

Abundance and production of ice algae in Resolute Passage, Canadian Arctic

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ABSTRACT: Abundance and photosynthetic activity of ice algae in Resolute Passage in the Canadian high Arctic were measured in relation to in situ irradiance throughout the main growth season in 1985 and 1986. A simple model was used to calculate in situ production rates and the theoretical maximum (light limited) size of crops and production rates. Both the observed and the maximum possible crop sizes and production rates varied directly with irradiance over the natural range of snow cover, and crops attained the theoretical maximum imposed by self-shading (77 to 225 mg m⁻² chlorophyll a under thin snow cover) in both years. Calculated in situ production of ice algae under thin snow cover (5 to 23 gC m⁻² yr⁻¹) could equal or exceed typical values for Arctic plankton. Comparison against observed biomass accumulation in the ice indicated that as much as 65% of the production could be exported from the ice during the growth season. Where light was artificially increased by maintaining snow-free areas, observed crops were much less than the theoretical maximum despite the absence of photosynthetic photoinhibition. Crops reported from some other arctic sites were also much less than their corresponding theoretical maxima. Low irradiance often limits ice algal growth, but our results suggest that losses associated with excessive irradiance and with grazing by amphipods at near-shore sites are additional factors determining algal abundance and production.

INTRODUCTION

Ice algae are proposed to be important primary producers in polar regions, not only for the absolute magnitude of their production but also for its timing and localization (Cross 1982, Horner 1985, Grossi et al. 1987). Subba Rao & Platt (1984) reviewed the relatively few production estimates for Arctic ice algae and assigned an average value of 10 gC m⁻² yr⁻¹, compared to 27 gC m⁻² yr⁻¹ for plankton of Arctic shelf waters. Recent data from the Antarctic indicated rates of 40 gC m⁻² yr⁻¹ or more under favorable snow cover (Grossi et al. 1987). The Antarctic results also indicated that much of the ice algal production can be lost to grazers or to the water column during the growth season (Grossi et al. 1987). If general, such export will cause production rates inferred from net biomass accumulation to underestimate total production, but direct measurements of production rate are still few for arctic as well as antarctic ice algae.

The availability of light influences ice algal abun-

dance and production in the Arctic, Antarctic and Subarctic (Apollonio 1961, 1965, Gosselin et al. 1985, 1986, Horner 1985, Sullivan et al. 1985, Grossi et al. 1987, Smith et al. 1988). In Hudson Bay, light was found limiting to algal photosynthesis in the first half of the growth season but increased to inhibitory levels in the later season (Gosselin et al. 1985, 1986), while in McMurdo Sound, Antarctica, light was found limiting to algal production throughout the growth season (Grossi et al. 1987). In the Arctic, both positive and negative correlations between algal abundance and light availability have been reported (Apollonio 1961, 1965, Clasby et al. 1976, Horner 1985). The absolute abundance of ice algae varies widely even under similar snow cover and presumably, light availability: from values of 100 to 300 mg m⁻² chlorophyll a in the Arctic and Antarctic respectively (Palmisano et al. 1987, Smith et al. 1988) to more typical values of 30 mg m⁻² or less. The larger crops (300 mg m⁻²) may represent the theoretical, light-limited, maximum (Palmisano & Sullivan 1985, McConville 1985) but the theoretical maximum has never been explicitly derived for ice algae.

More data on the season-integrated production of arctic ice algae in situ would help to resolve the controlling role of light more clearly, but such data are still difficult to collect and relatively rare. Alternatively,

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production rates in situ can, as for phytoplankton (Platt et al. 1980, Lewis et al. 1985), be calculated from the algal photosynthetic light response measured in samples from the natural community together with estimates of the available light in situ. The available light depends on incident solar radiation and its reflection and attenuation by ice and snow, but also on a self-shading effect that can be very strong in ice algal communities (Palmisano et al. 1987, SooHoo et al. 1987). Even if under-ice irradiance measurements are made, a transmission model must still be used to calculate the light available to the algae, and the photosynthetic rates attained in situ.

Our purpose here is to estimate the production rates of ice algae at our site in the Canadian Arctic, in order to test the hypothesis that production is light-limited and to determine whether total production is likely to greatly exceed the observed accumulation of algal biomass in the ice. Our estimates are based on measurements of light transmission and the photosynthetic-light response of the algae, and therefore entail the development and application of a simple model analogous to those used in similar calculations of phytoplankton production (Lewis et al. 1985). Because Antarctic ice is physically different in important ways, we restrict our detailed analysis to the Arctic at this stage. The model also defines the maximum theoretical standing crops and production rates expected if the populations reach the limits set by self-shading. We wished to test the hypothesis that ice algae at our site and elsewhere in the Arctic can attain the light-limited maxima of crop size and production rate.

Theory

Light. In the arctic, the ice algae are overwhelmingly concentrated in a thin (1 to 4 cm) layer at the bottom of an ice sheet that is typically 1.5 to 2.5 m thick (Horner 1985). The photon fluence rate (PFR) incident at the surface of the ice sheet (I') is partially reflected. A lesser proportion is reflected if the ice surface is free of snow. The light is then attenuated in passage through the ice and snow to a much smaller flux incident upon the algal layer (I_o). The flux is further attenuated in passage through the pigmented algal layer, which is most commonly confined to a narrow band of a few cm or less at the bottom of the ice sheet in the Arctic, leaving the amount I_u penetrating to the water column. To a first approximation, I_u can be modelled using the relatively simple relationship:

$$\ln(I_u/I') = -a - c \cdot X - k_i \cdot Z_i - k_s \cdot Z_s - k_{chl} \cdot [Chl] \quad (1)$$

where a = parameter for reflection from bare ice (dimensionless); c = (dimensionless) parameter for

extra reflection from snow ($X = 1$) vs bare ice ($X = 0$); Z_i and Z_s = ice and snow thickness (m); k_i and k_s = diffuse attenuation coefficients for ice and snow (m^{-1}). All parameters are variable; for example, 'a' varies with sun angle. For this first approximation, we will use constant values for the parameters as estimated by empirical analysis of light transmission data from our study area. $[Chl]$ denotes the areal concentration ($mg\ m^{-2}$) of chlorophyll *a*, and k_{chl} is the mean spectral extinction coefficient for chlorophyll ($m^2\ mg^{-1}$), more usually denoted k_c (Bannister & Weidemann 1984). We use the term k_{chl} to emphasize that, as we measure it, the parameter will be influenced by a number of factors other than purely algal light absorption. These factors, and the model's parameter values relative to those from more detailed investigations of light transmission (Warren 1982, Bannister & Weidemann 1984, Maykut 1985) will be described in the 'Discussion'.

If we assume, as is the case in the arctic sea ice we are considering, that the algal layer lies at the bottom of the ice sheet, then Equation 1 defines PFR at the top of the algal layer, I_o , as:

$$I_o = I' \exp(-a - c \cdot X - k_i \cdot Z_i - k_s \cdot Z_s) \quad (2)$$

where I_o = maximum PFR that algal cells may experience in situ. The lower PFR actually experienced by cells within the algal layer can be calculated as:

$$I(B) = I_o \cdot \exp(-k_{chl} \cdot B) \quad (3)$$

where $I(B)$ = PFR at some point in the algal layer above which the areal concentration of chlorophyll is B ($mg\ m^{-2}$). B ranges from zero at the top of the algal layer to $[Chl]$, the vertically-integrated areal concentration defined above, at the bottom. Equation 3 allows us to specify the PFR (ignoring selective spectral attenuation) received by a cell anywhere in the algal layer in terms of the areal concentration of chlorophyll, independent of its precise vertical distribution.

Photosynthesis. We use the following equation (Platt et al. 1980, Lewis et al. 1985) for the biomass-specific photosynthetic rate [P^B , $\mu gC\ (\mu g\ Chla)^{-1}\ h^{-1}$] as a function of PFR (I , $\mu mol\ quanta\ m^{-2}\ s^{-1}$):

$$P^B = P_m^B \cdot [1 - \exp(I/I_K)] \quad (4)$$

where P_m^B = light-saturated maximum in P^B ; I_K = 'adaptation parameter'. I_K in turn equals P_m^B/α , where α is the initial slope of the P^B vs I curve. Equation 4 fits the photosynthetic light response of ice algae adequately in our experience, so long as I does not greatly exceed values typical of the natural environment. Photoinhibition can occur at higher PFR (Cota 1985).

We assume that respiration rate (R^B , $\mu gC\ (\mu g\ Chla)^{-1}\ h^{-1}$) is independent of light, and is a constant fraction of P_m^B . This assumption is commonly made in models of microalgal growth (Wofsy 1983).

The rate of net photosynthesis, P_n , of the ice algal community ($\text{mgC m}^{-2} \text{ h}^{-1}$) is then given by integrating the quantity ($P^B - R^B$) from the top of the algal layer to the bottom:

$$P_n = \int_0^{[\text{chl}]} (P^B - R^B) \cdot dB$$

$$= P_m^B \cdot \int_0^{[\text{chl}]} [1 - \exp(-I/I_k)] \cdot dB - R^B \cdot [\text{Chl}] \quad (5)$$

Fig. 1 portrays the functional response of integrated photosynthesis and respiration and their difference (P_n)

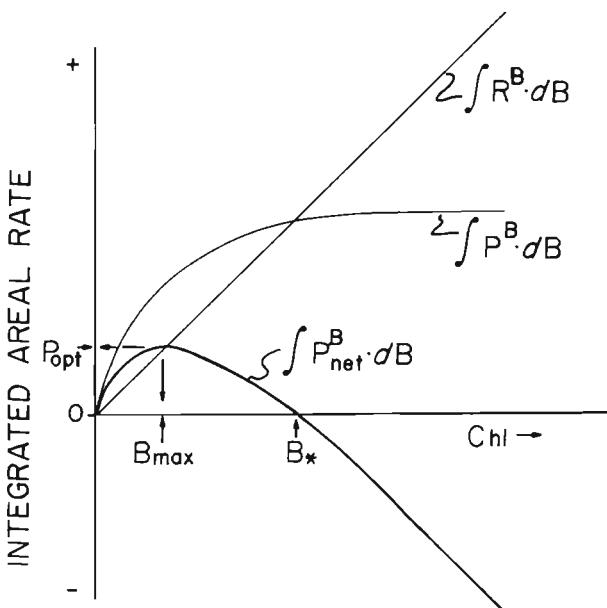


Fig. 1. Functional relation between vertically integrated areal production and respiration rates ($\text{mgC m}^{-2} \text{ h}^{-1}$) and integrated areal chlorophyll concentration, Chl (mg m^{-2}). All terms defined in the Introduction (Theory)

to increasing algal crop size, [Chl]. Substituting $I(B)$ from Equation (3) for I in Equation (5) and solving the integral leads to:

$$P_n = (P_m^B/k_{\text{chl}}) \cdot \int_{n=1}^{\infty} [(-I \cdot)^n \cdot (-1 + \exp(-n \cdot k_{\text{chl}} \cdot [\text{Chl}]))/(n \cdot n!)] - R^B \cdot [\text{Chl}] \quad (6)$$

where I = the quantity (I_o/I_k). In calculating production by Equation (6), we ignore variation of PFR through the 24 h photocycle, and assume instead that we can use a daily average value. This is not entirely accurate even during the period of nominally continuous days (April 23 onwards at Resolute) but is not a serious problem so long as the PFR experienced by the algae is usually close to or less than I_k .

Upper bounds. Fig. 1 shows that algal net production is at a light-limited maximum (termed P_{opt}) when the rate of increase of integrated photosynthesis with addi-

tional standing crop just equals the rate of increase of integrated respiration:

$$dP_n/dB = d[\int_0^{[\text{chl}]} P^B \cdot dB]/dB - d[\int_0^{[\text{chl}]} R^B \cdot dB]/dB = 0 \quad (7)$$

When the equality in Equation 7 holds, the biomass-specific rates of photosynthesis and respiration just balance at the bottom of the algal layer. The PFR at which photosynthesis just balances respiration is termed the light compensation point for photosynthesis, I_c , and setting Equation 4 equal to R^B :

$$I_c = I_k \cdot \ln(1 - R^B/P_m^B) \quad (8)$$

The algal standing crop, [Chl], that corresponds to P_{opt} can then be defined as the crop that reduces I_o to I_c and Equation 3 can be solved for the condition $I(B) = I_c$ to obtain:

$$\begin{aligned} B_{\text{max}} &= (-1/k_{\text{chl}}) \cdot \ln(I_o/I_c) \\ &= (-1/k_{\text{chl}}) \cdot \ln[(-I_k/I_o) \cdot \ln(1 - R^B/P_m^B)] \end{aligned} \quad (9)$$

P_{opt} is then given by evaluating Equation 6 for the condition $[\text{Chl}] = B_{\text{max}}$. B_{max} represents an upper limit to crop size as well as to production, inasmuch as any further increase would result in some proportion of the community being held continuously below the light compensation point for photosynthesis. This contrasts with the situation of phytoplankton in a well-mixed water column, for which the upper limit to crop size is reached only when the average PFR in the entire community is reduced to I_c (at standing crop B_* in Fig. 1; cf Sverdrup 1953, Wofsy 1983). In the case of ice algal communities that have attained B_{max} , populations in the upper algal layer could continue to increase if light alone regulated their growth while those below declined. If so, the algae should as a population penetrate ever upward into the ice. In practice, however, such penetration is severely constrained by the increasingly cold, dense and nutrient-poor nature of the ice algal habitat above a narrow (1 or 2 cm thick) porous layer adjoining the ice-water interface (the skeletal layer, Maykut 1985). Brine channels provide some exceptions to such a vertical gradient of conditions, but appear to offer much less habitat area than the porous skeletal layer. Observation shows that arctic ice algae normally remain overwhelmingly confined to the narrow bottom layer throughout the growth season (Poulin et al. 1983, Cota et al. 1987, R. Smith, A. Herman unpubl.). We assume that, as crops attain and begin to surpass B_{max} , further growth upward is effectively prevented by stresses other than light limitation in the upper layer. The maximum crop is therefore determined jointly and in a spatially organized way by light and other (not positively identified) factor(s), but should be predictable from the condition that cells at the lower bound of the community experience I_c . The maximum crop accordingly should be B_{max} (Equation 9).

MATERIALS AND METHODS

Sampling sites and methods. Study sites for 1985 and 1986 were located several km offshore from Resolute, N.W.T. ($74^{\circ}40'N$, $94^{\circ}54'W$) where the water column is roughly 100 m in depth. In 1984, routine sampling was carried out closer to shore, where the water column was about 30 m deep, but additional sampling was carried out along a transect extending several km offshore. The area is described more fully in Cota et al. (1987). Our period of observation was from late March to late May or early June in each year, spanning the main ice algal growth season.

The sampling program was designed to examine algal growth under 3 or, usually, 4 different depths of snow cover; 18 to 22, 8 to 12, or 2 to 4 cm, and an artificially-cleared area in 1984 and 1985. The cleared areas were established roughly at the outset of the sampling season and at least 3 wk before any samples for photosynthetic measurements were taken. For quantitative assessment of the areal concentration of algal biomass (chlorophyll *a*) we used a coring auger (SIPRE), cutting off and melting the lower 3 cm of each core which contained virtually all of the pigment. Aliquots of the melted core section were filtered through GF/F filters, the filters were extracted in 90 % acetone, and fluorescence was measured on a fluorometer calibrated against pure chlorophyll *a* (Smith et al. 1988). An acidification step was included to correct for phaeopigments which were rarely abundant in the ice alga samples. We collected triplicate cores from each of the different snow depths at intervals of 7 to 10 d through the observation period.

Photosynthesis and respiration measurements. Samples for physiological measurements were obtained by scraping the lower 1.0 cm or so of the ice (containing most of the visible pigment) into filtered seawater before melting (Bates & Cota 1986, Smith et al. 1987) at temperatures of -1.0 to $-1.5^{\circ}C$ in near-darkness. Suspensions so obtained were close to surfaced seawater salinity (ca 30 ppt) and usually contained 50 to 200 $\mu\text{g l}^{-1}$ of chlorophyll *a*. Other salinities (i.e. relative sea water contents) and sample preparation methods yielded only suspensions with lower photosynthetic rates (Bates & Cota 1986), suggesting that we achieved reasonably favorable conditions for ice algal photosynthetic measurements despite the unavoidable disruption of their natural physical and chemical environment (Smith et al. 1988). Photosynthesis was measured by both change in dissolved oxygen and by ^{14}C assimilation in separate, but usually concurrent, experiments on 6 (oxygen) or 15 (^{14}C) occasions throughout the observation period in 1985.

Experiments for dissolved oxygen change were conducted under fluorescent light filtered through a blue

acrylic screen, as previously described (Smith et al. 1987). Four different light levels (plus darkness) were available in the incubator. Dissolved oxygen was determined at the outset and after 6 and 24 h of incubation, using a high-precision, automated Winkler titration system and KIO_3 standards. The samples were incubated in borosilicate glass bottles of 30 or 60 ml volume. Frequent measurements showed that the incubator remained at $-1.0^{\circ}C$, close to the ambient natural temperature of -1.7 to $-1.8^{\circ}C$. PFR (400 to 700 nm) in the incubator was measured both with a LI-COR Inc. 4 π quantum probe and with a Biospherical Instruments 4 π quantum probe, the 2 probes agreeing to within 10 %. With change of position in each compartment of the incubator, PFR varied by up to 20 % of its value in the centre of the compartment. For present purposes the imprecise knowledge of PFR in the incubator is not important, since we will mainly be concerned only with the ratio of oxygen production at light saturation to consumption in the dark.

The same incubator was used to measure time courses of photosynthetic ^{14}C assimilation (Smith et al. 1987), which proved to be linear over intervals from one-half up to 24 h at least. Extracellular release of labelled dissolved organic carbon was also measured, and was found to be in the range of 5 to 15 % of total assimilation for the incubation periods of up to at least 24 h duration (Smith unpubl.).

Photosynthesis was also measured by ^{14}C , using a small-volume, short duration incubation system (Lewis & Smith 1983, Cota 1985). The incubator provided measurements of the rate of total (dissolved plus particulate) organic fixation over 1 h of incubation at 24 different irradiances. The estimated production rate should be close to gross photosynthesis because of the short incubation time (Smith & Geider 1985). Illumination was by tungsten-halogen lamp, filtered through a blue acrylic screen. The incubator design permitted precise determination of the PFR experienced by the samples, using the Biospherical Instruments 4 π quantum probe. Radioactive bicarbonate solution (New England Nuclear product, treated by us with UV radiation to eliminate any contaminating organic ^{14}C and then sterilized by autoclaving) was added at 1.0 $\mu\text{Ci ml}^{-1}$ from a stock solution of 1.0 mCi ml^{-1} . Incubations were terminated by acidification (to a final concentration of 1.25 $N \text{HCl}$), samples were de-gassed for 1 h, then neutralized (with NaOH) and mixed with a water-soluble scintillation cocktail. Activity was measured by liquid scintillation spectroscopy with external standards correction for quenching.

Both oxygen-based and ^{14}C -based photosynthetic light responses were fitted by non-linear least squares regression.

Light transmission. On each sampling date, meas-

urements of downwelling photon fluence rate (PFR) immediately beneath the ice (I_u , Equation 1) were taken using a LI-COR Inc. cosine collector quantum probe, measuring in the 400 to 700 nm band (PAR). The probe was deployed on an arm of 1 m length to avoid interference from the sampling hole, and was raised as gently as possible to the ice-water interface in order to minimize disturbance of the ice algal layer. Total downwelling solar radiation was measured simultaneously by Eppley pyranometer at Resolute airport, about 10 km distant (Environment Canada Atmospheric Environment Service 1982), and converted to PAR equivalent (I' of Equation 1) assuming that PAR is one-half of total solar radiation. The ratio could have been as low as 0.42 but might be expected to average closer to 0.50 due to the typically dry arctic air masses (Baker & Frouin 1987). Inaccuracy in the conversion of total to PAR radiation at the snow surface will influence interpretation of our estimates of the parameters for snow and ice albedo in Equation 1, but should not affect either the other parameters or the accuracy of estimated light reaching the ice algae.

The thickness of the ice sheet varied little during our study. It was therefore not possible to discriminate the effects of diffuse attenuation by the ice sheet from the effects of reflection from the ice surface, so the parameters a and k_i (Equation 1) were fitted as a single constant term ($a + k_i Z_i$, Table 1). Multiple linear least squares regression (Bevington 1969) of the observed $[\ln(I_u/I')]$ on corresponding observed values of Z_s and [Chl] yielded the parameter estimates summarized in Table 1.

RESULTS

Light transmission

Light transmission through ice, snow and algae in 1985 was clearly related to both the depth of snow cover and to the areal pigment concentration (Fig. 2). Our simple light transmission model (Equation 1) provided a highly significant fit to the data and explained 93 % of the variation. We excluded a single point representing the peak observed standing crop, 110 mg m⁻² of chlorophyll *a* under thin snow cover because its presence caused unacceptable pattern in the residuals of the model against [Chl]. The pattern, and implied lack of fit, disappeared when the point was removed, and the residuals were also free of pattern when plotted against snow cover depth. The chief effect of excluding the point was to increase k_{chl} from 0.028 to the final value of 0.035 m² mg⁻¹ (Table 1). This suggested that k_{chl} might decrease at the higher [Chl] values, but the single point was inadequate to resolve such a trend.

Transmission measurements were made again in 1986, with the fitted model explaining 83 % of the variation. The 1986 sampling was largely limited to 2 snow depths (thin snow cover, with or without the natural snow cover removed immediately before the light measurements) so the data base was more limited with regard to snow effects. The dynamic range in [Chl] was nearly twice as large in 1986 as in 1985, however, with peak crops exceeding 200 mg m⁻² of chlorophyll *a*. The fitted value of 0.0116 m² mg⁻¹ for k_{chl} in 1986 (Table 1) therefore

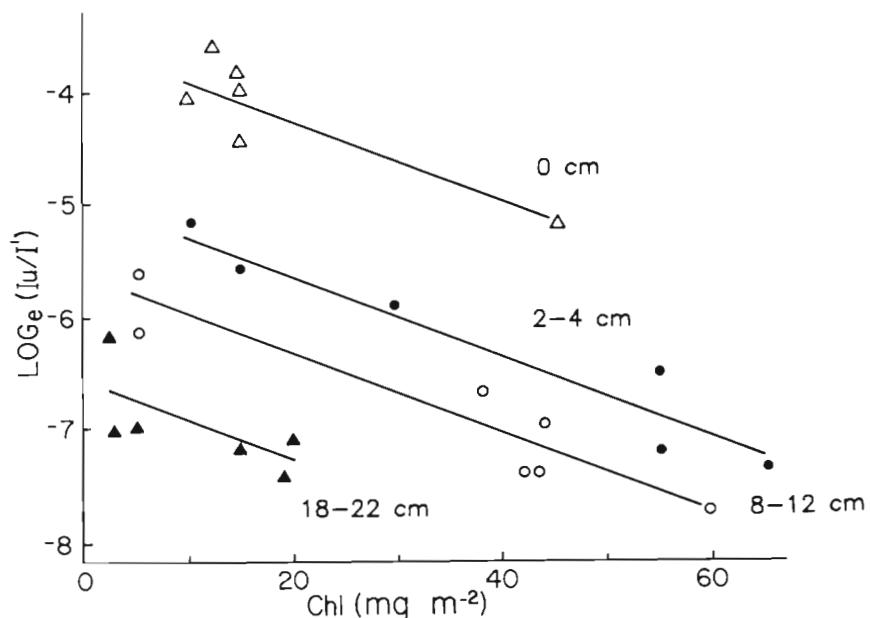


Fig. 2. Observed under-ice transmittance for 1985 versus areal chlorophyll standing crop, with the fitted model (Table 1) shown by solid lines. Snow depths were 0 cm, 2 to 4 cm, 8 to 12 cm and 18 to 22 cm

Table 1. Parameters (and their standard errors, SE) of a model for transmission of light through ice and snow in 1985 ($n = 25$) and 1986 ($n = 43$) near Resolute, N.W.T. Model (Equation 1) and parameters are explained in the Introduction; they were fitted by multiple linear regression. Fitted values of the model are shown for 1985 in Fig. 3

Parameter	1985		1986	
	Value	SE	Value	SE
$a + k_i Z_i$	2.469	0.356	3.277	0.332
k_{chl} ($m^2 \text{ mg}^{-1}$)	0.0350	0.0044	0.0116	0.0010
k_s (m^{-1})	9.44	1.47	10.75	3.11
c	1.134	0.254	0.570	0.172
$a + k_i Z_i + c$	3.603	0.437	3.847	0.374

might indeed indicate a decrease at higher values of [Chl], perhaps as a consequence of spectral narrowing. We tried to confirm this inference by fitting the transmission model only to those 1986 data for which [Chl] was less than 80 mg m^{-2} , anticipating a higher value of k_{chl} . The fitted k_{chl} changed only to $0.0102 \text{ m}^2 \text{ mg}^{-1}$, however, nor did the residuals of the full data set reveal any pattern suggestive of declining k_{chl} at higher [Chl]. Except for the single point in the 1985 data, therefore, we could find no direct evidence in our data set for a systematic decrease of k_{chl} at higher values of standing crop.

Variation in the fitted values of $(a + k_i Z_i)$ and (c) between 1985 and 1986 was not quite significant at the 95 % confidence level (Table 1), but the direction of the differences suggests that freshly-cleared ice (1986) has a higher albedo than ice kept continuously free of snow (1985). The fitted value for k_s was very similar between years (Table 1).

Photosynthesis and metabolism

Results of the experiments on oxygen exchange were pooled to form a common estimate of the relationship between net primary production and irradiance (Fig. 3). The data were pooled because individual experiments yielded only 5 points, too few for meaningful regressions, and we sought to determine a characteristic growth efficiency for the cells. Most of the measurements were on populations from low (2 to 4 cm) snow cover, but populations from heavier snow covers were also sampled twice. In all, the observations represent populations sampled from the beginning of May to early June, 1985.

Oxygen production rates represent net production (see Discussion), and so were fitted to Equation 4, with the addition of a respiration term R^B , by nonlinear least squares regression (Fig. 3). The residuals showed little trend against irradiance, indicating that the function was a reasonable description of the data. Growth efficiency $(1 - R^B/P_m^B)$ estimated from the fitted parameters was 87 % (with a standard error of 5.7 % calculated by propagating the error in R^B and P_m^B ; Bevington 1969). There was no indication of photoinhibition at any irradiance up to the maximum of $33 \mu\text{E m}^{-2} \text{ s}^{-1}$ used in the oxygen experiments.

The oxygen experiments could not resolve possible differences in photosynthetic response among populations from different snow covers. ^{14}C experiments offered much greater resolution of the light response (24 different PFR per curve), and the results of fitting Equation 4 are summarized in Table 2.

The photosynthetic parameters did not vary significantly among populations from different depths of

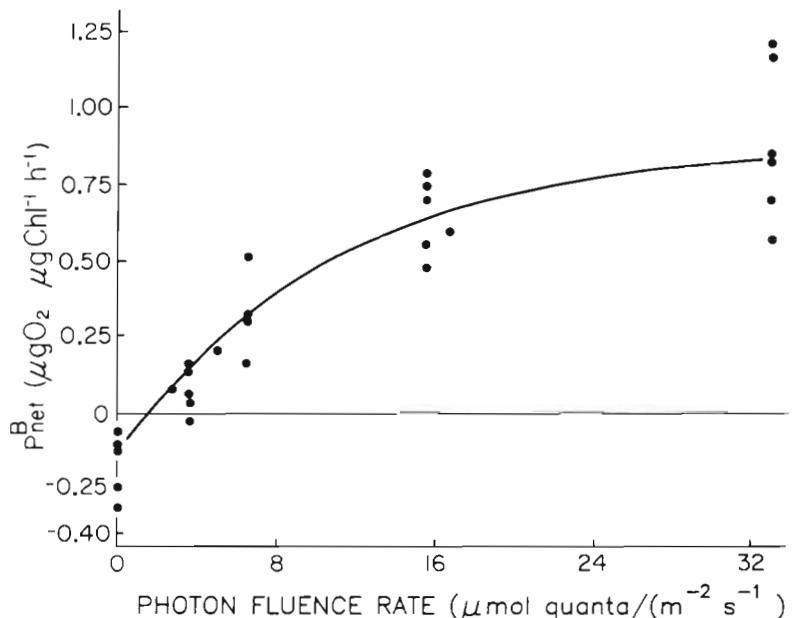


Fig. 3. Net oxygen evolution rate of ice algae as a function of PFD, together with the fitted model: $P_n^B = P_m^B [1 - \exp(-I/I_k)] - R^B$. The fitted parameter values and their standard errors were 1.010 ± 0.093 for P_m^B , 10.87 ± 3.01 for I_k ; and 0.130 ± 0.059 for R^B .

Table 2. Parameters (\pm SE) of the photosynthetic light response (Equation 4) of Arctic ice algae, measured by tracer carbon assimilation in 1985. Number n is the number of photosynthetic light response curves (24 rate measurements each) used to calculate the mean parameter values shown

Parameter	Snow cover (cm)	
	0	2–22
P_m^B *	1.170 \pm 0.844	0.600 \pm 0.130
α^{**}	0.061 \pm 0.047	0.125 \pm 0.030
I_k^{***}	19.1 \pm 1.7	4.8 \pm 0.6
n	5	17
• $\mu\text{gC} (\mu\text{gChla})^{-1} \text{h}^{-1}$		
•• $\mu\text{gC} (\mu\text{gChla})^{-1} \text{h}^{-1} (\mu\text{mol quanta m}^{-2} \text{s}^{-1})^{-1}$		
••• $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$		

snow cover ($p > 0.05$, multiple range t -test) but the populations from the cleared area had significantly higher P_m^B , lower α and higher I_k than populations from snow-covered areas ($p < 0.05$, paired t -test). We therefore used the mean parameter estimates for all the snow-covered populations, but a separate mean value for the clear populations (Table 2). The standard errors for P_m^B and α were large, especially for the clear populations, because the parameter values varied among sampling dates. The parameters did not increase or decrease systematically throughout the growth season, but instead appeared to oscillate in phase with the fortnightly rhythm of tidal amplitude (Cota & Horne unpubl.). Because P_m^B and α co-varied, the standard error of I_k was relatively small (Table 2).

Standing crops and production

B_{\max} was predicted from Equation 9, with I_o calculated from the fitted light transmission model (Table 1) and downwelling incident solar radiation (I' , PAR) averaged over 3 d periods to smooth the variations imposed by changing weather conditions. Over the main growth season (roughly Apr 1 to Jun 1), the resulting values for I_o ($\mu\text{E m}^{-2} \text{s}^{-1}$) ranged from about 14 to 40 (clear patch), 3 to 10 (2 to 4 cm snow cover), 1.6 to 6 (8 to 12 cm) and 0.7 to 2 (18 to 22 cm). There was little difference in I_o , under comparable snow covers, between 1985 and 1986.

B_{\max} increased during the main algal growth season, but most of the increase occurred before May 1 (Julian day 121, Figs. 4 and 5) with relatively stable values thereafter. B_{\max} increased with decreasing snow depth, except that populations growing under areas kept clear of snow were predicted to have a B_{\max} no larger than those under thin snow cover, a consequence of their elevated values of I_k (Table 2). The predicted maximum

crops were 70 to 80 and 200 to 250 mg m^{-2} of chlorophyll *a* under the lower snow covers in 1985 and 1986, respectively, reflecting the smaller value of k_{chl} in 1986.

B_{\max} appeared to be a realistic upper limit to the standing crops observed under natural snow cover in both 1985 and 1986 (Figs. 4 and 5). Instances of higher crops were observed, but were never observed to be sustained; the thin (2 to 4 cm) snow cover populations in 1985 in particular appeared to vary about B_{\max} through most of May. Populations under heavy snow cover in 1985 achieved a large standing crop on our last sampling date, but it is doubtful that the peak was sustained. Ice algae began to shed from the ice into the water column in early June (Smith et al. 1987) signalling the decline of the ice algal bloom shortly after the end of our 1985 observation period (Fig. 4).

B_{\max} greatly overestimated the crops actually attained in the artificially cleared area (Fig. 4). The observed crops in the cleared area were also lower than those under low or moderate snow cover. According to the measured photosynthetic light responses (Table 2) the algae should not have been photoinhibited in the clear area.

P_n was calculated from Equation 6, and the resulting values for net photosynthetic carbon production rate ($\text{mgC m}^{-2} \text{d}^{-1}$) were integrated by linear interpolation to calculate the expected rate of particulate organic carbon (POC) accumulation in the ice (Figs. 5 and 6). POC observed under natural snow cover in 1985 roughly paralleled the calculated values, but tended to be larger than the model predictions early in the growth season. In the late season, predicted POC accumulation exceeded the observed for 2 to 12 cm snow cover, but was less than the observed for 18 to 22 cm snow cover (Fig. 6). The calculated accumulation of POC was much larger than that observed under bare ice through most of the growth season.

Calculated POC accumulation was larger than the observed in 1986 (Fig. 5). The 1986 POC values were not measured directly, but were calculated from the observed chlorophyll crops and a POC:Chlorophyll *a* ratio of 21.9 derived from biochemical assays (Smith et al. 1988). The 1985 ratio was about 50 for algae under thin or no snow cover but even the larger ratio would not eliminate the disparity.

P_{opt} , the light-limited upper bound to production, was calculated by evaluating Equation 6 for $[\text{Chl}] = B_{\max}$ (Table 3). P_{opt} was much greater in 1986 than 1985, P_n attained P_{opt} , by definition, for all those populations for which observed $[\text{Chl}]$ equalled B_{\max} . The season-average values of P_n , calculated by dividing the predicted accumulation of POC (Figs. 5 and 6) by the length of the observation period, were less than P_{opt} because $[\text{Chl}]$ was often less than B_{\max} (Table 3).

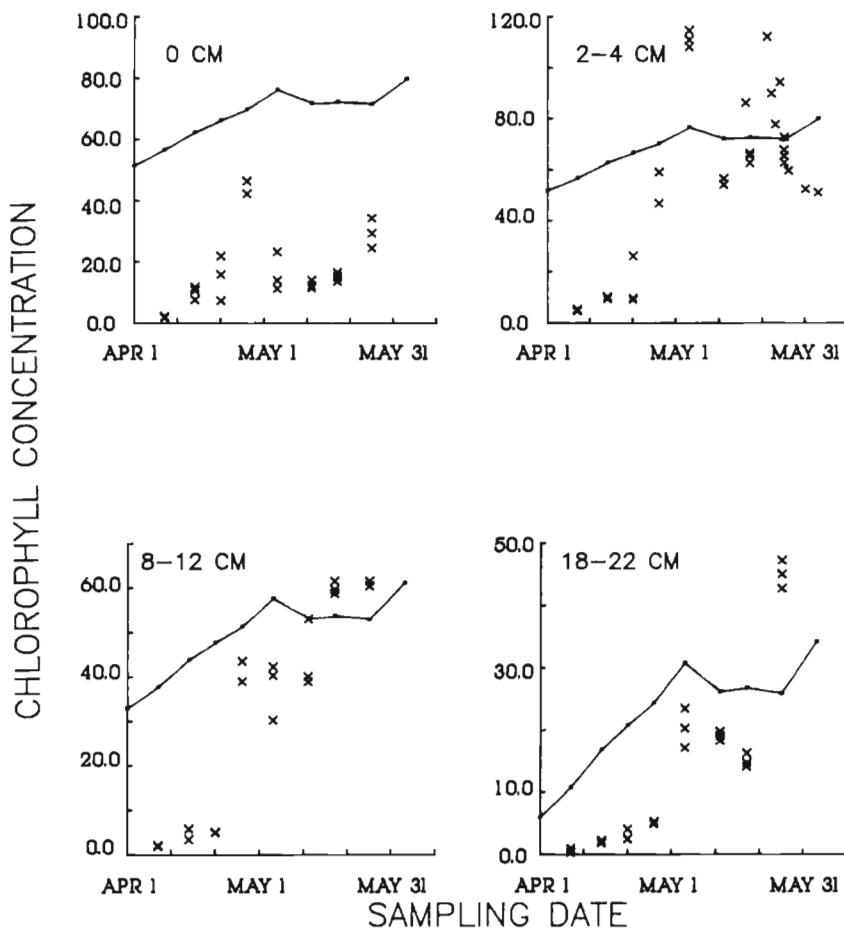


Fig. 4. Observed seasonal dynamics of chlorophyll *a* (mg m^{-2}) in sea ice in 1985 under 4 different depths of snow cover. Solid lines: B_{\max} (Equation 9). Note different scales for chlorophyll among panels

On season-average basis, observed rates of POC accumulation were similar to the rates calculated from P_n for natural snow cover in 1985, and the maximum rates of POC accumulation observed during the observation period approached or even exceeded P_{opt} (Table 3). The difference between observed POC accumulation and calculated production provides an estimate of potential export from the ice algal community, and ranged from a small negative value for heavy snow cover to a much larger positive value for the clear area in 1985 (Table 3). The export values so calculated are for the period preceding the decline of the algal bloom, when the major release of cells from the ice occurs. In 1986, the calculated production was much greater than the observed POC accumulation, leading to a large predicted export rate compared to any of the other populations we encountered (Table 3).

Other arctic sites

To calculate B_{\max} corresponding to crops reported from other locations in the arctic (Table 4), values of incident solar radiation for all locations except Resolute, 1984 and Point Barrow, Alaska, were obtained from reasonably proximate Environment Canada weather stations, in the same units and from the same instrumentation as the Resolute data. We used the 30 yr climatic norms rather than values specific to the particular years studied, a minor inaccuracy. Incident solar radiation, according to the climatic norms, ranged only about $\pm 10\%$ among all the locations at latitude $>60^\circ\text{N}$ during the ice algal growth season. Incident radiation for Point Barrow was estimated from the Environment Canada Inuvik weather station. The Resolute 1984 calculations, like those in 1985 and 1986, were based on daily radiation at Resolute. The parameter values used to predict B_{\max} (Equation 6) were those that we estimated and then used in our predictions for crops near Resolute in 1985.

All the literature values for arctic ice algal standing crop (except for one under deep snow) were less than the calculated B_{\max} (Table 4). The disparity would be yet greater had we used our 1986, rather than our 1985, value for k_{chl} . It would seem that our calculated maxima are indeed upper limits that published results to date do not surpass with any regularity.

Table 4 includes values for Resolute in 1984, col-

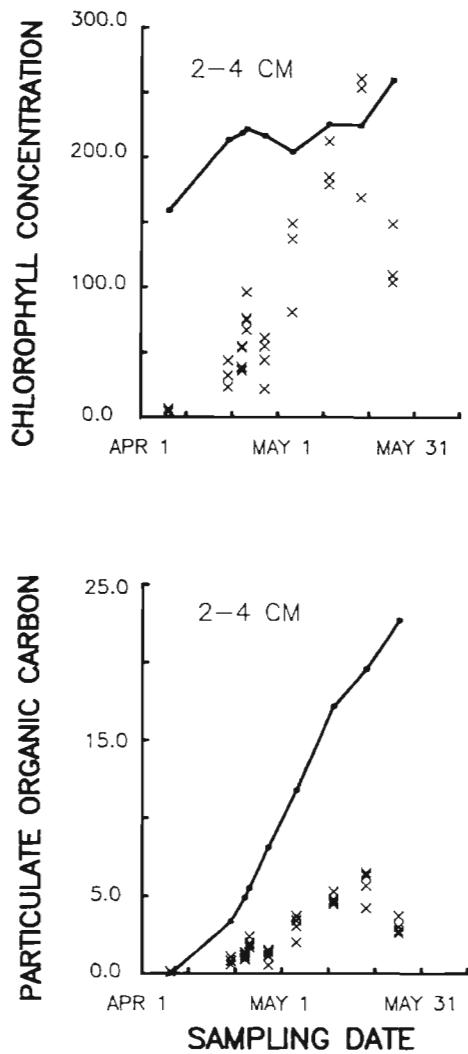


Fig. 5. Observed seasonal dynamics of chlorophyll *a* (mg m^{-2} , upper panel) and POC (mgC m^{-2} , bottom panel) in sea ice covered with 2 to 4 cm of snow in 1986. Line in the upper panel: B_{\max} ; line in the lower panel: cumulative POC calculated from net photosynthetic production rate, P_n

lected at sites closer to shore than in subsequent years. A transect was also sampled in 1984, from near-shore to several km offshore. Sampling again spanned the main algal growth season, as it did in 1985 and 1986, and the values reported are the maximum observed. Seasonal means follow similar patterns. Maximum crops were, like the literature values, less than B_{\max} . As the range of values for the 3 cm snow cover shows (Table 4), however, the standing crops increased about 4-fold in the offshore direction, a difference greatly exceeding the statistical uncertainty in the crop estimates. The abundance of amphipods, known consumers of ice algae, was simultaneously observed to decrease in the offshore direction (G. F. Cota unpubl.).

DISCUSSION

Previous studies in the Arctic have demonstrated positive correlations between light availability and ice algal abundance and production rates (Clasby et al. 1976, Horner & Schrader 1982) but have not pursued the effects of different light availabilities throughout the growth season. We have shown that ice algae growing under natural snow cover at our site near Resolute in 1985 and 1986 attained crops equalling the theoretical maximum imposed by self-shading (Figs. 4 and 5), and that through the main growth season of 1985 both calculated net production and observed POC accumulation rates in situ varied directly with light availability (Table 3). Crop sizes and production rates of ice algae (in bottom ice) also varied directly with available light through most of the growth season in McMurdo Sound, Antarctica (Grossi et al. 1987) and the early to mid season in Hudson Bay (Gosselin et al. 1986). Such results demonstrate that shortage of light is commonly a limiting factor to ice algal growth in a variety of polar marine ecosystems.

The crops observed under artificially cleared snow in 1985 (Fig. 4 and 6) and at sites elsewhere in the Arctic (Table 4) were much less than the theoretical maximum. The potential inadequacies of conventional sampling techniques (Clasby et al. 1976, Welch et al. 1988) are not systematically related to the apparent discrepancies of standing crops, but 3 other general factors could be involved. Our light transmission model might overestimate light availability in some cases, as discussed below. Alternatively, the efficiency of light use might differ from the values in the model; in particular, k_{chl} , I_k and R^B/P_m^B might be larger. The remaining major possibility is that natural populations are subject to additional losses (Apollonio 1965, Grossi et al. 1987) or to growth-limiting factors (Maestrini et al. 1986, Smith et al. 1987) other than light. In at least 2 cases, our results point to increased losses as important factors in addition to the available light in determining ice algal abundance.

Diminished algal crop sizes at high irradiance levels, as in our experimental snow-free area, have been reported before and attributed variously to photosynthetic inhibition (Gosselin et al. 1986) and to physical deterioration of the ice and bleaching of the algae (Apollonio 1961, 1965). Our measurements failed to reveal photoinhibition of photosynthesis in the clear ice populations, while direct measurements of POC production showed that bleaching was only a partial explanation (Fig. 6, Table 3). The light transmission model is not likely to be seriously wrong, since it was fitted, in part, to data from the clear patch without obvious systematic error. In fact, no error in our model would explain why observed pigment and carbon

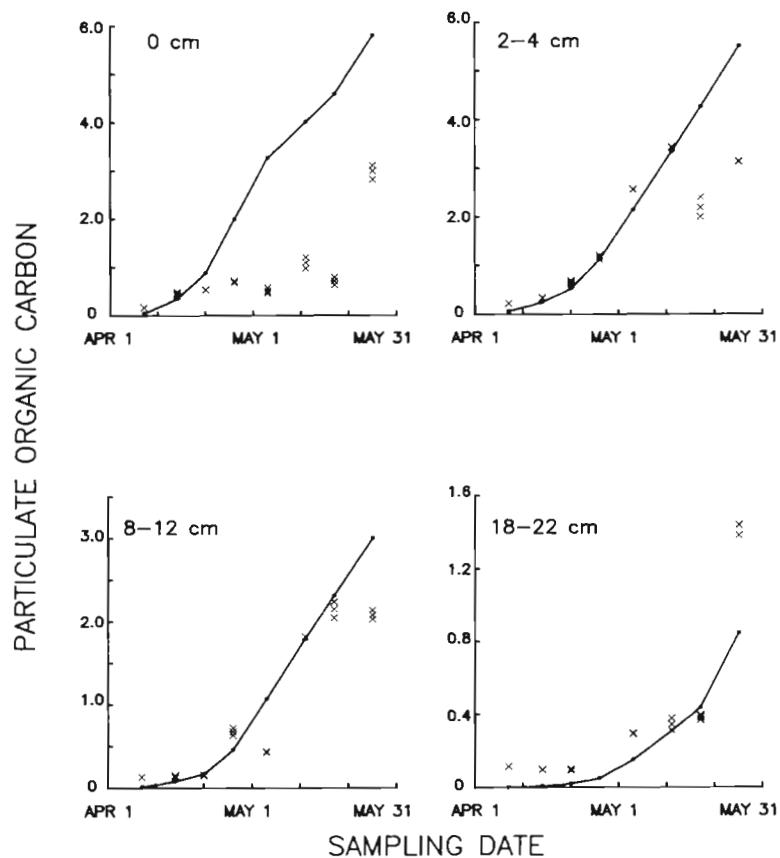


Fig. 6. Observed seasonal dynamics of POC (mgC m^{-2}) in sea ice in 1985 under 4 different depths of snow cover. Solid lines: cumulative POC calculated from net photosynthetic carbon production rate, P_n . Note different scales for POC among panels

standing crops were usually lower under snow-free ice than ice with thin snow cover. Increased losses from the clear ice populations, perhaps through excessive light absorption and consequent deterioration of the ice, therefore seem the likeliest explanation. If so, production under the thinnest snow covers was poised between light limitation and light excess. The rapid increase of light penetration accompanying snow-melt can be expected to induce losses similar to those we infer under the experimental clear patch, and may be instrumental in ending the ice algal bloom (Horner 1985).

The 1984 Resolute results present the other case for control of crops by loss rates. The observed crops were again smaller than the theoretical maximum, but the variation of crop sizes and amphipod abundance along the sampling transect suggested significant control of algal crops by amphipod grazing (Cross 1982). Apollonio (1965) reported the presence of amphipods in some ice cores, and also speculated that grazing influenced algal crop sizes in Frobisher Bay. It seems likely that amphipod grazing may have influenced many of the results culled from the literature (Table 4), which were also often from sites either nearshore or in shallow water columns. Both characteristics favour

higher amphipod abundance in the Resolute vicinity (Welch pers. comm.).

For sites other than Resolute, the low crops observed relative to B_{\max} (Table 4) may indicate that light alone is not limiting to maximum crop size and production at those sites. Alternatively, our model's theoretical maximum may be too high, i.e. extrapolation of our estimated parameter values to other sites and years may be unjustified. Our own observations in 1985 and 1986 showed that the theoretical maximum can vary widely even at the same site due solely to variability of the chlorophyll *a*-specific diffuse attenuation coefficient. Photosynthetic parameters and algal metabolism may also vary among sites and through the growth season in various ice communities (Cota 1985, Gosselin et al. 1985, 1986, Palmisano et al. 1985). Photoadaptive changes in photosynthetic parameters, including respiration rates and cell composition, could significantly alter the fundamental underpinnings of the model as expressed in Fig. 1. We were unable to demonstrate significant variation in the average values of photosynthetic parameters among populations grown under different snow covers and light regimes near Resolute, however, except for those under the (artificially) cleared areas. Photoadaptive differences probably do exist

Table 3. Carbon production rates of ice algae near Resolute, N.W.T. P_{opt} = theoretical maximum net production rate; P_n = in situ production rate calculated (Equation 6) for the observed populations; P_c = observed change of particulate organic carbon concentration in the ice. Export is the difference between production (P_n average) and accumulated POC (P_c average), representing loss of algal biomass from ice during growth season. Ranges are standard deviation, as percent of the mean, based on triplicate measurements of algal standing crop (for P_n) or POC concentration (for P_c) or both (for Export), so annual and daily rates have the same error range. Observations are from 1985 season except as noted

	Snow cover (cm)				
	0	2-4	8-12	18-22	2-4 (1986)
Daily rates (mgC m⁻² d⁻¹)					
P_{opt}	323.7	316.0	156.5	32.96	953.4
P_n (average)	116.8	121.2	66.3	20.61	462.9
	± 8.2	± 6.8	± 4.2	± 9.6	± 18.0
P_c (maximum)	283.2	198.9	199.5	132.2	319.6
	± 6.0	± 2.5	± 5.0	± 5.6	± 7.7
(Average)	58.5	94.2	50.3	27.6	132.2
	± 5.6	± 4.8	± 7.6	± 6.6	± 18.0
Annual rates for 50 d growth season (gC m⁻² yr⁻¹)					
P_n	5.8	6.1	3.3	1.15	23.1
P_c	2.9	4.7	2.5	1.40	6.6
Export	2.9	1.4	0.8	-0.25	16.5
	± 16.4	± 52.5	± 27.9	± 28.2	± 26.0

Table 4. Collected literature reports of areal concentration of ice algae chlorophyll in arctic locations, together with the predicted maximum possible light-limited concentrations, B_{max} , and the calculated PFD reaching the algae, I_o ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$). Sources are: Jones Sound, Apollonio (1961, 1965); Frobisher Bay, Grainger (1977); Point Barrow, Clasby et al. (1976); Barrow Strait, Robeson Channel and Hudson Bay, Dunbar and Acreman (1980); Resolute 1984, G. F. Cota (unpub.)

Location	Thickness of ice (cm)	Thickness of snow (cm)	I_o	Chlorophyll a conc. observed	B_{max} (mg m ⁻²)	B_{max} (mg m ⁻²)
Jones S.	165	21	1.62	23.0	30.0	
Jones S.	190	10	4.58	23.0	60.0	
Frobisher	150	5-20	3.00	4.6	48.0	
Frobisher	150	37	0.29	1.5	0.0	
Frobisher	150	10	3.92	9.1	55.6	
Pt. Barrow	162	5	6.43	30.0	69.8	
Pt. Barrow	162	5	6.43	24.0	69.8	
Robeson Ch.	194	1	10.09	10.3	82.6	
Barrow St.	160	2	8.93	13.8	79.2	
Hudson Bay	119	3	4.53	25.3	59.8	
Resolute 1984	180	0	34.8	12.2	77.1	
	180	3*	8.50	11.6	77.5	
	180	3**	8.50	45.6	77.5	
	180	10	4.39	18.3	58.6	
	180	20	1.71	20.7	31.6	

* Inshore site, ** offshore site

among populations from different natural snow covers, but were too small to be detectable with our moderate sample size. Similarly, photoadaptive differences in cell composition ratios such as chlorophyll:carbon were significant but small except for populations from the cleared areas (Smith et al. 1988). More work is required to characterize the variability and predictability of photoadaptive parameters in ice algal populations, but our data suggest that at least one important source of variability is the light attenuation parameter, k_{chl} .

Our fitted value for k_{chl} in 1986 ($0.0116 \text{ m}^2 \text{ mg}^{-1}$; Table 1) was similar to the mean spectral absorption coefficient recently reported for antarctic ice algae (SooHoo et al. 1987) and was likely near the minimum value that can be expected (Bannister & Weidemann 1984). The relatively large 1985 value of $0.035 \text{ m}^2 \text{ ml}^{-1}$ probably reflects the problems of measuring absorption coefficients by the regression of transmittance against chlorophyll concentrations (Bannister & Weidemann 1984), which mostly act to inflate the estimate. The strong narrowing of the light spectrum into the blue wavelengths in passage through sea ice (Grenfell & Maykut 1977, Maykut 1985) may also contribute to a high value for k_{chl} , but would not explain the inter-annual variability of k_{chl} . Non-algal light absorbing and scattering material that co-varies with the algae, and changes in the absorbing and scattering properties of the ice itself, are likely causes of the massive change in k_{chl} between years. Spectral narrowing of light transmitted through the ice and associated algae due to algal light absorption results in a predominantly green, rather than blue, spectrum and relatively low algal absorption coefficients (Bannister & Weidemann 1984, SooHoo et al. 1987). While our observed algal standing crops were certainly high enough to cause major spectral modification, we could not consistently demonstrate that biomass levels influenced our regression estimates of k_{chl} . We therefore have no positive evidence to suggest the factors responsible for apparently major variations in k_{chl} .

Although it is clear that our k_{chl} cannot be regarded as an accurate estimate of the algal absorption coefficient, it should be emphasized that it is the parameter needed in order to calculate the light reaching the algae, and also the amount ultimately passing through to the water column. Algal light absorption alone appears unlikely to explain the inter-annual variations in k_{chl} . Identifying the additional components of k_{chl} is important because the parameter is critical to the production and standing crops (Equations 6 and 9) that can be attained for a given supply of light, and its variation is one of the largest sources of uncertainty in our predictions.

Our model's fitted values for 'a' (Table 1) imply by difference an albedo for bare ice of 0.62 to 0.76 (1985 vs

1986) if we assume a typical attenuation coefficient of 0.01 cm^{-1} (Thomas 1963, Grenfell & Maykut 1977, Maykut 1985) for our average ice sheet thickness of 1.85 m, and our fitted value for 'c' would then imply an albedo of 0.86 to 0.88 for snow. Such albedos are at the high end of the range cited by Maykut (1985) but would be substantially smaller if we assumed a larger attenuation coefficient for ice from within the previously published range (ca 0.008 to 0.012 cm^{-1}) or a lower factor for converting total downwelling surface radiation to PAR downwelling. Our k_s values (Table 1) are definitely at the low end of the range of previously published values for dry snow (0.18 to 0.45 cm^{-1} : Thomas 1963, Grenfell & Maykut 1977, Warren 1982, Maykut 1985) so we may suspect that our estimates of light transmission to the algae are generous. More such measurements are needed to meet a long-standing need for better practical models for light transmission suitable to ecological applications (Welch et al. 1987).

The rate of planktonic primary production in Arctic shelf waters has been estimated to average $27 \text{ gC m}^{-2} \text{ yr}^{-1}$ for a 120 d growth season, or $13.5 \text{ gC m}^{-2} \text{ yr}^{-1}$ for a probably more realistic 60 d season in the High Arctic (Subba Rao & Platt 1984). Our calculated production rates, P_n , thus predict that production in the ice under thin snow cover, in 1986, could equal or even exceed that in the water column (Table 3). Our annual production estimates should be conservative because we assumed a 50 d growth season (matching our main observation period) but some production undoubtedly occurs outside that interval; the 1985 rates could be twice as large if production continued throughout June. The calculated export rates (Table 3) predict that half or more of production can be exported even during the main algal growth season, but mainly from areas of zero or thin snow cover. In situ measurements are needed to confirm the predicted export of production to the water column near Resolute, but a significant export rate is consistent with results obtained by in situ incubations elsewhere in the Arctic and Antarctic. Grossi et al. 1987 reported an even larger proportional export, about 90 % of total production in a snow-free area in McMurdo Sound. A smaller proportion, about 30 %, was exported from populations growing under 5 cm snow cover. Results from the Chukchi Sea (Clasby et al. 1976) suggest approximately 50 % export, if the observed increase of chlorophyll *a* standing crop during the observation period is converted using a ratio of 100 mgC:mg Chlorophyll *a*. At Resolute, copepods have been shown to feed upon ice algae throughout the algal growth season (Conover et al. 1986), confirming that algae do reach the water column. The mechanisms of export, and the fate of the exported material, are important subjects for further study (Grossi et al. 1987).

We have previously presented evidence, from

patterns of intracellular photosynthate allocation, for nutrient limitation of photosynthetic rates in the ice algal populations growing under thin snow cover in 1985 (Smith et al. 1987). The results presented here indicate that in situ production and standing crop were light limited. This seeming contradiction may reflect the vertical stratification of growth conditions, from relatively plentiful light but marginal nutrient supply at the top of the algal layer to extreme shade but better nutrient supply at the bottom. Measurements of photosynthesis in samples of the whole algal community will be influenced by cells adapted to both extremes even if, as our model assumes, light is the final limiting factor to crop size and production in situ. Results from Hudson Bay (Gosselin et al. 1986, Maestrini et al. 1986) and the bottom-ice community in Antarctica (McConville et al. 1985, Palmisano & Sullivan 1985, Grossi et al. 1987) have also given indications of both light and nutrient-limitation, and may similarly reflect the heterogeneity of physiological condition in natural populations. Ice algae are likely to adapt to strong vertical gradients in physical and chemical conditions, in their photosynthetic parameters, nutrient utilization kinetics, and other physiological features. Such adaptation may prove crucial to a more complete understanding of ice algae ecology.

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