Journal of Plankton Research Vol.21 no.8 pp.1519–1536, 1999

Phytoplankton growth rates in the Ross Sea, Antarctica, determined by independent methods: temporal variations

Walker O.Smith, Jr, David M.Nelson[1] and Sylvie Mathot

Virginia Institute of Marine Science, College of William and Mary, Gloucester Pt, VA 23062 and [1]College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331, USA

Abstract. The development of the seasonal phytoplankton bloom in the Ross Sea was studied during two cruises. The first, conducted in November–December 1994, investigated the initiation and rapid growth of the bloom, whereas the second (December 1995–January 1996) concentrated on the bloom's maximum biomass period and the subsequent decline in biomass. Central to the understanding of the controls of growth and the summer decline of the bloom is a quantitative assessment of the growth rate of phytoplankton. Growth rates were estimated over two time scales with different methods. The first estimated daily growth rates from isotopic incorporation under simulated *in situ* conditions, including ^{14}C, ^{15}N and ^{32}Si uptake measurements combined with estimates of standing stocks of particulate organic carbon, nitrogen and biogenic silica. The second method used daily to weekly changes in biomass at selected locations, with net growth rates being estimated from changes in standing stocks of phytoplankton. In addition, growth rates were estimated in large-volume experiments under optimal irradiances. Growth rates showed distinct temporal patterns. Early in the growing season, short-term estimates suggested that growth rates of *in situ* assemblages were less than maximum (relative to the temperature-limited maximum) and were likely reduced due to low irradiance regimes encountered under the ice. Growth rates increased thereafter and appeared to reach their maximum as biomass approached the seasonal peak, but decreased markedly in late December. Differences between the two major taxonomic groups present were also noted, especially from the isotopic tracer experiments. The haptophyte *Phaeocystis antarctica* was dominant in 1994 throughout the growing season, and it exhibited the greatest growth rates (mean 0.41 day^{-1}) during spring. Diatom standing stocks were low early in the growing season, and growth rates averaged 0.10 day^{-1}. In summer, diatoms were more abundant, but their growth rates remained much lower (mean of 0.08 day^{-1}) than the potential maximum. Understanding growth rate controls is essential to the development of predictive models of the carbon cycle and food webs in Antarctic waters.

Introduction

Quantifying phytoplankton growth rate in the ocean is of critical importance to understanding many oceanographic processes, because the growth rates of individual populations control the ultimate composition of the assemblage (Banse, 1991). This, in turn, controls a large number of ecosystem properties, such as vertical flux of organic matter, nutrient utilization patterns and yield from the food web. However, few detailed studies of growth rates of natural phytoplankton assemblages (especially those from Antarctica) have been completed.

The specific growth rate of phytoplankton (μ) is hard to measure *in situ.* Conceptually, it is the biomass-normalized, instantaneous rate of biomass increase of a species or assemblage in the absence of losses. Thus, in the absence of losses, the rate of phytoplankton biomass increase $\left(\frac{dB}{dt}\right)$ is given by:

$$\frac{dB}{dt} = \mu B \quad (1)$$

where B is the phytoplankton biomass and μ is expressed in h^{-1} or day^{-1}. In batch cultures, where the biomass per cell remains relatively constant and losses are essentially eliminated, μ can be estimated directly from changes in the numerical abundance of cells with time. Culture studies of this kind were compiled by Eppley (1972) to estimate an upper limit for the maximum growth rate (μ_{max}) of phytoplankton as a function of temperature:

$$\log_{10}(\mu_{max}) = 0.0275T - 0.070 \quad (2)$$

where T is the temperature in °C and μ_{max} is expressed in doublings day^{-1}. When μ is expressed in day^{-1}, equation (2) becomes:

$$\log_{10}(\mu_{max}) = 0.0275T - 0.229 \quad (3)$$

In most oceanic regions, μ never approaches the temperature-constrained μ_{max} because of limitation by nutrients and/or irradiance (Parsons *et al.*, 1984; Falkowski *et al.*, 1998). In addition, the observed $\frac{dB}{dt}$ is almost always considerably less than μB as defined by equation (1), even after taking into account the fact that $\mu < \mu_{max}$ because of losses due to grazing, sinking, mixing and advection. For the surface mixed layer at a given site, the net change in phytoplankton biomass through time can be expressed as:

$$\frac{dB}{dt} = \mu B - gZ - S - M \pm A \quad (4)$$

where Z is the zooplankton abundance, g is the mean rate of phytoplankton biomass ingestion per zooplankton individual, S is the removal of phytoplankton biomass by sinking, M is the removal of phytoplankton biomass by vertical mixing and A is the change (increase or decrease) in phytoplankton biomass due to lateral advection. Temporal changes in phytoplankton biomass in the ocean reflect the net imbalance among all growth and loss terms shown in equation (4), and can be either positive or negative. In the large portions of the ocean that exhibit fairly 'stable' environments, the growth and loss terms may be nearly equal $\left(\frac{dB}{dt} \approx 0\right)$ in certain periods of the year (Smetacek and Passow, 1990).

Several methods have been used to estimate phytoplankton growth rates in the sea. These differ in the loss terms that are included with growth in the estimate, and it is important to distinguish among them on that basis. Tracer methods that measure the uptake of an isotope during an incubation can be used to calculate the specific uptake rate (V) of the element whose uptake was measured (C, N or Si). The measured elemental uptake rate (ρ in $\mu mol^{-1}\ day^{-1}$ or $\mu g\ l^{-1}\ day^{-1}$) closely approximates μB when B is phytoplankton biomass in units of the element in question. That is, sinking, mixing and advection are eliminated because the sample is contained in a bottle, and grazing losses have little effect unless the tracer isotope is recycled back to a dissolved form during the incubation. This latter effect is almost always minor even if grazing is significant, because the specific activity of the isotope in the particulate matter remains much lower than

that in solution (e.g. Sheppard, 1962). V_C, V_N and V_{Si}, which are calculated as ρ_C/POC, ρ_N/PON and ρ_{Si}/BSi, respectively (POC is particulate organic carbon concentration, PON is particulate organic nitrogen concentration and BSi is biogenic silica concentration), yield minimum estimates of μ because of the contribution of POC, PON or BSi not associated with phytoplankton cells to the total measured 'biomass'. By definition, growth rates measured by isotope tracer methods cannot be negative.

In the past 15 years, a number of new methods have been developed to assess phytoplankton growth rates directly. Most prominent among these is the pigment labeling technique (Redalje and Laws, 1981; Gieskes *et al*., 1993; Goericke and Welshmeyer, 1993; Goericke, 1998), which involves the growth of phytoplankton with [^{14}C]bicarbonate and separation of the radiolabeled pigments using high-performance liquid chromatography (HPLC) at the end of the incubation. A few other methods for the assessment of growth rates have also been developed, but few have been used to measure phytoplankton growth rates over multiple time and space scales. One is the dilution method used to quantify grazing rates by microzooplankton (e.g. Landry, 1993; Landry *et al*., 1995), which involves diluting a water sample with filtered sea water (thereby changing both predator and prey density). Growth in the absence of grazing losses is considered to be the phytoplankton growth rate. Another method, the incorporation of $^{14}CO_2$ into protein for the determination of relative growth rate, has been applied infrequently (DiTullio and Laws, 1983; Lancelot *et al*., 1991; DiTullio, 1993). Finally, use of the frequency of dividing cells in natural populations has been limited by the method's restriction to only a few selected groups, such as dinoflagellates (e.g. Weiler and Chisholm, 1976; Weiler and Eppley, 1979).

Growth rates in polar oceans have not been rigorously addressed, and in studies where they have been investigated the results have been highly variable (Smith and Sakshaug, 1990). Maximum temperature-limited growth rates at –1.8, 0 and 2.0ºC calculated from equations (2) and (3) are 0.76, 0.85 and 0.97 doublings day^{-1}, or 0.53, 0.59 and 0.67 day^{-1}, respectively. However, Eppley (1972) did not include any cultures in his compilation that were grown below 2°C, and hence the accuracy of equation (2) at low temperatures is uncertain. Goldman and Carpenter (1974) analyzed data from continuous cultures to generate an equation similar to Eppley's, but their predicted μ_{max} values at –1.8, 0 and 2.0°C range from 0.23 to 0.33 day^{-1}, or less than half those predicted from equation (2). Average growth rates in Antarctic waters (determined by a variety of techniques) are generally less than those predicted from the Eppley (1972) temperature function [equation (2)]. For example, growth rates determined by Sakshaug and Holm-Hansen (1986) ranged from 0.15 to 0.49 doublings day^{-1}, and those measured by Holm-Hansen *et al*. (1977) ranged from 0.01 to 0.33 doublings day^{-1}. These data suggest that either equation (2) overestimates the maximum growth rate at low temperatures or that other factors (such as light or micronutrients) limit the growth of phytoplankton in the Southern Ocean (Fiala and Oriol, 1990). However, some studies (e.g. Spies, 1987) have found growth rates greater than those predicted by equation (2); hence, the absolute limit to growth in Antarctic waters remains equivocal.

To assess the growth rates of phytoplankton in the Ross Sea, we conducted short-term (e.g. 24 h) experiments using isotopic tracers ($[^{14}C]HCO_3$, $[^{15}N]NO_3$ and $[^{15}N]NH_4$, and $[^{32}Si]Si(OH)_4$). In addition, we measured the biomass of phytoplankton using a variety of methods to quantify the changes in biomass at a number of locations through time to assess the net growth rate over days to weeks. Finally, we conducted large-volume experiments using natural phytoplankton to measure growth rates under conditions which we believed to be near optimal. We expected that phytoplankton growth rates in the Ross Sea would be low initially due to irradiance limitation, maximal during late spring, decrease during late December, and near zero during January and February. We hypothesized that no differences in growth rates between diatoms and *Phaeocystis antarctica* (both of which are commonly encountered in the Ross Sea) would be observed, but that net growth rates $\left(\frac{dB}{dt}\right)$ would reveal substantial differences. To test these hypotheses, we measured growth rates and observations during two cruises to the Ross Sea continental shelf.

Method

Field studies

Samples were collected from the Ross Sea polynya (a region with reduced ice concentrations surrounded by dense ice) during two cruises on the RVIB 'Nathaniel B. Palmer'. The first, NBP94-06, sampled from 12 November to 8 December 1994 during a period of rapidly increasing phytoplankton biomass (Figure 1a), whereas the second, NBP95-08, sampled from 12 December 1995 to 8 January 1996 during the seasonal biomass maximum and decline (Figure 1b). Stations were occupied every 60 km along 76°30′S and many locations were sampled repeatedly through time. Water was collected using a Seabird 911 CTD system mounted on a rosette which contained 24 10-l Niskin bottles. Each Niskin bottle was fitted with a Teflon-coated stainless steel closing spring. At least 12 depths from the upper 150 m were sampled on each cast.

In addition, large-volume experiments were conducted to determine the chemical and biological changes which occur during the course of a bloom when irradiance effects are minimized. Twenty-five liter carboys of unamended sea water were incubated on deck and sampled through time (Smith *et al*., 1998), which allowed for growth rates to be determined through time as a function of environmental conditions.

Water samples

Subsamples were collected for nutrients, chlorophyll, particulate carbon and nitrogen, and biogenic silica concentrations. Nutrients (nitrate, nitrite, ammonium, phosphate, silicic acid) were analyzed using automated techniques at sea, and chlorophyll was assayed fluorometrically (Smith and Nelson, 1990). Particulate carbon and nitrogen concentrations were determined by high-temperature

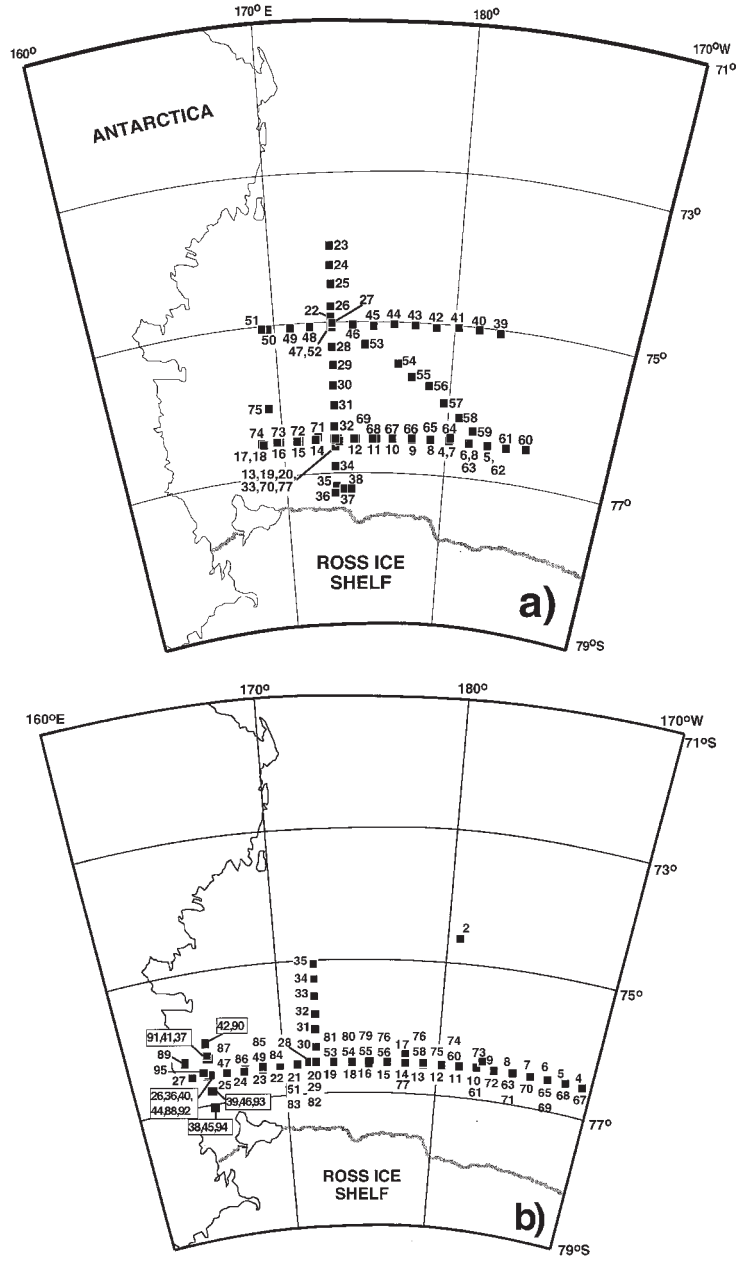

Fig. 1. Map showing the location of stations sampled during (**a**) NBP 94-06 (November–December 1994) and (**b**) NBP95-08 (December 1995–January 1996).

pyrolysis using a Carlo-Erba Model EA-1108 elemental analyzer (Smith and Gordon, 1997). Biogenic silica concentrations were measured using the methods of Brzezinski and Nelson (1989).

Uptake rates of carbon, nitrogen and silicon were determined using isotopic tracer methods under simulated *in situ* conditions. Carbon assimilation was measured on 280 ml samples using the uptake of [^{14}C]bicarbonate (Smith and Nelson, 1990), and nitrogen (nitrate and ammonium) uptake was measured in 550 ml samples from uptake of trace (10%) additions of ^{15}N and quantifying the ^{15}N incorporation by emission spectrometry (Smith and Nelson, 1990). Biogenic silica production was measured in 100 ml samples by quantifying the uptake of ^{32}Si (additions of tracer were ~50 000 d.p.m. per bottle, an increase of <0.01 μmol l^{-1}; Brzezinski and Phillips, 1997). Details of the methodologies are given elsewhere, but all used on-deck incubations under natural irradiance and lasted ~24 h.

Growth rate calculations

Growth rates were calculated by a number of independent methods. Short-term growth rates were calculated from ^{14}C, ^{15}N and ^{32}Si uptake rates:

$$\mu = \ln\left[\frac{B + \mathrm{d}B/\mathrm{d}t}{B}\right] \quad (5)$$

where μ is the growth rate (day^{-1}), B is an estimate of biomass (POC, PON or BSi) and $\frac{\mathrm{d}B}{\mathrm{d}t}$ is the rate of change of biomass determined from an isotopic rate measurement (Eppley, 1967). For carbon, the equation should use living algal carbon as POC to give an unbiased estimate of growth rate, since the use of total POC leads to an underestimate of μ to the extent that POC > POC_{living} (Eppley, 1967). In Antarctic phytoplankton blooms, much of the carbon found is considered as 'living' (identified with intact cells; Nelson and Smith, 1986; Nelson *et al.*, 1987), so that the underestimate caused by using total POC in equation (5) is not large. Similar arguments hold for nitrogen. Silicon has relatively small detrital pools (since it appears that detrital silica sinks rapidly from the surface layer; Nelson and Smith, 1986), so that the underestimate in silicon-based growth rates is small. Equation (5) is analogous to that used for determining the specific rate of nutrient uptake using the initial particulate matter concentration as the biomass estimate (Dugdale and Wilkerson, 1986), although these rates are generally expressed on an hourly basis rather than a daily rate.

Considerable attention has been given to the various models of algal growth with respect to nutrient uptake calculations. Specifically, it is possible to make different assumptions for the parameters in equation (5) that influence the calculated rates (Dugdale and Wilkerson, 1986; Brzezinski and Phillips, 1997). One major influencing variable is phytoplankton biomass. Since biomass can increase significantly during an incubation, particularly under conditions of rapid growth, using the particulate matter concentration at the end of the experiment actually causes an underestimate of μ when using equation (5). Conversely, using the particulate matter concentration from the beginning of an experiment results in an overestimate of μ. Furthermore, equation (5) assumes that the uptake of an element is constant through time and is not

influenced by the increased uptake by elevated algal biomass generated during the incubation. Dugdale and Wilkerson (1986) suggested using the arithmetic mean of the POM concentration (mean of initial and final POM) to give a more accurate estimate of uptake rate. However, they also noted that a model assuming exponential increase in specific uptake is more biologically realistic [their equation (5)], and suggested that comparable results are obtained using either the mean biomass during an incubation or an exponential model. Brzezinski and Phillips (1997) suggested that the exponential model was the most appropriate formulation for estimates of biomass-specific growth rates. We calculated growth rates using both of these approaches (linear and exponential) using data from large-volume experiments and biomass changes *in situ*. Nutrient or particulate matter concentrations [equation (5)] were derived from the arithmetic mean of the two data points.

Net growth rates were determined over longer time scales (e.g. weeks) by measuring the rates of change of either biomass or nutrients in the upper 150 m (e.g. Smith *et al*., 1991; Sambrotto *et al*., 1993). In essence, the approach quantifies the changes in phytoplankton biomass at a specific location by using equation (4). The use of 150 m as the surface layer allows for some redistribution of particles to subeuphotic depths (i.e. movement of slowly sinking particles into the layer between the base of the euphotic zone and 150 m). Losses during this period due to vertical mixing are minor, as mixed layers over most of the region averaged ~35 m, much less than the 150 m depth of the surface layer used in the calculations. Export due to rapidly sinking particles was measured at a few locations by short-term deployments of sediment traps (Asper and Smith, 1999), but not over a great range of locations or periods during the bloom. Changes in the DOC pool during the entire seasonal cycle were surprisingly small (Carlson *et al*., 1998), and no significant increases were noted below 150 m, suggesting that no introduction of DOC produced in the surface layer into deeper waters occurred during our study. We have no information on the losses due to incorporation into zooplankton biomass, but the losses due to zooplankton excretion of fecal material (generally the largest loss term in one-dimensional analyses; Daly *et al*., 1999) should be included in the estimates of vertical flux. In general, the standing stocks of zooplankton in the southern Ross Sea are quite low and represent <1% of the surface layer particulate matter standing stocks.

Such a calculation assumes that the vertical, one-dimensional effects are substantially greater than any horizontal variations induced by advection. Generally, this assumption is not rigorously tested, and as such the method's results often have a substantial degree of uncertainty. However, current meter data are available to assess advection in the southern Ross Sea. Current flow is seasonally dependent, with minima during summer (Asper and Smith, 1999). Maximum flows observed (~24 cm s^{-1}) represent a movement over 2 weeks of ~300 km; however, satellite images show that the bloom extends over at least 400 km (Arrigo and McClain, 1994). This suggests that movement of the surface layer at maximal rates will still allow the water patch to maintain its integrity, and therefore a one-dimensional approach might be reasonably appropriate to assess the growth and losses of the region.

Results

Phytoplankton growth rates

Growth rates calculated from isotope uptake using equation (5) for Si, C and N exhibited surprising variations both within and between cruises. Surface growth rates of carbon were on average higher than those determined from nitrogen and silicon during the November–December cruise (mean V_C, V_N and V_{Si} = 0.41, 0.12 and 0.10 day^{-1}, respectively; Table I), but the carbon-based growth rates decreased dramatically during the December–January cruise (mean V_C, V_N and V_{Si} = 0.15, 0.09 and 0.08 day^{-1}, respectively; Table I). ^{14}C-based growth rates during the first week of December averaged 0.47 day^{-1} (Smith and Gordon, 1997). The response of growth to irradiance as determined from the three tracers was similar, in that growth rates apparently saturated at ~5% of surface irradiance during spring and from 5 to 15% during summer (Figure 2a and b). Growth rates declined to lower values at lower photon flux densities. However, the extent of the reduction for carbon was much greater than for either silica or nitrogen, particularly in 1994. Carbon growth rates were significantly correlated with the assimilation number (the chlorophyll-specific primary productivity; Figure 3),

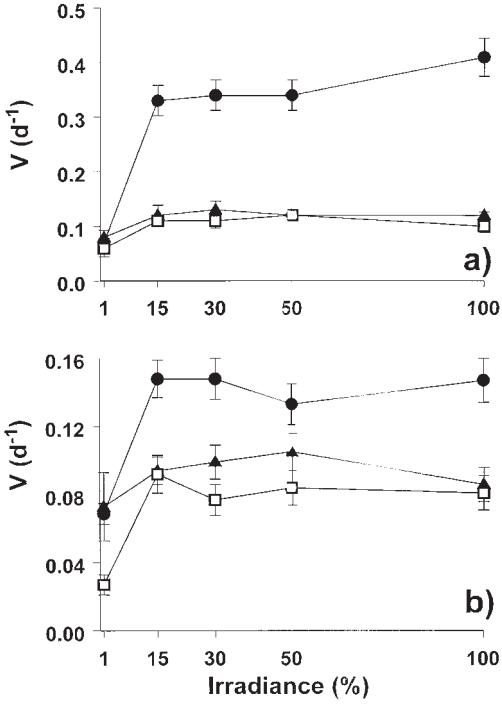

Fig. 2. The relationship of growth rates (based on carbon, nitrogen and silica uptake) and irradiance in (**a**) spring 1994 and (**b**) early summer 1995/96. Values represent means for the entire cruise and error bars represent standard errors. Surface irradiance averaged 49.9 and 49.5 mol m^{-2} day^{-1} during spring and summer, respectively.

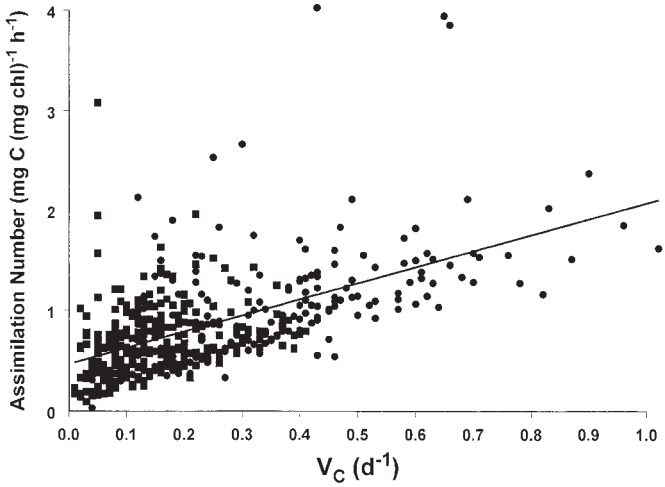

Fig. 3. Relationship of carbon-based growth rates and assimilation numbers (chlorophyll-specific growth rates) for both 1994 (●) and 1995/96 (■). Only values from above the 5% isolume were analyzed. The line represents the least squares Model I regression (AN = $1.60V_C + 0.47$; $r = 0.57$; $P << 0.001$).

Table I. Mean, ranges and standard deviations for all surface values of growth rates determined from carbon, nitrogen and silicon uptake measurements during NBP94-06 and NBP95-08

Growth rate	NBP94-06	NBP95-08
Mean carbon-based growth rate (V_C; day^{-1})	0.41	0.15
n	45	55
σ	0.23	0.09
Range	0.04–1.02	0.02–0.41
Mean nitrogen-based growth rate (V_N; day^{-1})	0.12	0.09
n	26	20
σ	0.05	0.04
Range	0.02–0.23	0.01–0.17
Mean silicon-based growth rate (V_{Si}; day^{-1})	0.10	0.08
n	7	11
σ	0.02	0.03
Range	0.08–0.12	0.03–0.15

n, number of observations used in analyses; σ, standard deviation.

which is not surprising given that the carbon:chlorophyll ratio did not vary dramatically. Because not all rates were measured at all stations, we can directly compare only six stations where V_C, V_N and V_{Si} were determined on the same samples. At Station 94-7, carbon-based growth rates were ~1.5 and 3.4 times greater than those determined using nitrogen and silicon isotopes, respectively (Figure 4a), while at Station 95-12 V_N and V_{Si} were approximately equal, but V_C was three times as high (Figure 4b). Growth rates for Station 95-28 were approximately equal regardless of the isotope used in their derivation (Figure 4c). Surface values for stations where all three rates were determined are listed in Table II.

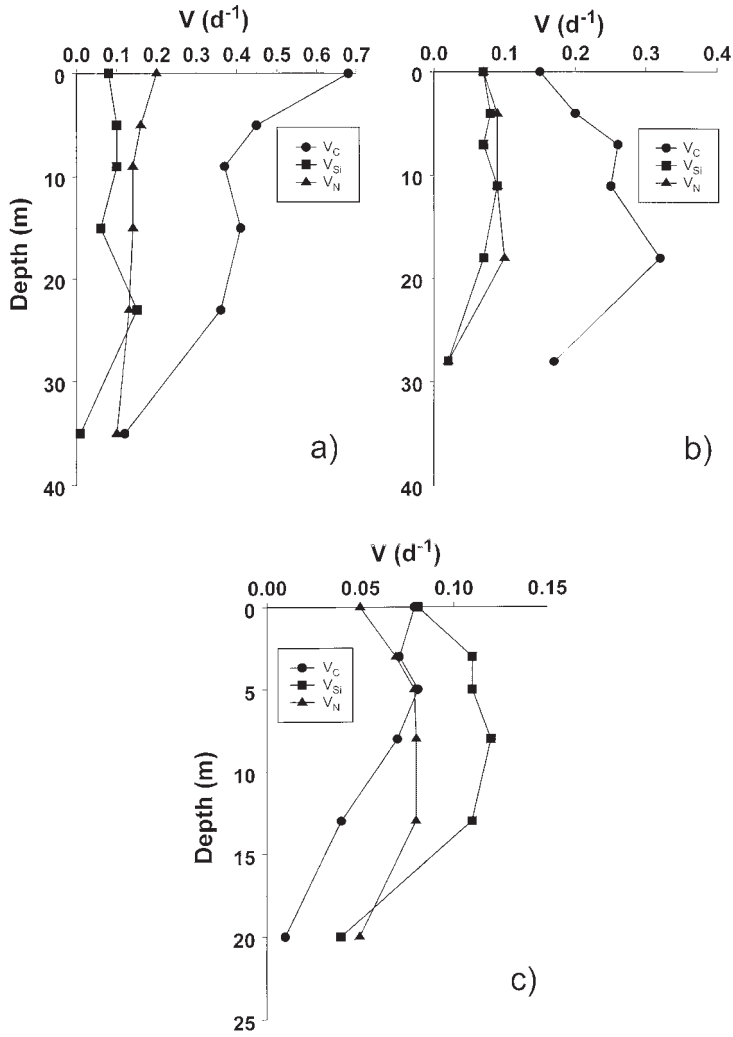

Fig. 4. Depth distribution of growth rates determined from carbon, nitrogen and silica uptake measurements at (**a**) Station 94-07, (**b**) Station 95-12 and (**c**) Station 95-19.

Net growth rates in large-volume experiments

Growth rates from large-volume studies were similar in magnitude to those from the isotopic studies (Table III; see also Smith *et al*., 1998). These growth rates were calculated from changes in biomass (PON and POC), as well as by calculating the changes observed in nutrients (nitrate + ammonium, phosphate, and silicic acid) and assuming that no significant amounts of dissolved organic matter were released by phytoplankton (an assumption supported by direct determination of

Table II. Surface growth rates based on carbon, nitrogen and silicon uptake measurements at those stations when all three were measured simultaneously

Station	V_C (day^{-1})	V_N (day^{-1})	V_{Si} (day^{-1})
94-07	0.26	0.17	0.11
94-15	0.04	0.09	0.08
94-19	0.68	0.20	0.08
94-64	0.57	0.05	0.12
94-70	0.53	0.06	0.11
94-72	0.51	0.23	0.12
Mean 1994	0.41	0.13	0.10
95-12	0.15	0.07	0.07
95-20	0.11	0.15	0.15
95-21	0.24	0.03	0.13
95-23	0.39	0.07	0.09
95-28	0.08	0.05	0.08
Mean 1995	0.25	0.07	0.10

Table III. Growth rates calculated from the disappearance of nutrients and by the appearance of particulate organic nitrogen and carbon in a large-volume experiment in 1994 (Smith *et al*., 1998). Growth rates are calculated by equation (5) assuming exponential (A) or linear growth (B). The experiment was overwhelmingly dominated by *P.antarctica*, and therefore growth rates based on silica removal are omitted. Growth rates were calculated from the start of the experiment through day 10, when nitrate depletion occurred. Biomass or nutrient concentrations for the calculation in B were those half-way through exponential growth

Variable used	Growth rate (day^{-1})	
	A	B
Particulate organic nitrogen	0.25	0.15
Particulate organic carbon	0.24	0.17
PO_4	0.17	0.16
NO_3	0.31	0.18

DON release rates; Hu and Smith, 1998). V_N and V_C varied as a function of time, and were maximal prior to nutrient depletion (Figure 5a and b), at which time they decreased greatly. Since the assemblage was overwhelmingly dominated by the haptophyte *P.antarctica* and diatoms did not contribute significantly to the standing stocks in these experiments, V_{Si} calculated from depletion of silicic acid was close to zero. Growth rates calculated using equation (5) and assuming an exponential model were slightly greater than those calculated assuming a linear model (Table III).

Net growth rates determined from changes in phytoplankton biomass in the surface layer at selected locations were generally lower than those determined from 24 h incubations, which was expected since growth rates determined from isotope incorporation do not include losses due to grazing, sinking or advection. Losses in the southern Ross Sea due to aggregate formation and zooplankton ingestion and fecal pellet formation and flux were temporally variable and not tightly coupled to phytoplankton production or biomass (Smith and Dunbar,

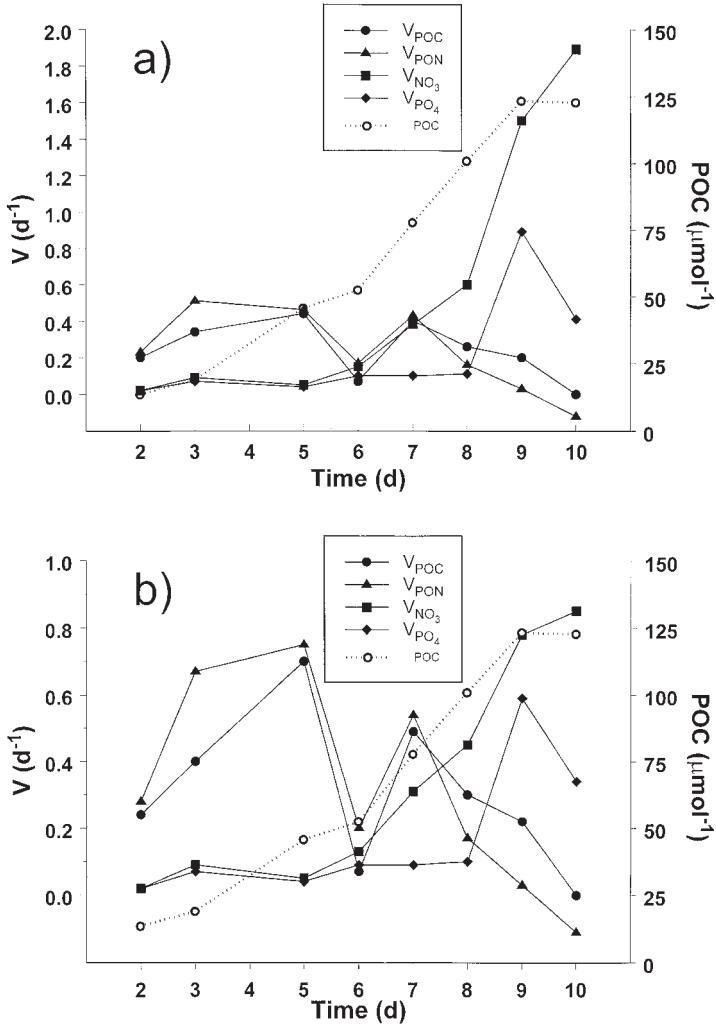

Fig. 5. Growth rates determined by the changes in dissolved nutrients during large-volume experiments using (**a**) a linear growth rate assumption and (**b**) an assumption of logarithmic growth. POC concentrations as a function of time are also listed (data from Smith *et al*., 1998).

1998; Asper and Smith, 1999), and biomass decreased in January and February (Arrigo and McClain, 1994; Smith *et al*., 1996; Asper and Smith, 1999). Such decreases will result in negative net growth rates based on a one-dimensional calculation, despite the fact that growth rates determined from isotopic measurements will be positive (Smith *et al*., 1996). Integrated stocks of particulate matter in the southern Ross Sea reach their seasonal maximum in mid-December and decline thereafter (Asper and Smith, 1999), and hence net growth rates calculated

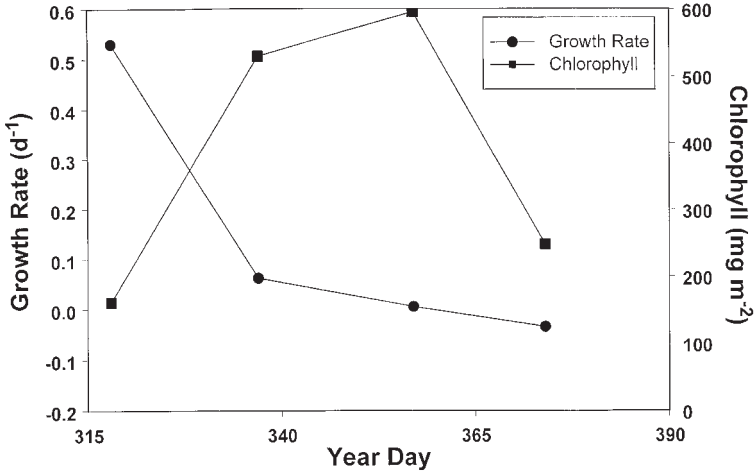

Fig. 6. Changes in integrated chlorophyll concentration and growth rate through time at 76°30′S, 180°.

from $\frac{dB}{dt}$ after the seasonal maximum are zero or negative (Figure 6). Growth rates calculated from changes in chlorophyll, POC and PON (Table IV) at selected sites along 76°30′S during spring and early summer ranged from 0.01 to 0.53 day^{-1} using equation (5) and assuming exponential growth, and from 0.01 to 1.22 day^{-1} assuming linear growth. The variations between the two estimates seem to result from the length of time over which biomass accumulates, as longer time intervals result in lower growth rate estimates.

Discussion

The growth rate (μ) of phytoplankton is a fundamental biological property in the surface layer of the ocean. It governs the productivity, carbon transformations within the food web, nutrient utilization and export to depth. Over days to weeks, the growth of one taxon relative to another controls the species composition of the phytoplankton (in conjunction with group-dependent loss processes such as grazing), so knowledge of growth rates of individual groups within the phytoplankton as well as the phytoplankton assemblage as a whole is critical to our understanding of the biotic responses to environmental forcing. Despite the clear need for growth rate data, few field studies attempt to measure this variable, mostly because the method requires independent estimates of both living biomass and the rate of change of biomass. All estimates of living biomass have uncertainties associated with them. For example, chlorophyll is often used to estimate phytoplankton carbon, but carbon:chlorophyll ratios can vary over an order of magnitude in field studies as a result of acclimation (Kirk, 1994; Smith *et al*., 1996). ATP is associated with living cells, but the carbon:ATP ratio

also varies significantly (Weiler and Karl, 1979); furthermore, ATP is also contained in heterotrophic cells and is not restricted to phytoplankton. POC and PON always contain a variable proportion of detrital material, but in areas and periods of rapid growth and elevated biomass, the contribution of detritus to the POC and PON standing stocks decreases substantially (Hobson *et al*., 1973; Nelson *et al*., 1989).

Upon the onset of phytoplankton growth in the Ross Sea, there is very little organic matter in the surface layer, and when substantial concentrations of phytoplankton are reached, most of the organic matter is associated with living phytoplankton. As such, estimates of living carbon from pigments, POC and PON determinations, and microscopic counts all converge. Because our estimates of growth rates were made during periods when biomass was high, a large fraction of the organic matter was contained in living cells. Growth rate estimates using POC or PON are likely to be underestimates of μ, but the magnitude of that underestimate is almost certainly <10%, and may approach 2% (the amount of detritus found in an earlier bloom study in the Ross Sea; Wilson *et al*., 1986).

Isotopic estimates of μ generally were lower than the predicted temperature-limited maximum of 0.52–0.59 day^{-1} at temperatures from –1.8 to 0°C (Eppley, 1972), but in 1994 (when productivity and biomass changes were greatest; Smith and Gordon, 1997) the carbon-based growth rate estimate approached the temperature-limited maximum. Indeed, for the entire spring cruise, carbon-based growth rates were high (mean V_C = 0.41 day^{-1}; Table I), and for the last week of the cruise growth rates were near the limit predicted by equation (2). This suggests that if the method is assessing growth rates accurately, then equation (2) is a reasonable estimate of temperature-limited growth rates in polar waters. Similarly, these data suggest that the relationship suggested by Goldman and Carpenter (1974) underestimates maximum growth rates in sub-zero waters of the Antarctic. Given the variability and uncertainty of μ_{max} estimates in polar systems (which range from 0 to nearly 1.5 doublings day^{-1}; Holm-Hansen *et al*., 1977; Sakshaug and Holm-Hansen, 1984; Spies, 1987; Fiala and Oriol, 1990), a more complete assessment of this relationship is required to predict any changes in phytoplankton growth rates induced by any future changes in sea-surface temperature in polar oceans.

One of the most striking aspects of the daily growth rate estimates is the difference among the growth rates as determined by different isotopes (Tables I and II). Carbon- and nitrogen-based growth rates represent the entire phytoplankton community, as all autotrophs incorporate $^{14}CO_2$ and require inorganic nitrogen for their growth. Silica-based rates, however, represent only diatoms, and there is no a priori reason to expect that diatoms and non-siliceous species will be growing at equal or similar rates. Indeed, estimated diatom growth rates (i.e. V_{Si}) are consistently lower than those of the entire phytoplankton community as estimated by V_C. *Phaeocystis antarctica* often accumulates extensively in the south-central Ross Sea, and it is possible that *P.antarctica* simply has a greater net growth rate as a result of being better acclimated to the spring environment (e.g. reduced photon flux densities, elevated iron concentrations, reduced losses due to grazing). However, it presently is not clear what environmental factor might

result in more rapid *Phaeocystis* growth in the Ross Sea. It is also possible that diatoms, particularly at these extremely low temperatures, do not have intrinsically high growth rates, and hence are genetically limited to maximal growth rates which are less than those of *Phaeocystis*.

A second aspect of these isotopic growth rate estimates is that the carbon- and nitrogen-based rates are generally not coupled. During balanced growth, the ratio of V_C to V_N (the ratio of biomass-specific uptake) should equal 1 (in contrast to the ratio of carbon and nitrogen uptake, which during balanced growth should approach the Redfield ratio, or ~6.6), and as a result the particulate C/N ratio will remain constant through time. However, the V_C/V_N ratio was greater than 1 during both cruises, and at times is greater than 3 (Figures 2 and 4). Elevated V_C/V_N ratios seem to be more common during spring, particularly during rapid growth of *P.antarctica*. We hypothesize that the 'extra' carbon is being partitioned to the extracellular mucoid sheath rather than into cellular synthesis. This would ultimately result in increased C/N ratios, and although such increases have been observed in the summer (Smith *et al*., 1996), no clear trend was seen within the 1994 cruise. It is also possible that this extracellular material might be remineralized to CO_2 over time scales longer than those of the measurements (24 h), but in less time than the reoccupation of station locations in the region (~5–20 day), thereby preventing any observable changes in the POC/PON ratios. The disparity between V_C and V_N is reduced during summer when the carbon-based growth rates decrease and become similar to the nitrogen-based growth rates. Also, growth rates based on nitrogen and carbon were similar in the large-volume experiments, suggesting that under certain conditions the upcoupling (or excess mucilage production, if that indeed is the cause of the quantitative difference) does not occur. The role of the extracellular mucilage of *P.antarctica* has received considerable attention in recent years (e.g. Davidson and Marchant, 1992), but its quantitative role in the partitioning of carbon relative to nitrogen remains uncertain.

Estimates of growth rates using equation (5), but assuming either exponential biomass increase during the incubation period or a constant, linear uptake of isotope, result in different calculated rates, and those that assume exponential growth during 24 h measurements are generally greater (Table III). Linear estimates of net growth rates produce much greater variations and often rates which are greater than those predicted from temperature alone (Table IV). Because exponential growth is biologically realistic in polar systems for intervals of days to weeks as well as for shorter intervals (≤24 h), at the modest growth rates encountered the two estimates should converge (Dugdale and Wilkerson, 1986; Brzezinski and Phillips, 1997). Similarly, at high growth rates or long time intervals, the two should diverge. It is important when growth rates are calculated that the assumptions made concerning growth be explicitly stated to allow for direct comparison of growth rates.

Growth rates are central to understanding of the changes in phytoplankton in the surface layer of the ocean, since the composition of surface communities results from the growth of various species of phytoplankton relative to the species-specific losses that occur as a result of grazing, sinking and aggregation.

Table IV. Growth rates determined from changes in biomass (chlorophyll, particulate organic carbon and particulate organic nitrogen) over time periods ranging from days to weeks at fixed locations. Biomass estimates integrated from the surface to 150 m. Growth rates were calculated using equation (5) and assuming an exponential (A) or a linear increase (B)

Station/variable	Time (day)	Growth rate (day^{-1})	
		A	B
Station 94-16, 94-73			
Chlorophyll	18.9	0.17	1.22
POC		ND	ND
PON		ND	ND
Station 94-15, 94-72			
Chlorophyll	19.0	0.16	0.98
POC		0.13	0.54
PON		0.13	0.52
Station 94-14, 94-71			
Chlorophyll	19.4	0.08	0.19
POC		0.09	0.24
PON		0.07	0.16
Station 94-13, 94-19			
Chlorophyll	2.25	0.10	0.23
POC		0.18	0.21
PON		0.01	0.01
Station 94-11, 94-68			
Chlorophyll	18.2	0.03	0.03
POC		0.05	0.09
PON		0.06	0.03
Station 94-4, 94-7			
Chlorophyll	0.65	0.53	0.70
POC		ND	ND
PON		ND	ND
Station 94-7, 94-64			
Chlorophyll	18.5	0.06	0.12
POC		0.02	0.03
PON		0.02	0.02
Station 94-9, 94-66			
Chlorophyll	19.1	0.09	0.23
POC		0.05	0.09
PON		0.08	0.03

ND, no data for these stations.

The losses which occur in turn markedly influence regional biogeochemical cycles by altering the quantity and quality of material exported from the surface layer. In addition, growth rates serve as the input to most numerical models of carbon dynamics of the ocean. Despite their importance, measurements of growth rates are made infrequently, especially in polar systems. Given that numerical models predict a significant impact on polar regions by atmospheric warming induced by anthropogenic change, the growth rate responses of polar phytoplankton to slight temperature changes remains poorly constrained. A more quantitative understanding of the rates of growth of polar phytoplankton will substantially add to our abilities to predict future changes in the food webs, carbon dynamics and biogeochemistry of the Antarctic.

Acknowledgements

We would like to thank L.Gordon for providing the nutrient analyses, and L.A.Monty, J.M.Arrington, S.Polk and A.-M.White for technical assistance. This research was supported by NSF grants OPP-9317587 and OPP-9317538. This is contribution no. 2232 of the Virginia Institute of Marine Science, The College of William and Mary.

References

Arrigo,K.R. and McClain,C.R. (1994) Spring phytoplankton production in the Western Ross Sea. *Science*, **266**, 261–263.

Asper,V.L. and Smith,W.O.,Jr (1999) Particle fluxes during austral spring and summer in the southern Ross Sea (Antarctica). *J. Geophys. Res.*, **104**, 5345–5360.

Banse,K. (1991) Rates of phytoplankton cell division in the field and in iron enrichment experiments. *Limnol. Oceanogr.*, **36**, 1886–1898.

Brzezinski,M.A. and Nelson,D.M. (1989) Seasonal changes in the silicon cycle within a Gulf Stream warm core ring. *Deep-Sea Res.*, **36**, 1009–1030.

Brzezinski,M.A. and Phillips,D.R. (1997) Evaluation of ^{32}Si as a tracer for measuring silica production rates in marine waters. *Limnol. Oceanogr.*, **42**, 856–865.

Carlson,C.A., Ducklow,H.W., Hansell,D.A. and Smith,W.O.,Jr (1998) Organic carbon partitioning during spring phytoplankton blooms in the Ross Sea polynya and the Sargasso Sea. *Limnol. Oceanogr.*, **43**, 375–386.

Daly,K.L., Wallace,D.W.R., Smith,W.O.,Jr, Skoog,A., Lara,R., Gosselin,M., Falk,E. and Yager,P.L. (1999) Anomalous carbon and nitrogen cycling in the Arctic: effects of ecosystem structure and dynamics. *J. Geophys. Res.*, **104**, 3185–3200.

Davidson,A.T. and Marchant,H.J. (1992) Protist abundance and carbon concentration during a *Phaeocystis*-dominated bloom at an Antarctic coastal site. *Polar Biol.*, **12**, 387–395.

DiTullio,G.R. (1993) Incorporation of $^{14}CO_2$ into protein as an estimate of phytoplankton N assimilation and relative growth rate. In Kemp,P.F., Sherr,B.F., Sherr,E.B. and Cole,J.J. (eds), *Handbook of Methods in Aquatic Microbial Ecology.* Lewis Publishers, Boca Raton, FL, pp. 573–578.

DiTullio,G.R. and Laws,E.A. (1983) Estimates of phytoplankton N uptake based on $^{14}CO_2$ incorporation into protein. *Limnol. Oceanogr.*, **28**, 177–185.

Dugdale,R.C. and Wilkerson,F.P. (1986) The use of ^{15}N to measure nitrogen uptake in eutrophic oceans; experimental considerations. *Limnol. Oceanogr.*, **31**, 673–689.

Eppley,R.W. (1967) An incubation method for estimating the carbon content of phytoplankton in natural samples. *Limnol. Oceanogr.*, **13**, 574–582.

Eppley,R.W. (1972) Temperature and phytoplankton growth in the sea. *Fish. Bull.*, **7**, 1063–1085.

Falkowski,P.G., Barber,R.T. and Smetecek,V. (1998) Biogeochemical controls and feedbacks on ocean primary production. *Science*, **281**, 200–206.

Fiala,M. and Oriol,L. (1990) Light-temperature interactions on the growth of Antarctic diatoms. *Polar Biol.*, **10**, 629–636.

Gieskes,W.W.J., Kraay,G.W. and Buma,A.G. (1993) ^{14}C labelling of algal pigments to estimate the contribution of different taxa to primary production in natural seawater samples. *ICES Mar. Sci. Symp.*, **197**, 114–120.

Goericke,R. (1998) Response of phytoplankton community structure and taxon-specific growth rates to seasonally varying physical forcing in the Sargasso Sea off Bermuda. *Limnol. Oceanogr.*, **43**, 921–935.

Goericke,R. and Welschmeyer,N.A. (1993) The chlorophyll-labeling method: measuring specific rates of chlorophyll a synthesis in cultures and in the open ocean. *Limnol. Oceanogr.*, **38**, 80–95.

Goldman,J.C. and Carpenter,E.J. (1974) A kinetic approach to the effect of temperature on algal growth. *Limnol. Oceanogr.*, **19**, 756–766.

Hobson,L.A., Menzel,D.W. and Barber,R.T. (1973) Primary productivity and sizes of pools of organic carbon in the mixed layer of the ocean. *Mar. Biol.*, **19**, 298–306.

Holm-Hansen,O., El-Sayed,S.Z., Franceschini,G.A. and Cuhel,R.L. (1977) Primary production and the factors controlling phytoplankton growth in the Southern Ocean. In Llano,G.A. (ed.), *Adaptations within Antarctic Ecosystems.* Smithsonian Institution, Washington, DC, pp. 11–50.

Hu,S. and Smith,W.O.,Jr (1998) The effects of irradiance on nitrate uptake and dissolved organic nitrogen release by phytoplankton in the Ross Sea. *Cont. Shelf Res.*, **18**, 975–990.

Kirk,J.T.O. (1994) *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge University Press, Cambridge, UK, 504 pp.
Lancelot,C.R., Veth,C. and Mathot,S. (1991) Modelling ice-edge phytoplankton bloom in the Scotia-Weddell Sea sector of the Southern Ocean during spring. *J. Mar. Syst.*, **2**, 333–346.
Landry,M.R. (1993) Estimating rates of growth and grazing mortality of phytoplankton by the dilution method. In Kemp,P.F., Sherr,B.F., Sherr,E.B. and Cole,J.J. (eds), *Handbook of Methods in Aquatic Microbial Ecology.* Lewis Publishers, Boca Raton, FL, pp. 715–722.
Landry,M.R., Kirshtein,J. and Constantinou,J. (1995) A refined dilution technique for measuring the community grazing impact of microzooplankton, with experiment tests in the central equatorial Pacific. *Mar. Ecol. Prog. Ser.*, **120**, 53–63.
Nelson,D.M. and Smith,W.O.,Jr (1986) Phytoplankton bloom dynamics of the western Ross Sea II. Mesoscale cycling of nitrogen and silicon. *Deep-Sea Res.*, **33**, 1389–1412.
Nelson,D.M., Smith,W.O.,Jr, Gordon,L.I. and Huber,B. (1987) Early spring distributions of nutrients and phytoplankton biomass in the ice-edge zone of the Weddell/Scotia Sea. *J. Geophys. Res.*, **92**, 7181–7190.
Nelson,D.M., Smith,W.O.,Jr, Muench,R.D., Gordon,L.I., Husby,D.M. and Sullivan,C.W. (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.
Parsons,T.R., Takahashi,M. and Hargrave,B. (1984) *Biological Oceanographic Processes.* Pergamon Press, Oxford, 330 pp.
Redalje,D.G. and Laws,E.A. (1981) A new method for estimating phytoplankton growth rates and carbon bimoass. *Mar. Biol.*, **62**, 73–83.
Sakshaug,E. and Holm-Hansen,O. (1986) Photoadaptation in Antarctic phytoplankton: variations in growth rate, chemical composition and P versus I curves. *J. Plankton Res.*, **8**, 459–473.
Sambrotto,R.N. *et al*. (1993) Elevated consumption of carbon relative to nitrogen in the surface ocean. *Nature*, **363**, 248–250.
Sheppard,C.W. (1962) *Basic Principles of the Tracer Method*. Wiley, New York, 282 pp.
Smetacek,V. and Passow,U. (1990) Spring bloom initiation and Sverdrup's critical-depth model. *Limnol. Oceanogr.*, **35**, 228–234.
Smith,W.O.,Jr and Dunbar,R.B. (1998) The relationship between new production and vertical flux on the Ross Sea continental shelf. *J. Mar. Syst.*, **17**, 445–457.
Smith,W.O.,Jr and Gordon,L.I. (1997) Hyperproductivity of the Ross Sea (Antarctica) polynya during austral spring. *Geophys. Res. Lett.*, **24**, 233–236.
Smith,W.O.,Jr and Nelson,D.M. (1990) Phytoplankton growth and new production in the Weddell Sea marginal ice zone in the austral spring and autumn. *Limnol. Oceanogr.*, **35**, 809–821.
Smith,W.O.,Jr and Sakshaug,E. (1990) Polar phytoplankton. In Smith,W.O.,Jr (ed.), *Polar Oceanography*, *Part B.* Academic Press, San Diego, CA, pp. 477–526.
Smith,W.O.,Jr, Codispoti,L.A., Nelson,D.M., Manley,T., Buskey,E.J., Niebauer,H.J. and Cota,G.F. (1991) Importance of *Phaeocystis* blooms in the high-latitude ocean carbon cycle. *Nature*, **352**, 514–516.
Smith,W.O.,Jr, Nelson,D.M., DiTullio,G.R. and Leventer,A.R. (1996) Temporal and spatial patterns in the Ross Sea, phytoplankton biomass, elemental composition productivity and growth rates. *J. Geophys. Res.*, **101**, 18455–18466.
Smith,W.O.,Jr, Carlson,C.A., Ducklow,H.W. and Hansell,D.A. (1998) Growth dynamics of *Phaeocystis antarctica*-dominated plankton assemblages from the Ross Sea. *Mar. Ecol. Prog. Ser.*, **168**, 229–244.
Spies,A. (1987) Growth rates of Antarctic marine phytoplankton in the Weddell Sea. *Mar. Ecol. Prog. Ser.*, **41**, 267–274.
Weiler,C.S. and Chisholm,S.W. (1976) Phased cell division in natural populations of marine dinoflagellates from shipboard cultures. *J. Exp. Mar. Biol. Ecol.*, **25**, 239–247.
Weiler,C.S. and Eppley,R.W. (1979) Temporal pattern of division in the dinoflagellate genus *Ceratium* and its application to the determination of growth rate. *J. Exp. Mar. Biol. Ecol.*, **39**, 1–24.
Weiler,C.S. and Karl,D.M. (1979) Diel changes in phased-dividing cultures of *Ceratium furca* (Dinophyceae): nucleotide triphosphates, adenylate energy charge, cell carbon, and patterns of vertical migration. *J. Phycol.*, **15**, 384–391.
Wilson,D.L., Smith,W.O.,Jr and Nelson,D.M. (1986) Phytoplankton bloom dynamics of the western Ross Sea Ice Edge—I. Primary productivity and species-specific production. *Deep-Sea Res.*, **33**, 1375–1388.

Received on September 18, 1998; accepted on April 19, 1999