Phytoplankton Growth and Regulation in the Labrador Sea: Light and Nutrient Limitation

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Abstract

The importance of light and nutrients in regulating phytoplankton growth in the Labrador Sea was evaluating using climatological data, 12 years of measurements made as part of the Labrador Sea Monitoring Program (LSMP) and physiological information from the literature. Light limits primary production and phytoplankton growth much of the year, even during summer when surface irradiance is at its seasonal peak. Nutrients, nitrogen (nitrate) and silicate, are reduced to low levels in surface waters in summer/autumn and can limit phytoplankton production and growth at this time of year. Nitrate appears to be the nutrient in shortest supply on the Labrador Shelf while silicate is in shortest supply in the central Labrador Basin. Multiyear trends in regional hydrography (increases in water temperatures, decreases in mixed layer depth) and changes in nitrate and silicate supply over the past decade (*i.e.* increases in nitrate and decreases in silicate) may be linked to changes in phytoplankton community composition and structure (*i.e.* decreases in large forms such as diatoms and increases in small picoplankton and nanoplankton forms).

Key words: primary production, phytoplankton, Labrador Sea, light, mixed-layer, nitrate, nutrients, silicate.

Introduction

The distribution, productivity and growth regulation of phytoplankton in high-latitude ecosystems have been the subject of numerous reviews and comprehensive studies (Longhurst, 1981, 2006; Gray and Christiansen, 1985; Francis, 1996; Skjoldal, 2004). Light and nutrients ("bottom-up" regulation) and herbivorous grazing ("top-down" regulation) are the principal factors that set limits on phytoplankton growth in these regions just as in other marine ecosystems. Viral lysis, a significant regulating factor in some systems has been little studied in these waters. Sub-polar and polar light conditions for phytoplankton growth, however, are subject to extreme seasonal variations, relative to other systems, due to the annual solar cycle and the presence of sea-ice. High-latitude ecosystems are also subject to strong meteorological forcing (cold temperatures, strong winds) and concomitant vigorous vertical mixing of the upper water column which influences the phytoplankton light environment (Rey and Loeng, 1985).

At the same time that strong vertical mixing diminishes light for phytoplankton growth, it enhances the supply of essential macro-nutrients (nitrate, phosphate, silicate) to the surface ocean that support growth. High latitude ecosystems, in general, are characterized by moderate to high nutrient concentrations much of the year (Kamykowski and Zentara, 1985, 1986; Louanchi and Najjar, 2000) and the nature and extent of nutrient limitation of phytoplankton growth in these regions continues to be the subject of inquiry (Harrison and Cota, 1991).

The Labrador Sea and adjacent shelves comprise a biologically productive high-latitude ecosystem (Fig. 1) that is strongly influenced by all of the factors that modify phytoplankton growth. The Labrador Sea system forms part of the Northwest Atlantic sub-polar gyre and is delineated by strong boundary currents, associated with shallow continental shelves (the East and West Greenland coastal currents to the east and the Labrador Current to the west), and a deep central basin that undergoes strong vertical convective mixing in late winter (Lazier *et al.*, 2002). Relatively warm, salty North Atlantic waters entering the central basin from the east and cold, fresh arctic waters enter over the continental shelves from the east and west, modifying water masses
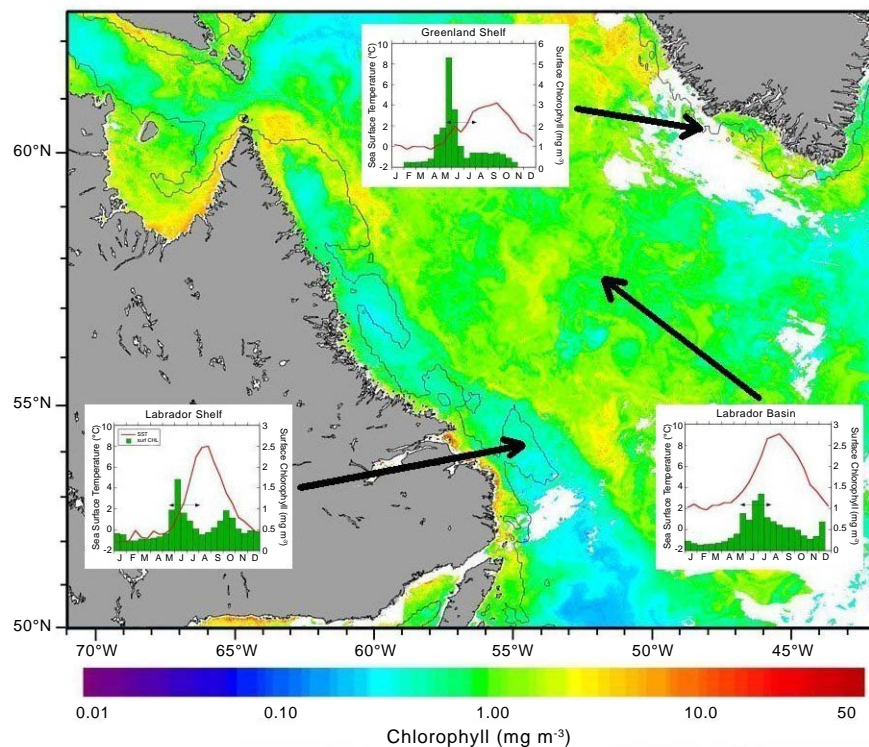
Fig. 1. Sea-viewing Wide Field-of-view Sensor (SeaWiFS) ocean colour composite im-
age (July) of the Labrador Sea and surrounding waters. Inset graphs show aver-
age (1998–2004) twice-monthly satellite (AVHRR) sea surface temperature, SST,
°C (red lines) and SeaWiFS surface chlorophyll concentration, mg m^{-3} (green verti-
cal bars) for: (lower left) the Labrador Shelf, (lower right) central Labrador basin
and (top center) Greenland Shelf, see also Fig. 3. Horizontal lines in inset graphs
indicate period of spring/summer LSMP observations.

and their physical, chemical and biological properties.
From the standpoint of phytoplankton, light conditions
and nutrient availability that determine seasonal growth
cycles and community structure will be strongly influ-
enced by the regional characteristics of circulation (mix-
ing and transport) imposed by the complex of water
masses making up the Labrador Sea system. As well,
seasonal sea-ice dynamics of the Labrador and Green-
land continental shelves will have a major effect on light
conditions and water column stability, the latter affect-
ing nutrient supply to the upper mixed-layer, that will
influence phytoplankton growth.

Systematic observations of physical (temperature,
salinity), chemical (nutrient concentrations) and biolog-
ical (phytoplankton biomass and productivity) proper-
ties in the Labrador Sea have been made over the past
12 years (1994–2005) as part of the Labrador Sea Moni-
toring Program (LSMP). An analysis of these data, along
with some historical data, provide most of the basic in-
formation required to evaluate the importance of light

and nutrients in limiting the growth of phytoplankton in
the region - the focus of this report.

Methods

Light and nutrient limitation, for the purposes of
this analysis, are defined as the resource (light level or
nutrient concentration) scaled by the physiological "rate
constant" that determines the threshold value (level of
light or concentration of nutrient) below which the rate
process (photosynthesis in the case of light and nutrient
uptake rate in the case of nutrients) is resource-limited.

For light, the resource is defined as the light level in
the upper mixed-layer, given by the equation:

$$I_{MLD} = I_0 \left(1 - e^{-Kz \times MLD}\right) \Big/ \left(Kz \times MLD\right) \qquad (1)$$

where I_{MLD} = average irradiance in the mixed-layer (W m^{-2}),
I_0 = surface irradiance (W m^{-2}), Kz = vertical attenuation
coefficient (m^{-1}) and MLD = mixed-layer depth (m). The

threshold parameter (I_t, W m^{-2}), often referred to as I_k in the literature, is derived from the photosythesis-irradiance (P-I) curve (Fig. 2a). For nutrients, the resource is defined by the concentration of nutrient in the upper mixed-layer and the threshold parameter (N_t, mmol m^{-3}), often referred to as K_s in the literature, is derived from the Michalis-Menten concentration-dependent uptake curve (Fig. 2b). Resource-limitation (light or nutrients), or the potential for resource-limitation, was evaluated using a number of lines of evidence, including a comparison of climatological and observed light and nutrient levels in the Labrador Sea with limitation-threshold levels and modeled phytoplankton growth where light and nutrients limitation are interactive.

Observations from the Labrador Sea Monitoring Program (LSMP) used in this analysis came from annual spring-summer expeditions from 1994–2005 (Table 1). Twenty-eight nominal stations were occupied along a transect from the southern coast of Labrador to the southern coast of West Greenland (Fig. 3). For this analysis, data were averaged over all years and aggregated by month (May, June, July) within three defined regions: the Labrador Shelf/Slope (LS), The Labrador Basin (LB) and the Greenland Shelf/Slope (GS).

Surface irradiance and in-water light attenuation were measured on selected expeditions (1996–1999, 2001–2002, 2004; see Table 1) using 4π photosynthetically active radiation (PAR, 400–700 nm) sensors (LICOR). Vertical attenuation coefficients (Kz) were determined from the extinction of light from profiles of the upper 50 m. Light was expressed in energy units based on the conversion factor: 1 W m^{-2} = 4.6 µmol quanta m^{-2} s^{-1}. On expeditions where light was not measured, clear-sky irradiance was calculated using the formulations of Bird (1984) and corrected for cloud-fog attenuation at the surface based on mean light conditions during the missions where direct measurements were made. Consistently, measured surface irradiance was 52% (± 2%) of clear sky irradiance across all cruises/years, largely
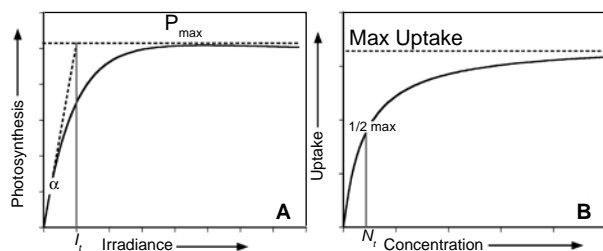
due to the prevailing meteorological conditions that characterize the spring/summer period in the Labrador Sea (Fig. 4). Mixed-layer depths (MLDs) were calculated from vertical density profiles of CTD (Seabird) casts and defined as the depth (z) of maximum density gradient in the upper water column ($z \leq 100$ m). Nutrient concentrations for nitrate (NO$_3$), phosphate (PO$_4$), and silicate (SiO$_3$), were determined by autoanalyzer using standard colorimetric methods (Hansen and Grasshoff, 1983). Ammonium (NH$_4$) was also measured during the latter part of the study period (1999–2005) using the manual method of Solórzano (1969).

Photosynthesis-irradiance (P-I) experiments in near-surface waters ($z \leq 25$ m) were conducted at a subset of stations (generally 5–8 of the 28 nominal stations) during each of the LSMP spring-summer missions (as well as during one mission in autumn and one in winter) using the method described by Platt *et al.*, (1980). The light limitation threshold parameter, I_t, varied by season (~30 W m^{-2} in winter to ~50 W m^{-2} in summer) but did not vary significantly by region. Nutrient uptake kinetics were not measured as part of the LSMP and, therefore, the nutrient limitation threshold parameter, N_t, for this analysis was taken from the literature. A number of recent studies in sub-polar seas suggest that the N_t for NO$_3$ and SiO$_3$ would be in the range of 2–6 mmol m^{-3} (Kristiansen *et al.*, 1994, 2000): a median value of 2 mmol m^{-3} was used for the present study (see also Hensen *et al.*, 2006).

Fig. 2. Resource-dependent rate processes and threshold levels (I_t and N_t) used in the analysis of: (**A**) light and (**B**) nutrient-limitation, respectively.

TABLE 1. Labrador Sea Monitoring Program (LSMP) missions and sampling dates, 1994–2005. NOTE: autumn/winter missions (96-026 and 02-075) were not included in this study.

| Mission	Year	L3 Line
94-008	1994	26 May – 08 June
95-016	1995	10 July – 13 July
96-006	1996	18 May – 27 May
96-026	1996	20 October – 28 October
97-009	1997	21 May – 28 May
98-023	1998	26 June – 02 July
99-022	1999	01 July – 10 July
00-009	2000	24 May – 05 June
01-022	2001	04 June – 11 June
02-032	2002	02 July – 08 July
02-075	2002	01 December – 09 December
03-038	2003	23 July – 29 July
04-016	2004	20 May – 27 May
05-016	2005	29 May – 03 June
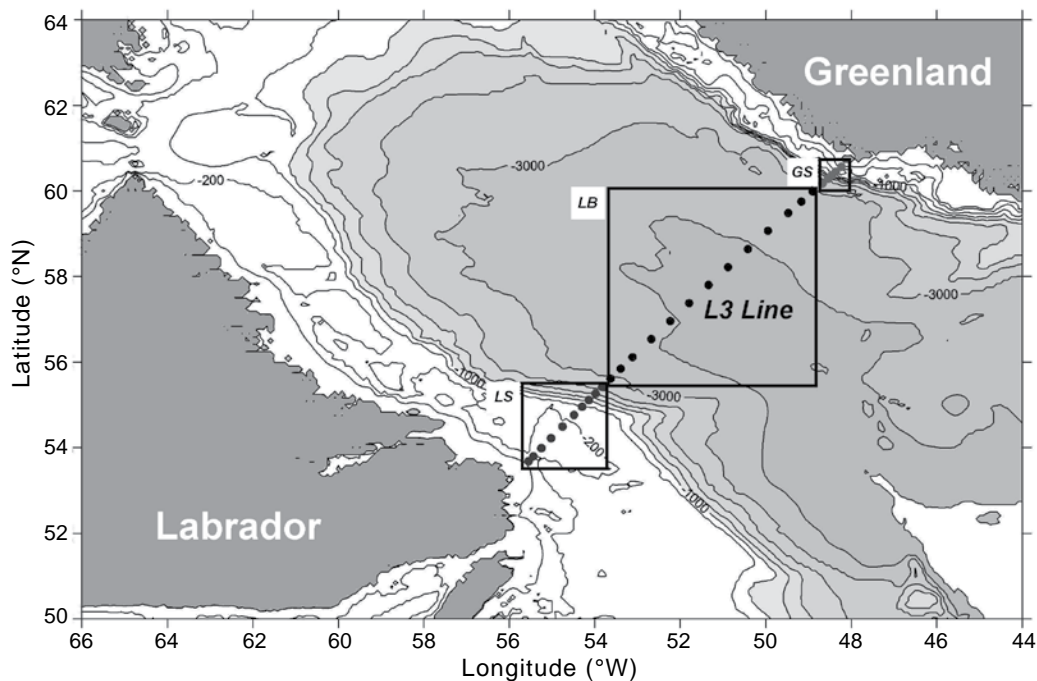
Fig. 3.   Labrador Sea Monitoring Program (LSMP) station locations, L3-01 (Labrador) to L3-28 (Green-
land) and sub-regions: Labrador Shelf/Slope, LS (L3-01 to L3-10); Labrador Basin, LB (L3-11 to
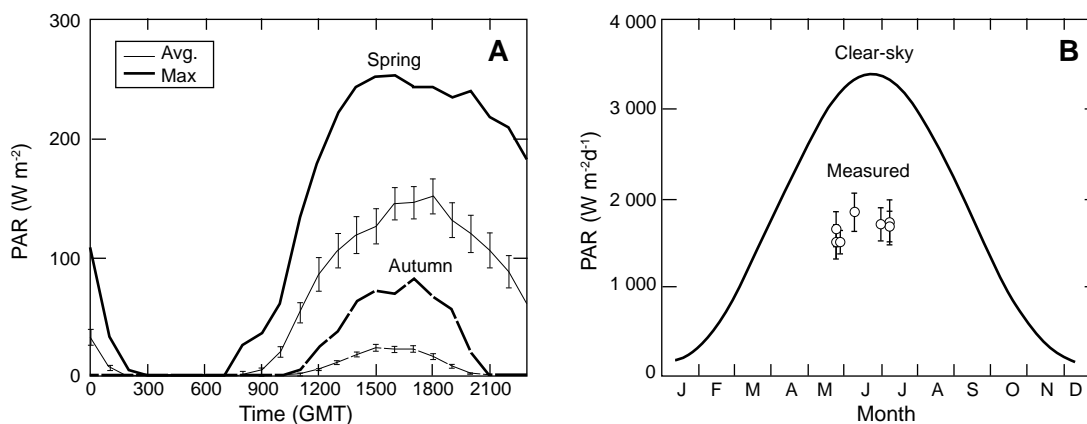L3-23); Greenland Shelf/Slope, GS (L3-24 to L3-28). Contours = bathymetry.

Fig. 4.   Surface incident solar irradiance (PAR) cycles in the Labrador Sea: (**A**) daily cycle (maximum and average) of hourly
energy fluxes from selected spring and autumn LSMP missions, (**B**) annual cycle of clear sky energy flux, (Bird, 1984)
compared with average daily energy flux measured during spring and summer LSMP missions. Vertical bars = standard
errors (SE).

PO_4 was not considered in this analysis since there is
little evidence that concentrations are reduced to levels
that would limit phytoplankton growth in sub-polar eco-
systems (Harrison and Cota, 1991).

Climatological data (1962–2002, objectively ana-
lyzed mean fields, one degree spatial resolution) of
mixed-layer depths and near-surface nutrient concentra-
tions for the Labrador Shelf/Slope, Labrador Basin and
the Greenland Shelf/Slope were extracted from the Na-
tional Oceanographic Data Center (NODC) databases
(http://www.nodc.noaa.gov/) (see also Monterey and
Levitus, 1997; Garcia *et al.*, 2006). Monthly mixed-layer
depth irradiances (I_{MLD}) were calculated (Eq. 1) using
the climatological *MLD*s and region/season averaged *Kz*
values from LSMP observations.

The evaluation of light and nutrient-limitation often
considers factors (thresholds of physiological processes)
operating independently when it is known that light and

nutrients act on phytoplankton growth and productivity in a synergistic way. To investigate the interplay of light and nutrient-limitation on phytoplankton growth *per se*, a simple phytoplankton growth model was employed which has been successfully used in coastal waters to quantify the sensitivity of phytoplankton growth to light and nutrients acting together (Cloern, 1999). This model, with some parameter adjustments, can be easily adapted for other marine environments such as the Labrador Sea. More complex mechanistic (cell-quota based) models may be considered a better choice for investigating the dynamics of multi-nutrient-light interactions (Flynn, 2001), however, parameter estimates required for these models from field observations is a real challenge and there are some circumstances where less complicated models are more appropriate (Flynn, 2003). The Cloern model, indeed, has the advantage of simplicity and parameterization that can be relatively easily derived from field observations, *i.e. N, I, N_t, I_t*. Moreover, it should adequately address questions of light and nutrient limitation under climatological mean conditions for large geographic areas which is the focus of our study. This growth model is based on the well-known saturation response of phytoplankton growth to light and nutrients (Fig. 2) and includes an interactive function such that, for example, phytoplankton growth at low light is enhanced by nutrient addition. This interactive term is not generally found in models that describe growth as the product or minimum of separate light and nutrient-limitation functions. More specifically, the model assesses the incremental change in phytoplankton growth with small, discrete changes in light or nutrient levels and expresses the relative effects of these changes on growth as a ratio (R). The resultant R ratios are indices that tell whether phytoplankton growth is more sensitive to light changes (R >1) or to nutrient changes (R <1). These ratios, in turn, can be plotted in a 2-D space where the major axes are another set of ratios, *i.e.* nutrient or light levels scaled to their corresponding threshold parameters, called the nutrient resource (N/N_t) and light resource (I/I_t) axes (Fig. 5). In this representation, although somewhat arbitrary (Cloern, 1999), R values >10 represent the growth domain where light sensitivity dominates and is thus considered to be indicative of light-limited conditions, R values <0.l, correspondingly, are considered indicative of nutrient-limited conditions and an R of 0.1–10 is indicative of conditions where co-limitation may occur.

Results

Mixed-layer depths (MLDs) varied by season and location (Fig. 6). Deepest MLDs occurred in March–April and were most pronounced in the central
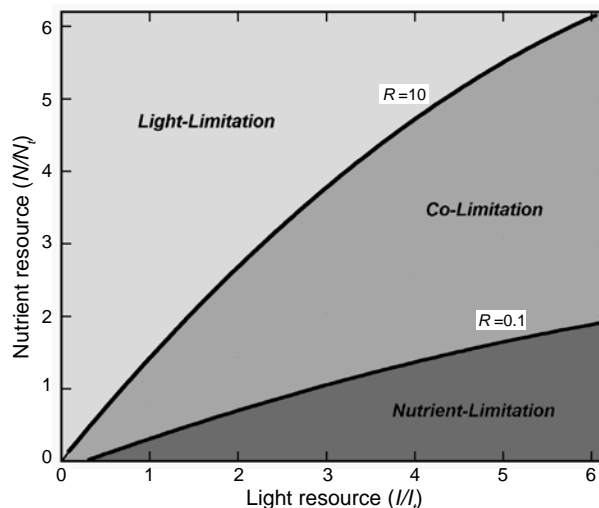

Fig. 5. Index (R) of resource-limitation based on the sensitivity of phytoplankton growth rate to light and nutrient changes. R = ratio of the incremental change in growth rate with change in light level or nutrient concentration; R values greater >10 indicate light-limitation, values <0.1 indicate nutrient limitation and values 0.1–10 indicate co-limitation. N = nutrient concentration, N_t = nutrient-limitation threshold concentration, I = light level, I_t = light-limitation threshold level. Modified from Cloern (1999).

basin (>300 m); shallowest MLDs (<10 m) occurred May–Aug in all sub-regions. MLDs observed during the LSMP spring-summer missions were notably deeper (statistically significant; p <0.01) than climatological MLDs; deepest spring-summer MLDs were observed in the Labrador Basin. In all sub-regions, spring-summer MLDs were shallower (statistically significant, p <0.01) than euphotic depths.

MLD light levels (I_{MLD}) also varied seasonally but were similar by location (Fig. 7). Maximum light levels (70–80 W m^{-2}) were observed in summer when solar light is at its peak and MLDs shallowest (June–August): I_{MLD} minimums (<10 W m^{-2}) occurred in winter–spring (November–March) when solar light is lowest and MLDs deepest. Mixed-layer light levels observed during the LSMP spring-summer missions were notably lower (20–50 W m^{-2}) and statistically different (p <0.01) from climatological levels (40–80 W m^{-2}) due principally to the considerably deeper LSMP MLDs compared to the climatologies (Fig. 5). Climatological I_{MLD} levels were higher than the light-limitation threshold (I_t) from May–September and lower the remainder of the year. I_{MLD} levels observed during the spring–summer LSMP missions, however, were similar to (Labrador Shelf) or somewhat lower than (Labrador Basin and Greenland

Shelf) but not statistically different from the I_t levels, even during summer peak light conditions.

Concentrations of nitrate (NO_3) in near-surface waters ($z \leq 25$ m) varied by season in all regions (Fig. 8). Maximum climatological values (9–10 mmol m^{-3}) were observed in spring (March–April), followed by a rapid decline due to biological consumption (Fig. 1, insets) with lowest concentrations throughout the summer and early autumn (July–September) after which concentra-

tions began increasing again. Concentrations observed during the spring-summer LSMP missions were higher than climatological means on the Labrador Shelf (statistically significant, $p < 0.05$) but similar to the climatologies in the Labrador Basin and on the Greenland Shelf. Similarly, minimum late summer (July) concentrations were lowest on the Labrador Shelf and below the 2 mmol m^{-3} limitation threshold, N_t; late summer levels were higher than N_t in the central basin and on the Greenland Shelf. Taking into consideration the climatological data
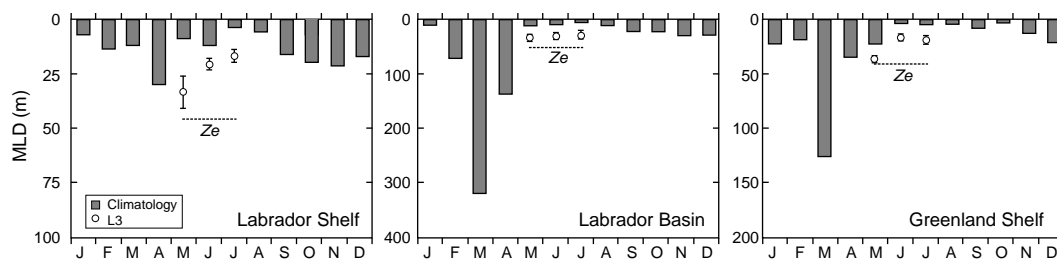

Fig. 6.   Annual cycle of mixed-layer depths (MLD) in the Labrador Sea (partitioned into shelves and central basin): vertical bars = climatology (Monterey and Levitus, 1997), points = average values derived from LSMP spring and summer missions (vertical lines = standard errors, SE). Horizontal dashed line = average observed spring-summer euphotic zone depth ($Ze = 4.6/Kz$). Note difference in vertical (depth) scales.
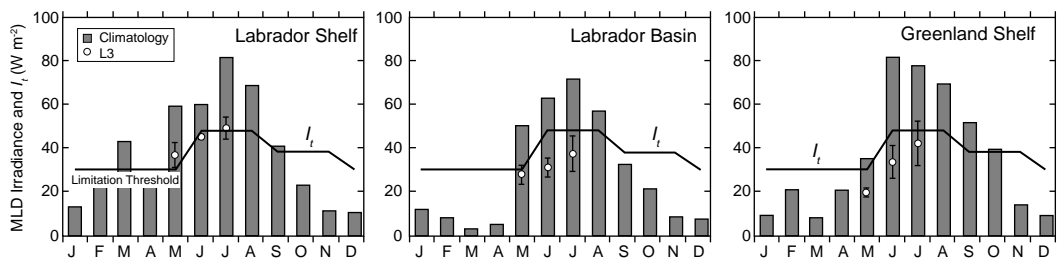

Fig. 7.   Annual cycle of mixed-later depth irradiance levels (I_{MLD}) in the Labrador Sea (partitioned into shelves and central basin): vertical bars = climatology, points = average values from LSMP spring and summer missions (vertical lines = standard errors, SE). Solid line = light-limitation threshold parameter (I_t). I_t levels in winter and spring were statistically indistinguishable but statistically different from summer ($p < 0.01$) and autumn ($p < 0.10$) levels.
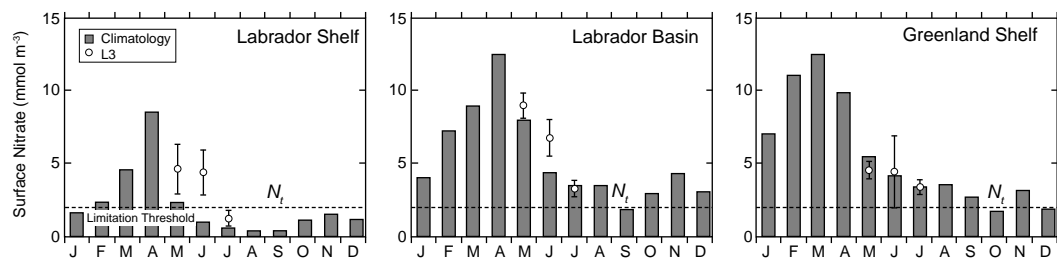

Fig. 8.   Annual cycle of surface nitrate (NO_3) concentrations (mmol m^{-3}) in the Labrador Sea (partitioned into shelves and central basin): vertical bars = climatology (Garcia et al., 2006), points = average values from LSMP spring and summer missions (vertical lines = standard errors, SE). Dashed line = NO_3-limitation threshold parameter (N_t).

and LSMP observations overall, NO₃ concentrations are higher in the central basin and on the Greenland Shelf than on the Labrador Shelf (statistically significant, p <0.05). Another consideration in evaluating nitrogen limitation in these waters is the fact that reduced forms of inorganic nitrogen (*e.g.* ammonium, NH_4) are also important for phytoplankton nitrogen nutrition. However, in the Labrador Sea, NH_4 concentrations are consistently low (<0.5 mmol m⁻³) in near surface waters in all regions and show no discernible pattern by geographic location or by season. It was determined that the inclusion of NH_4 (to get a more complete assessment of the nitrogen available for phytoplankton growth) would not have significantly changed the results or conclusions of this study and since only a subset of stations were sampled for NH_4, it was considered best to confine our analysis to NO₃ only.

Near-surface ($z \leq 25$ m) silicate (SiO_3) concentrations followed a similar seasonal cycle except that extremes (spring maxima-summer minima) were not as large and, overall, concentrations were similar among the three sub-regions, *i.e.* not statistically different (Fig. 9). Surface SiO_3 concentrations differed from NO₃, however, in that late summer (July) levels were at or be-

low the 2 mmol m⁻³ threshold concentration (N_t) in all sub-regions. Overall, regional differences in SiO_3 concentrations are less evident than differences in NO₃ concentrations.

NO₃ versus SiO_3 scatter plots for the LSMP data revealed some general patterns (Fig. 10, Table 2): (i) evidence of NO₃ depletion in the presence of measurable SiO_3 concentrations, seen predominantly on the Labrador Shelf in spring (Fig. 10, left panel); (ii) evidence of SiO_3 depletion in the presence of measurable NO₃, seen predominantly in the central Labrador Basin in summer (Fig. 10, center panel); and (iii) evidence of simultaneous NO₃ and SiO_3 depletion, a feature observed often on the Greenland Shelf in spring and summer (Fig. 10, right panel). These results provide strong site-specific evidence of both NO₃ and SiO_3 limitation that were less evident in analysis of climatolgical mean conditions where some degree of spatial and temporal averaging is used, *i.e.* Figs. 8 and 9.

Climatological and LSMP spring–summer light and nutrient data and their corresponding threshold values were used with Cloern's model (Fig. 5) to evaluate light and nutrient limitation in the Labrador Sea and results are
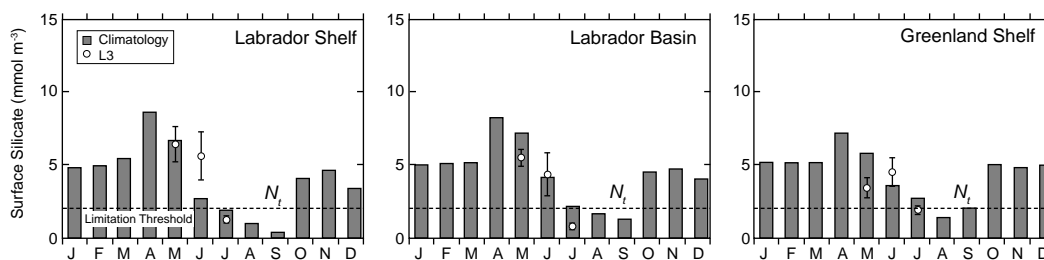

Fig. 9. Annual cycle of surface silicate (SiO_3) concentrations (mmol m⁻³) in the Labrador Sea (partitioned into shelves and central basin): vertical bars = climatology (Garcia *et al.*, 2006), points = average values from LSMP spring and summer missions (vertical lines = standard errors, SE). Dashed line = SiO_3-limitation threshold parameter (N_t).
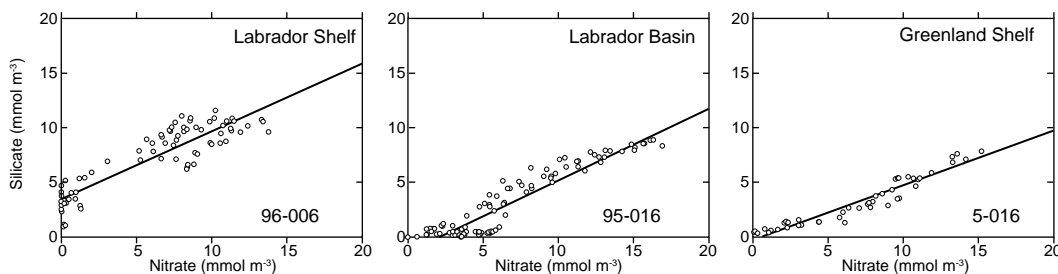

Fig. 10. Examples of nitrate (NO₃) versus silicate (SiO_3) concentration scatter plots of data from the upper 100 m for LSMP spring and summer missions showing: (left panel) NO₃-depleted conditions on the Labrador Shelf, (center panel) SiO_3-depleted condition in the central Labrador Basin, and (right panel) co-depleted conditions on the Greenland Shelf. Solid lines = least squares linear regression fits.

TABLE 2.   Least squares linear regression coefficients (slope, SiO_3:NO_3 and intercept, mmol m^{-3}) from nitrate versus silicate plots (data from <100 m): Labrador Sea (L3 Line) spring and summer missions. YD = year-day, Int-Si = intercept on SiO_3-axis, and Int-N = intercept on NO_3-axis.

| Mission	Mean YD	Labrador Shelf/Slope			Labrador Basin			GreenlandShelf/Slope		
		Slope	Int-Si	Int-N	Slope	Int-Si	Int-N	Slope	Int-Si	Int-N
96-006	143	0.62	3.52	–	0.44	1.52	–	0.12	4.60	–
04-016	145	-0.07	9.86	–	0.38	2.55	–	0.51	0.83	–
97-009	146	0.74	4.82	–	0.56	0.35	–	0.43	1.62	–
00-009	151	-0.13	9.96	–	0.28	4.14	–	0.33	4.26	–
05-016	152	0.49	3.98	–	0.45	0.56	–	0.50	–	0.52
01-022	159	0.24	6.19	–	0.51	0.27	–	0.56	0.30	–
98-023	181	0.75	1.14	–	0.58	–	2.90	0.75	1.14	–
02-032	186	0.55	0.39	–	0.64	–	2.42	0.49	0.76	–
99-022	187	0.61	0.90	–	0.65	–	2.68	0.54	–	0.44
95-016	193	1.07	0.54	–	0.66	–	1.97	0.45	0.85	–
03-038	208	0.68	1.13	–	0.51	–	0.25	0.33	1.04	–
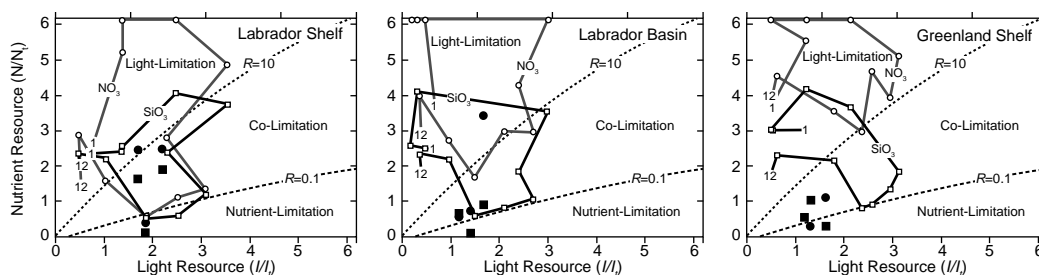
Fig. 11.   Light and/or nutrient-limitation of phytoplankton growth (see Fig. 5) under conditions observed in the Labrador Sea (partitioned into shelves and central basin): Solid grey (NO_3) and black (SiO_3) lines are based on monthly (1 = January, 12 = December) climatological conditions of light and nutrients and red and blue points are based on average spring and summer conditions observed during LSMP missions (1994–2005). For these plots, the Nutrient Resource axis = NO_3 conc. or SiO_3 conc./N_l and the Light Resource axis = I_{MLD}/I_l.

summarized in Fig. 11. Note that environmental growth conditions and physiological rate parmeters in the Labrador Sea were in some cases different from the input variables used in Cloern's coastal-temperate phytoplankton growth model (*e.g.* lower temperatures, deeper mixed-layers, less light attenuation, lower P-I parameters in the Labrador Sea). The *R* curves in Fig. 11 were adjusted accordingly. The solid lines in the figure trace the seasonal progression of the climatological data, indicating light-limited growth in late winter to early spring, co-limitation or nutrient-limited growth in summer/autumn back to light limitation in late autumn to end of the year. Noteworthy in these plots is the progressive separation of the NO_3 and SiO_3 traces, *i.e.* N-limited growth in summer is evident only on the Labrador Shelf whereas Si-

limited growth is evident in all sub-regions. On the other hand, LSMP data suggest some N- and Si-limited growth in all regions in summer.

Discussion

The importance of light in limiting the production and growth of high-latitude phytoplankton is well established and has been the subject of numerous studies and publications over the past several decades. Much of this work, however, due to limitations in accessibility to field study sites, has been restricted to peak phytoplankton growth season (summer) when light conditions are most favorable. In most studies, the physiological characteristics of the populations have been the focus (Har-

rison and Platt, 1986; Rey, 1991; Sakshaug and Slagstad, 1991). Only from established time-series stations has a more complete picture (annual time scale) of light influence on phytoplankton growth been possible, *e.g.* Ocean Weather Station M (66º N, 2º E) in the Norwegian Sea (Rey, 2004). Our study has consolidated information on seasonal mixed-layer dynamics, incident solar irradiance and in-water light attenuation in the Labrador Sea from the past 12 years to suggest that light is the principal limiting factor of phytoplankton production and growth for most of the year. Indeed, there is evidence from this analysis that light may limit growth even during summer when incident radiation is at its maximum. Sea-ice

dynamics will also have an additional strong influence on light conditions for phytoplankton growth in this region, particularly on the Labrador Shelf. This will be the subject of future analysis.

The influence of nutrients on phytoplankton production and growth, as the case with light, has been the subject of numerous studies in high-latitude ecosystems and again, most of this work has been confined to process studies during peak summer growth. In this case, however, it is only during peak summer growth that surface nutrients are reduced to levels limiting to phytoplankton. Therefore, information on annual nutrient
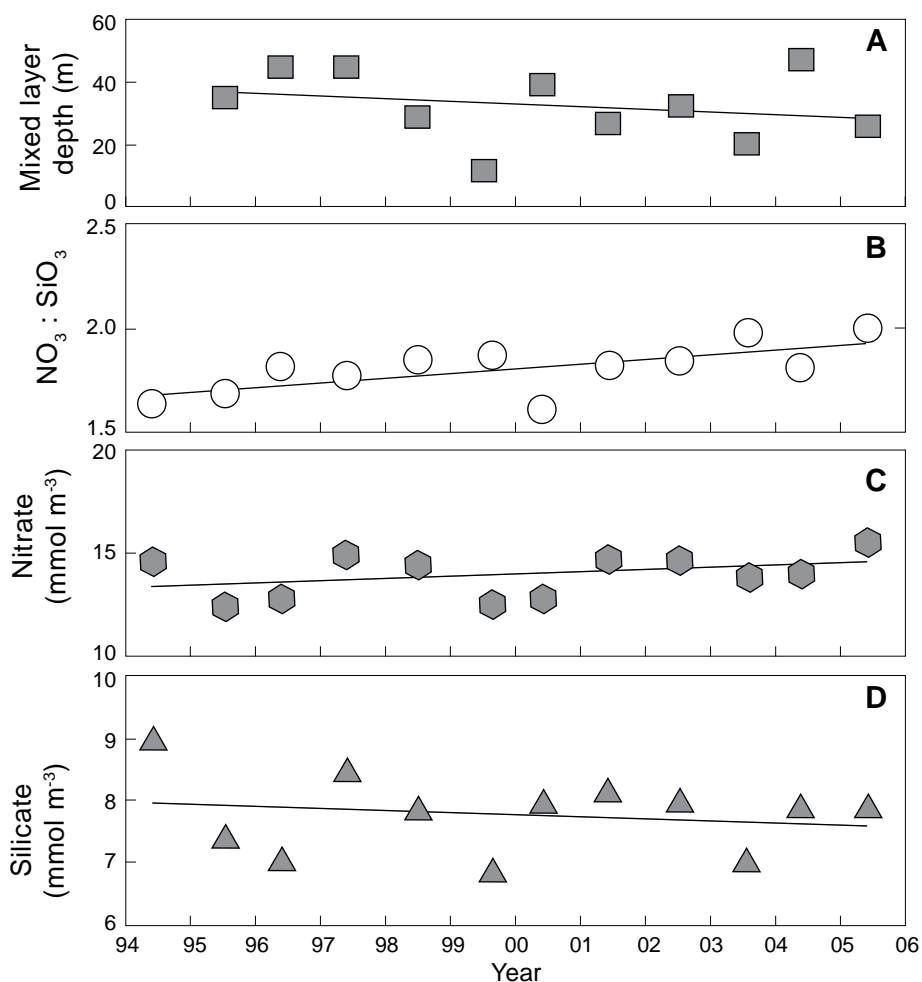

Fig. 12. Multiyear record of oceanographic conditions during spring/summer in the central Labrador Sea basin. (**A**) mixed layer depth: slope (b) = -0.852 m y^{-1}, correlation coef. (r) = 0.26, significance (p) = 0.44, (**B**) ratio of NO_3:SiO_3 at 100 ± 20 m: b = 0.0156 y^{-1}, r = 0.53, p = 0.06, (**C**) NO_3 concentration at 100 ± 20 m: b = 0.0897 mmol m^{-3} y^{-1}, r = 0.34, significance (p) = 0.25, (**D**) SiO_3 concentration at 100 ± 20 m: b = -0.0157 mmol m^{-3} y^{-1}, r = 0.10, p = 0.74.

dynamics may not add much more to the understand-
ing of phytoplankton nutrient-limitation *per se*, beyond
what seasonally restricted studies reveal. However,
knowledge of the extent of winter mixing (and recharge
of surface waters with nutrients) can contribute to a bet-
ter understanding of the amplitude and duration of the
phytoplankton growth cycle and the relative proportions
of macronutrients (*e.g.* NO_3 and SiO_3) in source waters
may help explain regional and/or temporal variability in
phytoplankton community structure (see below). In the
Labrador Sea where strong winter convective mixing
and summer density re-stratification are characteristic
features (Lazier *et al.*, 2002), where phytoplankton pro-
duction is significant (Fig. 1) and where surface nutri-
ent concentrations are reduced, the potential for some
degree of nutrient-limitation is certain. Several lines of
evidence presented here suggest that there is potential
for both nitrogen and silicon limitation in the Labrador
Sea in summer and that nitrate-limitation is more likely
on the Labrador Shelf while silicate-limitation is more
likely in the central basin. Furthermore, an evaluation of
the relative roles of light and nutrients on phytoplankton
growth based on a simple phytoplankton growth model,
suggests that co-limitation is likely in all regions during
the peak summer growth season.

The assumptions made in this study were based
on experimentally derived threshold values for light
(I_t or I_k) and literature-derived values for nutrients (N_t
or K_s). We are reasonably confident that our seasonally
varying I_t values are representative of phytoplankton for
sub-polar regions; we have made extensive measure-
ments during the LSMP and our values are consistent
with values reported in other regional studies, (Harrison
and Platt, 1986; Rey, 1991). The N_t values we used are
relatively conservative (*i.e.* median value of the re-
ported range) and assumed to be seasonally invariant.
There are a number of studies, however, that suggest
that the threshold parameter is not constant but is adap-
tive and adjusts to the prevailing nutrient conditions
(Harrison *et al.*, 1996; Kristiansen *et al.*, 1994, 2000),
i.e. as nutrient concentrations decrease the threshold
parameter decreases and thus the "affinity" for the di-
minishing nutrient resource increases. If the limitation
threshold values we used are too high for summer condi-
tions, for example, then the extent of nutrient-limitation
would be reduced relative to our assessment (*i.e.*, the
lines and data points in Fig. 11 would be shifted up more
into the light-limited domain). Cloern (1999) conducted
a detailed sensitivity analysis to explore the effects of
parameter estimates on his model results. His analysis
showed that resource limitation boundaries (*i.e.* the *R*
curves in Fig. 5) changed little with a change in growth
temperature of 20ºC, however, boundaries shifted as

much as ±30%, at high light resource (I/I_t) levels, when
N_t values were doubled/halved. This is on the order of
uncertainty we expect in applying this model to the Lab-
rador Sea, especially considering the relatively large ob-
served range in N_t levels in sub-polar waters.

There are additional considerations for silicate that
could influence the outcome of our analyses. For exam-
ple, N_t values have been seen to vary considerably during
the phytoplankton growth cycle in the Southern Ocean
for reasons unclear to the investigators (Nelson *et al.*,
2001). In other studies, concentration-dependent silicate
uptake does not saturate and continues to increase over
the full range of ambient silicate concentrations (Brown
et al., 2003). If the latter situation is relevant to the Lab-
rador Sea, then another approach altogether would be
required to assess silicate-limitation in these waters.

The analyses of LSMP data described thus far deal
with average conditions (1994–2005); inter-annual vari-
ability in mixing, nutrients and plankton are being ex-
plored but are not reported here. However, a preliminary
look at long-term trends in mixed-layer depths as well
as source water (below MLD, 100 ± 20 m) NO_3 and
SiO_3 concentrations suggests a shallowing (~0.9 m y^{-1})
in MLDs, an increase (~0.09 mmol m^{-3} y^{-1}) in NO_3 and a
decrease in SiO_3 (~0.02 mmol m^{-3} y^{-1}), the latter resulting
in a statistically significant ($p < 0.06$) increase in source-
water NO_3:SiO_3 ratios over the past 12 years in the cen-
tral Labrador Sea basin (Fig. 12). This has occurred at
the same time that surface seawater temperatures have
been increasing (Yashayaev *et al.*, 2003; Hendry, 2006;
Yashayaev and Clarke, 2006) and phytoplankton abun-
dance and community structure has been changing (Li
et al., 2006). Observations indicate that bulk chlorophyll
during spring has been decreasing in the Labrador Sea
while small forms, <10 µm (picoplankton and nano-
plankton), have been increasing over the past decade. By
inference (and difference), large (>10 µm) phytoplank-
ton have decreased over time. If a major component of
the large phytoplankton in these waters is comprised of
diatoms (Hensen *et al.*, 2006) then the question arises, is
the observed decrease in source-water SiO_3 linked to the
apparent decrease in silicate-requiring diatoms? More
generally, can the observed changes in NO_3 and SiO_3 be
linked to changes in larger-scale circulation (altered ad-
vective transport and modification of major water-mass
properties), *i.e.* are the increasing NO_3:SiO_3 ratios related
to changes in the relative contributions of North Atlantic
and arctic waters entering the Labrador Sea?

Recent analysis of decadal changes in satellite-based
sea-surface temperature and ocean colour (Behrenfeld
et al., 2006) suggest that global warming may enhance

phytoplankton productivity in high-latitude regions due to decreased surface mixing, shallowing MLDs and improved light conditions for phytoplankton growth (Doney, 2006). Our LSMP data suggest that MLDs may be decreasing as water temperatures increase, however, overall phytoplankton biomass (bulk chlorophyll) appears to be decreasing, not increasing (Li *et al.*, 2006). Changes we are seeing in source water nutrient ratios and in phytoplankton community structure suggest that Doney's conceptual model captures only part of the dynamics that will link climate change to response at the base of the marine food web. Understanding the primary environmental control factors (light, nutrients) on phytoplankton growth and community structure is a key element in establishing how "first-order" changes in environmental properties, such as temperature increase and ice melt through climate variability/change, will induce changes, "second-order effects", in mixing, light and nutrients conditions that more directly effect structure and function of biological communities.

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