Polar Biol (1984) 3:191–201

Polar Biology

Primary Production of Arctic Waters

D. V. Subba Rao and T. Platt

Marine Ecology Laboratory, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia B2Y 4A2, Canada

Received 30 January 1984; accepted 14 August 1984

Summary. Using data that have become available during the last ten years we have reestimated the annual production by phytoplankton in the arctic marine ecosystem. The new figure is some sixteen times higher than an estimate made in 1975. This is of considerable significance regionally, but still does not, of itself, imply that global phytoplankton production is underestimated at present.

Introduction

A previous estimate of total primary production for arctic waters was 13×10^6 t C y^{-1} (Platt and Subba Rao 1975). This calculation was made as a component of a wider estimate of global production by marine phytoplankton: it was based on very limited data, and sweeping assumptions had to be made.

In the intervening years, the Marine Ecology Laboratory (MEL) has conducted six cruises to the eastern arctic, during which studies on primary production have been carried out. Other groups have also accelerated their research on the primary production of the subarctic and arctic waters as is evident from the literature (see Nemoto and Harrison 1981, Harrison et al. 1982). Photosynthetic rates of ice-biota are becoming available (see Alexander 1981, Horner and Schrader 1982). Based on this enhanced data base a recalculation of annual total primary production in the arctic waters is justified, and is reported here. The figures require a substantial upward revision from those estimates made in the early 1970's.

Material and Methods

Geographic Region

In this paper, waters north of 65° which include the Arctic Basin and Norwegian Sea are considered as arctic waters: a variety of environmental conditions is represented. They occupy an area of 13.10×10^6 km^2 (see Tables 13 and 19, Moiseev 1971). Of this, the shelf area (<200 m) occupies 4.90×10^6 km^2, and the offshore slope covers 8.2×10^6 km^2 (Table 19, Moiseev 1971). Weeks (1976) estimated that 4% of the arctic basin (shelf area) and 5% of the offshore province are covered by young ice (first year ice) during summer, which corresponds to a total of about 0.6×10^6 km^2. Young ice serves as a substratum for algal growth. The extent of the sea ice cover varies with the season from a summer average minimum of 5.2×10^6 km^2 to a winter average maximum of 11.7×10^6 km^2 (CIA 1978). The ice thickness also varies between the thinner (0– <2 m), weaker first year ice and the thicker (up to 30 m), stronger multilayer ice (Weeks 1976).

Details of sampling during the arctic cruises from our laboratory are given in Table 1. At each station standard hydrographic measurements were made. Chlorophyll *a*, an index of phytoplankton biomass (B), was determined by the fluorometric method of Yentsch and Menzel (1963). The ^{14}C method (Steemann Nielsen 1952) was used to determine the rate of photosynthesis (P) at various levels of irradiance (I). Details of the experimental methods are given in Irwin et al. (1980, 1982, 1983a, 1983b). The mathematical formulation of the relationship between P and I is according to Jassby and Platt (1976) and Platt et al. (1980, 1982).

Total incident light was measured with an Eppley 40-junction black and white pyramometer and the output was integrated hourly using a Licor 550 printing integrator. Using a Licor Li 185A Quantum meter fitted with a 190 S underwater quantum sensor photosynthetically active radiation was measured in each bottle position.

The hyperbolic tangent equation of Jassby and Platt (1976)

$$P^B = P^B_m \cdot \tanh \cdot (\alpha I / P^B_m) \tag{1}$$

was used in the earlier investigations that employed low light incubators (Table 1, Labrador Sea, Baffin Bay Cruises 1977–1978). In this

Table 1. Sampling details during the MEL arctic cruises

Region	Period	No. expts.	Sampling depth (m)
Labrador Sea	15 Oct–31 Oct 1977	29	10–30
Labrador Sea	11 Feb–28 Feb 1978	32	10–30
Baffin Bay	25 Aug–15 Sept 1977	30	10–30
Baffin Bay and Lancaster Sound	30 Aug–14 Sept 1978	30	3–54
Baffin Bay	1 Aug– 3 Sep 1979	97	5–30
Eastern Canadian Arctic	16 July–26 Aug 1980	58	0–64
Foxe Basin	27 Aug– 7 Sep 1981	13	0–40

equation P^B_m, assimilation number, denotes maximum primary production (at light saturation) normalized to biomass and expressed as mg C · mg Chl $a^{-1}h^{-1}$; α is the inital slope of P-I curve expressed as mg C · mg Chl $a^{-1}h^{-1} \cdot W\,m^{-2}$ and I is the photosynthetically active radiation (PAR) measured in $W\,m^{-2}$.

I_k – the light adaptation index is derived as:

$$I_k \equiv P^B_m/\alpha\,. \tag{2}$$

In subsequent cruises when high light intensity incubators were used a continuous exponential function equation was used by Platt et al. (1980) which is expressed as follows:

$$P^B = P^B_s \cdot (1 - e^{-\alpha I/P^B_s}) \cdot e^{-\beta I/P^B_s} \tag{3}$$

where P^B_s is the rate of light saturated photosynthesis if there were no photoinhibition and expressed in units similar to P^B_m, i.e. mg C · Chl $a^{-1}h^{-1}$.

β denotes photoinhibition and has the same units as α, i.e. mg C · mg Chl $a^{-1}h^{-1} \cdot W\,m^{-2}$. In addition to the measured parameters P^B_m, P^B_s, α, β, I_K, two additional parameters I_m and I_b are also derived from the equation, as follows:

I_m = light intensity optimal for photosynthesis;

$$I_m = \frac{P^B_s}{\alpha} \log e \left(\frac{\alpha + \beta}{\beta}\right) \text{ in units of W m}^{-2}. \tag{4}$$

Simulated primary production profiles, a product of chlorophyll and primary production, were generated following the method of Herman and Platt (1983) and Platt and Herman (1983). An underwater light meter, attached to a submersible pump, was used to obtain the light irradiance profile and attenuation coefficient; chlorophyll values were based on fluorescence profile. Production per unit volume (mg C $m^{-3} \cdot h^{-1}$) was calculated by multiplying the chlorophyll with corresponding mg C Chl a h^{-1} obtained from the P-I curves (Jassby and Platt 1976) and values for the various depths were integrated for column rates. Locations of the Arctic stations discussed in this compendium are shown in Figs. 1 – 3.

Results and Discussion

The ranges of variation of phytoplankton biomass and primary production from our own arctic cruises are shown in Table 2. They are consistent with the ranges from a wider geographical area compiled from the literature and presented in Table 3.

Table 2. Biomass and primary production in the arctic seas based on MEL cruises

	Chlorophyll a µg l^{-1}	Primary production mg C h^{-1} m^{-3}
Range	0.05 – 15.0	0.02 – 14.01
$\bar{X}$	1.7	2.73
S. E.	0.12	0.18
N	320	320

The maximum specific production (assimilation number) ranged between 0.11 and 10.33 mg C mg h^{-1} Chl a^{-1} with a mean of 1.96 (Table 4). This mean is of similar magnitude to values found by other workers (Table 5) in the Arctic (1 – 1.5).

The assimilation numbers from the arctic, of course, are generally low compared to those from the temperate and tropical waters (Platt and Subba Rao 1975), but the ranges overlap with those from the Antarctic; 0.48 – 2.04 (Saijo and Kawashima 1964)), 0.63 – 2.65 (Burkholder and Mandelli 1965) 0.021 – 1.184 (Whitaker 1982), 0.5 – 5.2 (Jacques 1983), 0.37 – 0.74 (El-Sayed and Weber 1982), 0.07 – 2.91 (Neori and Holm-Hansen 1982).

The α values in the region of our sampling ranged between <0.01 and 0.23 mg C (mg Chl a)$^{-1}$ h^{-1} (W m^{-2})$^{-1}$. Smaller sub-sets of the data had ranges <0.01 – 0.14 from the eastern arctic (Gallegos et al. 1983) and 0.04 – 0.10 from the Foxe Basin (J. C. Smith et al. in press, and in preparation). The present mean I_k of 29 W m^{-2} and I_m of 122 W m^{-2} (Table 3) compare favourably with the sub-set means (I_k = 25 W m^{-2}, I_m = 126 W m^{-2}) reported from Baffin Bay (Platt et al.

Table 3. Comparison of biomass and primary production in the arctic seas

Region	Chlorophyll a µg l^{-1}	Primary production mg C h^{-1} m^{-3}	References	
High Arctic	0.0 – 5.72	0.11 – 4.90	English	1961
Resolute Bay	0.01 – 15	–	Welch and Kalfe	1975
Dumbell Bay	1.1 – 8.2	1.63 – 6.58	Appollonio	1980
Chuckchi Sea	0.25 – 40	0 – 44.20	Hameedi	1978
Brevoort Harbour	0.33 – 10.21	1.40 – 7.98	Hsiao and Trucco	1980
Frobisher Bay	≈0.3 – 5.0	0.42 – 4.17	Grainger	1979
Murman Coast	0.09 – 4.85	0.10 – 1.42	Sokolova and Solov'yeva	1971
W. Barents Sea	–	0.32 – 8.60	Corlett	1958
Barents Sea	0.20 – 1.59	0.03 – 2.40	Vedernikov and Solov'yeva	1972
Straumsbukta	–	0.05 – 13.50	Throndsen and Heimdal	1976
Beaufort Sea	–	0.10 – 8.80	Hsiao et al.	1977
Kugmallit Bay (Open Waters)	–	5.40 – 18.40	Duval	1977
West Iceland	–	0.01 – 6.0	Thordardottir	1973
Greenland Waters	–	0.5 – 7.0	Petersen	1979
Disko Fjord	–	0.004 – 1.84	Andersen	1977b
Godhavn	≈0.05 – 0.8	≈2 – 24	Andersen	1981
Liver Pool Bay	0.1 – 2.0	0.5 – 6.4	Grainger and Evans	1982

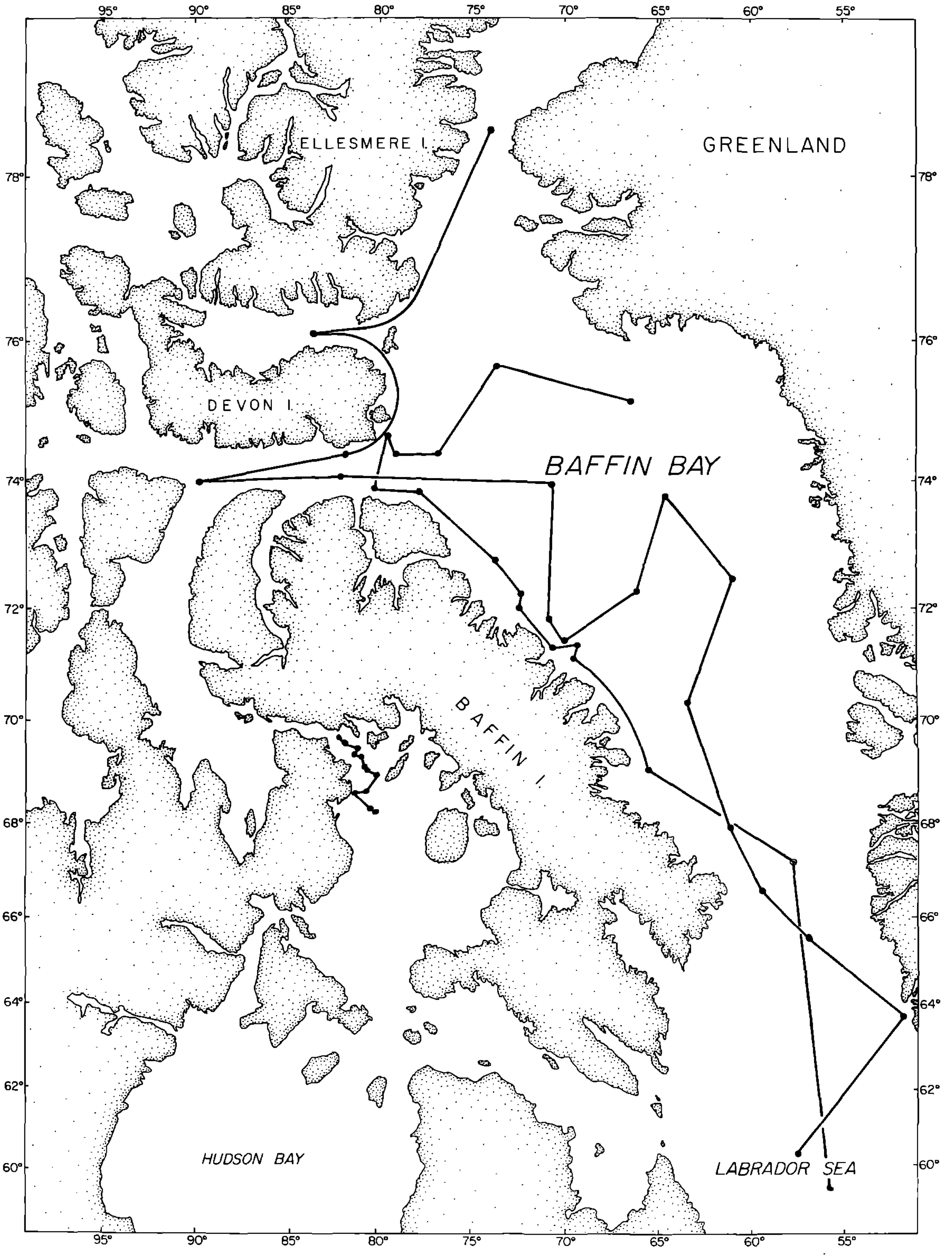

Fig. 1. Sampling locations in Baffin Bay, Davis Strait and Foxe Basin during MEL cruises

1982). In the Antarctic all the 3 parameters α, I_k, I_m were lower than those for the arctic; α ranged from 0.017 to 0.090, I_k 3 – 10 W m^{-2} and I_m 18 – 48 W m^{-2} (Jacques 1983). This departure could partly be due to the bias introduced when converting the light units (Klux) reported by Jacques to the W m^{-2} used here.

In the Arctic waters algal growth season is about 120 days; in the Northwest Greenland it is from April through October (Petersen 1964), off Murman coast, Scoresby Sound and Foxe Basin from May through October (see Bursa, 1961), at Resolute Bay between July and October (Welch and Kalff 1975), at Dumbell Bay

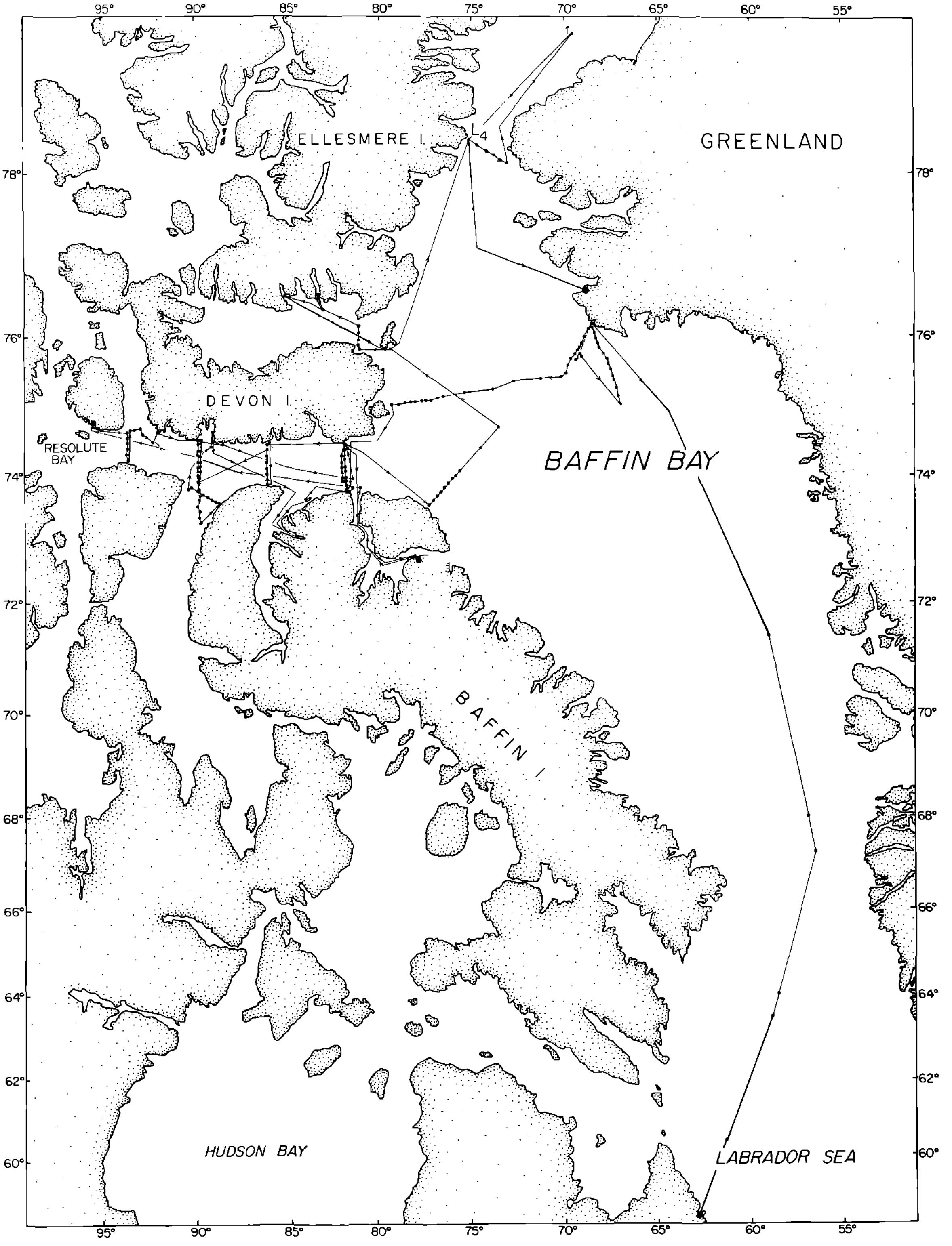

Fig. 2. Sampling locations in Baffin Bay and Eastern Canadian arctic during MEL cruises

from June to September (Apollonio 1980), off Straumsbukta during April to September (Throndsen and Heimdal 1976) and in the Arctic Basin during August and September (see Bursa 1961). Based on the Admirality Tables, a minimum of 2800 h of sunshine per growth season are available in these arctic waters and we have therefore based our annual primary production calculations on 120 d·24 h.

A wide range of daily integrated production values (0.004 – 4.89 g C d^{-1} m^{-2}) has been reported from the arctic (Table 6). In the arctic waters, because of extended photoperiod, hourly rates of primary production are

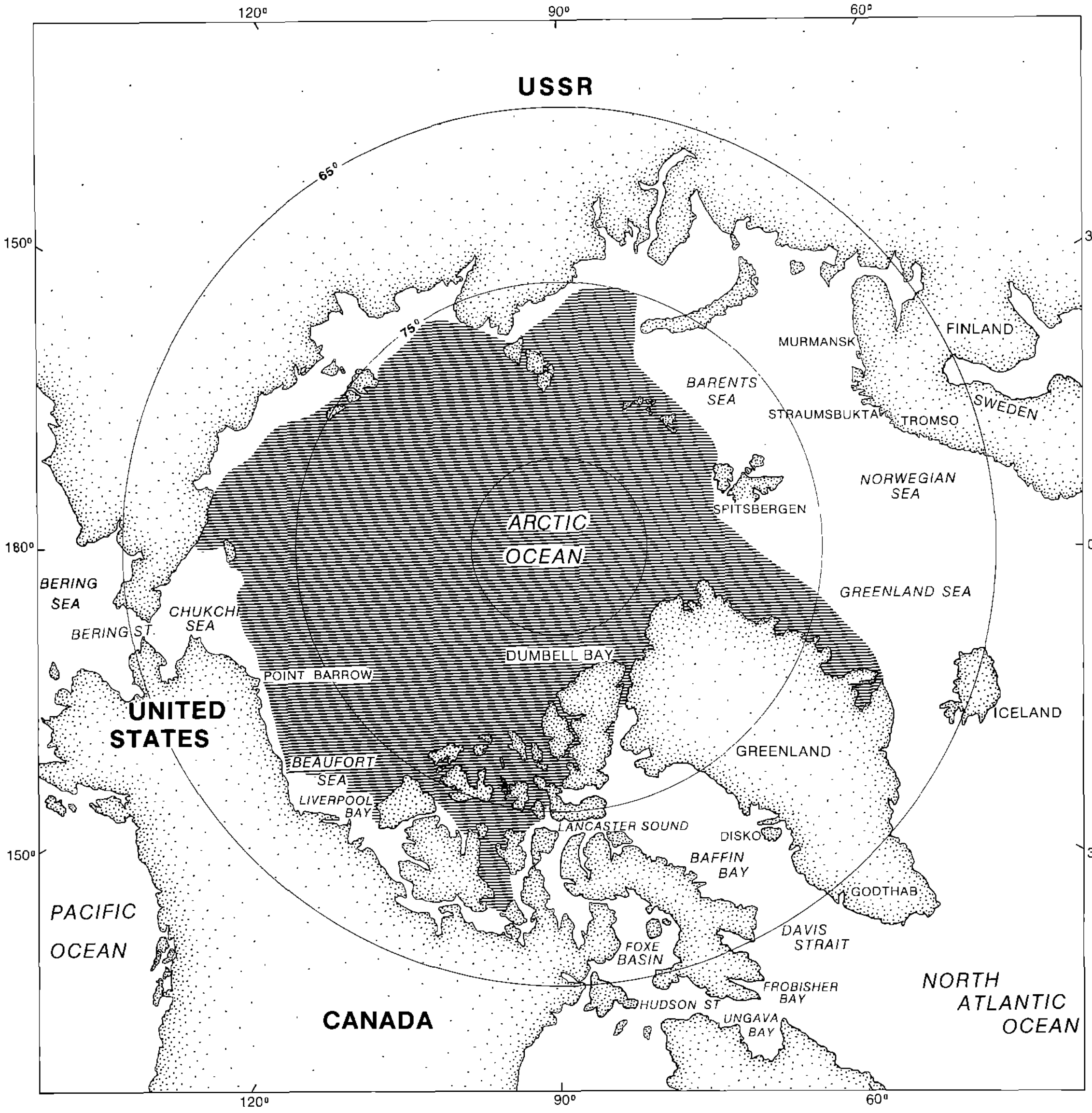

Fig. 3. Location map of arctic waters. Shaded area denotes the average extent of sea ice

multiplied by 24 to obtain daily rates. This is justified in view of the findings of Li and Harrison (1982) who demonstrated that in the Canadian arctic ^{14}C uptake rate was linear throughout the 24 h natural solar radiation period. Generally speaking the values were high in the shelf region such as the bays and including the fjords; for example Chuckchi Sea (3.0 g C), Beaufort Sea (2.54 g C), Bear Island (1.30 g C), western Barents Sea (1.33 g C), Straumsbukta (2.30 g C), Godhavn (1.93 g C), Lancaster Sound (4.75 g C), and Eastern Baffin Island (4.89 g C). These values are of similar magnitude as those recorded from the Antarctic waters around Gerlach Straits

Table 4. Light saturation parameters in the arctic seas based on MEL cruises

	P^B_m	α	I_k	I_m	β
Range	0.11 – 10.33	0.004 – 0.231	4 – 76	19 – 315	0 – 0.017
$\bar{X}$	1.96	0.069	29	122	0.002
S. E.	0.08	0.002	0.70	4.4	0
N	264	264	264	151	151

Units: P^B_m: mg C (mg Chl a)$^{-1}$ h^{-1};
α, β: mg C (mg Chl a)$^{-1}$ h^{-1} (W m^{-2})$^{-1}$;
I_k, I_m: W m^{-2}

Table 5. Summary of assimilation numbers from some arctic waters

Region	mg C h^{-1} mg Chl a^{-1}	References	
Arctic	1 – 1.5	Steemann Nielsen and Hansen	1959
High Arctic	3.6 – 7.2	Smith and English	1973[a]
Arctic Drift Station T-3	3.8	Pautzke	1974[a]
Disko Bay	0.19 – 0.83	Andersen	1977[a]
Chukchi Sea	1.3 – 1.5	Hameedi	1978
Chukchi Sea	0.3 – 2.0	Hameedi and Shaw	1975
Dumbell Bay	0.2 – 4.2	Apollonio	1980
Barents Sea – Murman Coast	0.09 – 2.66	Vedernikov and Solov'yeva	1972
Godhavn	0.09 – 8.9	Andersen	1981
Off Spitsbergen	<1.7	Heimdal	1983
Baffin Bay	0.79 – 1.22	Platt et al.	1982
E. Canadian Arctic	0.11 – 2.41	Gallegos et al.	1983
N. Foxe Basin	1.37 – 2.90	Smith et al.	in press
E. Canadian Arctic	0.1 – 10.33	Present studies	
E. Baffin Island	0.31 – 3.80	Hsiao and Trucco	1980

[a] See Hameedi 1978

Table 6. Summary of integrated production in the arctic seas

Region	g C d^{-1} m^{-2}	References	
Beaufort Sea	0.12 – 0.55	Alexander	1974
Beaufort Sea – Pt. Barrow	0.055 – 0.18	Alexander	1974
Beaufort Sea	0.01 – 2.54	Grainger and Evans	1982[a]
S. Beaufort Sea	0.10 – 1.19	Hsiao et al.	1977
N. Beaufort Sea	0.004	Horner and Schrader	1982
W. Iceland	0.17 – 0.50	Thordardottir	1973
Chukchi Sea	0.07 – 3.0	Hameedi	1978
Chukchi Sea	0.006 – 0.684	Matheke and Horner	1974
Dumbell Bay	0.14 – 0.83	Apollonio	1980
Straumsbukta	0.38 – 2.30	Throndsen and Heimdal	1976
Godthab	0.90	Petersen	1977
Disko Fjord	0.004 – 0.14	Andersen	1977[b]
Godhavn	0.34 – 1.93	Andersen	1981
Western Barents Sea	0.28 – 1.33	Corlett	1958
Off Spitsbergen	0.43 – 0.89	Heimdal	1983
E. Canadian Arctic	0.45	Grainger	1975
E. Canadian Arctic	0.227	Harrison et al.	1982
Davis Str.	0.02	Maclaren-Marex Co.	1979
Foxe Basin	0.20	Smith et al.	in press
E. Baffin Island	2.21 – 4.89	Hsiao and Trucco	1980
Baffin Bay	0.14 – 0.26	Herman	1983
E. Canadian Arctic	0.08 – 0.86	Harrison and Platt	in press
Bear Island	0.98 – 1.30	Marshall	1957
E. Canadian Arctic	1.09 – 4.75	Gallegos et al.	1983[a]
E. Arctic	0.058 – 0.190	Platt and Herman	1983[a]
Bering Sea	0.015 – 0.021	McRoy and Goering	1974
Central Arctic Basin	0.055 – 0.180	Alexander	1974
High Arctic	0.22	Nemoto and Harrison	1981
North Polar Sea	0.12 – 0.47	English	1961[a]
Murman Coast	0.007 – 0.262	Sokolova and Solov'yeva	1971
Murman Coast	0.045 – 0.594	Vedernikov and Solov'yeva	1972

[a] Hourly values ×24

[b] Simulated in situ measurements

Table 7. Incident radiation, temperature and nutrients in the arctic seas based on MEL cruises

	I W m^{-2}	Temp. °C	PO_4 mg at m^{-3}	NO_3 mg at m^{-3}	NH_4 mg at m^{-3}
Range	389 – 3500	−1.5 – 8.0	0.16 – 3.1	0 – 16.6	0 – 7.90
$\bar{X}$	1556	2.4	0.8	2.5	0.78
S. E.	83	0.1	0.02	0.2	0.05
N	87	304	320	301	305

(2.80 – 3.62 g C, Fogg 1977) or Signey Island (4.80 g C, Whitaker 1982) or from some of the highest productive temperate and tropical seas (see Platt and Subba Rao 1975). However, considerable variation in the magnitude of production probably also exists within these areas even though the growth season is short. In the Beaufort Sea the daily integrated production was 0.004 g C m^{-2} (Horner and Schrader 1982), 0.12 – 0.55 (Alexander 1974), 0.055 – 0.10 (Alexander 1974), 0.01 – 0.15 (Grainger and Evans 1982); in the Eastern Canadian Arctic 0.45 (Grainger 1975), 0.08 – 0.86 (Harrison and Platt in press), 1.09 – 4.75 (Gallegos et al. 1983) and in the Chuckchi Sea 0.006 – 0.684 (Matheke and Horner 1974), 0.07 – 3.0 (Hameedi 1978).

Based on the data given in Table 6, for the arctic shelf waters an average daily integrated production of 0.225 g C d^{-1} m^{-2} is calculated. These data include both short-term observations made over few days at one or more stations and as well as those extended over more than 7 months duration (Sokolova and Solov'yeva 1971, Andersen 1981) at a nearshore station. Production values of about 0.2 g C d^{-1} m^{-2} are frequently encountered during most of the studies listed in Table 6. This is about 25% of the estimate for Antarctic Shelf Waters (see Platt and Subba Rao 1975).

Based on the few seasonal studies (Grainger 1979, Grainger and Evans 1982; Appollonio 1980, Hameedi 1978, Matheke and Horner 1974, Hsiao et al. 1977) from the coastal arctic waters a spring peak in the primary production, somewhat similar to that observed in the temperate seas, can often be discerned. This peak may be complex for example in the vicinity of Murman Coast it may consist of four peaks of equal magnitude, corresponding to April, June – July, August and September (Sokolova and Solov'yeva 1971). In the Godhavn region there were three peaks occurring during April – May, June – July and September and during one year the first peak was of a higher magnitude (Andersen 1981). In Godthaab Fjord following a minor peak during March – April, a pronounced peak was observed during June (Petersen 1977); this was followed by another during August (Steemann Nielsen 1958). In Frobisher Bay where a seasonal study was carried out, production was unimodal with a peak development during July – August (Grainger 1979). In other regions such as Liverpool Bay (Grainger and Evans 1982), Dumbell Bay (Appollonio 1980), Beaufort Sea (Hsiao et al. 1977), Chuckchi Sea (Hameedi 1978, Matheke and Horner 1974) a well developed peak, probably the primary peak, was observed during August.

In the more offshore waters the integrated production values are lower when compared to the shelf waters (see Gorshkov 1983) and fall within the range (0.02 – 0.26 g C d^{-1} m^{-2}). Such regional differences in production are probably controlled by physical conditions. In the inshore waters of Manitounuk Sound, Hudson Bay, deepening of euphotic layer and stratified layer with progression of spring, seems to initiate development of phytoplankton blooms under the ice which upon melting releases the algae that initiate further blooms in the water (Legendre et al. 1981). In the Baffin Bay interaction between the surface irradiance, depth of mixed layer and concentration of chlorophyll seems to reflect in the magnitude of production (Herman 1983). In 50% of the production profiles, high chlorophylls ($\approx$0.5 mg m^{-3}) were associated with high production in the light abundant surface mixed layer whereas in the rest lower chlorophylls ($\leq$0.1 mg m^{-3}) in the surface layer resulted in insignificant production (Herman 1983). In the high arctic production was 0.22 g C d^{-1} m^{-2} (Nemoto and Harrison 1981), in Baffin Bay 0.14 – 0.26 g C (Herman 1983), and in Eastern Canadian Arctic 0.23 g C (Harrison et al. 1982), 0.058 – 0.19 g C (Platt and Herman 1983). These values are of the same magnitude as those from the open ocean waters of the Antarctic, 0.04 – 0.294 g C (El-Sayed and Turner 1977), 0.02 – 0.17 g C (Saijo and Kawashima 1964), <0.5 g C (Whitaker 1982) or the temperate and tropical regions (see Platt and Subba Rao 1975). Data for the arctic slope are not as extensive as those for the arctic shelf. In the Indian, Atlantic and Pacific oceans production in the offshore waters is about 30% of the adjacent shelf waters (see Platt and Subba Rao 1975) and in the arctic this is also assumed to be the case. In the Antarctic it is about 25% (El-Sayed et al. 1983), the average daily production for the arctic will then be 0.075 g C d^{-1} m^{-2}.

There is some evidence to suggest that production in the arctic is often not limited by nutrients. Nutrients during this study were generally high; $\bar{X}$ 0.8 mg at m^{-3} PO_4, 2.5 mg at NO_3, 0.78 mg at NH_4. Phosphate was never exhausted but occasionally NO_3 and NH_4 were (Table 7). Hameedi (1978) also made similar observations and in fact samples with high levels of biomass (7.56 – 40.17 µg Chl *a* l^{-1}) and production (43.67 – 530.64 mg C half-day^{-1} m^{-3}) had no nutrient exhaustion. There was no dramatic or systematic increase in production when samples were enriched with nitrate and or phospate (English 1961). In this respect also a similarity seems to exist between the arctic and Antarctic waters; in the Antarctic according to Fogg (1977) possibly some nutrient, rather than the macro-nutrients such as nitrate, phosphate and silicate or incident radiation which are in abundance, is a determining factor contributing to spatial variations in primary production. However, Whitaker (1982) did not observe any enhancement of photosynthetic rates in a variety of Antarctic and sub-antarctic surface waters enriched with vitamins, trace metals or chelators.

Euphotic layer extended from 19.5 m under the ice (Apollonio 1971) to 18 – 37 m in the Chukchi Sea (Hameedi 1978) and 70 m in the west Barents Sea (Corlett 1958). In the Baffin Bay the extent of the euphotic layer ranged between 27 – 45 m (Platt et al. 1982). Off Straumsbukta near Tromso, attenuation of different wavelengths of light varied with the season (Throndsen and Heimdal 1976); for red (653 nm) the winter, summer-autumn and spring attenuation depths corresponded to 12 m, 10.5 m and 9.5 m; for blue (450 nm) it was 40 m

Table 8. Summary of annual primary production in the arctic seas (calculations based on a 120 day growth season)

Region	$\mathrm{g\ C\ y^{-1}\ m^{-2}}$	References	
Godthaab Fjord	≈60	Steemann Nielsen	1958
W. Greenland	36	Petersen	1964
Godhavn	90	Andersen	1977
Godhavn	75 – 104	Andersen	1981
Frobisher Bay	41 – 70	Grainger	1979
Resolute Bay	45	Welch and Kalff	1975
Dumbell Bay	12	Apollonio	1980
Disko Fjord	4.7 – 13.7	Andersen	1977[b]
Northeast Chukchi Sea	18 – 28	Carey	1978
W. Greenland – Disko Bay	36	In Dunbar	1982
	29 – 98	In Dunbar	1982
Frobisher Bay (Land Locked Fjord)	12	In Dunbar	1982
Gulf of Finland	30 – 40	In Dunbar	1982
E. Canadian Arctic	27	Harrison et al.	1982
Off Alaska	10 – 15	Alexander et al.	1975
Beaufort Sea	15 – 40	Schell (Pers. com.)	

during winter and 17.5 m during autumn; green (522 nm) and yellow (583 nm) were similar with 53 m during winter and 30 m during fall. There is evidence to suggest the adequacy of light for photosynthetic growth of algal populations at the bottom of the Arctic Sea ice (Horner and Alexander 1972). In the Chukchi Sea at 4 out of 10 stations, interestingly the highest biomass (up to 40.17 μg Chl *a* $\mathrm{l^{-1}}$) and production (up to 95.61 mg C half $\mathrm{day^{-1}\ m^{-3}}$) in the column were at the bottom of the euphotic layer (18 – 37 m) where the light level ranged between 0.059 and 1.26 W $\mathrm{m^{-2}}$ (Hameedi 1978) but the assimilation numbers, however, were not high. In the Baffin Bay at 10 out of 14 stations chlorophyll and production values were higher at 1% light level than at 50% light level and at 5 stations the assimilation numbers were comparable (Platt et al. 1982). The compensation light in the Baffin Bay was at 0.3 W $\mathrm{m^{-2}}$, similar to that in the Antarctic waters (Fogg 1977) and favourably compares with 0.4 W $\mathrm{m^{-2}}$ calculated from the data of Holm-Hansen et al. (1977).

In these polar waters, which are persistently cold, temperature limits the rate of photosynthesis. Carbon assimilation rates increased 5 × as the in situ temperatures also increased in the range of −1.5 °C to 8 °C (Li et al. 1984). Phytoplankton from Labrador Shelf and Baffin Bay, collected at temperatures ranging between 0.2 °C and 2.1 °C showed about 2 – 3 × increase in their photosynthetic rates when incubated at temperatures up to <10 °C (Smith and Platt, in preparation). In the Antarctic waters also, a 2 × increase in assimilation numbers was observed when the experimental temperatures were elevated up to 7 °C from the ambient −0.8 to 1.0 °C (Neori and Holm-Hansen 1982).

Annual primary production in the arctic waters, based on a 120 day growth season, ranged between 12 – 98 g C $\mathrm{y^{-1}\ m^{-2}}$ (Table 8) and usually the higher values were observed in the coastal bays and fjords. A considerable variability in the annual primary production in the coastal arctic waters was noticed; for Frobisher Bay during the years 1967 – 1969 it was 41 – 70 g C $\mathrm{y^{-1}\ m^{-2}}$ (Grainger 1979) and for Disko Bugt during the years 1973 – 1975 production ranged from 75 to 104 g C $\mathrm{y^{-1}\ m^{-2}}$ (Andersen 1981). Both the magnitude and the total annual production at Frobisher Bay and Disko Bugt seem to be related to the duration of the growth season which in turn is governed by the removal of snow-ice cover and breaking up of ice (Grainger 1979, Andersen 1981). In the Antarctic also the annual production varied considerably; at Signey Island it was 130 g C $\mathrm{y^{-1}\ m^{-2}}$ for 1966 – 1967 (Horne et al. 1969), 86 – 289 g C $\mathrm{y^{-1}\ m^{-2}}$ during 1972 – 1974 (Whitaker 1982) and seems to be positively correlated with the stability of the water column. More data are needed from the offshore regions.

The calculated shelf and slope areas for the arctic are 4.90 and 8.20×10^6 $\mathrm{km^2}$ respectively and these are not as accurate as those for other oceans. Primary production rate for the shelf is about 27 g C $\mathrm{y^{-1}\ m^{-2}}$ and for the slope is assumed to be 9.0 g C $\mathrm{y^{-1}\ m^{-2}}$ (Table 9). The total primary production for the shelf and slope would then correspond to 132 and 73.8×10^6 t C $\mathrm{y^{-1}}$ (total 205.8×10^6 t C $\mathrm{y^{-1}}$) which is about 16 times higher than our earlier estimate (Platt and Subba Rao 1975).

Algal production in the sea-ice and ice-edge should be also included in calculating the total photosynthetic production of the arctic. There is a considerable range of estimates: 0.3 – 7.67 mg C $\mathrm{h^{-1}\ m^{-2}}$ (Clasby et al. 1973). Assuming a 24 h sunshine and 120 day growth season (see Horner and Schrader 1982) the annual production of the ice biota is about 0.9 to 22 g C $\mathrm{y^{-1}\ m^{-2}}$ (Clasby et al. 1973). Near Chukchi Sea, Matheke and Horner (1974) obtained rates between 0.5 and 57 mg C $\mathrm{h^{-1}\ m^{-2}}$ based on which we calculate annual rates of 1.4 – 164 g C $\mathrm{y^{-1}\ m^{-2}}$. Alexander (1974) obtained annual rates of 5 – 10 g C $\mathrm{y^{-1}\ m^{-2}}$ in the Beaufort Sea area. Horner and Schra-

Table 9. Revised estimates of total primary production in the arctic ocean

Region	Area[a] 10^6 km^2	Production g C y^{-1} m^{-2}	Total production (tons) 10^6 t C y^{-1}
Shelf (<200 m)	4.90	27	132
Offshore (>200 m)	8.20	9	73.8
Total	13.10		205.8

[a] Calculated from Moiseev (1971)

der (1982) reported rates of 0.7 g C m^{-2} at Narwhal Island and 5 g C m^{-2} at Barrow for the entire bloom period. These rates are similar to the 10 g C y^{-1} m^{-2} from the Antarctic (see Fogg 1977). In the Syowa Station area, Antarctica, the seasonal chlorophyll values of the algae when converted to production yielded values ranging between 1.5 and 3.25 g C y^{-1} m^{-2} which is <10% of the total phytoplankton production (Hoshiai 1981).

Assuming a nominal production rate of 10 g C y^{-1} m^{-2} for the young ice of the arctic which covers an area of 0.6 x 10^6 km^2 a conservative estimate of ice biota production would be 6 x 10^6 t C y^{-1} which is only <3% of the estimated total primary production occurring in the water column. This may change when more data similar to the substantially high rates (4.1 g C d^{-1} m^{-2}) from the bottom sea ice in McMurdo Sound, Antarctica (Palmisano and Sullivan 1983) are available. In the southern Bering Sea Alexander and Chapman (1981) estimated that the production due to ice algae is not a major component and is less than 1% of the annual primary production which is also the case in the Antarctic (Whitaker 1982). In the southern most Bering Sea a subarctic region, however, production due to ice edge algae is high (600 – 725 mg C h^{-1} m^{-2}) and important (Niebauer et al. 1981).

Although the revised total arctic production of 210 x 10^6 t C y^{-1} (205 x 10^6 t C due to arctic waters and 6 x 10^6 t C due to ice-biota) is about 16 times higher than the earlier estimates, it is not going to make a significant change in the annual global production of the oceans. This is because the area of the arctic waters is <4% of the total area of the world's oceans, the short duration of growth season; and a low level of production that, even though revised upwards, is still relatively low.

Because of increasing demands for living and mineral resources, research activity in the Arctic and Antarctic polar waters has been accelerated in recent years. Although the Antarctic has been the focus of oceanographic research over several decades, our understanding of the magnitude of its primary production, the basis of commercially exploitable resources, is far from complete. For example, in the Weddell Sea, Antarctic Ocean, based on the seasonal depletion of nitrate, phosphate and silicate Jennings et al. (1984) revised primary production estimates by 1.5 – 4 times higher than the earlier estimates. It should be pointed out that the revised production figure for the Arctic waters reported by us is a conservative estimate and probably needs substantiation with calculations based on nutrients budgets.

Acknowledgements. We are grateful to Drs. Donald M. Schell, Institute of Marine Science, University of Alaska, Fairbanks, Dr. W. G. Harrison and N. Watson, MEL, Bedford Institute of Oceanography for constructive discussion. Our thanks are also due to Mr. David Rudderham and Carla Caverhill for their excellent assistance with computations.

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