

The role of light and major nutrients

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Sverdrup revisited: Critical depths, maximum chlorophyll levels, and the control of Southern Ocean productivity by the irradiance-mixing regime

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Abstract

A reformulation of Sverdrup's critical-depth calculation, using recent optical and physiological information, is developed and applied to data from the Southern Ocean. Comparisons between calculated critical depths (Z_c) and mixed-layer depths (Z_m) indicate that both the marginal ice zone and the open waters of the Antarctic Circumpolar Current provide favorable irradiance-mixing regimes for the initiation and early development of phytoplankton blooms in summer (i.e. $Z_c > Z_m$) when phytoplankton biomass is low and the water clear; that when ice-edge blooms develop, Z_c shoals to depths about equal to Z_m , implying that phytoplankton standing stocks in ice-edge blooms may be self-limiting as a result of reduced penetration of irradiance; and that the highest chlorophyll levels that can be sustained in summer in open waters not stabilized by meltwater are $\sim 1.0 \mu\text{g liter}^{-1}$ in the Weddell and Scotia Seas and may be less in areas that experience stronger winds.

The waters south of the Antarctic Polar Front comprise an area of $\sim 38 \times 10^6 \text{ km}^2$, or 10% of the global ocean surface area (El-Sayed 1978). Within this region, the combined effects of wind stress and thermohaline circulation result in circumpolar surface divergence and upwelling, which maintain high concentrations of all major nutrients in the surface layer (e.g. Bainbridge 1980; Nelson et al. 1987). The light regime in both the northern and southern polar regions is highly seasonal, but during summer the maximum integrated daily irradiance is about equal to that in the tropics (Campbell

and Aarup 1989). Despite the permanently high nutrient concentrations and seasonally high light inputs that characterize Southern Ocean surface waters, primary productivity is generally $< 200 \text{ mg C m}^{-2} \text{ d}^{-1}$, even in summer (e.g. Holm-Hansen et al. 1977; El-Sayed 1978; Sakshaug and Holm-Hansen 1984). Mesoscale high-productivity events do occur, especially in the vicinity of the retreating ice edge and in shallow, coastal embayments (e.g. Smith and Nelson 1985; Holm-Hansen and Mitchell 1991). However, the integrated annual primary productivity of the Southern Ocean appears to be no more than $1 \times 10^9 \text{ t C yr}^{-1}$ ($< 5\%$ of the global total), even if the effect of ice-edge blooms is included (Smith and Nelson 1986; Smith et al. 1988).

It has been suggested that low productivity in the nutrient-rich surface waters of the Southern Ocean may result from a deficiency of Fe (Martin and Fitzwater 1988). Fe enrichment experiments conducted in the

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Ross Sea tend to support this hypothesis by showing that the final yield of phytoplankton biomass in long-term incubation experiments can be increased significantly by adding nanomolar concentrations of unchelated Fe (Martin et al. 1990). It is not clear what the mechanism of this Fe enrichment response might be (e.g. Dugdale and Wilkerson 1990), but similar results have now been reported by other groups from other Southern Ocean locations (de Baar et al. 1990).

There are other areas of the ocean where relatively low primary productivity is observed in nutrient-rich surface waters, most notably the equatorial and subarctic Pacific (e.g. Chavez and Barber 1987; Martin et al. 1989), and Fe limitation has been hypothesized to control productivity in these systems as well as in the Southern Ocean (Martin and Fitzwater 1988). However, the Southern Ocean differs from these other regions in a way that makes it an area of potentially great importance for the global ocean-atmosphere carbon balance and thus for regulation of atmospheric CO_2 concentrations. Because convergence zones at the Antarctic Polar Front are the only places in the ocean where globally significant quantities of surface water downwell to aphotic depths while still containing high concentrations of preformed nutrients (Gordon 1971), it has been suggested that utilization of these "excess nutrients" might have a substantial impact on atmospheric CO_2 . For example, model results have suggested that over the next 100 yr an average of $1.0\text{--}1.8 \times 10^9$ t of additional C per year could be removed from the atmosphere by biological pumping mechanisms in the Southern Ocean if phytoplankton growth were vigorous enough to remove all NO_3 and PO_4 from the water that sinks at the polar front (Peng and Broecker 1991; Joos et al. 1991).

Before the iron hypothesis was introduced, the prevailing view of the control of primary production in the Southern Ocean was that relatively weak vertical stability and strong winds combined to mix the upper ocean and its resident phytoplankton assemblages over depth intervals that resulted in a low time-integrated irradiance for the cells (e.g. Holm-Hansen et al. 1977;

Smith and Nelson 1985). Both the generally low productivity of the open waters of the Antarctic Circumpolar Current (ACC) and the occurrence of phytoplankton blooms in the marginal ice zone were interpreted as resulting from the balance between vertical light penetration and vertical mixing, in accordance with the "critical depth" concept first quantified by Sverdrup (1953). By this reasoning, the productivity of most of the Southern Ocean is low (even in summer) because the depth of the surface mixed layer (Z_m) approaches or exceeds the Sverdrup critical depth (Z_c), which is a function of the solar irradiance at the sea surface and the clarity of the water. Ice-edge phytoplankton blooms are permitted to develop when stabilization of the upper 20–50 m by meltwater from the receding ice diminishes Z_m to significantly less than Z_c (Smith and Nelson 1985; Wilson et al. 1986). If this view is correct, then the large, open-ocean areas of the ACC, where most of the nutrient-rich but unproductive surface waters are found, would be expected to show little or no growth response to fertilization with Fe or other micronutrients.

It has been difficult to test the critical-depth hypothesis rigorously in the Southern Ocean because of uncertainties in the numerical value of Z_c . These uncertainties have been attributed both to the approximations and assumptions used in the original formulation of the critical-depth equations and to selection of inappropriate values for certain terms (Kaiser and Schultz 1978; Smetacek and Passow 1990). In this paper we use recent optical and physiological information to develop a reformulation of Sverdrup's equations for Z_c , which we believe is subject to considerably less uncertainty. We apply this reformulated equation for Z_c to our own data from ice-edge phytoplankton blooms in the Weddell and Ross Seas and extend it to consider the control of primary production in open-water areas of the ACC.

A reformulation of Sverdrup's critical-depth equation

Starting from assumptions that appear to be valid for the polar oceans and for temperate waters in late winter, Sverdrup (1953)

defined the "critical depth" as that depth at which the vertically integrated rates of photosynthesis and respiration by the plankton were equal. Thus when $Z_m > Z_c$, the vertically integrated rate of phytoplankton photosynthesis is less than that needed to keep pace with respiratory consumption of organic C, and net increase of planktonic biomass cannot occur. Sverdrup showed that the value of Z_c depends on the time-averaged irradiance at the ocean surface (\bar{I}_0), the light attenuation coefficient of the surface water (K), and the irradiance at the photo-compensation depth (I_c). A simple rearrangement of terms in Sverdrup's equation 6 yields

$$Z_c = (0.18\bar{I}_0/KI_c) [1 - \exp(-KZ_c)] \quad (1)$$

where the 0.18 factor is a correction term that attempts to correct for surface reflectance (assumed to be 8%) and the absorption of ultraviolet, infrared, and far-red wavelengths in the upper few meters (assumed to be 80%). Because of the inverse proportionality between K and Z_c in Eq. 1, the exponential term depends only on \bar{I}_0 , and for all \bar{I}_0 values $> 100 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (i.e. all realistic \bar{I}_0 values for spring and summer), this term ranges from 0.98 to 1.0. Thus, to a good approximation Eq. 1 can be simplified to

$$Z_c = 0.18\bar{I}_0/KI_c \quad (2)$$

Although Sverdrup conceptually included zooplankton respiration in the I_c term (his equations 2 and 3), the numerical value of I_c was based on experimental data from phytoplankton cultures. That method of estimating I_c has been used in most subsequent applications of the critical-depth equations, and for many planktonic algae it is between 3 and $6 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (e.g. Raymont 1980). If an I_c value of $5 \mu\text{mol m}^{-2} \text{ s}^{-1}$ is used, \bar{I}_0 is expressed in $\mu\text{mol m}^{-2} \text{ s}^{-1}$ and K (m^{-1}), the value of Z_c (in m) can be calculated as

$$Z_c = 0.18\bar{I}_0/5K = 0.036\bar{I}_0/K \quad (3)$$

However, the value of Z_c calculated from Eq. 1–3 has been subject to large uncertainties for the following reasons. The time interval over which \bar{I}_0 is averaged has generally been unspecified. In the original

formulation I_0 was taken as total solar irradiance, rather than photosynthetically active radiation (PAR). Calculation of a photosynthetic-respiration balance on the basis of I_c values determined for phytoplankton cultures has meant that losses of photosynthetically produced organic C due to processes other than phytoplankton respiration (e.g. sinking, grazing, release of dissolved organic material) have not been considered. The 0.18 correction factor (i.e. eliminating 82% of the irradiance present just above the ocean surface because of surface reflectance and absorption in the upper few meters) was based on total solar energy and is much more extreme than can be justified optically for PAR. The 0.18 term has, nonetheless, been applied to PAR in virtually all calculations to estimate Z_c from field data (see Raymont 1980; Tett and Edwards 1984). It is clear that values of ~ 0.2 , applied to PAR rather than to total irradiance, have been necessary to give reasonable Z_c values, but we suggest that this is because a culture-derived value for I_c significantly underestimates this term in a mixed plankton assemblage.

Thus Eq. 1–3, as normally applied, contain two large compensating errors (an underestimate of I_c and an overestimate of the optical correction term for PAR) that were not part of their original derivation. The compensatory nature of these errors has resulted in reasonable values for Z_c , and so most estimates of the timing of spring blooms in temperate and subpolar regions based on critical-depth calculations have been reasonably good (see Raymont 1980; Tett and Edwards 1984). However, in spring Z_c is generally increasing rapidly with time due to the effects of the increasing daylength and solar elevation on \bar{I}_0 while Z_m is decreasing rapidly due to establishment of the seasonal thermocline (e.g. Pingree et al. 1976; Rey 1981; Sambrotto et al. 1986). Thus, even large uncertainties in Z_c would produce little uncertainty in the time at which Z_c first exceeds Z_m because these two depths are changing rapidly in opposite directions. Attempts to apply Z_c calculations spatially to observed distributions of K and Z_m within a given season are much more sensitive to uncertainty in the terms used to calculate Z_c , and in the Southern Ocean

only very broad generalizations about spatial relationships between Z_c and Z_m have been suggested (e.g. Smith and Nelson 1985; Jacques 1989).

Our reformulation of the equation for Z_c maintains the same form as that originally used by Sverdrup and is based on the same logic and mathematics (i.e. the original 1953 derivation of the critical-depth equation has not been altered in any way). We have simply substituted terms that are more consistent with present-day optical and biological data, with the purpose of eliminating or significantly reducing the sources of error listed above. Taking these in order, the changes we propose in a reformulated equation for Z_c follow.

For the time-averaged surface irradiance, \bar{I}_0 —We propose to use the mean PAR (400–700 nm) for the 24-h period during which observations are made. We believe it is obvious that using PAR is more appropriate than total energy, but the 24-h averaging period may or may not be applicable outside of polar regions. The 24-h period appears to be correct for polar systems because these areas typically receive at least some sunlight throughout the 24-h day in summer, and the specific growth rates of polar phytoplankton are generally <1 division d^{-1} (e.g. Nelson and Smith 1986; Smith and Nelson 1990). Thus, while a 24-h averaging period may have little meaning for a population that can undergo one to several division cycles between sunrise and sunset, the slower growing planktonic algae in polar oceans must integrate at least 24 h of light during each division cycle. Thus, we propose the following expression for \bar{I}_0 :

$$\bar{I}_0 (\mu\text{mol m}^{-2} \text{ s}^{-1}) = 11.57 \sum I_0 (\text{mol m}^{-2} \text{ d}^{-1}) \quad (4)$$

where $\sum I_0$ is the time-integrated PAR for a 24-h period (in $\text{mol m}^{-2} \text{ d}^{-1}$) and 11.57 converts $\text{mol m}^{-2} \text{ d}^{-1}$ to $\mu\text{mol m}^{-2} \text{ s}^{-1}$.

For the irradiance at the photocompensation depth, I_c —Clearly some value $>5 \mu\text{mol m}^{-2} \text{ s}^{-1}$ is required if the natural losses that result from grazing, sinking, release of dissolved organic C within the surface layer, etc. are to be accounted for in the calculation of Z_c (e.g. Smetacek and Passow 1990). Per-

ry and Marra (unpubl.) have calculated a “net photocompensation irradiance” (defined as the value of PAR that results in a net phytoplankton growth rate of zero in the presence of most naturally occurring losses) for natural plankton assemblages in the Gulf of Maine. Their values ranged from ~ 30 to $40 \mu\text{mol m}^{-2} \text{ s}^{-1}$. In concept, this net photocompensation irradiance (I_n) is much more realistic than an I_c value from pure algal cultures for calculating Z_c . Although site-specific values for I_n would be preferable, and indeed may be necessary to evaluate accurately the relationship between Z_c and Z_m in a given area at a given time, in the absence of other data we propose to use Perry and Marra’s average value from the Gulf of Maine ($35 \mu\text{mol m}^{-2} \text{ s}^{-1}$) as a first approximation. The use of an I_n value transposed from the Gulf of Maine is probably the greatest source of uncertainty in our reformulated equation for Z_c , and data from the Southern Ocean are needed to reduce or eliminate this uncertainty. Also, because Perry and Marra estimated I_n from flow-cytometric measurements before and after incubation experiments, sinking losses are not included and I_n represents a minimum value for the I_c term defined by Sverdrup (1953). However, we believe it is a much more realistic quantification of the photosynthesis-respiration balance of the upper water column than a culture-derived I_c .

For the 0.18 correction factor for reflectance and near-surface absorbance—The reflectance of global (i.e. direct + diffuse) PAR at the ocean surface averages 7% at subpolar latitudes in summer over a wide range of wind conditions and sea states (Campbell and Aarup 1989). In addition, PAR with wavelengths from 650 to 700 nm is absorbed quite strongly by seawater in the upper few meters of the ocean. This effect causes the attenuation coefficient for PAR to decrease with depth due to the changing spectral composition, and it represents a $\sim 15\%$ loss of PAR (e.g. Jerlov 1976). It thus seems necessary to reduce $\sum I_0$ by a total of $\sim 20\%$ to account for surface reflectance of global PAR and near-surface absorbance of >650 nm PAR, but an 82% reduction is far too great. We therefore propose an optical correction factor of 0.8 rather than 0.18.

When the above substitutions are made, when ΣI_0 is expressed in $\text{mol m}^{-2} \text{d}^{-1}$ and K is explicitly noted as K_{PAR} (in m^{-1}), the equation for Z_c becomes

$$Z_c = 0.8 \times 11.57 \times \Sigma I_0 / 35 K_{\text{PAR}} \quad (5)$$

or simply

$$Z_c = \Sigma I_0 / 3.78 K_{\text{PAR}} \quad (6)$$

Application to ice-edge phytoplankton blooms

We have previously interpreted the very close spatial association often found between phytoplankton biomass and meltwater in the marginal ice zone by invoking the critical-depth concept (Smith and Nelson 1985; Wilson et al. 1986). By that interpretation, stabilization of the upper water by low-salinity meltwater diminished Z_m to $\ll Z_c$ and permits an ice-edge phytoplankton bloom to develop. However, the uncertainties in Z_c described above have precluded the reporting of calculated Z_c values or of spatial comparisons with Z_m in the ice-edge zone. Martin et al. (1990) have proposed that their iron hypothesis can also explain the meltwater-phytoplankton association. They have suggested that airborne dust, rich in Fe, collects on the ice throughout the winter and is released as the ice melts in spring and summer, causing localized fertilization and a phytoplankton bloom. Data from the ice edge of the western Ross Sea (Smith and Nelson 1985; Martin et al. 1990) are consistent with either hypothesis; indeed, both processes (meltwater-induced stratification and Fe enrichment) must occur simultaneously if meltwater is a significant source of Fe.

Figure 1 presents vertical sections of density and chlorophyll in the ice-edge zone of the Weddell Sea in spring 1983 (Nelson et al. 1987) and the Ross Sea in summer 1991, with the Z_c we calculate from Eq. 6 superimposed on the density sections. Both Z_c and Z_m were between 100 and 150 m seaward of the meltwater lens and bloom in the Weddell Sea (Fig. 1a), but Z_c shoaled to <30 m within the core of the bloom as a result of higher values of K_{PAR} in the high-chlorophyll water. Under these conditions Z_c was actually $<Z_m$, even though meltwa-

ter had reduced Z_m to ~ 50 m. This relationship indicates that the irradiance-mixing regime in the vicinity of the melting ice is favorable for the *initiation* of a bloom, in the sense that when the water is relatively free of chlorophyll and K_{PAR} is low, Z_c would be $\gg Z_m$, but it suggests that the blooms also may be self-limiting because, as phytoplankton biomass accumulates and the resulting turbidity increases, Z_c becomes about equal to (and perhaps less than) Z_m .

Chlorophyll concentrations in the southern Ross Sea in January 1990 (Fig. 1d) were generally higher than those near the Weddell Sea ice edge in spring 1983 (Fig. 1b), resulting in Z_c values that were almost always <50 m, and at some locations were <20 m (Fig. 1c). Strong stabilization of the upper 20–25 m by meltwater near the receding pack ice reduced Z_m to $<Z_c$ in the marginal ice zone, but in the rest of the region Z_m was about equal to, and in places $>Z_c$. The entire region shown in Fig. 1c and d had been traversed by the receding ice during the previous 2 months (Nelson et al. 1991), and in mid- to late summer it is common to see persistent meltwater stabilization of the upper water at considerable distances from the ice in areas where surface currents are weak (e.g. Nelson et al. 1989; Muench et al. in press). In the Ross Sea in 1990 there was a stable surface layer 30–50 m deep extending at least 500 km seaward from the ice edge and reasonably high surface chlorophyll concentrations throughout the region (Fig. 1c,d). However, in January only the strongly stratified surface waters in the immediate vicinity of the ice edge produced a Z_m/Z_c relationship favorable to continued net increase in phytoplankton biomass. Thus, the Ross Sea seems to present another case in which stabilization by meltwater produces favorable irradiance-mixing conditions for the initiation of phytoplankton growth ($Z_m \ll Z_c$ when chlorophyll is low and the water clear), but phytoplankton biomass can become self-limiting when chlorophyll concentrations increase to levels that reduce Z_c to approximately Z_m (Fig. 1c).

Fe enrichment experiments were performed near the eastern and western ends of the transect shown in Fig. 1c and d (Mar-

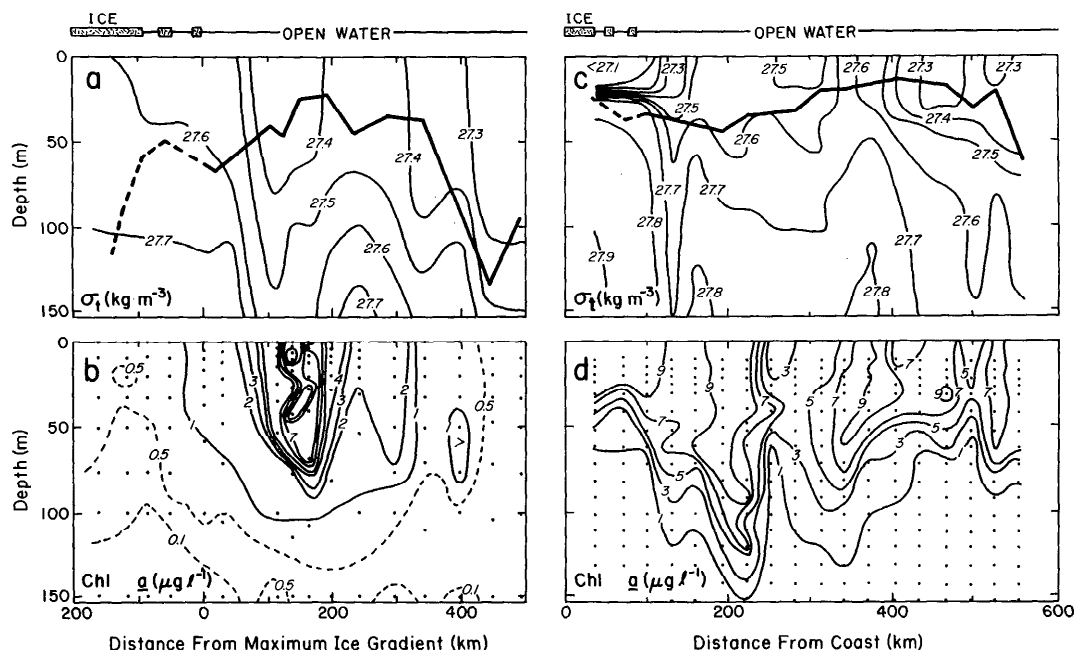


Fig. 1. Vertical sections of density (σ_t) and Chl *a* in the marginal ice zones of the Weddell Sea (a, b) in spring and the Ross Sea (c, d) in summer. All sections are oriented perpendicular to the main ice edge. The critical depth (Z_c) calculated from shipboard irradiance and attenuation coefficient data with Eq. 6 (bold line) is superimposed on the density sections. The dashed portion of the Z_c line denotes ice-covered waters, where productivity is strongly limited by light and the calculated Z_c represents the value that would pertain in the absence of ice. (Panels a and b redrawn from Nelson et al. 1987.)

tin et al. 1990). No effect of added Fe was noted in the water strongly stabilized by recent ice-melt in the west, but a clear response to added Fe occurred in the surface water ~ 500 km east of the ice edge. It thus appears likely that melting pack ice in the western Ross Sea stimulates phytoplankton growth by simultaneously stabilizing the upper 20–30 m and providing Fe.

The fact that Z_c apparently does not greatly exceed Z_m in well-developed ice-edge phytoplankton blooms in the Southern Ocean may help to explain the low specific growth rates of phytoplankton observed in these blooms. In ice-edge blooms in both the Ross and Weddell Seas, several independent estimates of specific growth rates of phytoplankton are in good agreement, and all indicate rates that very seldom exceed 0.3 divisions d^{-1} and are more typically <0.2 divisions d^{-1} (Wilson et al. 1986; Nelson and Smith 1986; Smith and Nelson 1990). The temperature-controlled upper limit on specific growth rates of phytoplank-

ton at $0 \pm 1^\circ\text{C}$ seems to be ~ 0.8 divisions d^{-1} (Eppley 1972), but rates this high are not approached in ice-edge blooms in either the Ross Sea or the Weddell Sea. The relationship between Z_c and Z_m in both systems (Fig. 1) appears to be such that growth at anywhere near maximum rates is prevented by light limitation in the relatively turbid surface waters that develop in ice-edge blooms.

Application to open waters of the ACC

The ice edge constitutes a specialized environment in the Southern Ocean, where local stabilization of the upper water by meltwater permits high phytoplankton biomass to accumulate. The high-nutrient, low-productivity condition that has generated interest in possible micronutrient fertilization experiments in the Southern Ocean (e.g. Martin et al. 1990) pertains over the much larger open-ocean areas of the ACC. These areas are not directly influenced by meltwater stabilization and are typically well mixed

to depths of 50–75 m in summer (e.g. Foster and Middleton 1984) and > 100 m in winter (Muench et al. 1990). This deeper mixing has been believed to prevent high productivity in most of the ACC in accordance with the Sverdrup critical-depth concept (e.g. Smith and Nelson 1985; Smith and Sakshaug 1990). However, it has been suggested that critical-depth–mixing-depth relationships in these open waters may generally be favorable to phytoplankton blooms for a 2–3-month period in summer (Jacques 1989), and our own experience has been that previous formulations of the critical-depth equation (i.e. Eq. 1–3) have been subject to too much uncertainty to permit useful spatial analyses (Smith and Nelson 1985; Wilson et al. 1986).

We believe that reformulation of the critical-depth calculation (Eq. 6), although still subject to uncertainty resulting from the lack of information on I_n values in the Southern Ocean, reduces the overall uncertainty of the calculation to a point that permits useful spatial comparisons to be made and general first-order biological conclusions to be drawn for the marginal ice zone (*see above*). Similar calculations can be applied to the open-ocean portions of the ACC to evaluate the vertical light penetration–mixing regime and to estimate the potential of these waters to support phytoplankton blooms if all (macro- and micro-) nutrients were sufficient. Here, we consider the Weddell–Scotia Confluence region and the eastern Scotia Sea during two periods for which data on ΣI_0 and Z_m are available: winter (June–August) and late spring through midsummer (November–February).

Winter—In June and July the Weddell–Scotia Confluence region is typically well mixed to depths > 100 m, even at the ice edge, and to ~150 m in areas > 200 km from the ice (Muench et al. 1990; Fig. 2a). By August localized areas of stabilization of the upper 50 m can be found, apparently as a result of accelerated ice melt by warm-core eddies generated at the Polar Front, but in areas unaffected by eddies the upper water remains well mixed to > 100 m. Due to short photoperiods, low solar elevations, and generally cloudy conditions, the integrated daily irradiance is low. For example, from

9 June to 14 August 1988, ΣI_0 ranged from 0.72 to 26.5 mol m⁻² d⁻¹ with a mean of 5.5 and a standard deviation of 4.9. During this period both chlorophyll concentrations and K_{PAR} were low, averaging 0.12 µg liter⁻¹ and 0.055 m⁻¹, respectively (Cota et al. in prep.). Thus, according to Eq. 6 the mean Z_c was 26.5 m, or <25% of the average Z_m . Also, at the low mean surface irradiance that characterized this region in winter, the exponential term in Eq. 1 diminishes from its spring–summer value of ~1.0 to 0.77, which would further reduce the mean Z_c to 20.3 m. However, to illustrate our finding that even the most favorable winter irradiance–mixing regime should be strongly limiting to productivity, we have calculated maximum Z_c values on the assumption of maximum clarity ($K_{PAR} = 0.044$ m⁻¹; Jerlov 1976) and have not adjusted Z_c downward by the exponential term.

Using these optimal assumptions, we find that the mean critical depth in winter calculated with Eq. 6 is 33.2 m (SD = 29.4). During the 1–14 August period, when some localized meltwater lenses were observed in the ice-edge zone (Muench et al. 1990), the mean ΣI_0 had increased to 10.1 mol m⁻² d⁻¹ (SD = 6.2), resulting in a calculated mean Z_c of 60.7 m (SD = 37.2). Thus the entire region seems to be mixed beyond the critical depth in winter, with the possible exception of areas where localized, eddy-driven ice melt decreases Z_m near the edge of the pack ice in late winter. This finding is consistent with the available data on Antarctic winter productivity (Brightman and Smith 1989, Cota et al. in prep.) and biogenic particle flux (Wefer et al. 1982; Fischer et al. 1988), which show very low rates through the June–August period. Persistence of species through several months of unfavorable light–mixing conditions in winter appears to result from a number of dark-survival strategies that enable cells to lower their respiratory rates (e.g. Smayda and Mitchell-Innes 1974; Hargraves and French 1983; Geider et al. 1986), and these physiological adaptations are not accounted for in either the original derivation of the equation for Z_c or our reformulation.

Late spring through midsummer—In January and early February the surface waters

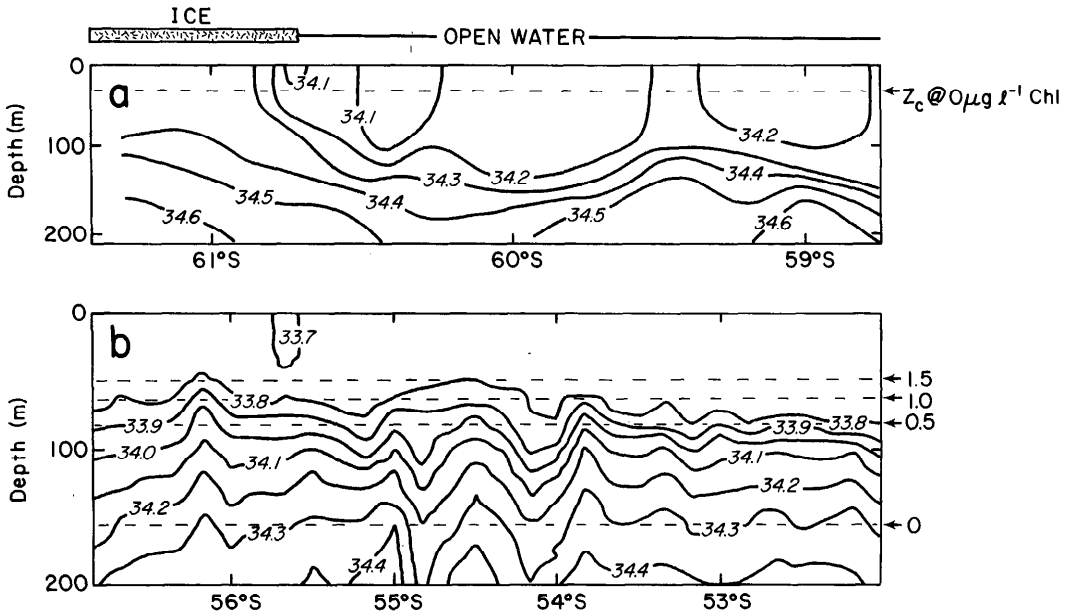


Fig. 2. [a.] Vertical section of salinity in the Weddell-Scotia Confluence region in winter (redrawn from Muench et al. 1990), showing the maximum Z_c value calculated from Eq. 6 for the mean daily irradiance measured in that region in winter ($5.5 \text{ mol m}^{-2} \text{ d}^{-1}$). [b.] Vertical section of salinity in the eastern Scotia Sea in summer (redrawn from Foster and Middleton 1984), showing the Z_c values calculated from Eq. 6 and 7 using Chl *a* concentrations of 0, 0.5, 1.0, and 1.5 $\mu\text{g liter}^{-1}$ and the mean daily irradiance measured in that region in late spring ($25.7 \text{ mol m}^{-2} \text{ d}^{-1}$).

of the Weddell-Scotia Confluence and eastern Scotia Sea are typically mixed to depths of 50–75 m, except in areas influenced by meltwater (Foster and Middleton 1984; Fig. 2b). The maximum daily irradiance for cloudless skies at 60°S in January would be $\sim 60 \text{ mol m}^{-2} \text{ d}^{-1}$ (Campbell and Aarup 1989), but on most days heavy cloud cover reduces ΣI_0 to less than half of its clear-sky value (e.g. Bishop and Rossow 1991). A record of integrated daily irradiance that we obtained in the Weddell-Scotia Confluence region over the 1 November–3 December 1983 period (a time that is seasonally symmetrical with January with respect to solar irradiance) shows a mean ΣI_0 of $25.7 \text{ mol m}^{-2} \text{ d}^{-1}$ (SD = 11.6). The highest daily ΣI_0 recorded during this period was $57.5 \text{ mol m}^{-2} \text{ d}^{-1}$, which is in good agreement with the maximum value predicted for this latitude and date (Campbell and Aarup 1989).

Critical-depth calculations for summer must take into account the dependence of K_{PAR} on the chlorophyll content of the sur-

face layer. The empirical relationship first proposed by Riley (1956),

$$K = 0.040 + 0.0088(\text{Chl}) + 0.054(\text{Chl})^{2/3}, \quad (7)$$

can be applied reasonably well to the dependence of K_{par} on chlorophyll for systems where most absorbance of irradiance is by water and chlorophyll (e.g. Parsons et al. 1977). This seems to be the case in the Weddell-Scotia Confluence area in late spring, where there is relatively little detrital or abiogenic particulate matter in the surface layer (Nelson et al. 1987). Combining Eq. 6 and 7 yields the relationship between Z_c and chlorophyll shown in Fig. 3a. A noteworthy aspect of this relationship is that the first few tenths of a microgram of chlorophyll per liter cause Z_c to shoal considerably from its value in the clearest (i.e. chlorophyll-free) ocean water, but that the dependence of Z_c on chlorophyll becomes much weaker at chlorophyll concentrations $> 2 \mu\text{g liter}^{-1}$.

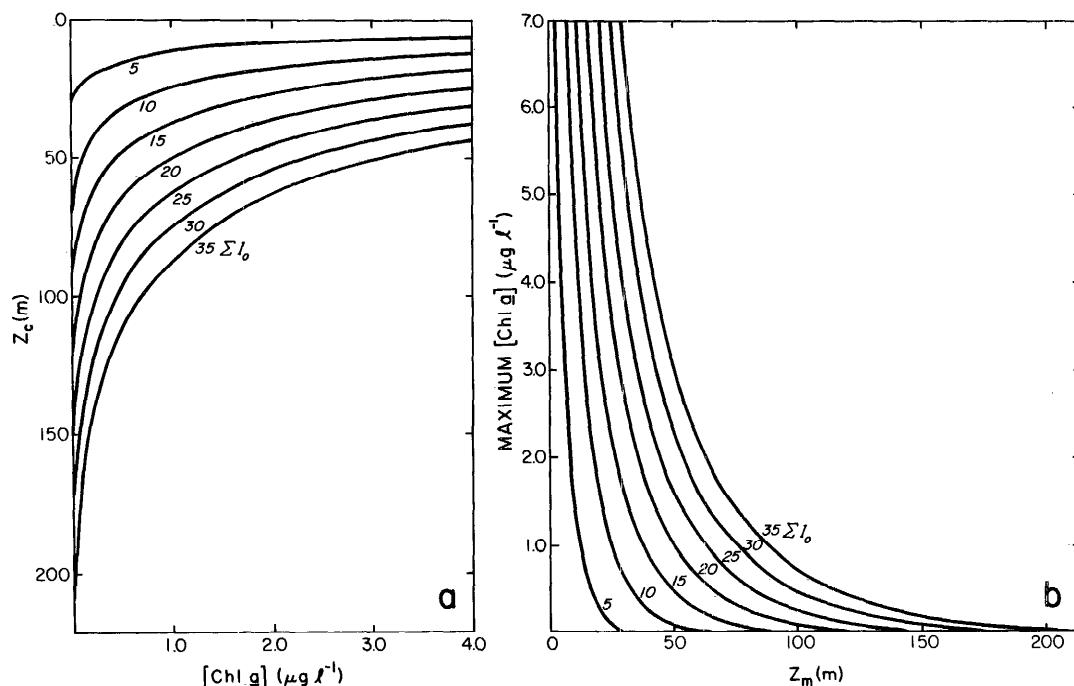


Fig. 3. [a.] Relationship between critical depth (Z_c), as calculated with Eq. 6 and 7, and mean chlorophyll concentration in the surface layer. [b.] Relationship between maximum sustainable chlorophyll concentration in the surface layer and the mixed-layer depth (Z_m), calculated with Eq. 6 and 7 and assuming that no increase in chlorophyll can be sustained unless $Z_m < Z_c$. In both panels the seven curves represent integrated daily irradiance values (ΣI_0 , in $Einst\ m^{-2}\ d^{-1}$) ranging from 5 to 35 $mol\ m^{-2}\ d^{-1}$ in steps of 5.

Figure 2b shows a salinity section through the eastern Scotia Sea in summer (Foster and Middleton 1984) in comparison with Z_c values calculated for a daily ΣI_0 of 25.7 $mol\ m^{-2}\ d^{-1}$ (the mean of our values for late spring 1983) at assumed chlorophyll concentrations of 0, 0.5, 1.0, and 1.5 $\mu g\ liter^{-1}$. It is apparent that, in the absence of chlorophyll, Z_c would significantly exceed Z_m throughout the region in spring and summer, but that Z_c and Z_m would become about equal at chlorophyll concentrations that range from 0.5 to 1.5 $\mu g\ liter^{-1}$, depending on Z_m . Thus, the open-ocean system is qualitatively similar to the ice-edge zone in summer; that is, the irradiance-mixing regime appears to be favorable for the initiation and early development of a phytoplankton bloom, but as chlorophyll increases in the surface layer, Z_c shoals. This makes any bloom self-limiting in the sense that above some chlorophyll concentration an unfavorable relationship between Z_c and Z_m

would prevent further increases in phytoplankton biomass. An important quantitative difference between open-water areas of the Scotia Sea and the marginal ice zone is that in the open ocean this self-limitation may keep chlorophyll levels below $\sim 1\ \mu g\ liter^{-1}$, where at the ice-edge concentrations of several micrograms per liter are both permitted (see Fig. 3) and observed (e.g. Smith and Nelson 1985; Nelson et al. 1987; see also Fig. 1).

The mathematical relationships shown in Fig. 3a can be expressed in plots of the maximum chlorophyll concentration in the surface layer predicted by the Z_c/Z_m relationship vs. Z_m (Fig. 3b). This relationship indicates that for a given mean daily irradiance the maximum chlorophyll concentration decreases quasi-exponentially with increasing Z_m . Observed chlorophyll concentrations could fall on or below (but not above) the quasi-exponential curve. A relationship like that shown in Fig. 3b has also

been predicted from a growth-loss model and shown empirically from a compilation of several Southern Ocean data sets (Mitchell and Holm-Hansen 1991). Thus it appears that critical-depth-mixing-depth relationships control the maximum chlorophyll concentrations that can be realized in Southern Ocean surface waters in summer and that in open-ocean areas this maximum may be $\sim 1 \mu\text{g liter}^{-1}$. Chlorophyll data collected in the Scotia Sea concurrently with the salinity section in Fig. 2b tend to support this conclusion; the highest observed chlorophyll concentrations were $\sim 1.5 \mu\text{g liter}^{-1}$ in the southern Scotia Sea, and chlorophyll decreased northward to $< 0.6 \mu\text{g liter}^{-1}$ as Z_m increased (Biggs et al. 1982).

Comparison with large-scale chlorophyll patterns

Figure 3b predicts that, as the depth of the wind-mixed surface layer increases, the vertical relationship between Z_m and Z_c should cause the maximum achievable chlorophyll concentration to decrease. Figures 2b and 3b both indicate that for the daily irradiance levels and mixing depths that characterize the Scotia Sea in late spring and summer ($\sim 25 \mu\text{mol m}^{-2} \text{d}^{-1}$ and 50–75 m), this maximum should be $\sim 1 \mu\text{g liter}^{-1}$. One implication of these relationships is that areas in the Southern Ocean that have summer mixed layers deeper than those in the Scotia Sea should also have lower maximum chlorophyll concentrations. (Note in Fig. 2b that as Z_m approaches 75 m in the northern portion of the section, $Z_c = Z_m$ at a chlorophyll concentration of $\sim 0.5 \mu\text{g liter}^{-1}$.) There is now large-scale spatial information to suggest that high winds and low phytoplankton biomass do coincide. Satellite-derived composite distributions of annual mean winds show a zone in the Indian Ocean sector of the ACC between 50 and 60°S where the mean wind stress is significantly greater than that for the Southern Ocean as a whole; furthermore, this area of high winds is also one from which composite ocean-color images from the Nimbus 7 Coastal Zone Color Scanner (CZCS) show virtually no chlorophyll concentrations $> 0.6 \mu\text{g liter}^{-1}$ (Mitchell et al. 1991). If the greater

winds in that sector of the ACC produce a Z_m generally greater than that in the Scotia Sea, diminished chlorophyll levels would be predicted on the basis of Eq. 6 and 7.

These same CZCS composite images also provide some support for the hypothesis of Fe limitation in the Southern Ocean, in that they show areas immediately east (i.e. downwind) of South Africa, Australia, and Argentina where pigment concentrations are higher than those in most other areas of the ACC. These observed pigment distributions are consistent with the hypothesis that airborne dust from the continents provides an Fe source that stimulates phytoplankton growth. However, the critical-depth-mixing-depth relationships we describe here, and the low chlorophyll concentrations that typify areas of above-average winds in the ACC, suggest that vertical mixing sets a rather modest upper limit on the phytoplankton biomass that can be achieved even when all chemical and biological conditions are ideal for phytoplankton growth.

More detailed, site-specific, predictions of maximum achievable chlorophyll levels may be possible by refining the critical-depth calculations presented here. In particular, the predictions can be improved significantly by obtaining data on the "net photocompensation irradiance" (Perry and Marra (unpubl.) for various Southern Ocean locations. However, if the Z_c values we have calculated by applying Eq. 6 and 7 to Southern Ocean data are even approximately correct, they imply that primary production over the greater portion of the ACC region could be stimulated little, if at all, by micronutrient fertilization. We suspect that Sverdrup might have predicted such an outcome in 1953.

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