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Contribution to the Themed Section: 'Revisiting Sverdrup's Critical Depth Hypothesis' Original Article

Vertical mixing, critical depths, and phytoplankton growth in the Ross Sea

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Phytoplankton growth and biomass accumulation vary spatially and temporally in the Ross Sea, largely as a function of ice concentrations, vertical mixing depths, and iron concentrations. To assess the role of vertical mixing in bloom initiation, we used a high-resolution numerical model to estimate changes in mixed layer depths from October 1 through early December, the period where phytoplankton growth begins and biomass accumulates, and estimate critical depths for this period. Mixed layers in October ranged from the complete water column (>600 m) to ca. 200 m; over a 60-day period, the mixed layers decreased on average by 70%. Estimated critical depths were exceeded in October, but would allow growth to proceed in late October due to shoaling of mixed layer depths, consistent with the known onset of the spring bloom in the Ross Sea. We also analysed a series of stations sampled near the Ross Ice Shelf during January 2012. Mean vertical profiles for the stations indicated deep vertical mixing; mixed layer depths averaged 60 m and ranged up to 96 m. Chlorophyll concentrations within the mixed layer averaged $6.60 \mu\text{g l}^{-1}$, and the pigment contributions were dominated by *Phaeocystis antarctica*. We suggest that this mesoscale region near the ice shelf is elevated in phytoplankton biomass due to frequent mixing events that redistribute biomass to depth and replenish nutrients, which in turn are utilized by an assemblage capable of utilizing low mean irradiance levels. Thus, the deep mixed layers and high biomass concentrations represent growth over long periods under reduced mixing punctuated by short periods of deeper vertical mixing that redistribute biomass. Water column vertical mixing and phytoplankton biomass in the Ross Sea are consistent with the critical depth concept as originally proposed by Sverdrup.

Keywords: biomass, chlorophyll, irradiance, phytoplankton, Ross Sea, vertical mixing.

Introduction

Southern Ocean phytoplankton experience exceptionally large variations in physical forcing variables, such as irradiance, vertical water column stratification, and nutrient supply, and also have relatively low growth rates due to low temperatures. The classical concepts formalized by Sverdrup (1953) have long been applied to Southern Ocean phytoplankton (Mitchell and Holm-Hansen, 1991; Nelson and Smith, 1991), in that it has largely been assumed that vertical mixing is deep in winter, and mixed layers shoal as less saline water from ice melt and heat from increased solar irradiance in spring increases vertical stratification in spring and summer. These concepts have been questioned by Behrenfeld (2010), who suggested that blooms in the North Atlantic were regulated by the tight coupling between grazers and phytoplankton, as well as the

dilution effect due to increased vertical mixing in winter. This “dilution-recoupling” hypothesis was further supported by drifter data from the North Atlantic (Boss and Behrenfeld, 2010). Mahadevan *et al.* (2012) suggested that eddy-derived mesoscale variations in mixed layer depths provided a mosaic of environments in which phytoplankton growth proceeded, and thus generated a bloom in spring that preceded one derived from temperature-induced stratification. Behrenfeld (2010) largely used satellite data to support his argument, as there are few direct observations collected during the onset of spring blooms in any environment. This is especially true in the Southern Ocean and its most southerly seas, such as the Ross Sea, where thick ice cover makes it difficult for ships to sample during the winter–spring transition.

Assessments of the role of irradiance on phytoplankton growth have shown the importance of vertical mixing in the Southern Ocean. Mitchell and Holm-Hansen (1991) suggested that mixed layers >40 m precluded phytoplankton growth and accumulation in the West Antarctic Peninsula; Nelson and Smith (1991) calculated critical depths for the Ross Sea and concluded that the critical depth concept indeed was applicable in describing phytoplankton growth and biomass accumulation. Smith *et al.* (2000) combined data from a series of cruises with a large range of mixed layer depths (some with mixed layers >600 m) and confirmed the conclusion of Mitchell and Holm-Hansen (1991) that growth was largely restricted to locations where mixed layers were <40 m. This was strong circumstantial evidence of the validity of the critical depth concept, but none of these studies sampled during early spring or conducted a time series of plankton development. Hence, while a relationship between vertical mixing and phytoplankton was established, a complete test of the Sverdrup concepts was lacking.

The Ross Sea is a heterogeneous system that becomes nearly completely ice covered in winter, with ice growing to ca. 1 m in thickness. There are regions near the coast, such as in Terra Nova Bay and near the central Ross Ice Shelf, where intense winds blow ice away from the coast and reduce ice concentrations in small areas. These areas continue to produce ice due to the very low air temperatures (ca. -60°C); ice formation results in brine rejection, the sinking of which in turn drives deep vertical mixing. The spatial extent of such mixing is, however, unknown. Indeed, very few observations on the water column are available for the winter and early spring period, given the difficulty of gaining access to the region at that time.

The waters close to the Ross Ice Shelf are different from those over much of the rest of the continental shelf, in that they often exhibit deep mixed layers throughout the year. They also are the sites of large blooms of the haptophyte *Phaeocystis antarctica* (El-Sayed *et al.*, 1983). In other parts of the Ross Sea, *P. antarctica* blooms appear early in spring (ca. late October; Smith and Gordon, 1997) and reach very high biomass (up to $15\ \mu\text{g l}^{-1}$ chlorophyll) by mid-December, after which the colonial forms disappear rapidly from the water column (Smith *et al.*, 2011). After *Phaeocystis* biomass is reduced, diatoms often grow, occasionally reaching chlorophyll concentrations that are equal to those of the primary *Phaeocystis* bloom (Smith *et al.*, 2006, 2011). The presence of *Phaeocystis* near the ice shelf is unusual, but also is quite predictable.

We present data from two sets of experiments. The first is the result of a model of Ross Sea circulation (Dinniman *et al.*, 2003, 2011) that accurately represents the essential physical processes on the continental shelf at a resolution that is relevant to phytoplankton growth and accumulation. The second is a set of measurements taken near the Ross Ice Shelf where deep mixed layers were detected along with enhanced concentrations of phytoplankton biomass. We use both of these to suggest that the concepts developed by Sverdrup (1953) indeed are applicable to the Ross Sea (and by extension, to much of the Southern Ocean), and to suggest a mechanism by which extensive accumulations of phytoplankton biomass can accumulate in the deep mixed layer despite the likely irradiance limitation.

Material and methods

Numerical model

The numerical model uses an implementation of the Regional Ocean Modeling System (Haidvogel *et al.*, 2008) for the Ross Sea

(Dinniman *et al.*, 2003, 2011). The circulation model uses a 5-km horizontal grid spacing with 24 terrain-following vertical layers, and its domain extends from 67.5°S to under the Ross Ice Shelf. The model includes a dynamic sea ice model (Budgell, 2005) that prognostically calculates sea ice concentration and thickness

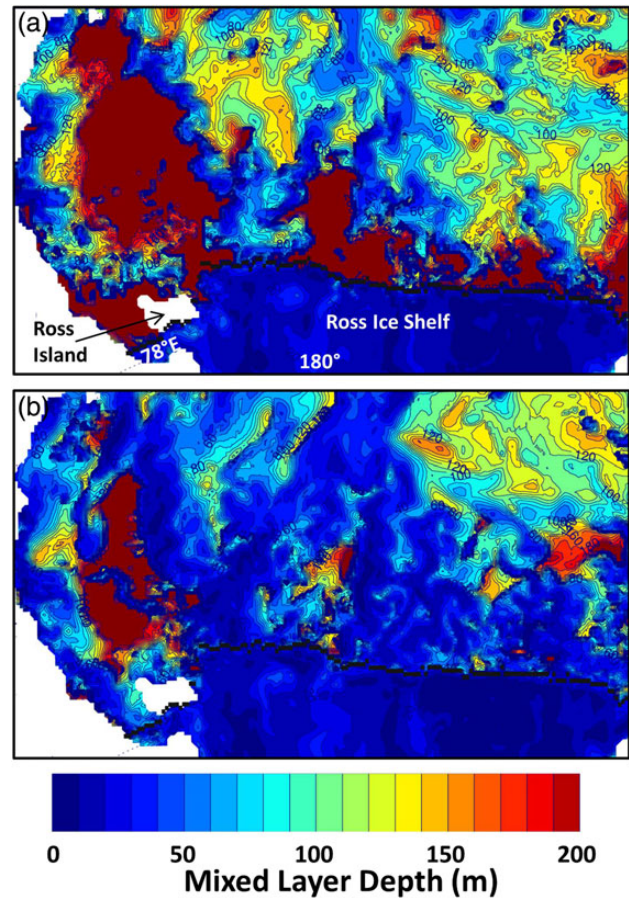


Figure 1. Modelled spatial distributions of the depth of mixing (m) in the Ross Sea from (a) October 1 and (b) November 27.

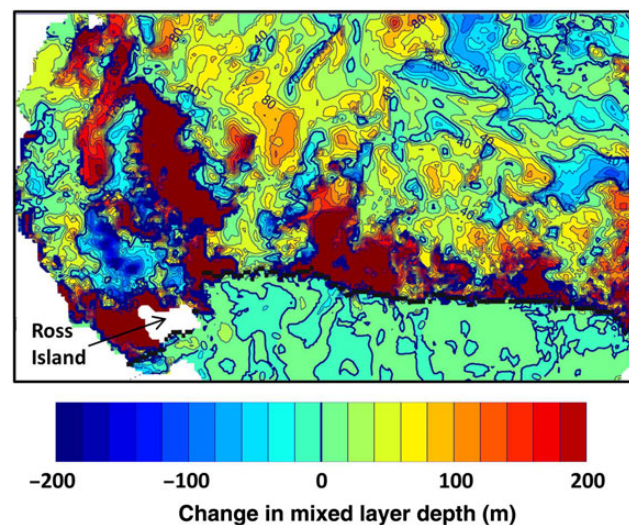


Figure 2. Modelled changes in the mixed layer depth between October 1 and November 27.

(Stern *et al.*, 2013) and accurately depicts circulation, shelf-water formation, and ice distribution (Dinniman *et al.*, 2007, 2011; Smith *et al.*, 2014a). Winds and air temperatures were taken every 6 h from the ERA-Interim (Dee *et al.*, 2011). The model also simulates the mechanical and thermodynamic interactions between the Ross Ice Shelf and the waters below (Holland and Jenkins, 1999; Dinniman *et al.*, 2011). Ocean tides are included. Mixed layers were derived from October 1 through November 27 at 2-week intervals. Mixed layers are defined by a change in σ_t of 0.01 kg m^{-3} from a stable surface layer (Thompson and Fine, 2003), as were observational mixed layers (see below).

Observations

Observations in the Ross Sea were collected as part of Processes Regulating Iron Supply at the Mesoscale (PRISM) in January–February 2012 from the *R/VIB Nathaniel B. Palmer* cruise NBP12-01. Hydrographic information was obtained using a Seabird 911+ CTD that was fitted with a WETLabs fluorometer and SeaTech transmissometer. Mixed layer depths were determined as with the model; that is, changes in σ_t from the stable surface layer (generally from 10 m) of 0.01 kg m^{-3} (Thompson and Fine, 2003; Sedwick *et al.*, 2011; Smith *et al.*, 2011, 2013). Kaufman *et al.* (2014) compared a number of independent methods of determining mixed layer depths and found no substantial difference among them, and also used a 0.01 kg m^{-3} threshold. Irradiance data (both surface and

submarine) were measured using BioSpherical Instruments quantum sensors. Water was collected from 12 depths in the upper 150 m for nutrients, phytoplankton biomass (chlorophyll *a*,

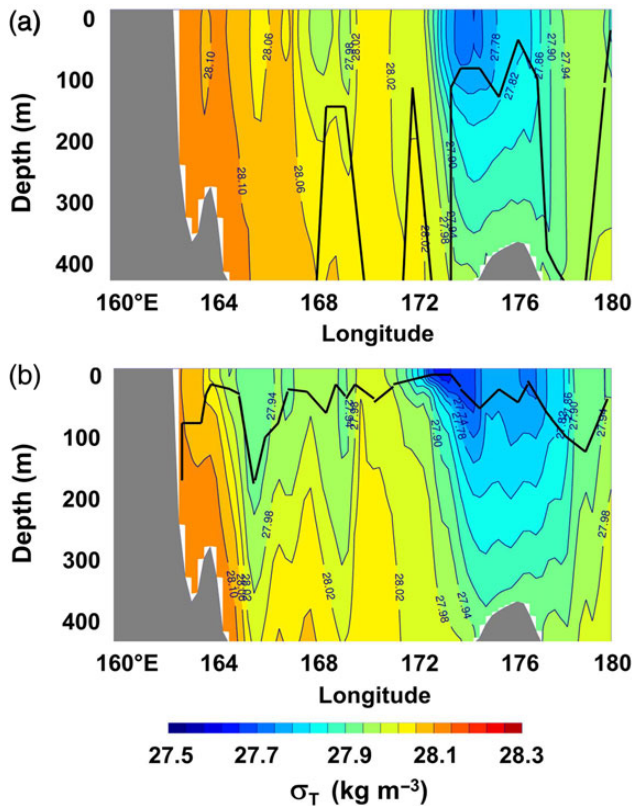


Figure 3. Modelled density distributions from the coast of Victoria Land to 180° along 77°S on (a) October 1 and (b) November 27. The mixed layer depth is indicated by the solid black line. Critical depths in October were 27 m, assuming an $\sum E_o$ of $5 \text{ mol photons m}^{-2} \text{ d}^{-1}$ and a $K_{\text{PAR}} = 0.048 \text{ m}^{-1}$, and in late November equalled 218 m, when $\sum E_o$ was assumed to increase to $40 \text{ mol photons m}^{-2} \text{ d}^{-1}$.

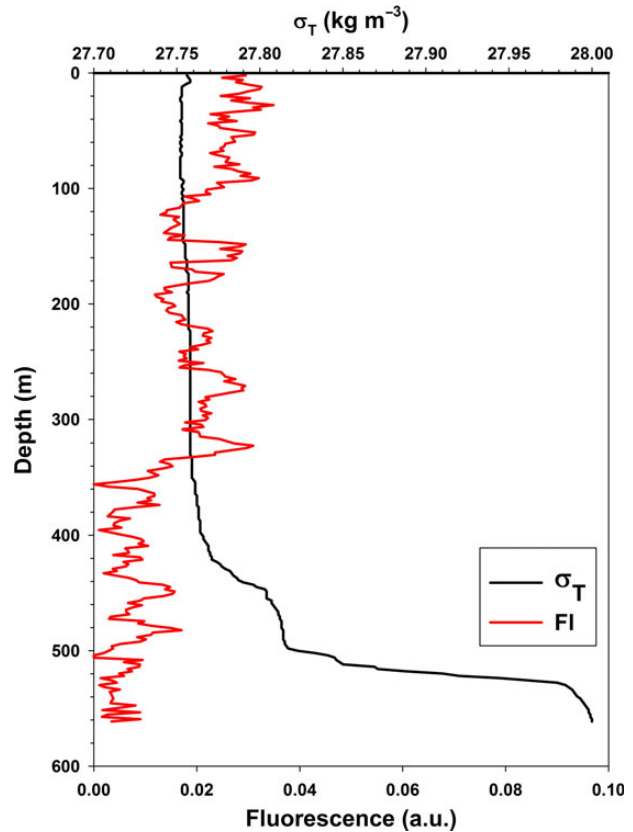


Figure 4. Vertical distribution of density (σ_t) and fluorescence in the entire water column ($z = 561 \text{ m}$) at St. 12 (occupied on 27 October 1996; 78.02°S , 175.91°E) within 20 km of the Ross Ice Shelf.

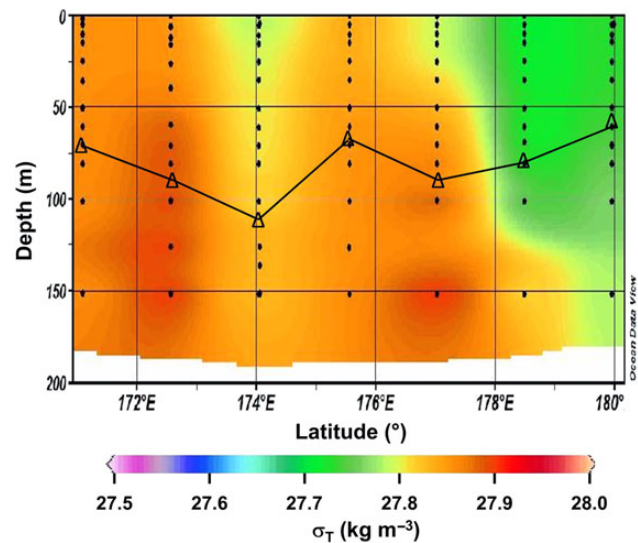


Figure 5. Distribution of density (σ_t) along 77°S on 16–17 November 2006 (Smith *et al.*, 2013). Mixed layer depths indicated by triangles and solid line.

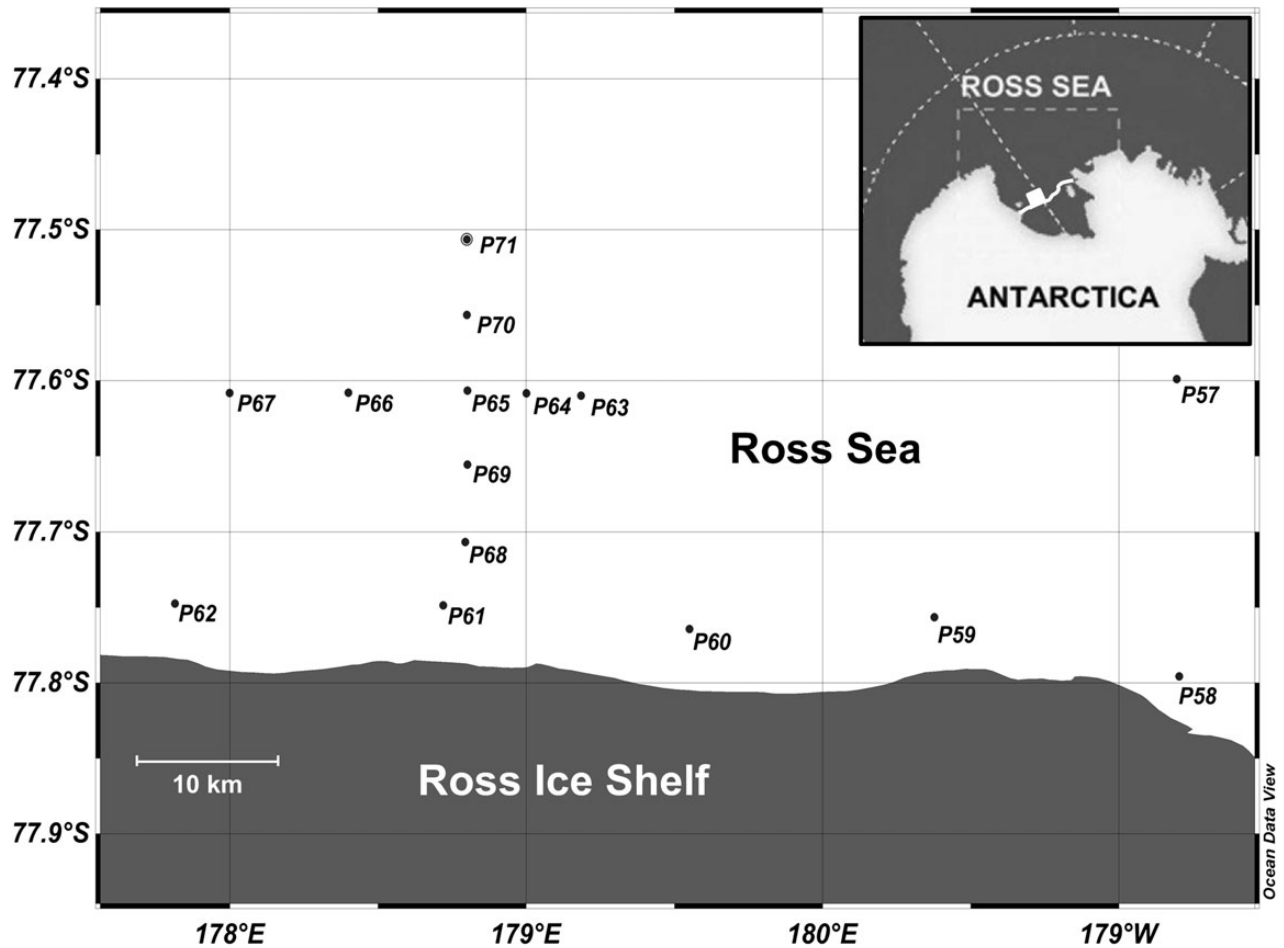


Figure 6. Location of the stations occupied near the Ross Ice Shelf in January 2012 during *NBP12-01*. White square in inset shows the location of the PRISM ice shelf stations.

Table 1. Calculated critical depths [from Equation (1)] and measured euphotic zone (1% isolume) depths, mixed layer depths, and mean mixed layer chlorophyll concentrations for PRISM stations located near the Ross Ice Shelf.

Station number	Mixed layer depth (m)	Euphotic zone depth (m)	Critical depth (m)	Mixed layer chlorophyll concentration ($\mu\text{g L}^{-1}$)
57	39	28	32	8.71
58	45	25	29	8.22
59	42	29	33	5.67
60	91	29	33	6.00
61	51	30	35	7.38
62	47	29	33	4.97
63	54	25	29	7.79
64	70	25	29	6.26
65	93	26	30	5.81
66	58	26	30	6.24
67	36	31	36	3.53
68	96	30	35	6.41
69	79	29	33	8.69
70	54	28	32	8.30
71	47	31	36	5.07
Mean \pm SD	60.1 \pm 20.5	28.1 \pm 2.15	32.2 \pm 2.47	6.60 \pm 1.53

Surface irradiance assumed to be 20 mol photons $\text{m}^{-2} \text{d}^{-1}$.

Table 2. Mean and SD of oceanographic variables at stations near the Ross Ice Shelf ($n = 15$).

Variable	Mean \pm SD
Mixed layer depth (m)	60.1 \pm 20.5
Euphotic zone depth (m)	28.1 \pm 2.15
Nitrate concentration (μM)	18.1 \pm 1.38
Silicic acid concentration (μM)	72.1 \pm 1.55
Chlorophyll <i>a</i> concentration ($\mu\text{g l}^{-1}$)	6.60 \pm 1.53
POC concentration ($\mu\text{mol l}^{-1}$)	35.1 \pm 7.83

particulate organic carbon (POC) and nitrogen, pigment, and biogenic silica concentrations; only chlorophyll *a* data are used in this analysis), and phytoplankton composition using Teflon-coated, external closure Niskin bottles. Methods for the determination of all variables are described in detail elsewhere (DiTullio and Smith, 1996; Gardner *et al.*, 2000; Smith *et al.*, 2006).

Critical depths (Z_c) were calculated using a reformulation of the Sverdrup (1953) equation (Nelson and Smith, 1991) or

$$Z_c = \frac{\sum E_0}{3.78K_{PAR}}, \quad (1)$$

where $\sum E_0$ is the surface photosynthetically active radiation (PAR) integrated over 24 h, K_{PAR} is the diffuse attenuation coefficient of PAR, and 3.78 is a combination of constants and conversion factors. Equation (1) was derived from the original Sverdrup (1953) formulation, but with slight changes with regard to photo-compensation depths and irradiance units. Specifically, Nelson and Smith (1991) used water column PAR values to avoid the assumptions of reflectance and differential absorption of wavelengths, and used more recent estimates of photocompensation depths from temperate regions.

The variable K_{PAR} was estimated as the slope of the line determined by regressing the natural logarithm of PAR values with depth, and the depth of the euphotic zone (1% of surface irradiance) calculated from K_{PAR} . Since the ship never was at a single location for 24 h, we estimated the minimum and maximum integrated irradiance values by fitting observed values for a clear sky at solar noon and local midnight to a sinusoidal function and a 24-h photoperiod (Hiscock *et al.*, 2003). We estimated that clouds reduced incident irradiance by 50%, although cloud-cover reductions can range 30–97%.

Results

Model and supporting observations

Modelled mixed layers in the Ross Sea are spatially variable and are a function of the magnitude and duration of brine rejection from the pack ice. For example, near the Ross Ice Shelf where southerly winds blow off the shelf and advect the pack ice to the north, new ice is continually generated in the polynya, and brine is continuously released, driving extremely deep mixing (Figure 1). Deep mixing also occurs over the shallow banks that parallel the coast of Victoria Land; conversely, lesser mixing occurs in the troughs where warmer water enters onto the shelf from the Ross Gyre. Changes in mixed layer depth over this 8-week period were large, and most areas had mixed layers that shoaled by 100 m or more, except in areas where pack ice remained (Figure 2). The modelled distribution of density along 77°S demonstrates the large temporal changes in mixed layer depths (Figure 3). Critical depths along this transect, assuming a constant irradiance, are shallower than the mixed layer depths in early October, but largely greater than the mixed layers in late November. Specifically, if a daily irradiance of $5 \text{ mol photons m}^{-2} \text{ d}^{-1}$ and chlorophyll concentrations of $<0.1 \mu\text{g l}^{-1}$ are assumed in early October, critical depths equal 27 m [derived from Equation (1)]; when daily integrated irradiance increases by late November and approaches 40 mol

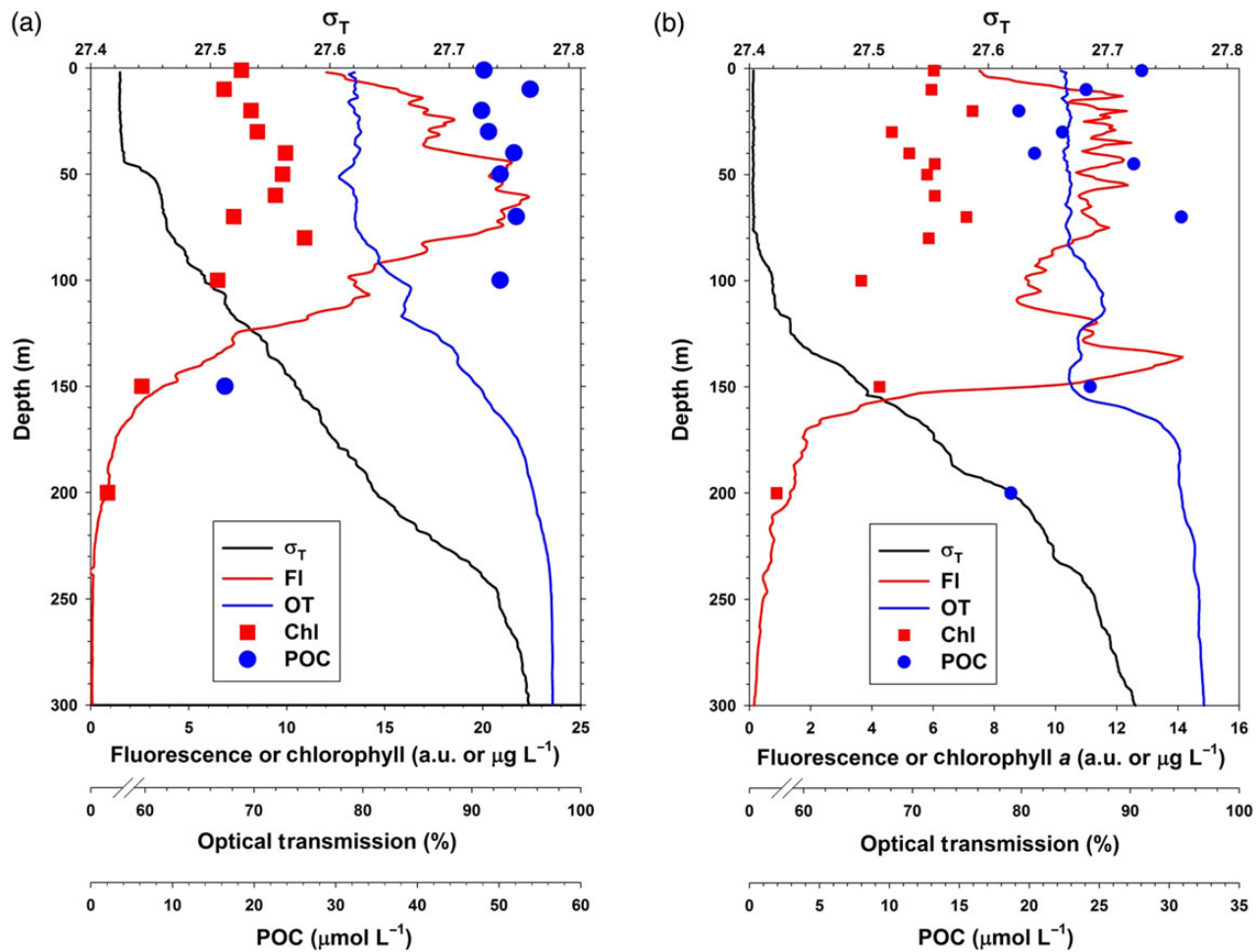


Figure 7. Vertical distribution of density, fluorescence, and optical transmission of two stations (a: St. 58 and b: St. 60) occupied during NBP12-01. Solid squares represent extracted chlorophyll concentrations, and solid circles represent POC concentrations.

photons $m^{-2} d^{-1}$ (but again with chlorophyll concentrations $< 0.1 \mu g l^{-1}$), critical depths exceed 200 m. As such, the model results and estimated critical depths are consistent with Sverdrup's (1953) original hypothesis.

Only limited numbers of oceanographic investigations have sampled the Ross Sea polynya in late winter or early spring. One station (at $78.02^{\circ}S$, $175.91^{\circ}E$) near the ice shelf was sampled on 27 October 1997 (http://usjgofs.who.edu/jg/dir/jgofs/southern/nbp96_4A/; Figure 4), and it showed a deep mixed layer (> 400 m) with no enhanced phytoplankton biomass. Other stations during the same cruise near $76.5^{\circ}S$ showed that mixed layers reached completely to the shelf floor. Another series of stations were completed from 16 to 17 November 2006 (Figure 5; Smith *et al.*, 2013), where mixed layers ranged from 58 to 112 m and where chlorophyll levels were $> 1 \mu g l^{-1}$. Thus, the limited observations in late winter–early spring support the modelled mixed layer depths, as well as the progression of reduced mixed layers associated with increasing phytoplankton biomass within the winter–spring transition.

Observations near the Ross Ice Shelf

Water columns near the Ross Ice Shelf (Figure 6) were characterized by deep mixed layers and large phytoplankton biomass. Mixed layer depths for the 15 PRISM stations near the ice shelf averaged 60.1 ± 20.5 m (Table 1); surface nitrate concentrations at these stations averaged $18.1 \mu M$. Mean euphotic zone depths and silicic acid, chlorophyll, and POC concentrations were 28.1 m, $72.1 \mu M$, $6.60 \mu g l^{-1}$, and $35.1 \mu mol l^{-1}$ (Table 2). Numerically, the phytoplankton assemblages were dominated by *Phaeocystis antarctica*, a condition also observed some 35 years earlier by El-Sayed *et al.* (1983).

Two stations (Sts 58 and 60), both similar in distance from the ice shelf, can be contrasted with respect to vertical density structure, fluorescence, optical transmission, and distributions of nitrate, chlorophyll, and POC (Figure 7). The mixed layer of St. 58 ($Z_{mix} = 45$ m) was slightly less than the mean for all stations (60.1 m; Table 1), and exhibited not only large phytoplankton biomass within the mixed layer, but also substantial concentrations below, which extended to 150 m. Optical transmission values supported the same conclusion of a large biomass through the upper 150 m. The depth of the euphotic zone was 25 m. St. 60 exhibited a deeper Z_{mix} (96 m), with large biomass accumulations within the mixed layer and below (again, through 150 m), as indicated by the large fluorescence and transmission values. St. 60's euphotic depth was 29 m.

Calculated critical depths strongly suggested that growth during sampling was largely limited by irradiance (Table 1); that is, critical depths were shallower in all cases than the mixed layer depths. We recognize that Sverdrup's original contribution was designed to predict the onset of a bloom rather than growth under high biomass conditions, but estimates of critical depths emphasize the primary role of irradiance in both growth initiation, biomass accumulation, and growth limitation. Critical depth estimates are highly dependent on integrated daily irradiance estimates (Table 3), which can vary greatly over space and time. Much of our sampling near the ice shelf was conducted under very cloudy skies, with substantial snow and strong winds. Our estimates of critical depths (Table 1) assumed a daily $\sum E_o$ of approximately half the maximum clear sky irradiance, but if the meteorological conditions that were encountered during sampling continued for 24 h or more, integrated irradiance would likely be substantially less, resulting in even more modest critical depths. Similarly, since spring conditions

Table 3. Dependence of estimated critical depths on surface irradiance.

Integrated daily surface irradiance (mol photons $m^{-2} d^{-1}$)	Calculated critical depths (m)
5	8.0
10	16.1
15	24.1
20	32.2
25	40.2
30	48.3
40	64.3
50	80.4
60	96.5
80	128

Critical depths calculated assuming a euphotic depth of 28 m and a K_{PAR} of $0.164 m^{-1}$, values similar to those measured during NBP12-01.

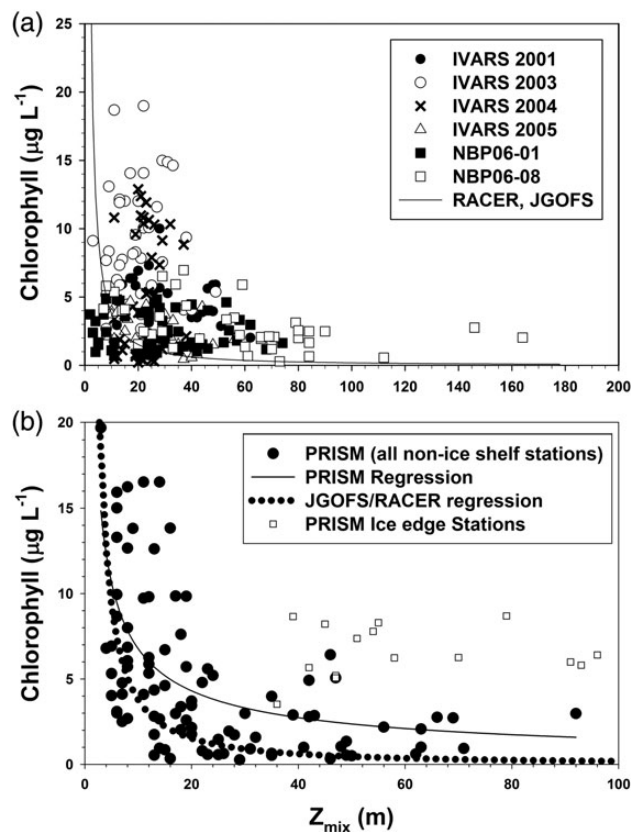


Figure 8. Relationship of mixed layer depth (Z_{mix}) and mean chlorophyll concentration in the mixed layer from (a) six cruises from 2000 to 2006 in the Ross Sea and (b) PRISM (both ice-shelf and non-ice-shelf stations). Included in both is the relationship determined by Mitchell and Holm-Hansen (1991), and in (b) the power relationship of PRISM non-ice-shelf stations ($CHL = 30.4Z_m^{-0.65}$; $R^2 = 0.31$, $p < 0.001$).

often are extremely cloudy, $\sum E_o$ values in spring would likely be reduced by far $> 50\%$.

Discussion

Although there are no data from the Southern Ocean to directly test Sverdrup's (1953) hypothesis, the Ross Sea appears to be an excellent region where these concepts can be verified. Our model results show

that for most of the continental shelf, mixed layers are very deep in winter and spring (driven by ice formation and brine rejection); furthermore, estimated critical depths for early spring (ca. 27 m assuming a euphotic depth of 95 m and 5 mol photons $\text{m}^{-2} \text{d}^{-1}$) remain far less than the mixed layer depths (Figure 3). As solar radiation increases seasonally and mixed layers become shallower, critical depths become deeper (ca. 211 m) and exceed the mixed layer depths. The critical depth concept appears completely consistent with phytoplankton temporal patterns observed in the past (Smith *et al.*, 2014b) and predicts the onset of growth (in late October; Smith and Gordon, 1997) well.

The role of vertical mixing and irradiance limitation has long been recognized as a dominant factor in controlling the annual productivity of the Southern Ocean (Smith *et al.*, 2014b). This remains true even with the realization that iron concentrations are exceptionally low throughout much of the Antarctic realm, even on continental shelves (Sedwick *et al.*, 2011). Mitchell and Holm-Hansen (1991) emphasized the importance of vertical mixing and suggested that mixed layers >40 m effectively precluded phytoplankton growth and biomass accumulation, a conclusion also supported by extensive data from the Ross Sea collected in the 1990s (Smith *et al.*, 2000). Many additional investigations have been completed in the past 15 years, and those suggest that the absolute depth of mixing is indeed important in regulating biomass, but that some environments support an elevated biomass in mixed layers up to 60 m (Figure 8a). Regardless of the absolute depth of mixing, the inverse relationship between mixing and chlorophyll concentration remains, emphasizing the importance of irradiance on the

regulation of phytoplankton biomass (Figure 8a). Mitchell and Holm-Hansen (1991) also emphasized that the duration of stratification was important to allow growth to proceed in a high-irradiance environment and permit biomass to accumulate. As such, loss terms from the surface mixed layer are important, and the stations where elevated biomass is observed in mixed layers deeper than 40 m may reflect a reduced loss rate. Data from the Ross Sea demonstrating substantial chlorophyll in deeper mixed layers suggest that these large accumulations may result from reduced loss rates when compared with the west Antarctic Peninsula. Conversely, there are many stations where shallow mixed layers support relatively low chlorophyll concentrations, and we suggest that these represent locations that have had stratification for substantial periods of time and the biomass levels have been reduced due to losses (grazing, sinking) and reduced growth rates from iron limitation (Sedwick *et al.*, 2011).

Data from the PRISM cruise, and specifically from the ice shelf stations (Figure 8b), are also markedly different from the relationship developed by Mitchell and Holm-Hansen (1991). Specifically, there are a substantial number of stations that exhibit elevated chlorophyll concentrations in mixed layers deeper than 40 m. This is especially true of the ice shelf stations, where there are extremely high chlorophyll concentrations that are nearly independent of mixed layer depth (Figure 8b). Based on our analysis of critical and euphotic depths, it is unlikely that these large biomass levels are the direct result of growth at depths below the euphotic zone. Such large concentrations of phytoplankton must have a different mechanism of generation.

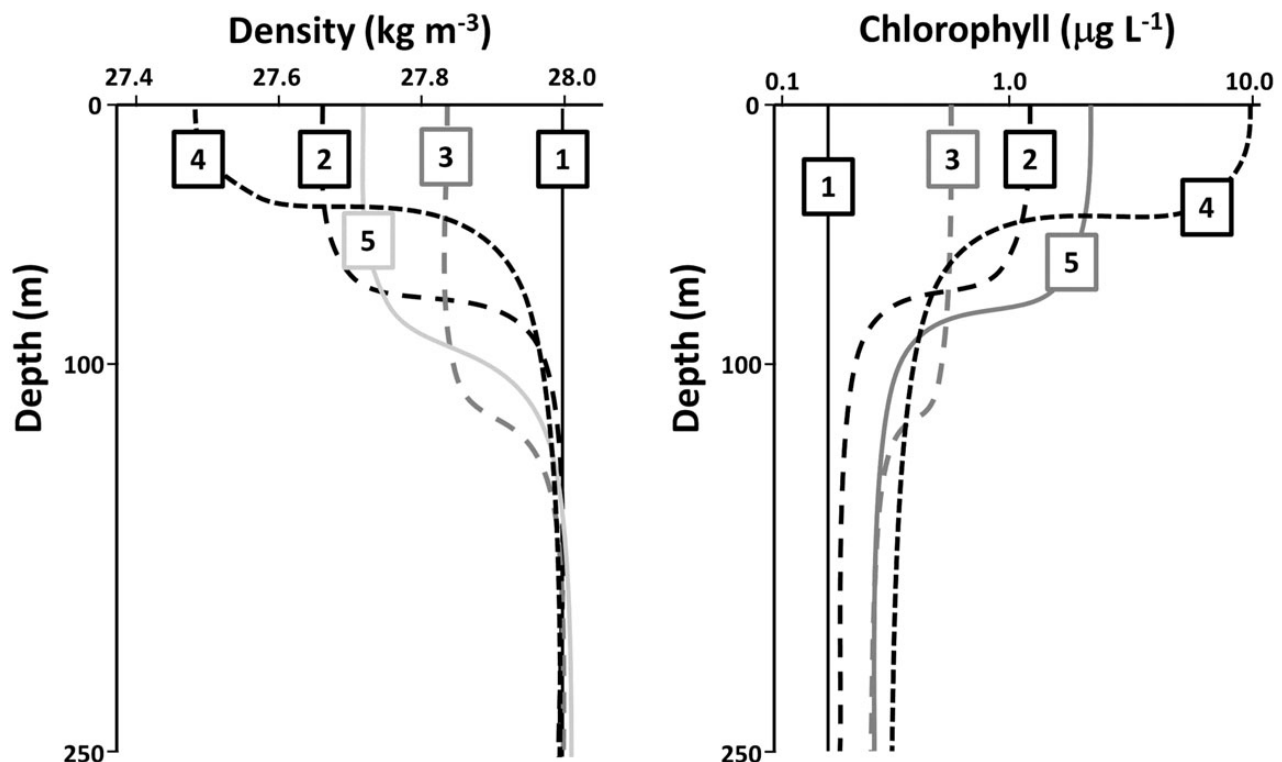


Figure 9. Schematic diagram of the generation of high biomass, deep mixing stations. Numbers indicate periods within the spring bloom: 1—initial, spring condition with deep mixing and low biomass; 2—generation of elevated biomass under relatively quiescent, stratified conditions; 3—redistribution of biomass and salt/heat during a wind event; 4—further growth and accumulation of biomass under quiescent, stratified conditions; and 5—redistribution of biomass and salt/heat during a wind event. Scales on axes are approximate.

We suggest the following as a means of accumulation of such large phytoplankton standing stocks (Figure 9): extensive growth during periods of significant water column stratification, followed by biomass redistribution by mixing induced by wind events, followed by further restratification of the surface water column, and followed by another redistribution of biomass during an intense wind event. Therefore, the growth/redistribution events would be driven by the timescales of local wind events. Furthermore, these blooms would be largely confined to the region near the ice shelf, as they are frequently the location of katabatic winds that blow off the continent over water. These katabatic winds likely only blow for ca. 20 km from the ice shelf, thus restricting the spatial extent of these blooms. Phytoplankton are dominated by the colonial haptophyte *Phaeocystis antarctica*, a species that is known to acclimate to low irradiances (Kropuenske *et al.*, 2009) and thrive in more deeply mixed water columns. It has also been suggested that the growth of *P. antarctica* becomes iron limited at the end of December in much of the Ross Sea (Smith *et al.*, 2000); however, the deep vertical mixing near the ice shelf, coupled with ice shelf iron inputs, likely precludes any iron limitation and allows mesoscale blooms to continue throughout summer.

In summary, phytoplankton growth in the Ross Sea in spring is clearly controlled by low irradiance levels imposed by surface pack ice and deep vertical mixing. While no data are available to directly test Sverdrup's (1953) critical depth hypothesis, model results are consistent with previous observations and confirm the validity of the classical paradigm in the Southern Ocean. An unusual region near the ice shelf is also irradiance limited, but the timescales of mixing likely allow for the development of a deeply mixed surface layer that maintains an elevated, though irradiance limited, phytoplankton biomass. Thus, irradiance can play a critical role in regulating phytoplankton growth in the Ross Sea at a variety of time and space scales, and the region would be an excellent location for an explicit observational test of Sverdrup's hypothesis.

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