of the silt had disappeared by July 10 and, in fact, a minor chlorophyll and photosynthesis maximum, confined to 2 m, is evident (Fig. 3) on July 10-25. This plankton activity declined in late July and early August as light penetration remained low.

The still-thick ice broke into separate and partially drifting flows by August 6-7. Relatively high incident radiation on August 10-12, combined with clear water (secchi disc depth of 15.5 m; Fig. 3), permitted notably higher light penetration into the bay (Fig. 2). This higher radiation was a brief phenomenon since low incident radiation values prevailed from August 14 for the rest of the period, and new, snow-covered, ice formed regularly from August 15 on. The increased light penetration on August 10-12 reached an intensity of 375 f.c. at 5 m and 200 f.c. at 10 m. The higher intensities were sufficient to stimulate chlorophyll synthesis from 3 to 4 mg m^{-2} to about 30 to 35 mg m^{-2} within 48 h, with accompanying high photosynthetic values. Steeman-Nielsen and Jorgensen (1968) reported that phytoplankton require up to 2 d to become fully adapted to high light intensities, a period of adjustment comparable to that observed in Dumbell Bay. It was in this period that assimilation numbers assumed a positive correlation with light intensities. The correlations of Fig. 4 are reminiscent of the experimental data of Steeman-Nielsen and Jorgensen (1968). Their Fig. 2 shows that algae grown at higher light intensities exhibit proportionately higher assimilation numbers at sub-optimal and at saturation intensities.

During the brief period of intense chlorophyll synthesis following that light stimulation in Dumbell Bay, the C-14 and O$_2$ photosynthesis measurements were almost identical (about 290 to 330 mg C m^{-2} d^{-1}), but after the chlorophyll biomass had reached its maximum concentration there were significant differences between the 2 measurements (Fig. 3). These discrepancies probably reflect the changing physiology of the phytoplankton. In seeking explanations of such large discrepancies, Eppley and Sloan (1965) found that the sum of particulate carbon formation (net production), respiration, and excretion approximated gross photosynthesis, and they suggested that excretion could account for much of the discrepancies between net and gross photosynthesis. In contrast to Antia et al. (1963), they suggest that high excretion is more characteristic of declining populations rather than those in vigorous growth. Excretion, they concluded, is inversely proportional to physiological activity and in diatoms it is related to low P/R values, to low assimilation numbers, and to declining growth rates.

Ignatiades and Fogg (1973) found relatively low rates of excretion during log growth in culture, and increasing percentages of excretion during stationary growth phase and with nutrient deficiency. Similarly, Berman and Holm-Hansen (1974) found, in actively growing cultures
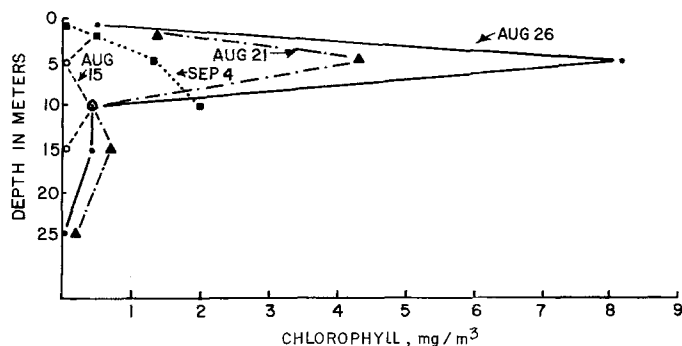
Fig. 6. Variations of chlorophyll concentrations in Dumbell Bay, August 14 - Sept. 4, 1959

and in natural plankton populations, that the percentages of extracellular releases of photosynthetic products were low (< 10%), but the percentages increased (8 to 39%) in flasks of stationary phase cells.

These experimental observations agree with the characteristics of the natural phytoplankton population found in Dumbell Bay. Between August 26-28 and September 4 the phytoplankton population sank from its point of abundance at 5 m (Fig. 6). Such sinking is considered (Steele and Yentsch, 1960; Strickland, 1965) a characteristic of a nutrient-deficient population. In fact nitrate was substantially reduced at 5 m, the depth of maximum phytoplankton growth, but it was not completely exhausted and a small concentration (0.2 μg A l^{-1}) was still measurable at the depth and time of maximum phytoplankton growth.

The characteristics of the phytoplankton in Dumbell Bay in late August (stationary growth phase, nutrient depletion, sinking) appear to conform to those associated with relatively high rates of excretion of photosynthetic products (Eppley and Sloan, 1965; Ignatiades and Fogg, 1973; Berman and Holm-Hansen, 1974) thereby accounting for the differences observed in the rates of gross and net photosynthesis.

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