Primary production in polar waters: relation to nutrient availability

W. G. HARRISON and G. F. COTA

Temperature, light and dissolved nutrients are considered the "master" abiotic properties *controlling* primary production in the ocean. Each of these properties, in turn, is influenced by water column stability and vertical mixing. Sustained research over the past several decades has endeavored to ascertain which of these properties is most important in regulating phytoplankton growth. In no region has this research effort been more evident than at high latitudes. For both polar regions, extremes in each of these properties is the rule in surface waters where phytoplankton grow: the lowest ocean temperatures, the greatest seasonal excursion in incident solar radiation, and the highest dissolved nutrient concentrations.

Based largely on indirect evidence, early researchers speculated that polar primary production was high relative to production at lower latitudes. This was commonly attributed to the abundant surface "macronutrients" (NO_3, PO_4, H_4SiO_4) since physiological adaptations to the suboptimum temperatures and light were thought to characterise these high latitude populations. Intensification of polar research since the late 1960's has in many respects modified this view. Current perspectives are that important differences exist between the Arctic and Antarctic with regard to the availability and role nutrients play in regulating primary production. In general much less emphasis is now placed on the significance of the macronutrients in the Antarctic although there is speculation and some evidence that "micronutrients" (Fe) may be important. Macronutrient availability appears to play a more important, though secondary, role in the Arctic, that of *sustaining* rather than *initiating* phytoplankton growth.

This paper reviews early, contemporary, and present research addressing the question, "What role does nutrient availability play in the distribution and magnitude of primary production in Arctic and Antarctic waters?" Emphasis is placed on new research on under-ice communities as well as on the historically studied pelagic communities.

W. G. Harrison, Biological Oceanography Division, Department of Fisheries and Oceans, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2; G. F. Cota, Graduate Program in Ecology, University of Tennessee, Knoxville, Tennessee 37996, USA.

Introduction

Over the past two decades, oceanographic research in polar oceans has made considerable progress in identifying the environmental (abiotic and biotic) properties which regulate the biomass and productivity of high-latitude phytoplankton (Fogg 1977; Holm-Hansen et al. 1977; Nemoto & Harrison 1981; Sakshaug & Holm-Hansen 1984; Priddle et al. 1986; Jacques 1989; Sakshaug 1989; Smith & Sakshaug 1990). Among the factors commonly considered are 1) temperature, 2) light, both solar variations and how it is influenced by the presence of sea-ice, 3) nutrients, 4) turbulence, or conversely, water column stability, and 5) food web interactions, e.g., grazing losses (El-Sayed 1984). Currently, it is believed that the environmental factors which exert the greatest control on polar phytoplankton growth are the low and relatively invariant temperatures, the presence (or absence) of sea ice and the extreme seasonal variations in the high-latitude light regimes (Smith & Sakshaug 1990). In general, therefore, turbulence/stability, food web interactions and nutrient availability (the latter determined by these physical and biological processes, i.e. "new" and "regenerated" nutrients, Dugdale & Goering 1967) may be considered to exert secondary effects on primary production or play a more confined role regionally or temporally. This paper deals with the specific role nutrients play in limiting, or more correctly *controlling* (Thingstad & Sakshaug 1990) primary production in both the pelagic and sea-ice phytoplankton communities of the Arctic and Antarctic. The emphasis is on the essential macro elements N, P, and Si, although we recognise that, strictly speaking, the term "nutrients" has a much

broader connotation which encompasses the trace elements essential for plant growth (e.g. Fe) as well as the non-essential elements (Holm-Hansen 1985).

Under natural conditions, unequivocal *proof* of "nutrient limitation" of primary production can infrequently, if not rarely, be established. Limitation is generally deduced from indirect evidence such as 1) the presence or absence of essential nutrients in the upper water column (usually the mixed layer), 2) covariance (direct or inverse) of nutrients with phytoplankton biomass and/or productivity, 3) nutrient bioassays, 4) cellular chemical composition, or 5) relative nutrient utilisation rates. These indirect indices will form the basis for the discussion developed in this paper.

There is an extensive amount of current literature dealing with this and allied topics, and our review merely touches on some of the highlights.

Why consider nutrients?

In the absence of any influence of nutrients, the general features of oceanic primary production

GEOSECS DATA

Fig. 2. Latitudinal variations in NO_3 and H_4SiO_4 concentrations in surface waters of the Atlantic and Pacific Oceans, GEOSECS Data (Bainbridge 1976a, b).
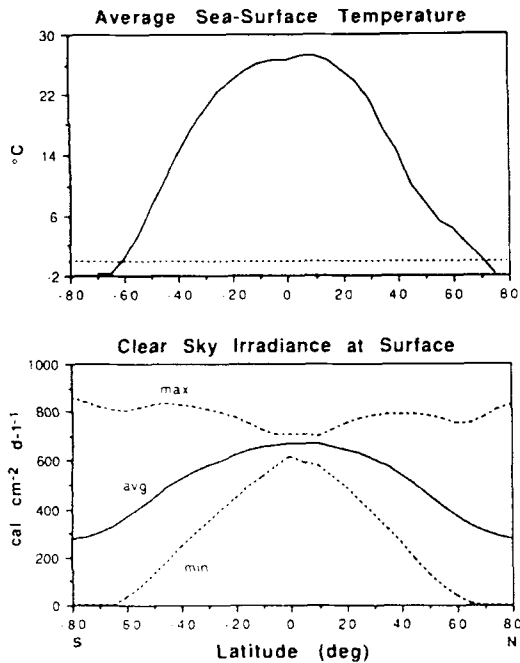
Fig. 1. Latitudinal variations in average sea surface temperature (Pickard 1964) and incident solar radiation (Ivanoff 1975, see also Campbell & Aarup 1989 for PAR variations). Lower panel also shows annual range based on monthly means.
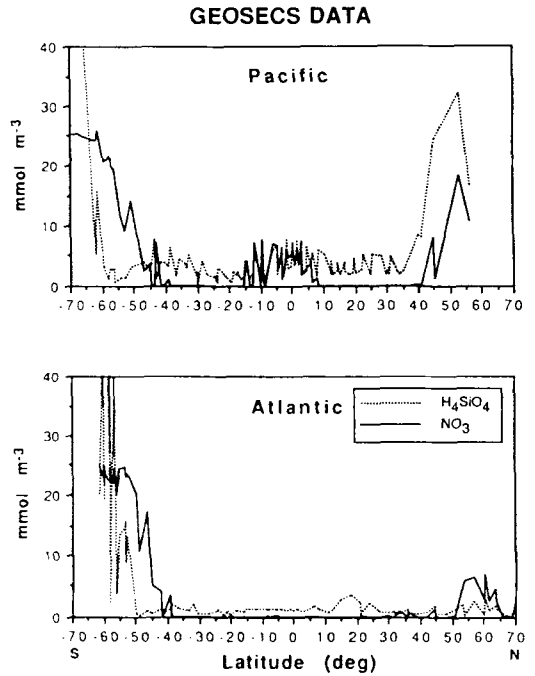
and phytoplankton biomass would be expected to follow the global ocean patterns in available light and temperature (Fig. 1) with the highest levels at low latitudes. It is clear, however, that the major patterns in the distribution of biological activity show lowest levels at low latitudes. Indeed, global plankton distributions are more closely correlated with the distributions of elevated sea surface nutrients (Reid 1962) which increase with latitude (Fig. 2). This apparent link between nutrients and biology led Sverdrup (1955) to construct the first global map of ocean productivity (Fig. 3) based on the tenet that, ". . . productivity depends on the rate at which plant nutrients of the surface layers are renewed and that the renewal takes place by physical processes, such as vertical convection, upwelling and turbulent diffusion. . .". This picture of the global distribution of ocean productivity and biomass is remarkably similar to our current views based on cumulative field measurements (Berger 1989) and ocean color satellite images (Lewis 1989), with one notable exception; Sverdrup's map depicts polar primary productivity in the highest category, for example on the same scale as that
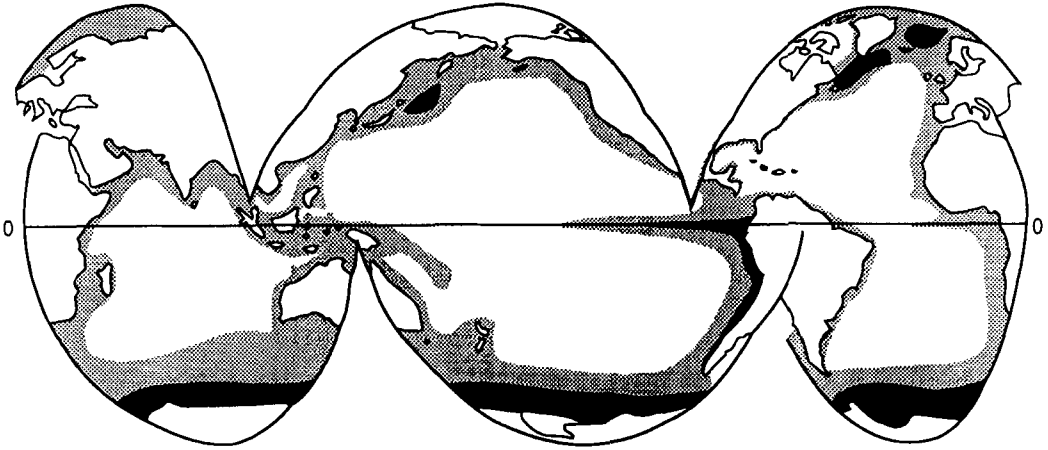
Fig. 3. Schematic representation of global productivity (relative) based on variations in nutrient "renewal" to surface waters by physical mixing processes (redrawn from Sverdrup 1955).

of coastal upwelling systems. We now know that this is clearly not the case, particularly for the Antarctic (Holm-Hansen et al. 1977; Subba Rao & Platt 1984). The prevailing contemporary view is that factors other than nutrient "replenishment" are comparable or of greater importance in setting the limits on primary production at high latitudes.

The pelagic production zone

Multidisciplinary investigations of the ecology of polar marine communities (distribution, productivity and their relationship to the environment) did not become an important component of ocean research until the late 1960s and early 1970s (Llano 1978; El-Sayed 1988). Studies have increased markedly in recent years: in the Arctic, the PROBES and ISHTAR programs (Bering-Chukchi Seas), the MIZEX and CEAREX programs (East Greenland Sea) and Pro mare (Barents Sea); and in the Antarctic, the AMERIEZ (Weddell-Scotia Seas) and RACER programs. Despite the relatively late start in multidisciplinary polar oceanography, most of the major Arctic and Antarctic water masses (Fig. 4) have been studied sufficiently to permit some generalisations about phytoplankton and the role nutrients play in its distribution and production.

Antarctic open waters

Persistently high nutrient concentrations,

especially nitrate (NO_3), phosphate (PO_4), and silicic acid (H_4SiO_4), in Antarctic surface waters are distinctive characteristics of the Southern Ocean (Fig. 2). Indeed, nutrient concentrations south of the Polar Front ($\sim 50°S$) are among the highest in any surface waters in the world; NO_3, H_4SiO_4, and PO_4 levels in summer can exceed 20 mmol m^{-3}, 50 mmol m^{-3}, and 2 mmol m^{-3}, respectively (Priddle et al. 1986; Jones et al. 1990). This is due largely to the massive-scale upwelling of deep North Atlantic waters at the Antarctic Divergence. From the standpoint of phytoplankton ecology, this system has been described as a "giant chemostat" (Holm-Hansen 1985) which provides an abundant, spatially uniform and continuous supply of nutrients for primary production. Though nutrient concentrations decrease in response to the phytoplankton growth cycle, they are rarely consumed to depletion, even during massive blooms (El-Sayed 1984). Moreover, classical nutrient enrichment assays have failed to demonstrate an increase in phytoplankton biomass or stimulation of production by the addition of the major or minor (trace) nutrients (Jacques 1983; Hayes et al. 1984). Elemental ratios of the particulate matter (C/N, N/P, C/P) deviate little from the expected Redfield ratios (Smith & Sakshaug 1990) which also argues against any significant N or P deficiencies. With respect to nitrogen limitation, the case is further weakened when one considers that, in addition to NO_3, reduced forms (NH_4, urea) are available and usually preferentially utilised;
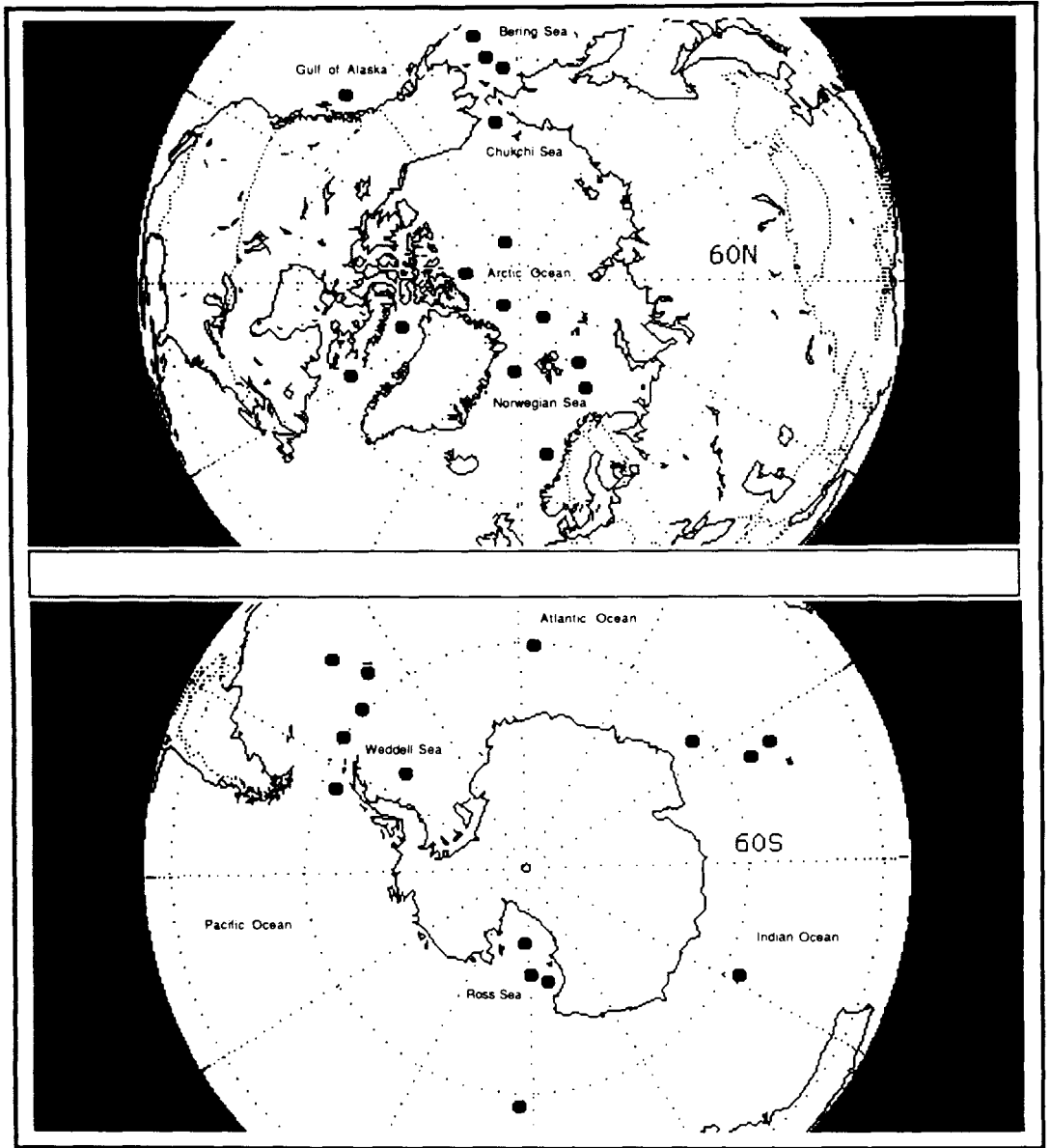
Fig. 4. Major present and past sites of ecological studies in polar oceans.

up to 50% or more of the phytoplankton nitrogen demand is met by this "regenerated" nitrogen produced locally as plankton metabolic wastes (Smith & Nelson 1990, and references cited therein).

Specific instances have been reported, however, where nutrient limitation was suspected. Holm-Hansen et al. (1989), for example, observed depletion of NO_3 and PO_4 in surface waters in the vicinity of Palmer Station during an intense phytoplankton bloom: chlorophyll   *a*   (CHL) = 4–30 mg m^{-3}.   Ancillary measurements of cellular biochemical properties also revealed abnormally high CHL/adenosine triphosphate (ATP) and particulate organic carbon (POC)/ATP ratios, indicative of nutrient-limited populations. Exhaustion of surface NO_3 and PO_4 have also been reported in some ice-

edge communities in the Ross Sea (Nelson & Smith 1986; see next section). Other findings have suggested that H_4SiO_4 may limit (or have the potential to limit) phytoplankton growth. Based on an analysis of NO_3-H_4SiO_4 and PO_4-H_4SiO_4 relationships in the world's oceans using the extensive NODC nutrient database, Zentara & Kamykowski (1977) and Kamykowski & Zentara (1985, 1989) have shown the potential for H_4SiO_4 depletion in surface waters in the Southern Ocean, particularly in waters south of the subtropical convergence and north of the Antarctic Divergence. Holm-Hansen et al. (1977) also drew attention to this region, noting that H_4SiO_4 concentrations decreased northward from the Divergence much more rapidly than did NO_3 and PO_4; this is clearly seen in the GEOSECS data in Fig. 2 (see also Le Jehan & Treguer 1985). Differential loss of the highly silicified phytoplankton (primarily diatoms) by sinking and low Si-dissolution rates (relative to regeneration of N and P) as a result of the prevailing low seawater temperatures has been the favored explanation (Nelson & Gordon 1982; Treguer et al. 1989). Biochemical and physiological characteristics of Antarctic diatoms also point to the potential for Si-limitation. Silicification appears much greater in Antarctic diatoms than in more temperate forms; often Si/C ratios are significantly elevated (see also section below) relative to normal ratios (Brzezinski 1985), suggesting an unusually high Si-demand for growth (Smith & Sakshaug 1990). Studies of Si uptake kinetics have also revealed very low substrate affinities in some strains of Antarctic diatoms; K_s values ranging from 12–90 mmol m^{-3} have been documented (Jacques 1983; Sommer 1986), as compared with normal values in the range of 1–5 mmol m^{-3}. Elevated K_s values imply the potential for Si-limitation even at the high ambient H_4SiO_4 levels characteristic of the Southern Ocean.

A discussion of the nutrient effects on productivity of Antarctic open waters would not be complete without commenting on several recent papers dealing with the possibility of "trace" nutrient (specifically, Fe) limitation in the Southern Ocean (Martin & Fitzwater 1988; Martin & Gordon 1988; Martin 1990; Martin et al. 1990b). Trace metal enrichment experiments have been done previously in the Antarctic (Jacques 1983; Hayes et al. 1984) but with negative results. Metal-free "clean" techniques were not used, and the findings have consequently been considered suspect. Using "clean" techniques, Martin and colleagues showed that despite the presence of high ambient concentrations of macro-nutrients, phytoplankton growth in the subarctic Pacific was stimulated only after the addition of nmolar amounts of Fe. This apparent Fe-deficiency was attributed to low inputs from the atmosphere (the primary source of Fe in the open ocean) in the region. They further speculated that the "Antarctic paradox" (low productivity despite high nutrients) may be explained using the same argument. Interestingly enough, Hart (1934) was one of the first to suggest Fe-deficiency as a controlling fact of Antarctic productivity. Martin et al. (1990b) subsequently showed that high productivity in Antarctic coastal waters was associated with high ambient Fe concentrations, whereas low productivity zones were extremely low in Fe offshore. Martin (1990) also noted an apparent link between Fe availability and glacial/interglacial CO_2 levels based on analysis of Antarctic ice cores. Martin's conclusions, however, have not been universally accepted because of questions arising from details of his methodology (Banse 1990, 1991; see also Martin et al. 1990a). Buma et al. (1990) have carried out contaminant-free enrichments experiments in the Weddell and Scotia Seas, showing Fe stimulation of chlorophyll *a* synthesis and nutrient assimilation, but growth in their control (unenriched) treatments also exceeded levels normally observed. They thus concluded that Fe was likely only one of several growth-limiting factors. Sakshaug & Holm-Hansen (1984) argue that observed variations in Antarctic productivity and biomass accumulation can be sufficiently explained by mixing and its effects on the phytoplankton light environment.

Antarctic marginal ice zone

The view of the Antarctic as an "oligotrophic" ocean (Jacques 1989) has been modified by recent findings that a substantial portion of the annual productivity is associated with the southward retreating ice edge during the austral spring-summer (Jennings et al. 1984; Smith & Nelson 1986). According to current estimates, the marginal ice zone accounts for about 40% of the total Antarctic primary production (Smith & Nelson 1986). Biomass and productivity associated with the ice edge are among the highest recorded for the Southern Ocean (El-Sayed 1971) and are typically higher than levels found in surrounding waters (Smith

& Nelson 1985); it therefore follows that the potential for nutrient limitation should be greatest there. Studies to date, however, do not generally bear this out although nutrient levels are reduced to a greater extent than in surrounding waters (El-Sayed & Taguchi 1981; Nelson & Smith 1986; Nelson et al. 1989). The one exception is the study of Nelson & Smith (1986) where NO_3 and PO_4 were reduced to levels below analytical detection in surface waters at two stations in the Ross Sea. These investigators have also noted exceptionally high H_4SiO_4 demand and Si/C compositional ratios (6–8× normal) of the ice edge diatoms in the Ross (Nelson & Smith 1986) and Weddell Seas, even in the late summer when the ice edge is stationary (Nelson et al. 1989). This fact along with observed low substrate affinities described previously (Jacques 1983; Sommer 1986) may potentially lead to Si-limitation, even if concentrations are not reduced to extremely low levels. Si-limitation, however, has not been conclusively demonstrated in the field yet. Overall, the link between nutrient availability and primary production in the Antarctic marginal ice zone seems weak at present.

In summary, despite isolated examples of nutrient exhaustion in intense bloom conditions in shallow waters or near the ice edge and evidence of atypically high nutrient demand (specifically, H_4SiO_4) by some phytoplankton species, it is presently felt that the distribution and production patterns of Southern Ocean phytoplankton bear little relationship to the distribution of the major nutrients. The converse apparently *is true* on the small to meso-scale, e.g. biological processes apparently have a major influence on the distribution of H_4SiO_4 (relative to that of NO_3 and PO_4) in waters flowing northward from the Antarctic Divergence (Jones et al. 1990). Other environmental or biological factors are currently felt to be more important in the initiation of Southern Ocean phytoplankton production and growth, with nutrients playing a secondary role (i.e. sustaining growth) at best. The exact role of "trace" nutrients is an intriguing question; however, their status as major controlling factors is as yet unresolved.

Arctic open waters

In marked contrast to the Antarctic, nutrient concentrations in Arctic/subarctic surface waters are considerably lower (see Fig. 2) and commonly reach exhaustion in summer (Codispoti & Richards 1968; Hameedi 1978; Alexander & Niebauer 1981; Harrison et al. 1982; Rey & Loeng 1985; Smith et al. 1985; Whitledge et al. 1986; MacDonald & Wong 1987; Spies et al. 1988). In fact, Sakshaug & Holm-Hansen (1984) have made the observation that *maximum* Arctic concentrations are typically lower than *minimum* Antarctic concentrations. Of the three macronutrients considered, PO_4 is almost universally present in excess in Arctic waters (but see MacDonald et al. 1987), even during summer when surface concentrations are usually at their lowest and the potential for nutrient limitation therefore generally focuses on NO_3 or H_4SiO_4. An inspection of Kamykowski & Zentara's (1985) analysis of NO_3-H_4SiO_4 relationships in the world's oceans revealed relatively few data sets for Arctic waters which permit an assessment of the prevalence of, or potential for, NO_3 versus H_4SiO_4 exhaustion in surface waters. The available results suggest excess H_4SiO_4 at NO_3 depletion in the Chukchi and western Beaufort Seas and *either* NO_3 *or* H_4SiO_4 depletion in the northern Bering Sea and the eastern Greenland/Norwegian Seas. A more selective but less comprehensive analysis of NO_3-H_4SiO_4 relationships for representative data sets in summer months suggests that the potential for NO_3 limitation may be more common (Fig. 5), even in the Arctic basin (English 1961). There are notable exceptions, however, to this pattern in other Arctic regions. For example, Rey & Skjoldal (1987) observed a regular and apparently extensive deep H_4SiO_4 depletion, extending well beyond the depth of the nitracline, in the Barents Sea during sedimentation of the spring diatom bloom. They suggested that subsequent diatom growth during summer could be retarded as a result since the positioning of the H_4SiO_4 gradient below that of the NO_3 and PO_4 gradients would mean relatively less H_4SiO_4 available to the base of the photic zone when mixing occurred. In a long term study of NO_3-H_4SiO_4 relationships in waters off Iceland, Stefansson & Olafsson (1990) described years where H_4SiO_4 was in excess as "anomalous", occurring only when the spring bloom was dominated by non-diatom algae such as the prymnesiophyte, *Phaeocystis pouchetii*. Codispoti et al. (1990) noted a similar residual of H_4SiO_4 in surface waters of the Greenland Sea coincident with *Phaeocystis* blooms. In any event, surface nutrient exhaustion in summer and concomitant reduction in phytoplankton productivity

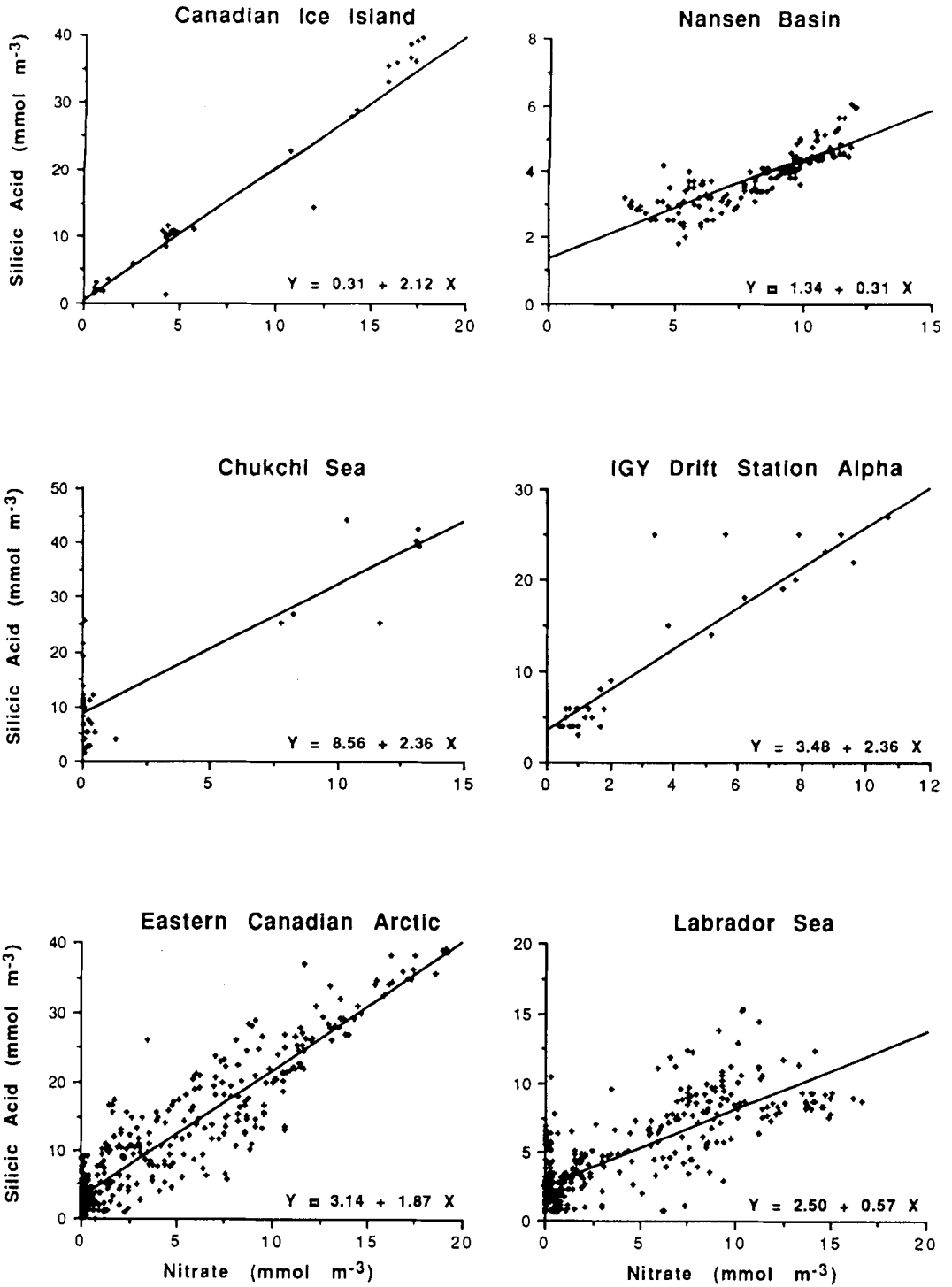*Fig. 5.* NO$_3$-H$_4$SiO$_4$ relationships for selected sites in the Arctic. Line represents least-squares linear regression fit. Data sources: Canadian Ice Island – B. T. Hargrave (unpubl. data). Nansen Basin – E. P. Jones (unpubl. data), Chukchi Sea – Hameedi (1978), Eastern Arctic – Irwin et al. (1978a, 1982, 1983, 1984, 1985, 1987, 1988), Labrador Sea – Irwin et al. (1978b, 1978c, 1986a, 1986b, 1988, 1989).

and biomass are widespread features of the Arctic.

Establishing a direct link between nutrients and phytoplankton variations in the Arctic summer is not always straightforward. Extensive studies over several years in the eastern Arctic (Labrador sea to northern Baffin Bay) have failed to demonstrate any statistical relationship between phytoplankton biomass or productivity indices and ambient nutrient concentrations (Harrison & Platt 1986). Multivariate analysis (step-wise regression) of an updated and more extensive (627 observations) data set of photosynthesis-irradiance parameters and environmental factors (Fig. 6, Table 1) confirm Harrison & Platt's earlier conclusions; only temperature and light contributed significantly to the variance in P_m^B, the maximum photosynthetic rate at light saturation, while biomass contributed (but only marginally) to the variance in α^B, the photosynthetic efficiency parameter (Table 2). A similar analytical

Table 1. Range and mean values for chlorophyll a (CHL, mg m^{-3}), photosynthesis-irradiance parameters (P_m^B = mgC mgCHL^{-1} h^{-1}, α^B = mgC mgCHL^{-1} h^{-1} (μmol m^{-2} s^{-1})$^{-1}$, and selected environmental properties of the upper water column in the Labrador Sea and eastern Canadian Arctic (see Fig. 6). Sample depth = metres. temperature (t) = °C, NO$_3$ concentration = mmol m^{-3}.

	No. Obs	Minimum	Maximum	Mean
P_m^B	674	0.11	12.84	2.04
α^B	673	0.001	0.188	0.018
CHL	672	0.03	25.27	2.44
Depth	674	0	80	18
t	653	−1.8	11.5	1.9
NO$_3$ conc.	650	0.00	16.55	2.17

approach was taken in assessing nutrient effects on water-column integrated productivity of a subset of the above data (29 stations) from Baffin Bay and adjoining waters (Table 3). In this analysis, neither nutrient *concentrations* nor nutrient *util-*
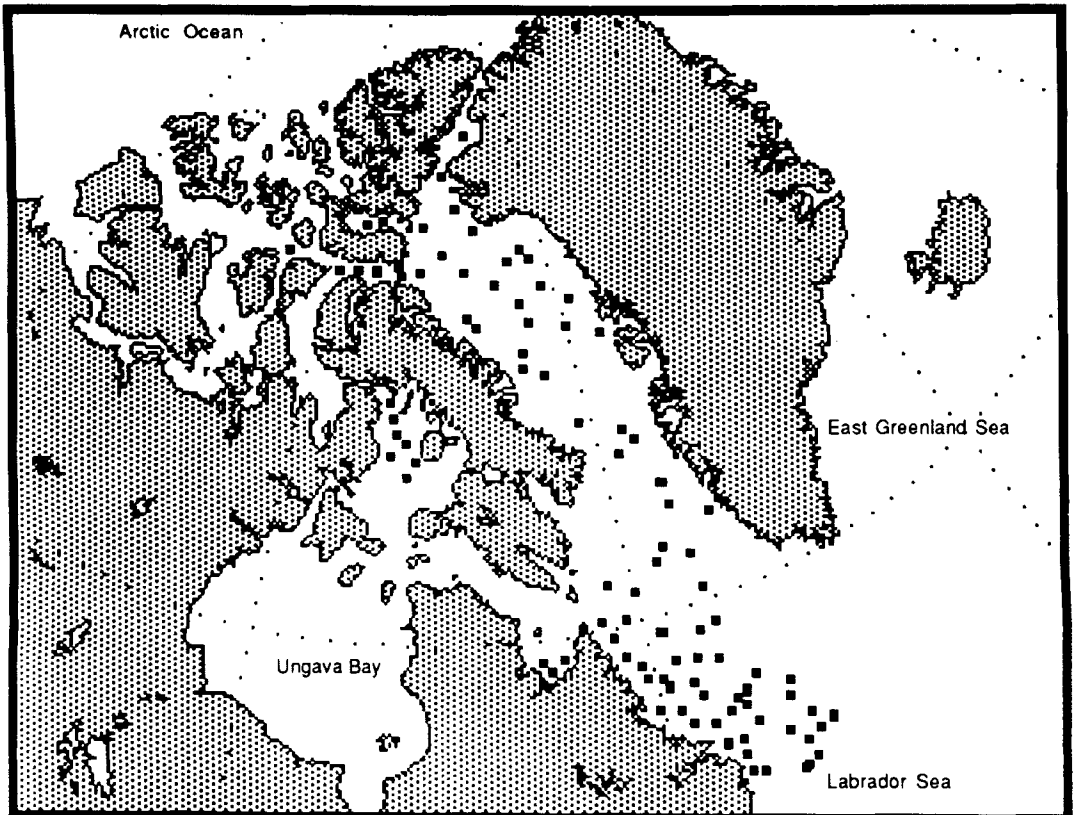

Fig. 6. Station locations in the eastern Canadian Arctic (Labrador Sea, Baffin Bay and adjoining waters) where photosynthesis-irradiance (P-I) measurements have been made (see also Table 1).

Table 2. Stepwise regression analysis of photosynthesis-irradiance parameters and selected environmental factors from field work covering summer periods from 1977–1984 and including regions from ca. 55°N–79°N latitude (data summarised in Table 1).

	Adjusted R^2	RMS Residual	F
A. Dependent variable: P_m^B			
Independent variables included:			
Temperature	0.252	1.338	164.52
Sample depth	0.274	1.318	20.06
Variables excluded:			
NO_3 conc.			2.49
Chlorophyll *a*			1.42
B. Dependent variable: α^B			
Independent variables included:			
Chlorophyll *a*	0.011	0.069	7.67
Variables excluded:			
Sample depth			3.14
Temperature			2.51
NO_3 conc.			0.37

isation rates contributed to the observed variation in primary productivity; incident radiation and phytoplankton biomass were the only significant co-variates (Table 4). Studies in the Bering Sea, on the other hand, have clearly established the link between NO_3 and productivity/biomass levels in late spring and summer, e.g. in association with shelf-break mixing (Iverson et al. 1979), wind mixing events (Sambrotto et al. 1986), and ice edge upwelling (Alexander & Niebauer 1981). The availability of NO_3 appears to be a major determinant in the spatial and temporal distribution of phytoplankton in that region (McRoy et al. 1972; Whitledge et al. 1986; Walsh et al. 1989; Hansell et al. 1989). Further south in the Gulf of Alaska, surface NO_3 concentrations rarely reach undetectable levels even in summer (Anderson et al. 1969). Martin & Fitzwater (1988) attribute this and the relatively low productivity of the region to Fe-limitation, although suppression of NO_3 uptake by NH_4 has also been suggested (Wheeler & Kokkinakis 1990). In the eastern Arctic, Rey et al. (1987) established a clear relationship among chlorophyll *a* biomass, NO_3 utilisation rates, and water column stability in temporal studies in the Barents Sea over a several year period.

Despite the common absence of NO_3 from summer surface waters, reduced-N forms (NH_4, urea), which are often not routinely measured, constitute a significant fraction of the nitrogen available for phytoplankton growth in the Arctic and may mitigate to some extent the potential limiting effects of NO_3 depletion (Harrison et al. 1982, 1985); uptake patterns of the reduced-N compounds to date have provided no evidence that the summer phytoplankton populations are severely N-limited (Harrison et al. 1982; Harrison 1983; Kristiansen & Lund 1989). This may help to explain the lack of correlation between phytoplankton indices and nutrients in the eastern Arctic. It seems clear, in any event, that other environmental factors may be more important on the time/space scales characterising these data (Harrison et al. 1982; Harrison & Platt 1986). Regenerated-N forms constitute a surprisingly

Table 3. Range and mean values for chlorophyll *a* (CHL, mg m^{-2}), carbon productivity (PP, mgC m^{-2} d^{-1}), nitrogen productivity (ρNO_3 & ρNH_4, mmol m^{-2} d^{-1}) and selected environmental properties of the upper water column in the eastern Canadian Arctic during summer 1978 & 1980 (Harrison et al. 1982, 1985). Average daily incident radiation (I_o) = mol m^{-2} h^{-1}, temperature (t) = °C, photic depth (Z_c) and mixed-layer depth (Z_m) = metres, NO_3 & NH_4 concentration (mmol m^{-2}), and f-ratio = $\rho NO_3/(\rho NO_3 + \rho NH_4)$.

	No. Obs	Minimum	Maximum	Mean
CHL	29	12.8	121.7	49.2
PP	29	105	1076	298
ρNO_3	29	0.34	8.00	2.22
ρNH_4	29	0.19	3.20	1.49
f-ratio	29	0.19	0.88	0.54
I_o	29	0.47	3.00	1.51
t	27	−1.0	7.8	1.1
Z_c	29	24	54	34
Z_m	29	0	22	13
NO_3 conc.	29	0.7	227.1	59.8
NH_4 conc.	29	0.7	16.5	4.9

Table 4. Stepwise regression analysis of water-column integrated primary productivity and selected environmental factors from summer field work in Baffin Bay and adjoining waters, eastern Canadian Arctic, 1978 and 1980 (data summarised in Table 3).

	Adjusted R^2	RMS Residual	F
A. Dependent variable: Chlorophyll a (CHL)			
Independent variables included:			
Incident radiation	0.299	25.90	12.07
Variables excluded:			
f-ratio			1.70
Inorganic-N conc.			0.49
Temperature			0.43
N-Uptake			0.37
B. Dependent variable: Primary productivity (PP)			
Independent variables included:			
Chlorophyll a	0.395	159.67	43.49
Incident radiation	0.614	127.54	15.19
Variables excluded:			
f-ratio			1.22
Temperature			0.98
N-uptake			0.65
Inorganic-N conc.			0.34

Inorganic-N = NO_3 + NH_4, N-uptake = NO_3 + NH_4 uptake. f-ratio = NO_3 uptake/(NO_3 + NH_4) uptake.

large portion of the nitrogen productivity in both the Arctic (Harrison et al. 1982; Muller-Karger & Alexander 1987; Kristiansen & Lund 1989; Smith & Kattner 1989) and the Antarctic (Slawyk 1979; Olson 1980, Gilbert et al. 1982; Rönner et al. 1983; Collos & Slawyk 1986; Koike et al. 1986; Smith & Nelson 1990), which suggests that biotic controls on nutrient availability need more serious consideration than in the past.

Arctic marginal ice zone

Biological activity in the marginal ice zones is as important to the annual primary production cycle in the Arctic as it is in the Antarctic (Smith 1987). Detailed calculations for the Bering Sea, for example, show that the ice-edge communities account for 40–50% of the total regional production (McRoy & Goering 1976; V. Alexander, cited in Smith 1987). Although the effects of melting ice on vertical stability is considered the major factor in the *initiation* of the ice edge blooms, its consequences in the Arctic are markedly different from those in the Antarctic. Meltwater stability provides a more suitable light environment for phytoplankton growth but it also imposes a barrier to nutrient resupply once mixed layer reserves are depleted. In the Antarctic, of course, this presents little problem since nutrient concentrations are usually well in excess of growth requirements. However, in the Arctic, surface concentrations are much lower and are generally depleted early in the growing season, particularly in the marginal ice zone (Alexander & Niebauer 1981; 1989; Rey & Loeng 1985; Smith et al. 1985; Spies et al. 1988). In the Arctic, therefore, nutrient availability (i.e. resupply) is a major factor in the *maintenance* of ice edge production. Mixing processes such as ice edge upwelling and eddy formation are considered the principal resupply mechanisms in both the Bering (Alexander & Niebauer 1981; Muller-Karger & Alexander 1987) and East Greenland (Buckley et al 1979; Smith et al. 1985; Johannessen et al. 1987) Seas. Rey & Loeng (1985) found no evidence of upwelling in their studies of the ice edge production cycle in the western Barents Sea but noted a seasonally progressive deepening of the phytoplankton biomass, tracking the nitracline and residing well below the pycnocline by late summer. Post bloom production appeared to be supported principally by biotic nitrogen sources, i.e. "regenerated"-N (Harrison et al. 1982, 1985; Muller-Karger & Alexander 1987; Kristiansen & Lund 1989) as is the case in temperate waters.

In summary, whereas nutrient availability may only rarely influence phytoplankton dynamics in the Antarctic, some degree of nutrient limitation seems the rule in Arctic waters, especially in summer. The link between nutrients (NO_3 or H_4SiO_4) and phytoplankton biomass and productivity has been clear in some studies, par-

ticularly where physical mixing processes dominate (for example the marginal ice zone), but more difficult to establish in other studies where regenerative, "biotic", processes apparently dominate (for example the summer open waters condition of the eastern Canadian Arctic). In polar waters in general, it is clear that several environmental factors collectively determine the distribution and activity of phytoplankton, however, nutrient availability appears to rank high among these in the Arctic.

The under-ice production zone

Besides being vast, remote and inhospitable with planetary extremes in temperature, light and nutrients, polar oceans have an annual fluctuation in ice cover of about $23 \times 10^6 \text{ km}^2$, most of which is first-year ice. Sea ice influences heat flux, thermohaline structure of the upper ocean, air-sea interactions such as gas exchange and momentum transfer, albedo, the transmission of irradiance, and biological activity, especially primary productivity. Acute undersampling and bias in polar observations reflect the historical emphasis on ice-free areas during the summer navigable season. The proliferation of studies near ice edges and in ice-covered systems over the last decade or two has greatly improved our appreciation for the space/time variability of primary productivity.

Initially, primary productivity under seasonal or permanent ice cover was thought to be negligible because of very low irradiance and temperature (English 1961), but several groups of algae are capable of growing in ice-covered waters or on sea ice. Benthic algae, including microphytes and macrophytes, phytoplankton, and ice algae, all have been found to display net production under certain ice-covered conditions (Horner & Schrader 1982; Dunton 1985; Dayton et al. 1986; Rivkin et al. 1989). These algal groups have characteristic distributions and periods of maximum growth. The benthic algae are restricted to shallow regions (<20–50 m), and although most algae have summer growth maxima during open water periods, some macrophytes utilise stored carbon reserves and display winter growth peaks when nutrients are highest and competition lowest (Dunton 1985). Ice algae are associated with most types of sea ice, but particularly annual (first-year) ice. Little is known about pack ice assemblages except that biomass levels are rela-

tively low with little seasonal variability; evidence for in situ growth is limited to a slight nutrient depletion in ice (Dieckmann et al. 1990). Bottom ice algae on land-fast ice, by contrast, have been studied intensively and the largest blooms occur during local spring when there is little competition for nutrients. Benthic algae with summer growth maxima, on the other hand, are in direct competition with phytoplankton for light and nutrients. Over large scales phytoplankton and ice algae dominate polar productivity because of their wider distributions.

Ice algal productivity appears to be most pronounced under land-fast annual ice in regions with high nutrients and low snow cover. In providing a highly concentrated resource for grazers and augmenting phytoplankton production, they are important in prolonging the brief polar growth season. During their peak growth season, ice algae dominate local autotrophic activity (Horner & Schrader 1982). Bottom ice algal assemblages are confined to the ice water interface because of low temperatures; this represents the top of the seasonal euphotic zone. Photosynthetically active radiation incident on bottom ice algae is usually 1–5% or less of surface irradiance, and when heavily colonised 80–90% is absorbed within the algal layer (Welch & Bergmann 1989). Accumulations of 100–300 mg CHL m^{-2}, predominantly pennate diatoms, are common in productive regions (Smith et al. 1988; Cota & Sullivan 1990; Welch & Bergmann 1989). Visible bands of pigments are confined to a few cm. Intense gradients of nutrients and light across this layer suggest that cells at the top receive elevated irradiances but may be nutrient-limited whereas the reverse occurs at the bottom of the layer, i.e. light-limited and nutrient replete (Cota & Horne 1989; Cota et al. 1990; Smith et al. 1988, 1990). In this regard, the ice algal layer may be largely analogous to phytoplankton in the water column but vertically compressed.

Nutrients available to ice algae come from three principal sources: ice desalination, biological regeneration in situ, and mixing of the adjacent water column (Cota et al. 1987). The largest pool of nutrients is the latter (Fig. 7). Most salts (70–80%) are excluded from sea ice during formation while ice growth, which persists over about half of the vernal bloom, promotes convective fluxes at the interface (Reeburgh 1984). Subsequent brine drainage is almost continuous, but most salts in sea ice are locked within the ice until the
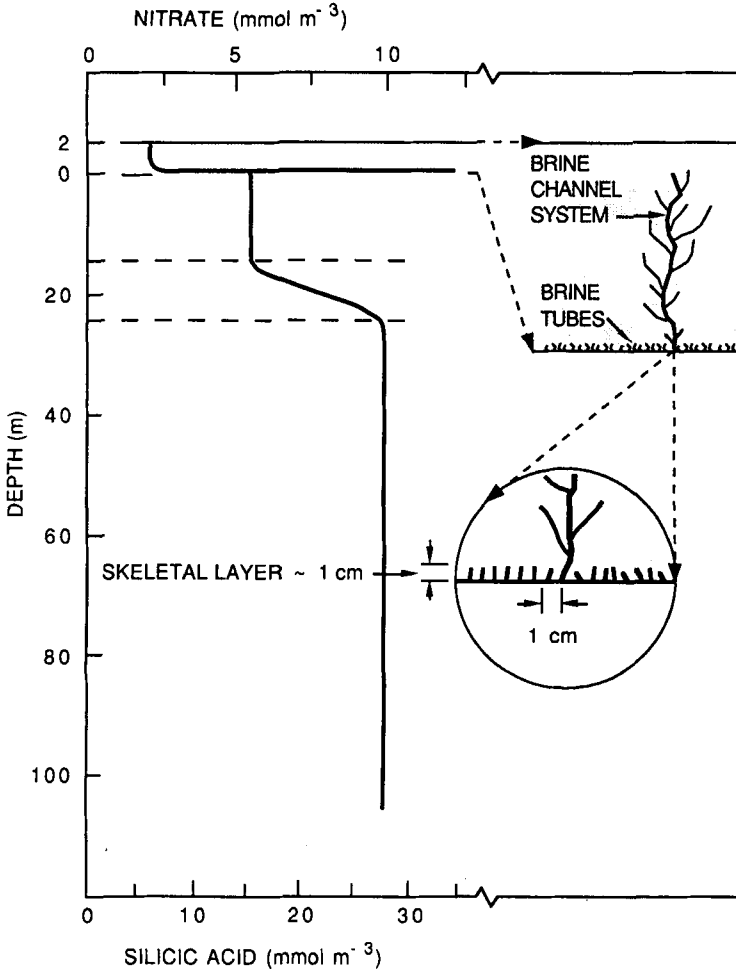
Fig. 7. Schematic representation of $\dot{N}O_3$ and H_4SiO_4 distribution through ice and water column.

late spring melt when concentrated brines exit from particular sites (50–200 brine channels m^{-2}), maintaining their identity well below the interface. Biomass accumulations indicate that large amounts of nitrogen and silicon are needed to account for minimal requirements of net population growth. Regenerative fluxes can supply only a small portion of algal demand, especially for silicon. However, nutrients in seawater are more than adequate to satisfy demand, but fluxes are episodic (Cota et al. 1987; Cota & Sullivan 1990).

Productivity and maximum biomass accumulation of bottom ice algae in some cases appear to be related to nutrient availability. In southeastern Hudson Bay classical enrichment bioassays have

shown that nitrogen limits ice algal biomass in estuarine waters (Maestrini et al. 1986). Moreover, Welch et al. (1991) suggest that the maximum ice algal biomass is directly proportional to mean water column NO_3 for 5 shallow (<150 m) sites in the Canadian Arctic. Welch and co-workers also hypothesised that NO_3 consumption by macrophytes in winter may reduce nearshore nitrogen concentrations in northwestern Hudson Bay. They also found that depletion of H_4SiO_4 in Barrow Strait exceeded 275 mmol m^{-2} between April and June in the top 100 m of the water column well before any phytoplankton bloom (Welch & Begmann 1989; see also Cota et al. 1990). Even in areas with relatively strong currents, steep and persistent nutrient gradients

with near surface minima have been observed in "well mixed" surface layers beneath heavily colonised sea ice, confirming a strong source-sink relationship (Cota et al. 1987, 1990; Cota & Horne 1989). At sites in the Arctic and subarctic, vertical nutrient fluxes appear to be linked closely to tidal forcing, and fluctuations in supply can influence ice algal photosynthetic response and biomass (Gosselin et al. 1985; Cota et al. 1987; Cota & Horne 1989; Demers et al. 1989); other environmental forcing may dominate currents and mixing in McMurdo Sound, Antarctica (Cota & Sullivan 1990). Ice algae are apparently capable of storing significant amounts of phosphorus and nitrogen so that nutrient ratios and concentrations in melted bottom ice cores may exceed those in seawater (Cota et al. 1990; Smith et al. 1990). Ammonium concentrations in bottom ice are also elevated, but about half of the nitrogen utilisation by ice algae is NO_3 (Table 5, Cota et al. 1988; Harrison et al. 1990). Significant internal nitrogen stores and compositional ratios (C:N, C:CHL) in the Redfield proportions are indicative of N-sufficient populations (Harrison et al. 1990). Several lines of evidence, however, suggest that H_4SiO_4 is likely to be limiting for bottom ice algae in fully marine waters (Cota et al. 1990; Cota & Sullivan 1990; Gosselin et al. 1990).

Microalgal populations colonising the interstices of sea ice represent a special situation with extreme and prolonged vertical stability where temperature, salinity and irradiance are often relatively constant compared to planktonic systems. Nutrients, on the other hand, may be depleted and resupplied episodically as in pelagic environments; in sea ice, nutrients must be available within, or delivered to, a narrow stratum. Except in the lowest few centimetres, nutrient concentrations are low in sea ice and could sustain only a brief ice algal bloom if they were readily available. Regenerative processes satisfy a portion of the required nitrogen and phosphorus, but dissolution of biogenic silica appears to be too slow to provide much H_4SiO_4. If high standing stocks of ice algae are attained and have sufficient light to continue growing, then rates of external nutrient supply, particularly from the water column, may become limiting even in the most nutrient-rich polar waters.

Summary

Nutrient availability varies in its importance for phytoplankton growth in polar oceans. Generally speaking, the Antarctic is characterised by a continuous and ample supply of nutrients. Nutrient limitation (or the potential for nutrient limitation) is apparently rare, but local depletion can occur if other growth-limiting conditions (for example water-column stability) are conducive to optimum production, biomass accumulation, and elevated nutrient demand (Mitchell & Holm-Hansen 1991). Such conditions occur in shallow coastal

Table 5. Range and mean values for ice algal chlorophyll *a* (CHL, mg m^{-2}), photosynthesis-irradiance parameters (P_m^B = mgC mgCHL^{-1} h^{-1}), α^B = mgC mgCHL^{-1} h^{-1} (µmol m^{-2} s^{-1})$^{-1}$, and selected environmental properties for bottom ice assemblages under low snow cover from Barrow Strait, NWT, Canada and McMurdo Sound, Antarctica in 1985 and 1986. Temperature (t) = °C, NO_3 & NH_4 concentration = mmol m^{-3}, ρNH_3 & ρNH_4 = mmol m^{-3} h^{-1}, f-ratio = $\rho NO_3/(\rho NO_3 + \rho NH_4)$.

	No. Obs	Minimum	Maximum	Mean
P_m^B	60	0.01	1.80	0.37
α^B	60	0.002	0.362	0.050
t	60	−1.90	−1.80	−1.85
CHL	96	4.5	182.0	68.9
NO_3* conc.	95	1.80	72.3	18.3
NO_3** conc.	14	3.91	123.40	40.39
NH_4** conc.	14	4.05	40.39	16.38
H_4SiO_4* conc.	95	2.90	14.40	6.90
ρNO_3	52	0.02	80.04	6.05
ρNH_4	50	0.05	36.15	3.45
f-ratio	45	0.08	0.92	0.53

* Concentrations based on bottom 3–5 cm of ice cores, Resolute 1985 (Cota et al. 1990). Directly comparable measurements were not available from the Antarctic.

** Concentrations based on bottom 1–3 cm of ice cores, Resolute 1985 and 1986 (Harrison et al. 1990). Directly comparable measurements were not available from the Antarctic.

waters, along receding ice edges and in under-ice (epontic) communities where vertical stratification is more persistent or prolonged. The generally more favorable growth conditions in the northern ocean, i.e. water-column stability (e.g. Dunbar 1968), combined with lower overall nutrient concentrations result in nutrient depletion being a common feature in subarctic and Arctic surface waters, in open waters as well as along ice edges. In both polar regions, factors other than nutrients are apparently most important in the *initiation* of growth whereas nutrients may be relegated to a more secondary role of *sustaining* growth and setting the upper limit on biomass accumulation.

Studies to date have provided a convincing picture of the interaction of ocean physics and phytoplankton as manifest through the supply of nutrients for growth. In both polar oceans, physically-mediated nutrient supply ("new" production, Eppley & Peterson 1979) is more important than at lower latitudes (Fig. 8), accounting for over 50% of the total primary production, particularly in the marginal ice zones (Smith & Nelson 1990). This high proportion of new production, however, is not commensurate with the level of primary production predicted if nutrient-limitation were the only consideration (Fig. 9). Clearly, other factors come into play in setting the upper limits on polar productivity, even in

Fig. 9. Relationship between f-ratio (new/total nitrogen production) and total primary production. Open symbols and curve = temperate/tropical data (Eppley & Peterson 1979); closed symbols = polar data, circles are pelagic studies, triangles are ice edge studies (Smith & Nelson 1990).

the Arctic where nutrient depletion is prevalent. Nonetheless, the close link between new production and the export (and redistribution) of biogenic materials (Eppley & Peterson 1979) points to the importance of nutrient-phytoplankton relationships in developing a better understanding of the role of polar oceans in global biogeochemical cycles (Dugdale & Wilkerson 1989; Jones et al. 1990; Smith & Sakshaug 1990).

The so-called "biotic" factors have received surprisingly little attention in studies of polar phytoplankton (El-Sayed 1984; Holm-Hansen 1985). In view of the large proportion (almost half) of the primary production that is supported by locally regenerated nutrients (NH_4, urea), despite often high "new" nutrient (NO_3) concentrations, attempts to model polar phytoplankton growth dynamics will be incomplete until plankton food web interactions (both in terms of grazing losses and nutrient resupply) are incorporated.
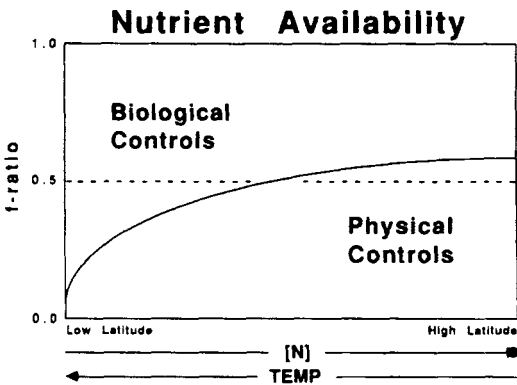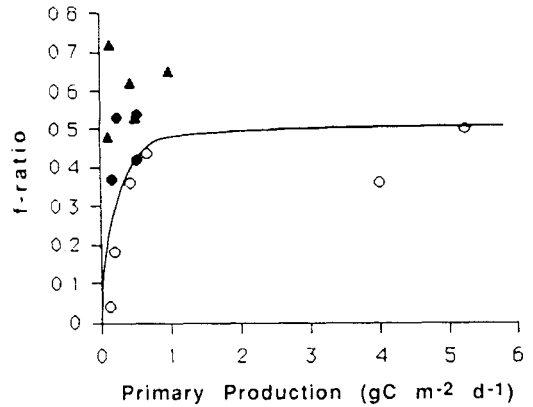

Fig. 8. Schematic representation of the relative importance of physical and biological sources of nutrients for phytoplankton growth along a latitudinal axis. [N] = surface nutrient concentration. TEMP = seawater temperature. Physical sources ("new" nutrients) are scaled by the f-ratio (Eppley & Peterson 1979) and range from approximately 0.1 (10% of total) in tropical oceans to approximately 0.6 (60% of total) in polar oceans. "Regenerated" nutrients (biological sources) make up the balance.

References

Alexander, V. & Niebauer, H. J. 1981: Oceanography of the eastern Bering Sea ice-edge in spring. *Limnol. Oceanogr. 26*, 1111–1125.

Alexander, V. & Niebauer, H. J. 1989: Recent studies of phytoplankton blooms at the ice edge in the Southeast Bering Sea. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer 188*, 98–107.

Anderson, G. C., Parsons, T. R. & Stephens, K. 1969: Nitrate distribution in the subarctic Northeast Pacific Ocean. *Deep-Sea Res. 16*, 329–334.

Bainbridge, A. E. 1976a: GEOSECS Atlantic final hydrographic data report. *GEOSECS Operations Group*, Scripps Institution of Oceanography, La Jolla, California.

Bainbridge, A. E. 1976b: GEOSECS Pacific final hydrographic data report. *GEOSECS Operations Group*, Scripps Institution of Oceanography, La Jolla, California.

Banse, K. 1990: Does iron really limit phytoplankton production in the offshore subarctic Pacific? *Limnol. Oceanogr. 35*, 772–775.

Banse, K. 1991: Iron availability, nitrate uptake, and exportable production in the subarctic Pacific. *J. Geophys. Res. 96*, 741–748.

Berger, W. H. 1989: Global maps of ocean productivity. Pp. 429–455 in Berger, W. H., Smetacek, V. S. & Wefer, G. (eds.): *Productivity of the Ocean: Present and Past.* Wiley Interscience, New York.

Brzezinski, M. A. 1985: The Si:C:N ratio of marine diatoms: interspecific variability and the effect of some environmental variables. *J. Phycol. 21*, 347–357.

Buckley, J. R., Gammelsrød, T., Johannessen, J. A., Johannessen, O. M. & Røed, L. P. 1979: Upwelling: Oceanic structure at the edge of the Arctic pack ice in winter. *Science 203*, 165–167.

Buma, A. G. J., Nolting, R. F. de Baar, H. J. W. & Cadee, G. C. 1990: Testing the iron limitation hypothesis for phytoplankton from the Southern Ocean. *EOS 71*, 67.

Campbell, J. W. & Aarup, T. 1989: Photosynthetically available radiation at high latitudes. *Limnol. Oceanogr. 34*, 1490–1499.

Codispoti, L. A. & Richards, F. A. 1968: Micronutrient distributions in the East Siberian and Laptev seas during summer, 1963. *Arctic 21*, 67–83.

Codispoti, L. A., Freiderich, G. E., Whaling, P. & Friebertshauser, M. E. 1990: Some implications of the nutrient observations made during the 1989 CEAREX experiment. *Eos 71*, 79.

Collos, Y. & Slawyk, G. 1986: ^{13}C and ^{15}N uptake by Marine phytoplankton -IV. Uptake ratios and the contribution of nitrate to the productivity of Antarctic waters (Indian Ocean sector). *Deep-Sea Res. 33*, 1039–1051.

Cota, G. F. & Horne, E. P. W. 1989: Physical control of ice algal production in the high Arctic. *Mar. Ecol. Prog. Ser. 52*, 111–21.

Cota, G. F. & Sullivan, C. W. 1990: Photoadaptation, growth and production of bottom ice algae in the Antarctic. *J. Phycol. 26*, 399–411.

Cota, G. F., Prinsenberg, S. J., Bennett, E. B., Loder, J. W., Lewis, M. R., Anning, J. L., Watson, N. & Harris, L. R. 1987: Nutrient fluxes during extended blooms of Arctic ice algae. *J. Geophys. Res. 92*, 1951–1962.

Cota, G. F., Sullivan, C. W. & Priscu, J. C. 1988: Uptake of inorganic nitrogen by ice algae in McMurdo Sound, Antarctica. *Eos 69*, 1104.

Cota, G. F., Anning, J. L., Harris, L. R., Harrison, W. G. & Smith, R. E. H. 1990: The impact of ice algae on inorganic nutrients in seawater and sea ice in Barrow Strait, NWT, Canada during spring. *Can. J. Fish. Aq. Sci. 47*, 1402–1415.

Dayton, P. K., Watson, D., Palmisano, A., Barry, J. P., Oliver, J. S. & Rivera, D. 1986: Distribution patterns of benthic microalgal standing stock at McMurdo Sound, Antarctica. *Polar Biol. 6*, 207–213.

Demers, S., Legendre, L., Maestrini, S. Y., Rochet, M. & Ingram, R. G. 1989: Nitrogenous nutrition of sea-ice microalgae. *Polar Biol. 9*, 377–383.

Diekmann, G., Sullivan, C. W. & Garrison, D. L. 1990:

Seasonal standing crop of ice algae in pack ice of the Weddell Sea, Antarctica. *Eos 71*, 79.

Dugdale, R. C. & Goering, J. J. 1967: Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnol. Oceanogr. 12*, 196–206.

Dugdale, R. C. & Wilkerson, F. P. 1989: Regional perspectives in global new production. Pp. 289–308 in Denis, M. M. (ed.): *Oceanologie, actualite et prospective.* Centre d'Oceanologie de Marseille.

Dunbar, M. J. 1968: *Ecological Development in Polar Regions.* Prentice-Hall, Englewood Cliffs, N.J.

Dunton, K. H. 1985: Growth of dark-exposed *Laminaria saccharina* (L.) Lamour, and *Laminaria solidungula* J. Ag. (Lamipariales: Phaeophyta) in the Alaskan Beaufort Sea. *J. Exp. Mar. Biol. Ecol. 94*, 181–189.

El-Sayed, S. Z. 1971: Observations on phytoplankton bloom in the Weddell Sea. Pp. 301–312 in Llano, G. & Wallen, I. (eds.): *Biology of the Antarctic Seas.* Am. Geophys. Union., Washington, D.C.

El-Sayed, S. Z. 1984: Productivity of Antarctic waters: A reappraisal. Pp. 19–34 in Holm-Hansen, O., Bolis, L. & Gilles, R. (eds.): *Marine Phytoplankton and Productivity.* Springer-Verlag, Berlin.

El-Sayed, S. Z. 1988: The BIOMASS Program. *Oceanus 31*, 75–79.

El-Sayed, S. Z. & Taguchi, S. 1981: Primary production and standing crop of phytoplankton along the ice-edge in the Weddell Sea. *Deep-Sea Res. 28*, 1017–1032.

English, T. S. 1961: Some biological observations in the central North Polar Sea. Drift Station Alpha. 1957–1958. *Arct. Inst. N. Am. Res. Paper 13*, 8–80.

Eppley, R. W. & Peterson, B. J. 1979: Particulate organic matter flux and plankton new production in the deep ocean. *Nature 282*, 677–680.

Fogg, G. E. 1977: Aquatic primary production in the Antarctic. *Phil. Trans. R. Soc. Lond. B279*, 27–38.

Gilbert, P. M., Biggs, D. C. & McCarthy, J. J. 1982: Utilization of ammonium and nitrate during austral summer in the Scotia Sea. *Deep-Sea Res. 29*, 837–850.

Gosselin, M. L., Legendre, L., Demers, S., Ingram, R. G. 1985: Responses of sea-ice microalgae to climatic and fortnightly tidal energy inputs (Manitounuk Sound, Hudson Bay). *Can. J. Fish. Aquat. Sci. 42*, 999–1006.

Gosselin, M., Legendre, L., Therriault, J-C. & Demers, S. 1990: Light and nutrient limitation of sea-ice microalgae (Hudson Bay, Canadian Arctic). *J. Phycol. 26*, 220–232.

Hameedi, M. J. 1978: Aspects of water column primary productivity in the Chukchi Sea during summer. *Mar. Biol. 48*, 37–46.

Hansell, D. A., Goering, J. J., Walsh, J. J., McRoy, C. P., Coachman, L. K. & Whitledge, T. E. 1989: Summer phytoplankton production and transport along the shelf break in the Bering Sea. *Cont. Shelf Res. 9*, 1085–1104.

Harrison, W. G. 1983: The time-course of uptake of inorganic and organic nitrogen compounds by phytoplankton from the eastern Canadian Arctic: a comparison with temperate and tropical populations. *Limnol. Oceanogr. 28*, 1231–1237.

Harrison, W. G. & Platt, T. 1986: Photosynthesis-irradiance relationships in polar and temperate phytoplankton populations. *Polar Biol. 5*, 153–164.

Harrison, W. G., Platt, T. & Irwin, B. 1982: Primary production and nutrient assimilation by natural phytoplankton populations of the eastern Canadian Arctic. *Can. J. Fish. Aq. Sci. 39*, 335–345.

Harrison, W. G., Head, E. J. H., Conover, R. J., Longhurst, A. R. & Sameoto, D. D. 1985: The distribution and metabolism of urea in the eastern Canadian Arctic. *Deep-Sea Res. 32*, 23–42.

Harrison, W. G., Cota, G. F. & Smith, R. E. H. 1990: Nitrogen utilization in ice algal communities of Barrow Strait, Northwest Territories, Canada. *Mar. Ecol. Prog. Ser. 67*, 275–283.

Hart, T. J. 1934: On the phytoplankton of the south-west Atlantic and Bellingshausen Sea *Disc. Rep. 8*, 1–268.

Hayes, P. K., Whitaker, T. M. & Fogg, G. E. 1984: The distribution and nutrient status of phytoplankton in the Southern Ocean between 20° and 70° W. *Polar Biol. 3*, 153–165.

Holm-Hansen, O. 1985: Nutrient cycles in Antarctic marine ecosystems. Pp. 6–10 in Siegfried, W. R., Condy, P. R. & Laws, R. M. (eds.): *Antarctic Nutrient Cycles and Food Webs*. Springer-Verlag, Berlin.

Holm-Hansen, O., El-Sayed, S. Z., Franceschini, G. A. & Cuhel, R. L. 1977: Primary production and factors controlling phytoplankton growth in the southern ocean. Pp. 11–50 in Llano, G. A. (ed.): *Adaptations Within Antarctic Ecosystems*. Gulf Publ. Co., Houston.

Holm-Hansen, O., Mitchell, B. G., Hewes, C. D. & Karl, D. M. 1989: Phytoplankton blooms in the vicinity of Palmer Station, Antarctica. *Polar Biol. 10*, 49–57.

Horner, R. A. & Schrader, G. C. 1982: Relative contributions of ice algae, phytoplankton and benthic microalgae to primary production in nearshore regions of the Beaufort Sea. *Arctic 35*, 485–503.

Irwin, B., Hodgson, M., Dickie, P. & Platt, T. 1978a: Phytoplankton productivity experiments in Baffin Bay and adjacent inlets 22 Aug. to 18 Sept. 1977. *Fisheries and Marine Service Data Report, No. 82*.

Irwin, B., Evans, P. & Platt, T. 1978b: Phytoplankton productivity experiments and nutrient measurements in the Labrador Sea from 15 Oct. to 31 Oct. 1977. *Fisheries and Marine Service Data Report, No. 83*.

Irwin, B., Evans, P. & Dickie, P. 1978c: Phytoplankton productivity experiments and nutrient measurements in the Labrador Sea from 11 February to 28 February 1978. *Fisheries and Marine Service Data Report, No. 114*.

Irwin, B., Platt, T., Harrison, W. G., Gallegos, C. L. & Lindley, P. 1982: Phytoplankton productivity experiments and nutrient measurements in Ungava Bay NWT from 1 August to 3 September, 1979. *Fisheries and Marine Service Data Report, No. 287*.

Irwin, B., Harris, L., Hodgson, M., Horne, E. & Platt, T. 1983: Primary productivity and nutrient measurements in northern Foxe Basin, NWT from 27 August to 7 September 1981. *Fisheries and Marine Service Data Report, No. 385*.

Irwin, B., Dickie, P., Lindley, P. & Platt, T. 1984: Phytoplankton productivity in Lancaster Sound and approaches during the summer of 1979. *Fisheries and Marine Service Data Report, No. 423*.

Irwin, B., Platt, T. & Caverhill, C. 1985: Primary production and other related measurements in the eastern Canadian Arctic during the summer of 1983. *Fisheries and Marine Service Data Report, No. 510*.

Irwin, B., Caverhill, C., Dickie, P., Hodgson, M. & Platt, T. 1986a: Primary productivity of ice algae on the Labrador Shelf from 16 March to 27 March 1984. *Fisheries and Marine Service Data Report, No. 559*.

Irwin, B., Caverhill, C., Dickie, P., Horne, E. & Platt, T. 1986b: Primary productivity on the Labrador Shelf during June and July 1984. *Fisheries and Marine Service Data Report, No. 577*.

Irwin, B., Horne, E. P. W., Boulding, E. & Platt, T. 1987: Phytoplankton productivity in Jones Sound during August and September 1984. *Fisheries and Marine Service Data Report, No. 676*.

Irwin, B., Dickie, P., Hodgson, M. & Platt, T. 1988: Primary production and nutrients on the Labrador Shelf, in Hudson Strait and Hudson Bay in August and September 1983. *Fisheries and Marine Service Data Report, No. 692*.

Irwin, B., Caverhill, C., Mossman, D., Anning, J., Horne, E. & Platt, T. 1989: Primary productivity on the Labrador Shelf during July 1985. *Fisheries and Marine Service Data Report, No. 760*.

Ivanoff, A. 1977: Oceanic absorption of solar energy. Pp. 47–71 in Kraus, E. B. (ed.): *Modelling and Prediction of the Upper Layers of the Ocean*. Pergamon Press, Oxford.

Iverson, R. L., Whitledge, T. E. & Goering, J. J. 1979: Chlorophyll and nitrate fine structure in the southeastern Bering Sea shelf break front. *Nature 281*, 664–666.

Jacques, G. 1983: Some ecophysiological aspects of the Antarctic phytoplankton. *Polar Biol. 2*, 27–33.

Jacques, G. 1989: Primary production in the open Antarctic Ocean during the austral summer. A review. *Vie Milieu 39*, 1–17.

Jennings, J. C., Jr., Gordon, L. I. & Nelson, D. M. 1984: Nutrient depletion indicates high primary productivity in the Weddell Sea. *Nature 308*, 51–54.

Johannessen, O. M., Johannessen, J. A., Svendsen, E. A. S., Shuchman, R. A., Campbell, W. J. & Josberger, E. 1987: Ice edge eddies in the Fram Strait marginal ice zone. *Science 236*, 427–429.

Jones, E. P., Nelson, D. M. & Treguer, P. 1990: 7. Chemical Oceanography. Pp. 407–476 in Smith, W. O. Jr. (ed.): *Polar Oceanography Part B: Chemistry, Biology and Geology*. Academic Press, New York.

Kamykowski, D. & Zentara, S.-J. 1985: Nitrate and silicic acid in the world ocean: patterns and processes. *Mar. Ecol. Prog. Ser. 26*, 47–59.

Kamykowski, D. & Zentara, S.-J. 1989: Circumpolar plant nutrient covariation in the Southern Ocean: patterns and processes. *Mar. Ecol. Prog. Ser. 58*, 101–111.

Koike, I., Holm-Hansen, O. & Biggs, D. C. 1986: Inorganic nitrogen metabolism by Antarctic phytoplankton with special reference to ammonium cycling. *Mar. Ecol. Prog. Ser. 30*, 105–116.

Kristiansen, S. & Lund, B. A. 1989: Nitrogen cycling in the Barents Sea – I. Uptake of nitrogen in the water column. *Deep-Sea Res. 36*, 255–268.

Le Jehan, S. & Treguer, P. 1985: The distribution of inorganic nitrogen, phosphorus, silicon and dissolved organic matter in surface and deep waters of the Southern Ocean. Pp. 22–29 in Siegfried, W. R., Condy, P. R. & Laws, R. M. (eds.): *Antarctic Nutrient Cycles and Food Webs*. Springer-Verlag, Berlin.

Lewis, M. R. 1989: The variegated ocean: a view from space. *New Scientist 124*, 37–40.

Llano, G. A. 1978: Polar Research: a synthesis with special reference to biology. Pp. 27–61 in Llano, G. A. (ed.): *Polar Research: to the Present, and the Future*. AAAS Selected Symp. 7. Westview Press.

MacDonald, R. W., Wong, C. S. & Erickson, P. E. 1987: The distribution of nutrients in the Southeastern Beaufort Sea: Implications for water circulation and primary production. *J. Geophys. Res. 92*, 2939–2952.

Maestrini, S. Y., Rochet, M., Legendre, L., Demers, S. 1986: Nutrient limitation of the bottom-ice microalgal biomass

(southeastern Hudson Bay, Canadian Arctic). *Limnol. Oceanogr. 31*, 969–982.

Martin, J. H. 1990: Glacial-interglacial CO₂ change: the iron hypothesis. *Paleooceanogr. 5*, 1–13.

Martin, J. H. & Fitzwater, S. 1988: Iron deficiency limits phytoplankton growth in the north-east Pacific subarctic. *Nature 331*, 341–343.

Martin, J. H. & Gordon, R. M. 1988: Northeast Pacific iron distribution in relation to phytoplankton production. *Deep-Sea Res. 35*, 177–196.

Martin, J. H., Broenkow, W. W., Fitzwater, S. E. & Gordon, R. M. 1990a: Yes it does: a reply to the comment by Banse. *Limnol. Oceanogr. 35*, 775–777.

Martin, J. H. & Gordon, R. M. & Fitzwater, S. 1990b: Iron in Antarctic waters. *Nature 345*, 156–158.

McRoy, C. P. & Goering, J. J. 1976: Annual budget of primary production in the Bering Sea. *Mar. Sci. Comm. 2*, 255–267.

McRoy, C. P., Goering, J. J. & Shiels, W. E. 1972: Studies of primary productivity of the Bering Sea. Pp. 199–216 in Takenouti, A. (ed): *Biological Oceanography of the Northern North Pacific Ocean.* Idemitsu Shoten, Tokyo.

Mitchell, B. G. & Holm-Hansen, O. 1991: Observations and modeling of the Antarctic phytoplankton crop in relation to mixing depth. *Deep-Sea Res. 38*, 981–1007.

Muller-Karger, F. & Alexander, V. 1987: Nitrogen dynamics in a marginal sea-ice zone. *Cont. Shelf Res. 7*, 805–823.

Nemoto, T. & Harrison, G. 1981: High latitude ecosystems. Pp. 95–126 in Longhurst, A. R. (ed.): *Analysis of Marine Ecosystems.* Academic Press, London.

Nelson, D. M. & Gordon, L. I. 1982: Production and pelagic dissolution of biogenic silica in the southern ocean. *Geochim. Cosmochim. Acta 46*, 491–501.

Nelson, D. M. & Smith, W. O., Jr. 1986: Phytoplankton bloom dynamics of the western Ross Sea ice edge – II. Mesoscale cycling of nitrogen and silicon. *Deep-Sea Res. 33*, 1389–1412.

Nelson, D. M., Smith, W. O., Jr., Muench, R. D., Gordon, L. I., Sullivan, C. W. & Husby, D. M. 1989: Particulate matter and nutrient distributions in the ice-edge zone of the Weddell Sea: relationship to hydrography during late summer. *Deep-Sea Res. 36*, 191–209.

Olson, R. J. 1980: Nitrate and ammonium uptake in Antarctic waters. *Limnol. Oceanogr. 25*, 1064–1074.

Pickard, G. L. 1964: *Descriptive Physical Oceanography.* Pergamon Press, New York.

Priddle, J., Hawes, I. & Ellis-Evans, J. C. 1986: Antarctic aquatic ecosystems as habitats for phytoplankton. *Biol. Rev. 61*, 199–238.

Reeburgh, W. S. 1984: Fluxes associated with brine motion in growing sea ice. *Polar Biol. 3*, 29–33.

Reid, J. L. 1962: On circulation, phosphate phosphorus content, and zooplankton volumes in the upper part of the Pacific Ocean. *Limnol. Oceanogr. 7*, 287–306.

Rey, F. & Loeng, H. 1985: The influence of ice and hydrographic conditions on the development of phytoplankton in the Barents Sea. Pp. 49–64 in Gray, J. S. & Christiansen, M. E. (eds.): *Marine Biology of Polar Regions and Effects of Stress on Marine Organisms.* J. Wiley & Sons, Chichester.

Rey, F. & Skjoldal, H. R. 1987: Consumption of silicic acid below the euphotic zone by sedimenting diatom blooms in the Barents Sea. *Mar. Ecol. Prog. Ser. 36*, 307–312.

Rey, F., Skjoldal, H. R. & Slagstad, D. 1987: Primary production in relation to climatic changes in the Barents Sea. Pp. 29–46 in Loeng, H. (ed.): *The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea.* Proc. 3rd Soviet-

Norwegian Symp., Murmansk, 26–28 May 1986. Institute of Marine Research, Bergen.

Rivkin, R. B., Putt, M., Alexander, S. P., Meritt, D. & Gaudet, L. 1989: Biomass and production in polar planktonic and sea ice microbial communities: a comparative study. *Mar. Biol. 101*, 273–283.

Rönner, U., Sörensson, F. & Holm-Hansen, O. 1983: Nitrogen assimilation by phytoplankton in the Scotia Sea. *Polar Biol. 2*, 137–147.

Sakshaug, E. 1989: The physiological ecology of polar phytoplankton. Pp. 61–89 in Rey, L. & Alexander, V. (eds.): *Proc. 6th Conf. Com. Arct. Internatl 13–15 May 1985.* E. J. Brill, Leiden.

Sakshaug, E. & Holm-Hansen, O. 1984: Factors governing pelagic production in polar oceans. Pp. 1–18 in Holm-Hansen, O., Bolis, L. & Gilles, R. (eds.): *Marine Phytoplankton and Productivity.* Springer-Verlag, Berlin.

Sambrotto, R. N., Niebauer, H. J., Goering, J. J. & Iverson, R. L. 1986: Relationships among vertical mixing, nitrate uptake, and phytoplankton growth during the spring bloom in the southeast Bering Sea middle shelf. *Cont. Shelf Res. 5*, 161–168.

Slawyk, G. 1979: ¹³C and ¹⁵N uptake by phytoplankton in the Antarctic upwelling area: Results from the Antiprod I cruise in the Indian Ocean Sector. *Aust. J. Mar. Freshwater Res. 30*, 431–448.

Smith, R. E. H., Anning, J., Clement, P. & Cota, G. 1988: Abundance and production of ice algae in Resolute Passage, Canadian Arctic. *Mar. Ecol. Prog. Ser. 48*, 251–63.

Smith, R. E. H., Harrison, W. G., Harris, L. R. & Herman, A. W. 1990: Vertical fine structure of particulate matter and nutrients in sea ice of the high Arctic. *Can. J. Fish. Aquat. Sci. 47*, 1348–1355.

Smith, S. L., Smith, W. O., Jr., Codispoti, L. A. & Wilson, D. L. 1985: Biological observations in the marginal ice zone of the East Greenland Sea. *J. Mar. Res. 43*, 693–717.

Smith, W. O., Jr., 1987: Phytoplankton dynamics in marginal ice zones. *Oceanogr. Mar. Biol. Ann. Rev. 25*, 11–38.

Smith, W. O., Jr. & Kattner, G. 1989: Inorganic nitrogen uptake by phytoplankton in the marginal ice zone of the Fram Strait. *J. Cons. Perm. Int. Explor. Mer 188*, 90–97.

Smith, W. O., Jr. & Nelson, D. M. 1985: Phytoplankton bloom produced by the receding ice idge in the Ross Sea: spatial coherence with the density field. *Science 227*, 163–166.

Smith, W. O., Jr. & Nelson, D. M. 1986: Importance of ice edge phytoplankton production in the Southern Ocean. *BioScience 36*, 251–257.

Smith, W. O., Jr. & Nelson, D. M. 1990: Phytoplankton growth and new production in the Weddell Sea marginal ice zone during austral spring and autumn. *Limnol. Oceanogr. 35*, 809–821.

Smith, W. O., Jr. & Sakshaug, E. 1990: Polar Phytoplankton. Pp. 477–525 in Smith, W. O., Jr. (ed.): *Polar Oceanography Part B: Chemistry, Biology and Geology.* Academic Press, New York.

Sommer, U. 1986: Nitrate- and silicate-competition among Antarctic phytoplankton. *Mar. Biol. 91*, 345–351.

Spies, A., Brockmann, U. H. & Kattner, G. 1988: Nutrient regimes in the marginal ice zone of the Greenland Sea in summer. *Mar. Ecol. Prog. Ser. 47*, 195–204.

Stefansson, U. & Olafsson, J. 1990: Anomalous silicate-nitrate relationships associated with *Phaeocystis pouchetii* blooms. *EOS 71*, 66.

Subba Rao, D. V. & Platt, T. 1984: Primary production of Arctic waters. *Polar Biol. 3*, 191–201.

Sverdrup, H. U. 1955: The place of physical oceanography in oceanographic research. *J. Mar. Res. 14*, 287–294.

Thingstad, T. F. & Sakshaug, E. 1990: Control of phytoplankton growth in nutrient recycling ecosystems. Theory and terminology. *Mar. Ecol. Prog. Res. 63*, 261–272.

Treguer, P., Kamatani, A., Gueneley, S. & Queguiner, B. 1989: Kinetics of dissolution of Antarctic diatom frustules and the biogeochemical cycle of silicon in the Southern Ocean. *Polar Biol. 9*, 397–403.

Walsh, J. J., McRoy, C. P., Coachman, L. K., Goering, J. J., Nihoul, J. J., Whitledge, T. E., Blackburn, T. H., Parker, P. L., Wirick, C. D., Shuert, P. G., Grebmeier, J. M., Springer, A. M., Tripp, R. D., Hansell, D. A., Djenidi, S., Deleersnijder, E., Henriksen, K., Lund, B. A., Andersen, P., Muller-Karger, F. E. & Dean, K. 1989: Carbon and nitrogen cycling within the Bering/Chukchi Seas: source regions for organic matter effecting AOU demands of the Arctic Ocean. *Prog. Oceanogr. 22*, 277–359.

Welch, H. E. & Bergmann, M. A. 1989: Seasonal development of ice algae and its prediction from environmental factors near Resolute, N.W.T., Canada. *Can. J. Fish. Aquat. Sci. 46*, 1793–1804.

Welch, H. E., Bergmann, M. A., Siferd, T. D. & Amarulik, P. S. 1991: The seasonal development of ice algae near Chesterfield Inlet, N.W.T. Canada. *Can. J. Fish. Aquat. Sci.* In press.

Wheeler, P. A. & Kokkinakis, S. A. 1990: Inhibition of nitrate uptake by submicromolar ammonium in the oceanic Subarctic Pacific: ammonium recycling limits new production. *Limnol. Oceanogr. 35*, 1267–1278.

Whitledge, T. E., Reeburgh, W. S. & Walsh, J. J. 1986: Seasonal inorganic nitrogen distributions and dynamics in the southeastern Bering Sea. *Cont. Shelf Res. 5*, 109–132.

Zentara, S.-J. & Kamykowski, D. 1977: Latitudinal relationship among temperature and selected plant nutrients along the west coast of North and South America. *J. Mar. Res. 35*, 321–337.