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Aquatic primary production in the Antarctic

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A review is presented of studies, including recent work by members of the British Antarctic Survey, on the primary productivity of plankton, ice-flora and benthos in both marine and freshwater habitats in the Antarctic. Those members of the flora so far studied have low compensation points enabling slow growth in low light intensities but otherwise show no apparent adaptation to temperatures around freezing point. Certain sea areas, mostly inshore, have dense standing crops with daily and annual productivities as high as those of productive areas elsewhere in the oceans but in the open Southern Ocean productivity seems generally low even although nutrient concentrations are high, probably because of excessive turbulence carrying plankton out of the photic zone. There is as yet insufficient data to show whether, as a whole, the photosynthetic efficiency of the Southern Ocean is greater or less than that of other sea areas. Antarctic algae liberate extracellular products of photosynthesis but there is no definite evidence that these are reassimilated to support growth when light intensities are low and it may be that this material, carried by currents, supports heterotrophic production in other parts of the ocean. Comparison of data for adjacent marine and freshwater systems shows that their rates of primary production are much the same but the marine phytoplankton shows characteristics of shade-adapted cells consistent with the greater turbulence to which it is exposed.

INTRODUCTION

On 28 November 1771, the company at the Club of the Royal Philosophers included James Cook, Jan Ingenhousz and Joseph Banks (Allibone 1976). Their conversation was not recorded; it is perhaps unlikely that they discussed the subject of this paper but, nevertheless, these three men provided its starting points. On his second voyage Cook circumnavigated the Antarctic continent and in his account of this drew attention to the biological productivity of the Southern Ocean. Ingenhousz, with Priestley, was to be the discoverer of the process of photosynthesis, on which primary production, and hence biological production generally, depends, and Banks appears to have been the first to give a scientific description of the phytoplankton (Beaglehole 1963, vol. 1, p. 182 and vol. 2, p. 139) which carries out photosynthesis in the sea. The presence of diatoms in certain parts of the Southern Ocean was reported by several explorers following Cook but intensive study of phytoplankton abundance and the factors controlling its increase was not carried out until the *Discovery* investigations (Hart 1934). The introduction of the radiocarbon method enabled direct measurement of primary production in Antarctic seas (Klyashtorin 1961; Saijo & Kawashima 1964; El-Sayed, Mandelli & Sugimura 1964) and the information now available is sufficient to warrant some general conclusions to be drawn. Studies on primary production in freshwaters, which began with those of Goldman, Mason & Wood (1963), have been less extensive.

THE PHYSIOLOGY OF COLD-WATER PLANTS

The abundance of phytoplankton in waters near freezing point is often striking but this does not, of course, necessarily imply high primary production. Under light limited conditions, photosynthesis becomes nearly independent of temperature so that the contribution to primary production by phytoplankton in the lower part of the photic zone would be much the same, other things being equal, in the Antarctic and the tropics. However, Steemann Nielsen & Hansen (1959) reported that, relative to their chlorophyll content, the light-saturated rates of photosynthesis (mg carbon mg^{-1} chlorophyll *a* h^{-1} = *assimilation number*) of low- and high-temperature grown algal cells were nearly the same. To explain this the hypothesis was advanced that the retarding effect of low temperature on the dark reactions of photosynthesis is offset in cold-adapted cells by increase in enzyme concentrations. In support it was shown that although under otherwise similar conditions rates of photosynthesis are nearly the same in cells of the marine diatom *Skeletonema costatum* adapted to grow in culture at 7 and 20 °C, the relative growth rate is less than half at the lower temperature of what it is at the higher and the cells are larger and contain more protein than those adapted at 20 °C (Steemann Nielsen & Jørgensen 1968; Jørgensen 1968). However, Morris & Glover (1974) have pointed out that in batch cultures like those used in this work there is a peak in photosynthetic activity after a period the duration of which depends on temperature, and, in using material harvested after the same time period from low and high temperature, cells in different physiological conditions were being compared. When account is taken of this no evidence remains to show that adaptation to lower temperatures is a consequence of increased cell concentrations of enzymes. There are still the possibilities that cold water species contain isozymes which are more active at low temperatures or that their control mechanisms allow higher rates of enzyme action to be achieved. These mechanisms evidently occur in Antarctic animals (Feeney & Osuga 1971) but do not appear to have been so far demonstrated in algae.

It seems likely that a large part of the success of cold-water (psychrophilic) algae depends on the different responses of photosynthesis, photorespiration and respiration, acting to produce a relatively greater excess of production over consumption the lower the temperature. Bunt, Owens & Hoch (1966) found in a study of the sea-ice diatom, *Fragilaria sublinearis*, that whereas the optimum for oxygen production occurred round about 7 °C, oxygen uptake (either in the light or dark) was maximum between 10 and 24 °C so that in this temperature range net oxygen production could not occur and the organism was thus obligately psychrophilic. The compensation point for *F. sublinearis* at 6.8 °C was about 0.0005 ly min^{-1} (*ca.* 70 lux), that is about 0.17 of the intensity usually taken as the compensation point for planktonic algae, and at lower temperatures even lower intensities would be expected to be sufficient (Bunt 1967). For a freshwater cryptomonad, grown at 4 °C, Morgan & Kalff (1975) found the compensation point to be 0.00002 ly min^{-1}. Although an excess of photosynthate may thus be produced at low temperatures the relative rate of its production may not be sufficient to support high growth rates. From observations on natural Antarctic phytoplankton populations Holm-Hansen, El-Sayed, Franceschini & Cuhel (1977) estimated the highest relative growth rate as 0.33 doublings per day. This figure, which may be compared with 1 doubling per day which is often the maximum rate exhibited by phytoplankton in temperate waters, is less than that predicted by Eppley (1972) for phytoplankton at temperatures around zero. There thus does not seem to be any physiological adaptation enabling high relative growth rates to be achieved by Antarctic phytoplankton.

Phytoplankton survives a period of several months of minimal light intensity during the Antarctic winter and even in summer is likely to be carried down below the photic zone for long periods by turbulence. Of four strains of algae isolated from Antarctic sea-ice (a chlamydomonad, a chrysomonad, *Fragilaria sublinearis* and *Chaetoceros fragile*) only the chrysomonad failed to survive 3 months in complete darkness (Bunt & Lee 1972). Smayda & Mitchell-Innes (1974) found that 7 out of 9 strains of diatoms from temperate coastal waters remained viable after 90 days in the dark. Survival in the dark of *Skeletonema costatum* was prolonged at low temperature – it remained viable at least 24 weeks at 2 °C as compared with 1–4 weeks at 20 °C. Survival time of the green alga *Dunaliella tertiolecta* was prolonged by occasional illumination at sub-compensation intensities. Morgan & Kalff (1975) found that low temperatures reduced cell division rates of *Cryptomonas erosa* relative to carbon fixation, so that the cells accumulated carbohydrate. Long survival in the dark (over 2 months at 1 °C) was largely dependent on the slow respiration of this storage material at low temperatures. Thus there does not seem to be any reason to doubt the ability of Antarctic phytoplankton to survive the inevitable long periods of darkness and to resume growth when the water mass containing them returns to the light. Presumably, survival depends largely on the rate of respiration being extremely low at low temperatures. The hypothesis that survival of both marine and freshwater algae in near darkness is assisted by heterotrophic or phototrophic assimilation of dissolved organic substances is an attractive one (see Rodhe 1955; Wilce 1967; Fogg & Horne 1970) but there is so far little laboratory evidence that this is actually important (Bunt & Lee 1972).

Determinations of primary productivity

(*a*) *In the sea*

Plankton

Many determinations of primary productivity have now been made in Antarctic seas using the radiocarbon technique. Mostly these consist of single sets of measurements, made in simulated *in situ* experiments or at a limited number of depths for any given station, carried out during cruises of many weeks duration. It is consequently difficult to distinguish between variations related to time and those related to place. No authors have taken account of the possibility that the photosynthetic behaviour of phytoplankton is different under the conditions of such determinations from that in highly turbulent water in which cells are exposed to a fluctuating light climate. The results, which have been reviewed by El-Sayed (1966, 1968, 1970*a*), Platt & Subba Rao (1975) and Fogg (1975*a*) need only be summarized briefly here together with comments on some of the more recent contributions.

Primary production is generally correlated with density of the standing crop of phytoplankton. In the Antarctic Peninsula sector low values (< 0.4 g carbon m^{-2} d^{-1}) have usually been found in Drake Passage but high values have been reported for certain areas, e.g. around the South Orkney Islands, in the southwestern Weddell Sea, in the Bransfield and Gerlache Straits, and waters just west of the Antarctic Peninsula. El-Sayed (1967), for example, recorded 3.2 g C m^{-2} d^{-1} in February 1965 in the Gerlache Strait (64° 30′ S, 62° 30′ W), Mandelli & Burkholder (1966) reported 3.62 g C m^{-2} d^{-1} in February 1965 near Deception Island (63° 0′ S 60° 30′ W), and Horne, Fogg & Eagle (1969) found a peak of productivity of 2.8 g C m^{-2} d^{-1} in early February 1967 in the inshore waters of Signy Island (60° 43′ S, 45° 38′ W), estimating the total for the season to be 130 g C m^{-2}. Whitaker (unpublished), who made determinations at a station off Signy Island near that used by Horne *et al.* (1969), found the annual rates to be 25 and 80 g C m^{-2} respectively for 1972–3 and 1973–4. Further east in the Atlantic sector, in the eastern Weddell Sea, and south of the South Sandwich Islands, values are again on the low side. No radiocarbon determinations appear to have been made so far in the areas around South Georgia studied by the *Discovery* investigations but from the density of phytoplankton reported by Hart (1934) it would be expected that primary production should be high.

In the Pacific sector the values recorded between 75° and 150° W have generally been low (Saijo & Kawashima 1964; El-Sayed 1970*a*, *b*). The primary production of the Bellingshausen Sea also appears to be low but high values have been reported from the Ross Sea (El-Sayed 1970*b*; Holm-Hansen *et al.* 1977).

The Indian Ocean sector likewise appears to have generally low rates of primary production (El-Sayed & Jitts 1973; Holm-Hansen *et al.* 1977). Steyaert (1977) found distinct increases in primary production in the vicinity of the Crozet Islands (46° S, 51° E) and on the eastern side of the Kerguelen-Heard plateau (49° S, 70° E) as compared with adjacent areas of the SW Indian Ocean.

The maximum rates of primary production recorded in Antarctic waters are among the highest reported for any sea areas; the figures given above may be compared, for example, with maximum values of 3.4 g C m^{-2} d^{-1} for Walvis Bay, 3.5 g C m^{-2} d^{-1} for the English Channel and 11.74 g C m^{-2} d^{-1} for the Peru Current (Platt & Subba Rao 1975). Most of the Southern Ocean, however, is much less productive and El-Sayed (1967) has emphasized the contrast between the high productivity of neritic regions and the barrenness of the open ocean. El-Sayed (1967) estimated that the average gross production south of the Antarctic Convergence is 0.33×10^{10} tonnes of carbon per year. This is about 10 % of the gross production for all the oceans, 3.1×10^{10} t of carbon per year (Platt & Subba Rao 1975), and implies that area for area Antarctic waters are about twice as productive as the rest. However, on the basis of their own measurements only, Holm-Hansen *et al.* (1977) estimate the primary production of a larger area (3.2×10^{7} km^2) as 0.65×10^{9} t C per annum, which suggests that Antarctic waters are less than half as efficient as other parts of the world's oceans.

High primary production in the Antarctic is generally considered to be related to the high concentrations of nutrients found in the Southern Ocean. South of the Antarctic Convergence average surface concentrations are more than 20 μmol l^{-1} for nitrate-N, 2 μmol l^{-1} for phosphate-P and 50 μmol l^{-1} for silicon (El-Sayed 1968). These concentrations are about twice those found during the winter in fertile temperate waters and even at the peak of phytoplankton production they are not reduced to much less than one quarter of their maximum values (Whitaker, unpublished). Immediately north of the Antarctic Convergence concentrations are distinctly lower but still high compared with most moderately productive waters elsewhere. The availability in Antarctic waters of iron and other trace metals, which sometimes has a decisive rôle in determining phytoplankton activity (Ryther & Guillard 1959), does not appear to have been studied. Nothing definite is known about the vitamin requirements of the Antarctic phytoplankton flora but since diatoms predominate and since most of the marine representatives of this group which have been examined in culture have a requirement for vitamin B_{12} it seems that the concentrations of this substance could also be important. Carlucci & Cuhel (1977) found that concentrations of vitamin B_{12} ranged from less than 0.05 to 3.3 ng l^{-1} in the Southern Indian Ocean. 20 % of samples contained no detectable amount of vitamin B_{12} but most of those from the more southerly stations contained appreciable amounts. Samples from the upper 75 m contained low concentrations of the dissolved vitamin but high concentrations in particulate form. It is possible that the concentration of vitamin B_{12} may have important effects on the composition of the Antarctic phytoplankton flora but there does not seem to be any evidence that it affects primary productivity to any appreciable extent. Carlucci & Cuhel (1977) found that thiamin was usually lacking in detectable concentrations in Antarctic waters but that biotin was often present in high concentrations. Since only a few phytoplankton species require these vitamins their concentrations are probably not of great ecological importance. In accordance with the idea that nutrients are not normally limiting for the phytoplankton population as a whole, Holm-Hansen *et al.* (1977) found a good correlation between photosynthetic rates in antarctic waters and the intensity of incident solar radiation.

In considering spatial variations in primary production in waters south of the Antarctic Convergence it seems safe to dismiss incident radiation, surface water temperatures and concentrations of nitrate, phosphate and silicate as contributing to these variations since all these have much the same values over the area in question. It remains possible, however, that some micronutrient is a determining factor. Hardy (1967), in discussing the dense phytoplankton growth which occurs southwest of South Georgia in an area of mixing of Bellingshausen and Weddell Sea waters, makes the suggestion that it results from each water mass contributing a trace growth factor in which the other is deficient. The observations of Carlucci & Cuhel (1977) lend colour to this suggestion but there does not appear to be any positive evidence of it as yet.

The depth of mixing in the Southern Ocean is generally such that phytoplankton is carried below the photic zone and the average amount of light received by the cells in a population is correspondingly reduced. The low compensation point characteristic of cold-water plankton offsets this to some extent – Holm-Hansen *et al.* (1977) occasionally found photosynthesis at 0.01 % of incident intensity – but with the almost continuous westerly gales in the northern part of the area the turbulence may frequently be such that net photosynthesis is not possible. Several authors (Hart 1934; El-Sayed & Mandelli 1965; Saijo & Kawashima 1964) attribute the generally low primary productivity of the Southern Ocean to this factor and suggest that areas of high primary productivity are those in which comparative stability of the water column occurs. There is much qualitative evidence in support of this view. Thus Hart (1934) noted that short periods of fine weather in the pack promote the formation of strongly marked discontinuity layers at shallow depths and corresponding growth of phytoplankton. A high value of primary production (1.56 g C m^{-2} d^{-1}) recorded by El-Sayed (1971 *a*) for a part of the Weddell Sea (74° 59′ S, 60° 57′ W) only accessible by ice-breaker may be explained in this way. On the other hand, Hart (1934) suggested that a 'desert area' NE of King George Island owes its existence to the presence of a submarine ridge inducing strong vertical mixing. Inspection of the large number of depth profiles published by El-Sayed (1967) shows that low rates of primary production are associated with strong vertical mixing as indicated by uniform distribution with depth of temperature and chlorophyll *a*. Phytoplankton abundance and primary productivity also tend to be low at the Antarctic Convergence where vertical mixing is intense (El-Sayed & Mandelli 1965; Hasle 1969; Walsh 1971). Whitaker (unpublished) has found that the period of maximum production coincides with moderate stabilization of the water column in inshore water off Signy Island and that the major decline in production was a sudden one following a severe storm causing mixing, rather than a gradual decline which might be related to decreasing nutrient concentrations or light intensity. Pingree, Pugh, Holligan & Forster (1975) have drawn attention to the way in which fronts between different water bodies may provide an optimum balance between stabilization and turbulence for development of phytoplankton blooms. A similar analysis for the area SW of South Georgia, referred to in the previous paragraph, would be interesting but sufficiently detailed data is not available.

Release of extracellular products of photosynthesis by phytoplankton, now a well-attested phenomenon (see Fogg 1975*b*), would be expected to occur in Antarctic seas. It seems to be a general rule that although the absolute amount of extracellular products decreases with decreasing phytoplankton concentration the percentage release increases (Anderson & Zeutschel 1970; Thomas 1971) and in accordance with this Horne *et al.* (1969) found the percentage extracellular release to be low, generally about 1%, in water off Signy Island with dense phytoplankton. Less productive areas have not yet been investigated from this point of view. Glycollic acid, which is an important component of the material released, has been detected in concentrations up to 15 μg l^{-1} in a few seawater samples from south of the Convergence (Fogg *et al.* 1975). This may be compared with concentrations of up to 78 μg l^{-1} found in more extensive series of analyses of temperate waters.

Sea-ice

Sea-ice, which at its maximum extent may cover 25.5×10^6 km^2 in the Antarctic (Lewis & Weeks 1971), provides a comparatively complex environment (Bunt 1963; El-Sayed 1971*b*) in which algae are often prominent. The ice-flora appears to be distinct from the planktonic flora (Bunt 1966). One habitat is provided by the lenses of low salinity melt water on the surface of the upper layer of sea-ice but primary production in this situation does not appear to have been studied. Whitaker (1977) studied a population of *Navicula glaciei* which developed in the slush and frozen infiltration ice, through which seawater percolates freely, in a tide-crack. Chlorophyll *a* reached 148 mg m^{-2} at the peak of growth but it was concluded that the maximum primary productivity of inshore sea-ice habitats around Signy Island was small, 1–2 g C m^{-2} a^{-1}. A few studies have been made on the algae occurring in the dimly-lit underlayer of loosely aggregated ice-crystals. The chlorophyll *a* concentration in this situation was found by Bunt (1963) to be high (150 mg m^{-3}) as compared with that in the water below the sea-ice (16 mg m^{-3}). However, because of the low light intensity the rate of photosynthesis was low, the peak rate reported by Bunt (1966) being 3.8 mg C m^{-3} h^{-1}. From this a tentative estimate was made of the annual primary production as 10 g C m^{-2}, which is rather less than values for unproductive open water. Measurements made under arctic sea-ice have given similarly low values ranging from 7.7 mg C m^{-2} h^{-1} near the peak of an algal bloom to a low of 0.3 mg C m^{-2} h^{-1} just before a thaw (Clasby, Horner & Alexander 1973).

From the studies of Bunt *et al.* (1966) and Bunt (1967), which were discussed above (p. 28), it seems likely that the principal physiological attribute enabling algae to grow under sea-ice is a low compensation point. The possibility that the algae may photoassimilate dissolved organic substances (Bunt 1967) is worth considering since these substances presumably become concentrated in the interstitial water as ice crystals form. However, photoassimilation of organic substances by sea-ice algae does not appear to have been studied in the laboratory and *in situ* observations by Horner & Alexander (1972) on algal populations occurring in the bottom few centimetres of arctic sea-ice suggest that it is negligible. Uptake was assayed following supply of [^{14}C]glycine, [^{14}C]glucose and [^{3}H]acetate. Total uptake was slow and, from radioautography, assimilation of these substrates appeared to have been largely carried out by bacteria.

Benthic algae

Large brown and red seaweeds are abundant in Antarctic inshore waters in a zone the upper limit of which, about 10 m below low tide mark, is determined by the scour of ice, and the lower limit, about 70 m below low tide mark, presumably by the penetration of light (Zaneveld 1966; Arnaud 1974). Between 10 m and low tide mark benthic diatoms are usually abundant and green filamentous algae are often conspicuous in the intertidal zone in the summer (Arnaud 1974). Although the biomass per unit area is often considerable, scarcely anything is known of the primary production or growth rates of the seaweeds. Hastings (unpublished) has observed that the growing season of *Phyllogigas grandifolius* around Signy Island begins immediately after the departure of the sea-ice but that growth may be reduced if light penetration is reduced by a phytoplankton bloom. The presence of large seaweeds in areas covered by thick sea-ice for most of the year has excited comment because the amount of light reaching them has seemed scarcely sufficient to support growth (Zaneveld 1966; Wilce 1967). It has been suggested that such algae may survive by assimilation of dissolved organic substances (Wilce 1967) but it seems likely that the low compensation points shown by cold water algae are sufficient to explain their presence in these situations (Zaneveld 1966).

(*b*) *In lakes*

Plankton

The principal studies on primary productivity have been on small lakes; two, Algal Lake (0.08 ha, $z_{\max}$ 0.9 m) and Skua Lake (0.46 ha, $z_{\max}$ 1.0 m) on Ross Island (Goldman, Mason & Wood 1972), and one, Heywood Lake (4.07 ha, $z_{\max}$ 6.0 m) on Signy Island (Light 1977). In the two Ross Island lakes at 77° 38′ S the maximum crops of phytoplankton occurred around mid-summer and there was indication that growth might sometimes be controlled by release of nutrients or trapped algal cells as the ice melted. Both nitrate-N and phosphate-P fell to low levels in both lakes by midsummer. Inhibition of phytoplankton photosynthesis at high light intensities (Goldman *et al.* 1963) was marked and at midsummer photosynthesis was least at mid-day and maxima occurred in morning or afternoon or even at midnight on bright days. The maximum chlorophyll *a* concentrations were about 40 and 10 $\mu g\ l^{-1}$ respectively for Skua Lake and Algal Lakes, the greater standing crop in the former being attributable to eutrophication by birds. The average planktonic photosynthetic rates were 1.55 and 6.72 $g\ C\ m^{-3}\ d^{-1}$ for Skua Lake and 0.26 and 0.19 $g\ C\ m^{-3}\ d^{-1}$ for Algal Lake for the 1961–2 and 1962–3 seasons respectively. However, in Algal Lake rates varied erratically probably as a result of the repeated partial freezing of this small body of water. The considerably higher primary production by phytoplankton in Skua Lake in the second season is attributed to increased avian fertilization and decreased volume (Goldman *et al.* 1972).

Light's (1977) results for Heywood Lake on Signy Island at 60° 43′ S are similar to those for the Ross Island lakes but because this lake is deeper and did not freeze completely there is the difference that the main peak of phytoplankton occurred in the spring at low light intensities when the ice cover was still present. Snow cover of the ice appeared to be the main factor controlling production. Maximum concentrations of nitrate-N and phosphate-P have been reported as 535 and 50 $mg\ l^{-1}$ respectively by Heywood (1968) and contamination from seals may have increased the nutrient status of the lake in recent years. The maximum chlorophyll *a* concentration and rates of primary productivity found by Light are given in table 1.

A single set of observations, reported by Fogg & Horne (1970), showed that a phytoplankton sample from Knob Lake, Signy Island, released in extracellular form 43% of the carbon fixed in photosynthesis in surface illumination under overcast conditions. This is in agreement with results from temperate waters and suggests that release of extracellular products is a normal feature of phytoplankton photosynthesis in Antarctic lakes. Glycollic acid, a probable extracellular product, has been found in water from Heywood Lake, Signy Island at a concentration of 40 μg l^{-1} (Fogg *et al.* 1975).

The question of whether the phytoplankton of polar lakes is able to assimilate dissolved organic substances is a much discussed one (see, for example, Fogg & Horne 1970). Suitable substrates may be released as extracellular products in the photosynthesis of plankton and benthos, or be produced by decomposition of plankton, or be derived allochthonously from birds and seals. The relatively high concentrations, up to 32 mg C l^{-1}, found in Lake Bonney (77° 40′ S, 162° 25′ E) which is situated in a dry valley, must presumably be derived from primary production within the lake itself (Parker, Whitehurst & Hoehn 1974). The apparent rapid recycling of this organic matter is unexplained, there being no evidence to show whether its utilization is heterotrophic or phototrophic. An indication that phytoplankton in Heywood Lake, Signy Island, may assimilate organic matter has been obtained by Light (unpublished). In the spring, when the lake was still ice-covered, a chlorophyll *a* maximum at 6 m, just above the bottom coincided with a marked peak in uptake of [^{14}C]acetate. The uptake may, of course, have been by bacteria associated with the algae.

Benthos

Benthic felts of blue green algae are often conspicuous around the margins of Antarctic lakes and extend to the depth of 1 m or more. The felt, which consists mainly of *Phormidium* spp., shows an orange or rusty red layer above and a blue-green layer below – a structure which may give protection against excessively high intensities of radiation and promote solar heating. In the Signy Island lakes, temperature differences of 1–2.3 °C between the algal felt and the water surface have been observed (Fogg & Horne 1970) and in the Ross Island lakes felt temperatures may be 10 °C higher than in the overlying water (Goldman *et al.* 1972). Similar higher temperatures have been found to increase the rate of photosynthesis of phytoplankton from the same lakes even when light-limited (Goldman *et al.* 1972) and a similar effect on the felt would be expected to give it an advantage. This is so; Fogg & Horne (1970) found in a Signy Island lake that in water of 1 m depth the primary production of the felt was 25 times as great as that of the phytoplankton in the water column overlying it. Goldman *et al.* (1972) found the benthic felt contained between 4.0 and 35.0 mg cm^{-2} of chlorophyll *a*, with average photosynthetic rates of 1.56 and 2.56 g C m^{-2} d^{-1} in Skua Lake and of 1.91 and 3.63 g C m^{-2} d^{-1} in Algal Lake for the 1961–2 and 1962–3 season respectively. Primary production by these felts increased throughout the open water period to a peak in February. For the lakes as wholes the ratios of the total planktonic primary production to that for the benthos were 0.33 and 0.72 for Skua Lake and 0.03 and 0.01 for Algal Lake for the 1961–2 and 1962–3 seasons respectively. Fogg & Horne (1970) and Parker *et al.* (1974) found that benthic felts release extracellular products of photosynthesis.

Mosses, such as *Amblystegum* sp., *Calliergon sarmentosum*, *Drepanocladus* spp. and *Pohlia nutans*, frequently occur in abundance in the deeper waters (2–36 m) of Antarctic lakes (Light & Heywood 1973, 1975). No studies of the physiology or primary production of such mosses appear to have been reported so far but although their biomass is impressive it may be surmised that it is made possible by the low compensation points of the plants and achieved by slow growth at limiting light intensities.

DISCUSSION

The primary productivity of Antarctic seas and lakes may have been exaggerated in the past but there is no doubt that rates as high as those elsewhere in the world are sometimes achieved and that Light & Heywood (1975) are right in asserting that the primary productivity, even of continental Antarctica, is mainly aquatic. Much remains to be learnt about the physiology of cold-water plants but it appears that they survive and grow largely by virtue of having low compensation points and that high productivity is generally the result of slow growth of a large biomass.

TABLE 1. PRIMARY PRODUCTION ON AND AROUND SIGNY ISLAND (60° 43′ S, 45° 38′ W)

	annual production	max. daily production	chlorophyll *a* maximum		assimil. no.
	g C m^{-2}	mg C m^{-2}	mg m^{-3}	mg m^{-2}	
Heywood Lake					
(J. Light 1970–2)	100–200	4500	35	175[a]	10.5
sea					
(A. Horne 1966–7)	130	2800	40	1200[b]	1.07
(T. Whitaker 1972–4)	25–80	5000	47	605[c]	1.15

a In the water column to the lake bottom at 6.2 m.
b In the water column down to 50 m.
c In the water column down to 16.5 m.

The suggestion that Antarctic plants are able to grow at minimal light intensities because they are capable of heterotrophic or phototrophic assimilation of dissolved organic substances has been made in relation to plankton, the ice flora and seaweeds, but there is as yet no definite evidence to show that it occurs. One is tempted to think that a process of such obvious biological advantage must occur if suitable substrates are available but growth as a result of normal photosynthetic assimilation of carbon dioxide exceeding respiration even at very low light intensities at near zero temperatures seems adequate to account for the observed biomasses. Large quantities of organic matter are released in extracellular form in the course of photosynthesis in Antarctic waters but the fate of these is not known. Kriss, Mishustina, Mitskevich & Zemtsova (1967) concluded that Antarctic waters contain relatively few heterotrophic microorganisms and Sorokin (1973) may well be correct in suggesting that dissolved organic matter produced by phytoplankton in the region of the Antarctic Convergence becomes available for extensive bacterial growth in tropical latitudes by advection of deep and intermediate waters.

The existence of primary productivity data for a sea-area and a lake of about the same nutrient status within about 2 km of each other offers a unique opportunity for comparison (table 1). The maximum daily and annual productions per unit area of water surface, which are for plankton only, are of the same order and, considering the variation from year to year, the differences are not significant. In terms of chlorophyll *a* the maximum concentrations of phytoplankton are also much the same in the lake and the sea (Fogg & Horne (1970) were premature in commenting on the apparently low concentration of chlorophyll in the Signy lakes as compared with the adjacent sea). The maximum chlorophyll *a* values in the water column under unit area of water surface show differences which, being as much as sixfold, are probably real. Talling (1961) concluded that the maximum chlorophyll *a* content for a photic zone was 300 mg m^{-2}. The value for Heywood Lake is below this, in accordance with the success of benthic plants. The amount in the sea was much greater for both periods examined and suggests that only a portion of the population was in the photic zone at any one moment. There are also considerable differences in the assimilation numbers, those for the sea being about the usual value for Antarctic waters (e.g. Saijo & Kawashima 1964) whereas that for the lake is almost 10 times higher. The interpretation of assimilation numbers is difficult (Fogg 1975*a*). It is unlikely that differences in nutrient concentrations could be important here and although Eppley (1972) has shown that assimilation number decreases with temperature this would be insufficient to account for the difference. It seems most likely that we are dealing here with a shade adapted population in the sea and a high light adapted population in the lake. Mixing in the sea is sufficient to ensure that the average intensity received per cell is low and, as Bunt (1967) has shown, such cells have a high chlorophyll content and low assimilation number. In the lake the whole population remains in the photic zone and the chlorophyll content per cell is correspondingly less and the assimilation number higher. From this it would be expected that assimilation number would show a correlation with the stability of the water column but an examination of the data of El-Sayed (1967) and Holm-Hansen *et al.* (1977), which permit approximate calculations of assimilation numbers and relative stability coefficients, showed positive correlations which are not statistically significant.

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