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Pelagic primary production during summer along 65 to 72°N off West Greenland

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Abstract The distribution of phytoplankton biomass and primary production were studied during summer 1993 at 16 stations from 65 to 72°N off West Greenland, ranging more than 900 km. Hydrography, nutrients and chlorophyll *a* profiles revealed a significant change in structure from south to north. Nitrate was depleted in the euphotic zone at most stations except close to the ice edge (West Ice) or close to outflow from large glaciers. The vertical distribution of phosphate followed that of nitrate, but was never depleted. Despite two stations with relatively high surface concentrations, silica showed the same distribution as the other two nutrients. In the south, chlorophyll *a* concentration and primary production were lower than north of Disko Bay (69°N), associated with a well-mixed versus a salinity-generated stratification, respectively. In Vaigat, a high-production station was identified, (st. 910, 69°52′69N–51°30′61W) with a chlorophyll *a* concentration in the euphotic zone of >13 μg l^{-1} and an area primary production of 3.2 g C m^{-2} day^{-1}. This is seldom encountered in arctic waters and was presumably due to nutrient-rich melt-water originating from the Iluliíssat Glacier. The overall primary production for the studied area was 67–3207 mg C m^{-2} day^{-1} (mean ± SD = 341 ± 743 mg C m^{-2} day^{-1}), which is within the range of the few results published for West Greenland and eastern Canadian Arctic waters.

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Introduction

The sea along West Greenland represents a dynamic transition zone between cold polar water and warmer water of Atlantic origin (Kiilerich 1943; Buch 1984, 1990). The water masses along West Greenland represent a mixture of water from the East Greenland Polar Current and Atlantic water from a branch of the Irminger Current which flows towards East Greenland and south of Cape Farewel where it is mixed with the Polar Water (Dunbar 1946). This mixture, which flows northwards along the west coast, makes up the West Greenland Current (see Fig. 1A). The West Greenland Current meets the Baffin Land Current which flows southwards from Arctic Canada. Part of the West Greenland Current bends eastwards to the Baffin Land Current, creating a dynamic zone (front) in the region 69–71°N (Buch 1984).

The sea along West Greenland is seasonally partly ice-covered. The ice cover varies greatly from year to year depending on the degree of atmospheric cooling (Buch 1990). The average ice-cover extension along West Greenland in February reaches the coastline between Sisimiut and Assiat (66°56′–68°45′), covering the Davis Strait south to the Baffin Island (Buch 1990). The waters close to the ice edge are particularly productive because of significant release of nutrients and stabilization of the water column (e.g. Smith 1987; Andersen 1989; Smith and Sakshaug 1990).

In spring, a diatom phytoplankton bloom follows the withdrawal of the sea ice, depleting the surface layer of nutrients (e.g. Nielsen and Hansen 1995). After the spring bloom, pelagic primary production depends mainly on remineralization of nutrients (Nielsen and Hansen, in press).

Very few measurements of depth-integrated primary production from West Greenland waters have been reported (Steemann Nielsen 1958, 1975; Petersen 1964; Smidt 1979; Andersen 1981; Nielsen and Hansen 1995, in press) and only Steemann Nielsen's (1958, 1975)

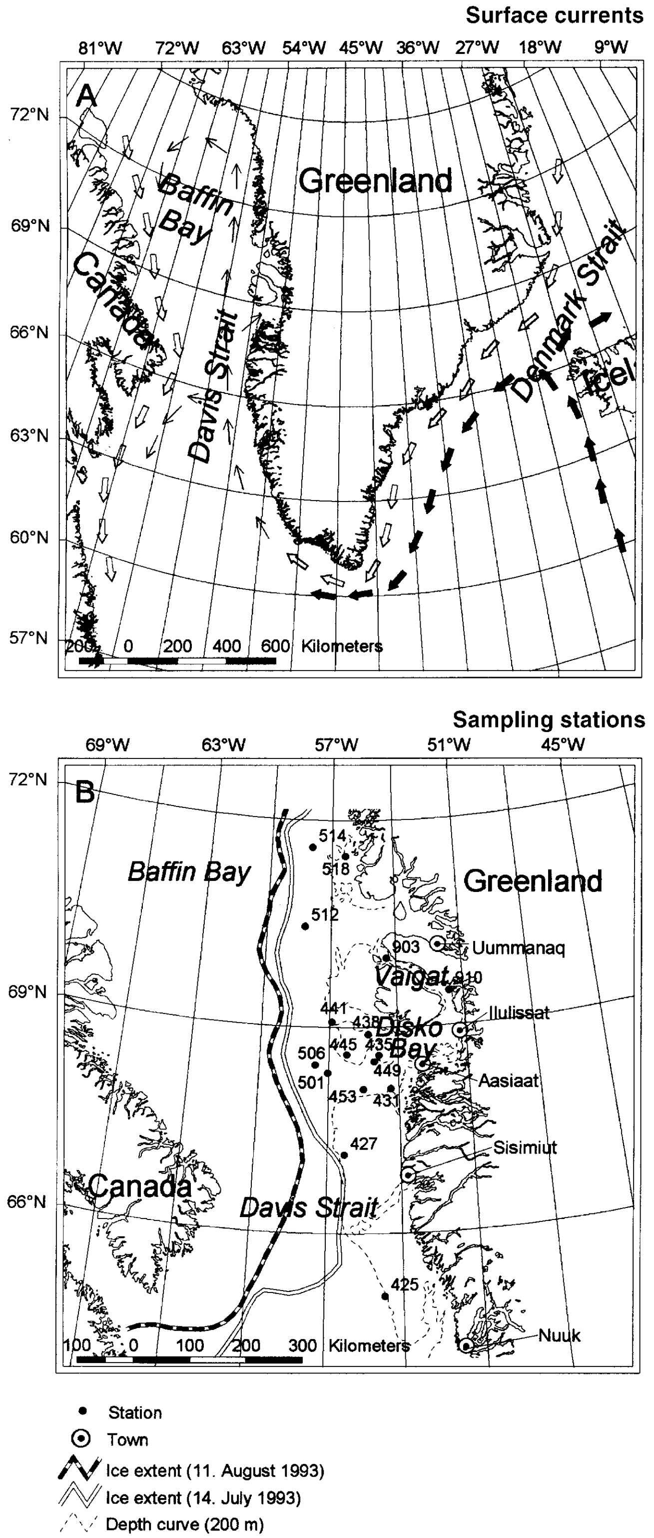

Fig. 1A Map of the study area with the currents around Greenland. ⇧ East Greenland Polar Current, ⬆ Irminger Current, together these currents mix and create the Polar Current, → West Greenland Current, ⇧ Baffin Land Current; redrawn from Herman et al. (1965). **B** Location of the sampling stations covering a transect 65–72°N off West Greenland. *Double line* and *broken line* refer to the approximate border of close drift ice of the west-ice at 14 July and 11 August 1993, respectively. *Dotted line* represents the 200-m depth curve

measurements from July/August 1954 were made in the more open waters off West Greenland. Moreover, little research has focused on primary production in this area in the last four decades, a period in which large-scale hydrographical changes seem to have taken place (Buch et al. 1994). Such data could be essential when potential global change effects on Arctic marine systems are to be evaluated.

The present study was conducted during July/August, the period after the phytoplankton spring bloom, and reports on photosynthetic characteristics of the phytoplankton communities, primary production, and vertical profiles of chlorophyll *a* and inorganic nutrient concentrations along the south-north gradient. The object was to add further to the limited knowledge of pelagic primary production in West Greenland marine waters.

Materials and methods

Hydrography, ice cover and solar irradiance

The present study was carried out off the west coast of Greenland from the "Royal Greenland" prawn-trawler Pâmiut, from 17 July to 9 August 1993. A total of 16 stations were investigated, ranging from along 65°N to 72°N (Fig. 1B, Table 1). The stations were visited around local 12 noon, when maximum irradiance was expected. Vertical temperature and salinity profiles were measured at nine of the stations, using conductivity, temperature and salinity probes (Seabird SBE 25 Datalogger).

Information on sea-ice cover was obtained from Navy maps – NOAA Joint Ice Center (Navy Polar Oceanography Center, Suitland) – via the Danish Meteorological Institute in Copenhagen. The ice cover is given as the approximate border of drift ice at the beginning and end of the investigation.

Solar downwelling irradiance was measured continuously using a 2 π Licor PAR (200–700 nm) quantum sensor connected to a Licor LI-1000 datalogger. The sensor was placed in an unshaded position on top of the ship and was set to log irradiance data six times each hour. The light attenuation in water was determined with a 4 π Licor PAR quantum sensor and made relative to the 2 π surface sensor readings. They were made at 2-m intervals to a final depth of about 22 m.

Sampling

Samples for determination of inorganic nutrients, chlorophyll *a* and primary production were collected using a Jolly Jet water pump (Model 1100 Marina, 70 l min^{-1}) connected to a pre-washed 80-m-long hose, (2.5 cm in diameter). Water from the integrated depth intervals of 0–5, 5–10, 10–20, 20–35, 35–50 and 50–75 m was collected in six 25-l acid-washed polyethylene containers (held in darkness). The "true" depth was calculated from depth marks on the hose and the angle between the sea water surface and the hose.

Samples for determination of nitrate, phosphate and silicate (approximately 30 ml of seawater from each depth interval) were stored at −25°C in acid-washed polyethylene bottles after addition of a droplet of chloroform to prevent microbial activity. The samples were later analysed on an automatic nutrient analyser (Dansk Havteknik) following Grasshoff (1976).

For determination of chlorophyll *a*, duplicate samples of 3–5 l from each depth interval were filtered onto Whatman GF/F filters and extracted in 96% ethanol for 24 h, whereafter the filtrates were

Table 1 Date, positions, water depths, time for water sampling, providing a guide (time difference of approximately 1 h from sampling) for initial time for primary production incubations at the 16 stations along 65–72°N off West Greenland during July/August 1993 (* stations on fishing banks)

Station	Date	Latitude	Longitude	Depth (m)	Sampling time (hours)
Southern part					
425	18 July	65°02′20N	54°42′01W	342	1300–1400
427*	19 July	67°16′44N	56°18′60W	146	1300–1415
431	20 July	68°20′13N	54°19′70W	415	1200–1300
435	21 July	68°52′45N	54°48′44W	295	1600–1630
438*	22 July	69°12′46N	55°16′35W	151	1400–1415
441	23 July	69°24′64W	56°54′83W	208	1210–1300
445*	24 July	68°53′13N	56°14′41W	176	1330–1400
449	25 July	68°46′08N	55°01′34W	278	1330–1400
453	26 July	68°19′72N	55°30′20W	506	1355–1430
501	30 July	68°34′90N	57°04′19W	358	1230–1300
506	31 July	68°42′83N	57°37′88W	312	1315–1345
Northern part					
512	2 August	70°55′36N	58°17′82W	348	1300–1330
514	3 August	72°11′30N	58°04′58W	311	1330–1400
518	4 August	72°02′82N	56°21′75W	315	1300–1330
Vaigat					
903	7 August	70°25′20N	54°23′45W	435	1430–1500
910	9 August	69°52′69N	51°30′61W	394	1315–1345

measured spectrophotometrically (Jespersen and Christoffersen 1987).

Primary production

Primary production in a depth-integrated sample assumed to be representing the euphotic zone was determined using the ^{14}C tracer method (Steemann Nielsen 1952). Euphotic zone depth was calculated as 1% of surface irradiance. An integrated seawater sample was gently mixed in a 1-l acid-washed blue-cap bottle and 1.48 MBq ^{14}C was added. The sample was transferred to ten acid-washed Jena bottles (100 ml) and incubated for 2 h at sea-surface temperature in a deck-incubator. Two of the ten bottles were incubated as dark bottles and the eight remaining light bottles were incubated at 1–75% of solar irradiance (provided by shading with nylon nets). After incubation, the samples were pressure-filtered (max. 0.2 bar pressure difference) on Whatman GF/F filters. The filters were placed in 20-ml scintillation vials, 200 µl of 0.1 N Hcl was added, after which they were stored at −25°C. In the laboratory, the unfrozen samples were fumed by giving an airflow to remove inorganic ^{14}C, and 10 ml Instagel Filtercount was added. After about 5 h, the ^{14}C concentration was measured in a Wallack liquid scintillation counter.

Integrated primary production was calculated for every 10 min of the day at 1 m intervals throughout the euphotic zone on the basis of daily solar irradiance pattern, light attenuation, chlorophyll *a* concentration and photosynthesis/light intensity (P vs E) relationship specific for each day/station. Water surface reflection was set to be constant at 10% of downwelling irradiance. The total CO_2 concentration was assumed to be 2.1 µM (Richardson 1991). No correction was done for algal respiration.

The P versus E relationship was fitted iteratively to a functional expression inspired by Bannister (1979) and modified by Markager et al. (1994):

$$P^* = \frac{\alpha E P^*_{max}}{\left(\left((P^*_{max})^m + (\alpha E)^m\right)^{1/m}\right) - C}$$

where P^* is the chlorophyll *a*-specific photosynthetic rate, α is the initial slope of the curve, E is the irradiance, P^*_{max} is the maximum photosynthetic rate, m is a shape parameter and C is the y-axis intercept.

Results

Hydrography

All water masses in the study area were dominated by water originating from the West Greenland Current, except at the three northernmost stations (sts. 512, 514, 518) which were influenced by inflow from the high Arctic, by the melting sea ice and by land runoff (Fig. 1A,B). The area was generally deeper than 140 m water. Three of the stations were positioned on fishing banks (st. 427 on Store Hellefiske Bank, st. 438 and 445 on Disko Bank).

The surface temperature was generally close to 5°C, decreasing towards −1°C to 0°C at the bottom of the euphotic zone (Fig. 2). In the southern part of the Davis Strait, the salinity profile was nearly uniform (Fig. 2). Only at the stations nearest the border of the West Ice (st. 501 and especially 506) was the water column somewhat influenced by melting ice. Lower salinities in the surface layer resulted in a marked pycnocline.

In the northern part of the Davis Strait, and southern Baffin Bay (sts. 512, 514), the water column was influenced by Polar Water and melting sea ice due to later withdrawal of the West Ice. The low-salinity surface layer (31.8–32.5 pss) resulted in the formation of a marked pycnocline. Station 518 was situated close to land, from which glacier outflow from Uummanaq Fjord generated low-salinity surface water with a very marked pycnocline. From the pycnocline and to the bottom of the euphotic zone (51 m) salinity increased to 33.6 pss.

In Vaigat at station 903, a low-salinity surface layer created a pycnocline that conformed with the depth of

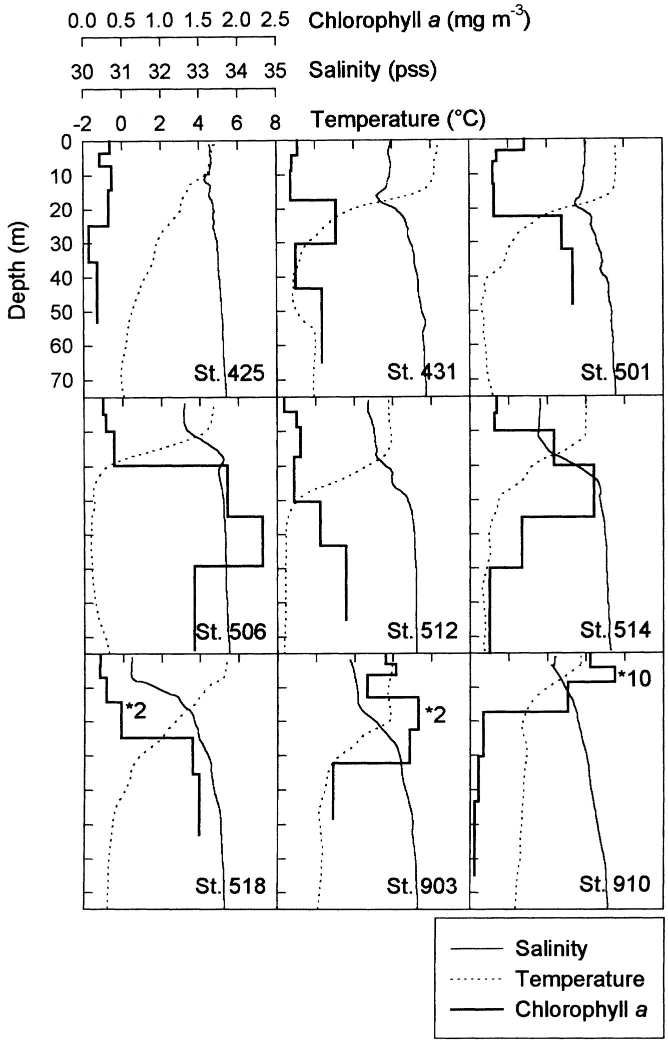

Fig. 2 Vertical distribution of temperature, salinity and chlorophyll *a* at selected stations along a transect 65–72°N off West Greenland during July/August 1993. Note the multiplication factors for chlorophyll *a*

the euphotic zone, whereas at station 910, a much weaker pycnocline was observed.

Due to the strong vertical salinity gradient in the surface layer at several stations during the summer, all energy transferred to the surface was presumably preserved in this layer since turbulent mixing cannot normally erode the pycnocline (Buch 1990).

Vertical distribution of nutrients and chlorophyll *a*

The vertical distribution of nutrients and chlorophyll *a* was closely related to water column stability (Fig. 2, Table 2). Nutrient concentrations were typically low in the upper layer, increasing below the pycnocline, which was at 2- to 25-m depth (Table 3). Nitrate was generally not detectable within the upper 10 m of the water column (not shown). However, at some stations, nitrate was detectable in the euphotic zone (up to >2 mmol m^{-3}). The vertical distribution of orthophosphate followed the distribution of nitrate, but it was never depleted, being 0.1–0.2 mmol m^{-3} in the upper 10 m. Mean values were 0.1–0.4 mmol m^{-3} in the euphotic zone (Table 2). Silicate was distributed in the same pattern as nitrate and phosphate. In the upper 10 m, the concentration ranged from 0.3 to 1.1 mmol m^{-3}, with a mean of 0.5–1.8 mmol m^{-3} in the euphotic zone (Table 2).

The chlorophyll *a* concentration typically showed a peak at or slightly below the pycnocline (Fig. 2). At sts. 903 and 910, the chlorophyll *a* concentration was also relatively high in the upper 5 m. The highest chlorophyll *a* concentrations were found at Vaigat, especially at st. 910, where the concentration reached 18.7 mg m^{-3} in the upper 10 m. At sts. 431 and 518 there were indications of relatively high chlorophyll *a* concentrations deeper in the water column, presumably also below the euphotic zone.

Nutrient relationships

The relationship between nitrate and phosphate is shown in Fig. 3A. The line representing the Redfield ratio (Redfield 1958) can be compared with the imaginary slope between values of nitrate and phosphate of the measured samples. For high nitrate concentrations, the slope of the samples and the line representing the Redfield ratio correspond, but for low values of nitrate the slope of the actual samples is higher (Fig. 3A). For values of nitrate below detection limit (plotted as 0), phosphate is still detectable (0.13 ± 0.05 mmol m^{-3}), also indicating that nitrate could be the limiting nutrient.

The relationship between nitrate and silicate (Fig. 3B) cannot be described by a constant imaginary slope. Going from a slope of about zero, the slope increases for higher nitrate concentrations (>4 mmol m^{-3}). For nitrate concentrations below detection limit, silicate reached 0.78 ± 0.43 mmol m^{-3}, again suggesting nitrate consumption.

P versus *E* relationships

The chlorophyll *a*-specific carbon assimilation was plotted as a function of irradiance (Fig. 4). The initial slope of the function, α, expresses photosynthetic efficiency at low irradiances, and P^*_{max} the maximal chlorophyll *a* (biomass) specific production rate for the integrated phytoplankton community. However, the calculated P^*_{max} must be considered just an approximation, since only in few cases (6 out of 15) did specific production reach a maximum. Phytoplankton acclimated to low irradiances often shows high levels of α and low levels of P^*_{max}, whereas phytoplankton acclimated to high irradiances displays low α values and high P^*_{max} values. This can be expressed by the light saturation index (E_k), $E_k = P^*_{max}/\alpha$ (Talling 1957), where a rela-

Table 2 Mean ± SD concentrations (mmol m^{-3}) of inorganic nutrients in the euphotic zone and in deeper water strata at the 16 stations along 65 to 72°N off West Greenland during July/August 1993 (*n* number of duplicate samples, see Materials and methods; *nd* no data)

Station	Water depth	NO_3^-	PO_4^{3-}	SiO_2	*n*
Southern part					
425	Euphotic zone	2.2 ± 2.3	0.4 ± 0.2	1.8 ± 0.7	6
	Deeper water	nd	nd	nd	
427	Euphotic zone	1.8 ± 1.7	0.4 ± 0.2	1.4 ± 0.6	5
	Deeper water	4.7	0.7	2.6	1
431	Euphotic zone	2.4 ± 2.7	0.4 ± 0.3	1.5 ± 1.3	6
	Deeper water	nd	nd	nd	
435	Euphotic zone	1.0 ± 1.8	0.3 ± 0.2	1.1 ± 0.6	4
	Deeper water	2.5 ± 0.3	0.6 ± 0.1	0.4 ± 0.3	2
438	Euphotic zone	0.0 ± 0.0	0.1 ± 0.1	1.3 ± 0.8	6
	Deeper water	nd	nd	nd	
441	Euphotic zone	0.8 ± 2.1	0.3 ± 0.2	1.1 ± 0.7	6
	Deeper water	nd	nd	nd	
445	Euphotic zone	0.4 ± 0.9	0.2 ± 0.1	0.7 ± 0.1	6
	Deeper water	nd	nd	nd	
449	Euphotic zone	0.0 ± 0.0	0.2 ± 0.0	0.8 ± 0.1	4
	Deeper water	2.3 ± 1.6	0.5 ± 0.6	1.6 ± 0.7	2
453	Euphotic zone	1.8 ± 3.0	0.3 ± 0.4	1.1 ± 1.0	6
	Deeper water	nd	nd	nd	
501	Euphotic zone	0.2 ± 0.5	0.2 ± 0.1	0.8 ± 0.1	6
	Deeper water	nd	nd	nd	
506	Euphotic zone	0.6 ± 1.2	0.2 ± 0.2	0.6 ± 0.5	5
	Deeper water	8.5	1.0	5.8	1
Northern part					
512	Euphotic zone	0.0 ± 0.0	0.2 ± 0.05	0.5 ± 0.0	5
	Deeper water	3.5	0.6	2.3	1
514	Euphotic zone	0.8 ± 0.6	0.3 ± 0.1	0.9 ± 0.4	4
	Deeper water	5.8 ± 2.5	0.8 ± 0.1	4.4 ± 1.2	2
518	Euphotic zone	0.5 ± 1.2	0.2 ± 0.2	1.7 ± 0.8	6
	Deeper water	nd	nd	nd	
Vaigat					
903	Euphotic zone	0.0 ± 0.0	0.1 ± 0.0	0.7 ± 0.1	3
	Deeper water	2.4 ± 2.7	0.5 ± 0.3	2.3 ± 1.3	3
910	Euphotic zone	2.0 ± 1.5	0.4 ± 0.1	1.6 ± 1.4	3
	Deeper water	8.3 ± 1.0	0.8 ± 0.0	6.9 ± 1.3	3

tively low E_k value represents acclimation to low irradiances and a relatively high E_k value represents acclimation to high irradiances. Data on the depth of the pycnocline and euphotic zone, P^*_{max}, α, E_k, average chlorophyll *a*-specific production in the euphotic zone, and the calculated daily area primary production rate are presented in Table 3. The E_k values ranged between 23 and 131 μmol photons m^{-2} s^{-1} (one extreme value of 354) and there was no obvious correlation with light saturation value and location characteristics for the sampling stations. The lowest E_k value was observed at st. 512, north of Disko, and the highest at st. 903 in Vaigat. Phytoplankton communities close to the edge of the West Ice showed, however, a relatively low E_k. Vaigat phytoplankton showed an extremely high acclimation to high irradiances at st. 903.

Horizontal distribution of chlorophyll *a* and daily primary production

The average chlorophyll *a* concentration in the euphotic zone (Fig. 5A) was relatively low at the southern stations (0.2–0.4 mg Chl *a* m^{-3}). The highest concentrations were found in the southern Vaigat, with 13.2 mg Chl *a* m^{-3}, and chlorophyll *a* levels were generally high at the outlet of Disko Bay (Table 3, Fig. 5A). A positive relationship between phytoplankton biomass and latitude was observed when the Vaigat stations were not taken into account (see also L. Pedersen, H.M. Jensen, A.D. Burmeister, B.W. Hansen, unpublished work).

The horizontal distribution of integrated primary production (Fig. 5B) mainly reflects the distribution of chlorophyll *a*. The primary production was lowest in the southern part of the sampling area when the stations close to drift ice and glaciers were omitted (and except Vaigat) (<100 mg C m^{-2} day^{-1}). The highest primary production rate was found in Vaigat. St. 910 in the southern Vaigat was outstanding, with a primary production of 3207 mg C m^{-2} day^{-1}, measured 9 August (Table 3). No overall relationship between primary production and distance from shore was found, except for an increase in the primary production from outside Disko Bay towards the West Ice, probably due to higher nutrients supply associated with the melt water (Fig. 5B).

Table 3 Depth of pycnocline and euphotic zone, P versus E parameters, integrated daily P* and primary production in the euphotic zone on 16 stations along 65 to 72°N off West Greenland during July/August 1993 (*nd* no data due to technical problems; *nd** missing data at high light intensities impeded the estimation; ** close to the West Ice; *** land run off)

Station	Pycnocline (m)	Euphotic zone (m)	P^*_{max}	α	E_k	Chl *a* ($\mu g\ l^{-1}$)	Integrated daily P* (mg C mg $Chla^{-1}$ m^{-2} day^{-1})	Integrated daily primary prod. (mg C m^{-2} day^{-1})
Southern part								
425	12	50	1.76	0.0277	68	0.22	6.94	78
427**	nd	36	0.75	0.0097	87	0.42	5.28	80
431	2	55	1.53	0.0141	118	0.40	4.77	113
435	nd	34	0.94	0.0142	67	0.51	9.11	155
438	nd	45	nd*	0.0590	nd	0.68	2.15	67
441	nd	60	0.67	0.0131	52	0.54	4.10	135
445	nd	56	1.42	0.0123	115	1.78	1.80	190
449	nd	29	0.90	0.0068	131	1.15	4.68	160
453	nd	67	0.83	0.0180	53	0.74	2.18	109
501**	20	53	1.30	0.0511	29	0.89	6.64	318
506**	15	50	0.88	0.0167	54	1.34	4.49	314
Mean ± SD						0.79 ± 0.45		156 ± 83
Northern part								
512	25	50	1.74	0.0861	23	0.39	7.52	151
514	20	41	1.14	0.0092	128	0.98	4.02	170
518***	10	51	0.57	0.0120	50	1.77	2.64	245
Mean ± SD						1.05 ± 0.57		189 ± 41
Vaigat								
903	20	16	1.45	0.0043	354	2.82	5.54	251
910	10	21	1.74	0.0218	84	13.24	12.12	3207
Avg	16.9	44.6	1.17	0.0235	94.2	1.74	5.22	340.8
± SD	5.3	14.1	0.41	0.0225	79.7	3.14	2.67	743.0

Discussion

The hydrography was characteristic for a summer situation throughout the investigated area. The surface layer had been warmed up to around 5°C, which is typical for this area (Andersen 1981; Nielsen and Hansen 1995). Pronounced differences in the melting of sea ice produced differences in the stratification of the water column.

The stabilization of the water column has a great influence on the conditions for phytoplankton growth. At all stations the vertical distribution of nutrients followed the density of the water column (sigma-t, not shown), as a result of isolation of the upper mixed surface layer and the depletion of nutrients due to phytoplankton growth. This is typical for the Arctic post-bloom period (e.g. Andersen 1981; Platt et al. 1987; Nielsen and Hansen 1995, in press, and references in Smith and Sakshaug 1990). In particular, nitrate was depleted in the surface layers, which is consistent with other measurements in Arctic waters (Andersen 1981; Platt et al. 1987; Nielsen and Hansen 1995, in press, and references in Smith and Sakshaug 1990). A comparison of all the nutrient measurements from the present study with nutrient levels monitored in Disko Bay 1992 and 1994 by Nielsen and Hansen (1995, in press) reveals ratios between NO_3^- and PO_4^{3-} and between NO_3^- and SiO_2 (Fig. 3A,B) similar to those we have found, indicating that the 1993 cruise actually described a typical situation for these waters during summer. Potentially, nitrate seems to be limiting for phytoplankton growth since it was the only one of the measured nutrients that became depleted and was below the Redfield ratio (Redfield 1958) in the surface waters. This is in accordance with the findings of Nielsen and Hansen (1995, in press) at the outlet of Disko Bay and of Harrison et al. (1982) in Baffin Bay and the Davis Strait. Despite low concentrations of nitrate and ammonium in the euphotic zone, Harrison et al. (1982) did not find any signs of nutrient limitation in the phytoplankton population, and they concluded that nutrients may play a less important role than temperature and light in controlling phytoplankton production. Sakshaug (1989) stated that, although the majority of individual phytoplankton species are not necessarily nutrient limited, the system is nutrient-limited relative to a system based on "new" nutrients (i.e. early in the productive season). For the Barents Sea it has been shown that nitrate is the dominant nitrogen source when phytoplankton biomass is high and that it is less important in the oligotrophic post-bloom period (Kristiansen and Lund 1989). It therefore seems likely that phytoplankton species acclimated to low nutrient levels prevail in the oligotrophic system (Sakshaug 1989).

Silicate concentrations were generally low in the surface layers, but it did not reach a level lower than about 0.5 mmol m^{-3}. This could indicate a shift in the

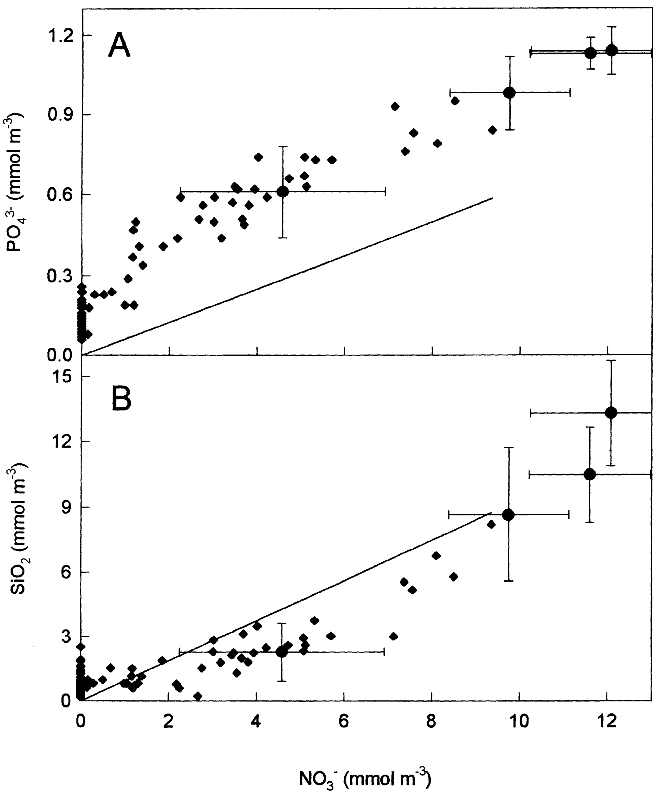

Fig. 3 Phosphate versus nitrate (**A**), and silicate versus nitrate (**B**). The *lines* indicates the Redfield ratio (N:Si:P – 16:15:1) by atoms of the nutrients ($n = 96$ samples). The *dots* with *standard deviation bars* show measured values from Disko Bay (69°15′N, 53°33′W) (Nielsen and Hansen 1995, in press)

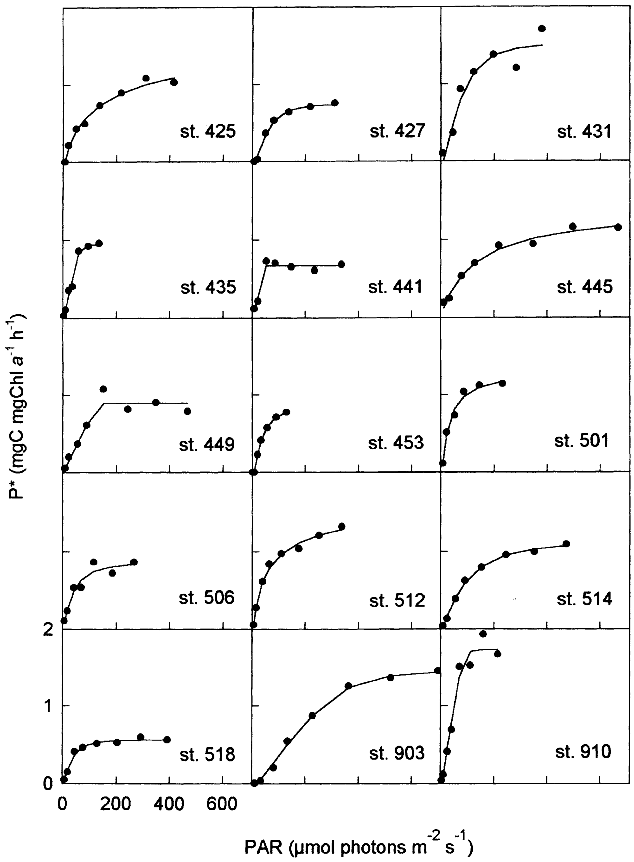

Fig. 4 Relationships between integrated chlorophyll *a*-specific photosynthetic rate (*P**) and irradiance on 16 stations along 65–72°N off West Greenland during July/August 1993

algal population from silicate-demanding diatoms in the bloom situation to flagellates after the depletion of nutrients (Nielsen and Hansen, in press). Phytoplankton identification from the area (L. Pedersen, H.M. Jensen, A.D. Burmeister, B.W. Hansen, unpublished work) showed that diatoms were relatively insignificant in biomass in open waters, but somewhat more so at the northern part of the study area. However, at Vaigat diatoms contributed half or more to the phytoplankton biomass (not shown) reflecting a well-mixed environment. Egge and Aksnes (1992) suggested that diatoms are always numerically predominant at silicate concentrations above 2 mmol m^{-3}. The diatom dominance was probably caused by higher growth rates at non-limiting silicate concentrations (Egge and Aksnes 1992). Silicate was therefore potentially limiting for diatom growth in the open waters we have studied.

The observed distribution of chlorophyll *a* characterized by low concentrations and a local maximum at or slightly below the pycnocline is typical for the late summer situation in Arctic waters (e.g. Andersen 1981; Harrison et al. 1982; Rey and Loeng 1985; Sakshaug 1989; Skjoldal and Rey 1989; Nielsen and Hansen 1995, in press). The horizontal pattern observed for chlorophyll *a* in our investigation is comparable to those found in the few previous investigations from the area (e.g. Hansen and Steemann Nielsen 1959; Andersen 1981; Harrison et al. 1982; Nielsen and Hansen 1995). The high chlorophyll *a* concentrations in Vaigat resemble concentrations found in Lancaster and Jones Sound, in the eastern Canadian Arctic (Borstad and Gower 1984).

The high chlorophyll *a* concentration in Vaigat with maximum concentration at 5- to 10-m depth indicated a bloom that was initiated shortly before our observation and glacial runoff from land presumably was responsible for this bloom. A similar situation was also observed at the same site in summer 1994 (Clausen et al. 1994). The chlorophyll *a*-specific integrated primary production rates were within the same range as reported for August 1979 from Brevoort Harbour, Arctic Canada by Hsiao and Trucco (1980).

Our chlorophyll *a* normalized photosynthetic parameters, α and P^*_{max} (Table 3), are not related to any particular environmental variable measured. The observed values are, despite their obvious methodological limitations because primary production was performed on integrated water instead of water from discrete depths and the P versus E curves were in some cases not reaching P^*_{max}, however, comparable to data reported from other Arctic waters (e.g. Subba Rao and Platt 1984; Smith and Sakshaug 1990). Harrison and Platt (1986) presented grand median values of $\alpha = 0.057$ and

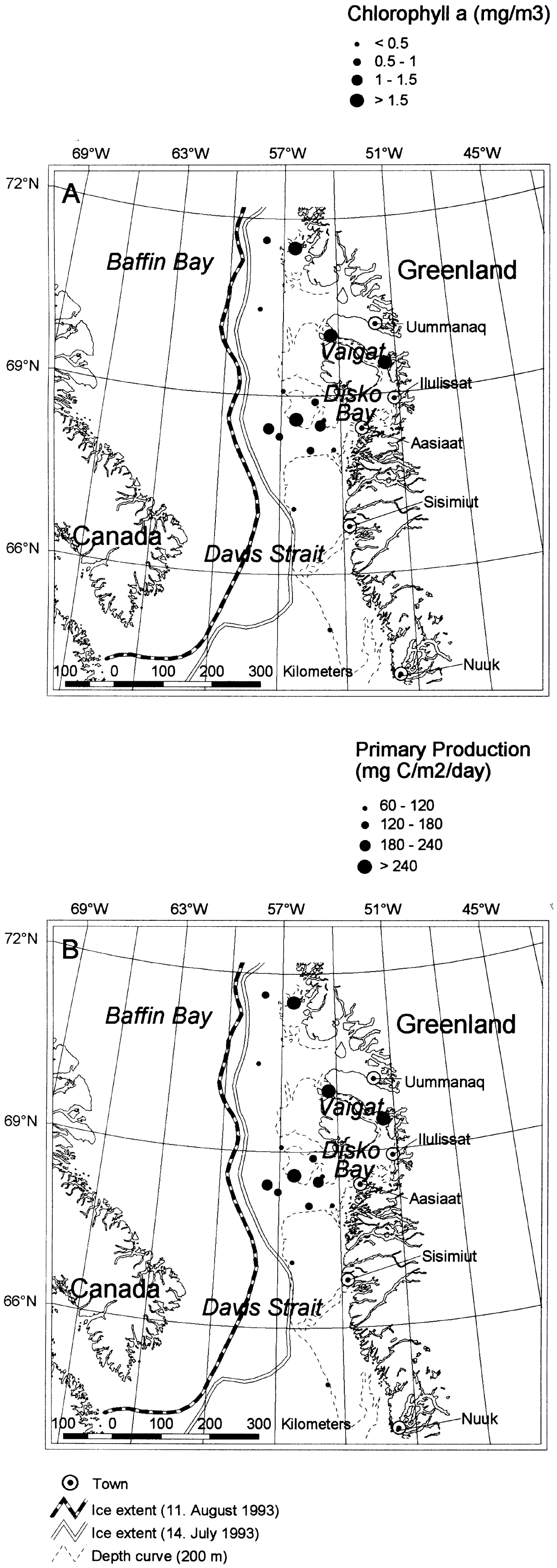

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Fig. 5A Horizontal distribution of mean phytoplankton biomass (mg chlorophyll *a* m^{-3}) in the euphotic zone **B** Horizontal mean area distribution of integrated primary production in terms of mg C m^{-2} day^{-1} in the euphotic zone along 65–72°N off West Greenland during July/August 1993

$P^*_{max} = 1.21$, based on a total of 424 *P* versus *E* experiments performed in the Labrador Sea and the Canadian high Arctic. Our values are well within these ranges. However, our mean value for the light saturation index E_k is generally and for no obvious reason higher than reported elsewhere. One of the stations on Disko Bank (st. 445), however, showed high light acclimation despite a great difference in chlorophyll *a* concentration and in depth of euphotic zone, presumablye due to sub-surface blooms (data not shown). The very high E_k values, chlorophyll *a* concentration, as well as primary production in Vaigat, cannot be explained by a deep euphotic zone, as the euphotic zone was only 16–20 m, but must be due to surface turbulence in the upper 20 m frequently exposing the phytoplankters (diatom-dominant) to high light and to nutrients from the Ilulissat glacier.

In Table 4 we present primary production data primarily from West Greenland and also from the region around the present study site (see also Subba Rao and Platt 1984; Andersen 1989; Rysgaard et al., in press, for a comprehensive collection of arctic primary production data). Most of the data in Table 4 are from coastal stations, which explains the relatively higher production rates than those found in open waters in the present study. At our open-water stations primary production rates of 67–318 mg C m^{-2} day^{-1} were found. This is slightly lower than reported data from Disko Bay and Baffin Bay. However, the high primary production rates in Vaigat have never been published from this area before. Only primary production rates from the outlet of Nuuk Fjord (Steeman Nielsen 1975) and from West Baffin Bay (Hsiao and Trucco 1980) reach comparable levels. In July/August 1954, however, Steemann Nielsen (1975) measured >500 mg C m^{-2} day^{-1} in the central Davis Strait where Polar Water (Labrador Current) meets the oceanic water, and close to the coast of West Greenland, over the shallow fishing banks between about 62 and 67°N.

In 1954 the primary production was higher near the west coast of Greenland (in the range 300–500 mg C m^{-2} day^{-1}) and decreased with increasing distance from the coast (150–300 mg C m^{-2} day^{-1}). In contrast, our data show an increase in the primary production rate going from the outlet of Disko Bay and westwards into the Davis Strait. One reason for this fundamental difference could be the late withdrawal of sea ice in 1993 giving rise to different hydrographic conditions (see Rysgaard et al., in press). The primary production in 1954 was generally a factor of 2 higher than in the present study. It is, however, problematic to compare instantaneous measurements made on one particular day despite the fact

Table 4 Primary production rates in the euphotic zone from West Greenland and the eastern Canadian Arctic. Data pertain to July/August unless specified otherwise

Site	*P* (mg C $m^{-2}day^{-1}$)	Date	Reference
Nuuk Fjord	150–2400	1955–1957	Steemann Nielsen 1975
Nuuk Fjord	150–1250	1961–1966	Smidt 1979
Nuuk Fjord	900[a]		Petersen 1977
Disko Bay	100–850	1959–1960	Petersen 1964
Disko Bay	250–1300	1973–1975	Andersen 1981
Disko Bay	690 ± 450	1992 (June/July)	Nielsen and Hansen 1995
Disko Bay	153 ± 33	1994 (Aug/Sept.)	Nielsen and Hansen, in press
Davis Strait	54	(Aug)	Booth 1984
West Greenland	67–318 (3207[b])	1993	Present study
West Baffin Bay	2110–4890	1979	Hsiao and Trucco 1980
Baffin Bay	227	1978 (Aug/Sep.)	Harrison et al. 1982
Baffin Bay	140–260		Herman 1983 (in Andersen 1989)
Frobisher Bay	300 ± 1175	1967–1969	Grainger 1979

[a] In connection with ice
[b] Vaigat st. 910

that the exact same method was applied (e.g. Petersen 1964; Smidt 1979; Andersen 1981).

The present horizontal phytoplankton biomass and primary production data provide basic information for West Greenland waters. This information is of interest for ecological modelling and for comparison between older data sets and future discussions concerning potential effects of global change on Arctic marine systems.

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References

Andersen OGN (1981) The annual cycle of phytoplankton primary production and hydrography in the Disko Bugt area, West Greenland. Medd Grøn Biosci 6:1–65
Andersen OGN (1989) Primary production, chlorophyll, light, and nutrients beneath the Arctic sea ice. In: Herman Y (ed) The Arctic Seas. Climatology, oceanography, geology, and biology. Van Nostrand Reinhold, New York, pp 147–191
Bannister TT (1979) Quantitative description of steady state, nutrient-saturated algal growth, including adaption. Limnol Oceanogr 24:76–96
Booth JA (1984) The epontic algal community of the ice edge zone and its significance to the Davis Strait ecosystem. Arctic 37:234–243
Borstad GA, Gower JFR (1984) Phytoplankton distribution in the Eastern Canadian Arctic. Arctic 37:224–233
Buch E (1984) Variations in temperature and salinity of West Greenland Waters, 1970–82. NAFO Sci Counc Stud 7:39–43
Buch E (1990) A monograph on the physical environment of Greenland waters. Greenland Fisheries Research Institute, Copenhagen
Buch E, Horsted SA, Hovgrd H (1994) Fluctuations in the occurrence of cod in Greenland waters and their possible causes. ICES Mar Sci Symp 198:158–174
Clausen S, Gedde D, Grastrup-Hansen D, Levinsen H, Riis T, Vestergaard O (1994) Danish course report (in Danish with English summary). In: Ehrhardt C, Gedde D, Grastrup-Hansen D, Heldbjerg H, Vestergaard O (eds). Botanical Institute, Copenhagen University, pp 83–102
Dunbar MJ (1946) The state of the West Greenland Current up to 1944. J Fish Res Board Can 6:460–471
Egge JK, Aksnes DL (1992) Silicate as regulating nutrient in phytoplankton competition. Mar Ecol Prog Ser 83:281–289
Grainger EH (1979) Primary production in Frobisher Bay, Arctic Canada. In: Dunbar MJ (ed) Marine production mechanisms. International Biological Programme 20. Cambridge University Press, Cambridge, pp 9–30
Grasshof K (1976) Methods for sea water analysis. Weinheim, New York
Hansen VK, Steemann Nielsen E (1959) The primary production in the waters west of Greenland during July 1958. Cons Perm Int Explor Mer XLIV:158–159
Harrison WG, Platt T (1986) Photosynthesis-irradiance relationships in polar and temperate phytoplankton populations. Polar Biol 5:153–164
Harrison WG, Platt T, Irwin B (1982) Primary production and nutrient assimilation by natural phytoplankton populations of the Eastern Canadian Arctic. Can J Fish Aquat Sci 39:335–345
Herman F, Hansen PM, Horsted SA (1965) The effect of temperature and currents on the distribution and survival of cod larvae at West Greenland. Int Comm Northwest Atl Fish Spec Publ 6:389–395
Hsiao SIC, Trucco R (1980) A marine biological study of Brevoort Harbour and nearby waters of Eastern Baffin Island phytoplankton. Can Mar Rep Fish Aquat Sci, no, 1557
Jespersen AM, Christoffersen K (1987) Measurements of chlorophyll-a from phytoplankton using ethanol as extracting solvent. Arch Hydrobiol 109:445–454
Kiilerich A (1943) The hydrography of the West Greenland Fishing Banks. Medd Komm Dan Fisk Havunders II
Kristiansen S, Lund BA (1989) Nitrogen cycling in the Barents Sea. I. Uptake of nitrogen in the water column. Deep Sea Res 36:255–268
Markager S, Hansen B, Søndergaard M (1994) Pelagic carbon metabolism in a eutrophic lake during a clear-water phase. J Plankton Res 16:1247–1267
Nielsen TG, Hansen BW (1995) Plankton community structure and carbon cycling on the western coast of Greenland during and after the sedimentation of a diatom bloom. Mar Ecol Prog Ser 125:239–257
Nielsen TG, Hansen BW (in press) Plankton community structure and carbon cycling on the western coast of Greenland during

the stratified summer situation. I. Hydrography, phytoplankton and bacterioplankton. Aquat Microb Ecol

Petersen GH (1964) The hydrography, primary production, bathymetry, and "Tagsâq" of Disko Bugt, West Greenland. Medd Grøn 159:1–45

Petersen GH (1977) Biological effects of sea ice and icebergs in Greenland. In: Dunbar MJ (ed) Polar oceans. 1974 Proceedings of the Polar Ocean Conference. McGill University, Montreal, pp 319–329

Platt T, Harrison WG, Horne EPW, Irwin B (1987) Carbon fixation and oxygen evolution by phytoplankton in the Canadian High Arctic. Polar Biol 8:103–113

Redfield AC (1958) The biological control of chemical factors in the environment. Am Sci 46:205–222

Rey F, Loeng H (1985) The influence of ice and hydrographic condition on the development of phytoplankton in the Barents Sea. In: Gray JS, Christiansen ME (eds) Marine biology of polar regions and effects of stress on marine organisms. Wiley, New York, pp 49–63

Richardson K (1991) Comparison of ^{14}C primary production determinations made by different laboratories. Mar Ecol Prog Ser 72:189–201

Rysgaard S, Nielsen TG, Hansen BW (in press) Seasonal variation in nutrients, pelagic primary production and grazing in a high-Arctic coastal marine ecosystem, Young Sound, Northeast Greenland. Mar Ecol Prog Ser

Sakshaug E (1989) The physiological ecology of polar phytoplankton. In: Rey L, Alexander V (eds) Proceedings of the Sixth Conference of the Comité Arctique International, 13–15 May 1985. Brill, New York, pp 61–89

Skjoldal HR, Rey F (1989) Pelagic production and variability of the Barents Sea ecosystem. In: Sherman K, Alexander LM (eds) Biomass yield and geography of large marine ecosystems. AAAS Selected Symposia Series III. Westview Press, Colorado, pp 241–286

Smidt ELB (1979) Annual cycles of primary production and of zooplankton at Southwest Greenland. Medd Grøn Biosci 1:1–53

Smith WO Jr (1987) Phytoplankton dynamics in marginal ice zones. Oceanogr Mar Biol 25:11–38

Smith WO Jr, Sakshaug E (1990) Polar phytoplankton. In: Smith WO (ed) Polar oceanography. Part B: chemistry, biology and geology. Academic Press, New York, pp 477–525

Steemann Nielsen E (1952) The use of radio-active carbon (C^{14}) for measuring organic production in the sea. J Cons Perm Int Explor Mer 18:117–140

Steemann Nielsen E (1958) A survey of recent Danish measurements of the organic productivity in the sea. Rapp P-V Reún Cons Perm Int Explor Mer 144:92–95

Steemann Nielsen E (1975) Marine photosynthesis with special emphasis on the ecological aspects. Elsevier Oceanography Series, 13. Elsevier, Amsterdam

Subba Rao DV, Platt T (1984) Primary production in Arctic waters. Polar Biol 3:191–201

Talling JF (1957) The phytoplankton population as a compound photosynthetic system. New Phytol 56:133–149