REVIEW

ENVIRONMENTAL FACTORS CONTROLLING PHYTOPLANKTON PROCESSES IN THE SOUTHERN OCEAN[1]

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The factors controlling the distribution of phytoplankton stocks, species composition, and their physiological status in the Southern Ocean are reviewed. In the last decade, the key data sources have been observational and experimental. Together, they provide a framework to understand the complex temporal and spatial patterns of environmental control within the distinct basins and ecological provinces. High resolution remotely sensed observational data have overcome the issue of geographical remoteness. Furthermore, by exploiting seasonal and spatial differences in algal distributions, observational data have enabled the cross-correlation of such trends with patterns in other environmental properties. Perturbation experiments have offered a mechanistic understanding to help interpret observational data by altering environmental properties under carefully controlled conditions. A consistent set of trends, on the modes of environmental control of phytoplankton processes, is now emerging across the different basins and provinces. The key determinants are light, iron, and silicic acid supply (top-down control was not considered). However, their interplay in time and space (i.e. simultaneous limitation of phytoplankton processes) is less clear, requires further study, and is discussed. Future challenges include the need to understand better the mode(s) of environmental control on key algal functional groups via more taxon- and species-specific studies. The initiation of more time-series moorings with "smart" bio-optical and sampling sensors are needed to define the seasonal distributions of algal taxa. Moreover, new perturbation experiments are required to investigate the influence on phytoplankton processes of projected climate-mediated alteration of mixed layer depth and nutrient supply as widely predicted by modelers.

Key index words: Antarctic; environmental control; irradiance; nutrients; phytoplankton; trace metals

Abbreviations: CZCS, coastal zone color scanner; DMS, dimethyl sulfide; DMSP, dimethylsulfonioproprionate; HNLC, high nitrogen-low chl; JGOFS, Joint Global Ocean Flux Study; PF, polar front; POOZ, permanently open ocean zone; SIZ, seasonal ice zone

The Southern Ocean comprises around 20% of the area of the World Ocean but is viewed to play a disproportionately important role in controlling the climate of both the present day (Sarmiento et al. 1998) and geological past (Broecker and Henderson 1998, Moore et al. 2000). This region has the greatest inventory of unused macronutrients in the World Ocean (Levitus et al. 1993) and is the most important province for the export and burial of biogenic silica (Trèguer et al. 1995) and for the production of dimethyl sulfide (DMS) (Kettle et al. 1999). Variations in the rate of synthesis of the precursor of DMS (DMSP), the utilization rate of macronutrients, and subsequent changes in the rate of export of photosynthetically fixed carbon in polar waters are all mediated by phytoplankton. Such variations over geological time may be key determinants of the atmospheric concentration of biogenic gases, such as carbon dioxide and DMS and hence climate (Moore et al. 2000, Watson et al. 2000).

These waters encompass the Atlantic, Indian, and Pacific Oceans and four basins—Weddell-Enderby, South-Indian, Southwest Pacific, and Southeast Pacific (Carmack 1990). Around the Antarctic continent are a series of circumpolar fronts, such as the Antarctic Circumpolar Current (Deacon 1982, Orsi et al. 1995, Belkin and Gordon 1996), that are characterized by large geostrophic surface velocities (Nowlin and Klinck 1986). Between these fronts are water masses with distinct physical (Rintoul and Bullister 1999) and chemical (Zentara and Kamykowski 1981) signatures that result in the definition of different oceanographic provinces such as the Sub-Antarctic Water Ring (Banse 1996, Longhurst 1998). A further level of complexity is introduced by the seasonal advance and retreat of sea ice around the continent (Comiso et al. 1993, Moore et al. 2000). Any classification scheme must include sea-ice extent, which contributes to the differentiation of ecological provinces (Trèquer and Jacques 1992) such as the permanently open ocean zone (POOZ) and the seasonal ice zone (SIZ). Such a range of conditions and provinces make the study of environmental control of algal processes more difficult, because

each has a different seasonal cycle of biomass and production (Arrigo et al. 1998, Moore and Abbott 2000).

The detailed study of phytoplankton in the Southern Ocean commenced in the 1930s with expeditions by the Norwegians (Gran 1931) and British (Hart 1934, Hendey 1937). Their theories on the environmental control of phytoplankton are reviewed by de Baar (1994), but in brief their findings were seminal with respect to the concept of the "Antarctic Paradox," i.e. low chl concentrations despite perennially high macronutrient levels, subsequently referred to as high nitrogen-low chl (HNLC) (Chisholm and Morel 1991), and the potential role of iron and silicic acid in controlling algal stocks in polar and subpolar waters, respectively. In the following decades few conceptual advances were made in resolving environmental control, with major research efforts in the 1960s and 1970s being directed on better understanding polar physical oceanography (e.g. Gordon et al. 1977), and algal studies focused mainly on improving estimates of primary production rates (El-Sayed et al. 1964, El-Sayed 1978, Holm-Hansen et al. 1977).

A key advance in assessing patterns of phytoplankton stocks was made in 1978 with the launch of the coastal zone color scanner (CZCS), which provided unprecedented spatial and temporal coverage of chl concentrations until 1986 (see later). In the 1980s a series of biological and multidisciplinary projects investigated algal dynamics associated with the SIZ in the Weddell/Scotia (Nelson et al. 1987, 1989) and Ross Seas (Smith and Nelson 1985, Nelson and Smith 1986, Wilson et al. 1986). Late in the decade, other programs, such as RACER (Research on Antarctic Coastal Ecosystem Rates, Huntley et al. 1991) and EPOS (European Polar Stern Study) took place near the Antarctic Peninsula and in the POOZ and SIZ regions of the Atlantic sector (Buma et al. 1991), respectively (Fig. 1). These large-scale interdisciplinary studies were the forerunners of a proliferation of biogeochemical studies in the 1990s. During the 1980s, the experiments of Martin et al. (1990a,b) most significantly advanced our understanding of the environmental control of phytoplankton processes. They reported that the supply of iron to phytoplankton resulted in marked increases in both carbon fixation and nitrate utilization rates and thus provided an explanation for the Antarctic Paradox of Hart (1934), which subsequently led to the Iron Hypothesis of Martin (1990), that linked iron supply, phytoplankton, and changes in climate over geological time scales.
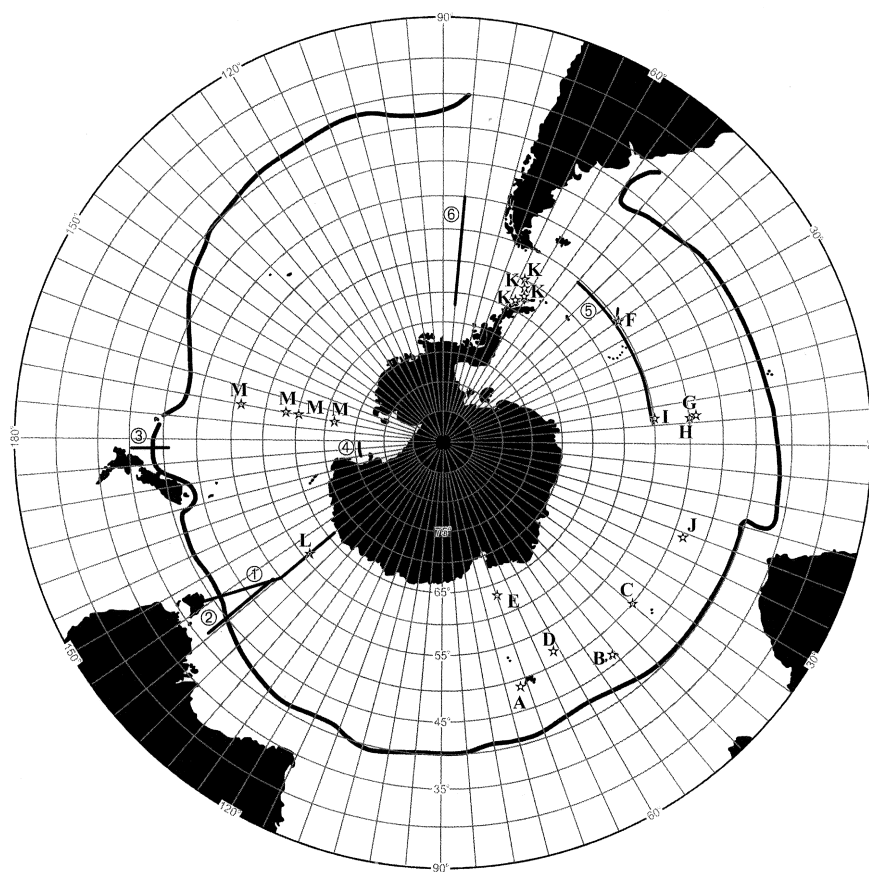

FIG. 1. A map of the Southern Ocean centered on the Antarctic and annotated with research voyages, transects, experiments, and time series during the last decade. The circumpolar line denotes the approximate mean position of the subtropical front (taken here as the northern limit of the Southern Ocean). A, the KERFIX time station (Jeandel 1997); B, Crozet Basin (Read et al. 2000); C, Prince Edward Island (Froneman and Perissinotto 1996); D and E, stations occupied during the ANTARES program (Gaillard 1997); F, the South Georgia time-series site (Atkinson et al. 2001); G, H, and I, stations occupied during EPOS (Buma et al. 1991) and German JGOFS (Smetacek et al. 1997); J, site of EISENEX (Smetacek 2001); K, the RACER grid of stations (Huntley et al. 1991); L, the site of the SOIREE (Boyd et al. 2000); M, stations occupied during AESOPS (Antarctic Environment and Southern Ocean Process Study) (Smith et al. 2000). Line 1, the SR3 repeat transect (Trull et al. 2001a, Rintoul et al. 1997); 2, the SAZ (Sub-Antarctic zone) experiment (Trull et al. 2001b); 3, the Ocean Ecosystem repeat transect (Bradford-Grieve et al. 1999); 4, W-E transects during AESOPS (Smith et al. 2000) and ROAVERRS (Arrigo et al. 1999, 2000); 5, the EPOS transect (Smetacek et al. 1997); and 6, the STERNA study (Turner and Owens 1995).

The initiation of the Joint Global Ocean Flux Study (JGOFS) in 1989 provided a sustained international effort to investigate the biogeochemistry of polar waters. Vessels from the United Kingdom, France, Germany, and the United States conducted major studies in the western Atlantic Ocean (Turner and Owens 1995), eastern Atlantic/Weddell Sea (Smetacek et al. 1997), Indian Ocean (Read et al. 2000, Blain et al. 2001), and Pacific/Ross Sea (Smith et al. 2000) sectors of the Southern Ocean, respectively (Fig. 1). Moreover, other programs contributed shorter term research studies in subpolar regions (Laubscher et al. 1993, Froneman and Perissinotto 1996, Sedwick et al. 1997, 1999, Boyd et al. 1999, Bradford-Grieve et al. 1999, Trull et al. 2001a,b), and other regional programs were initiated, such as ROAVERRS (Research on Ocean Atmosphere Variability and Ecosystem Response in the Ross Sea, Arrigo et al. 1999, 2000) (Fig. 1).

Toward the end of the century, a more advanced ocean color sensor (SeaWiFS, Sea-viewing Wide-Field of view Sensor) was launched and provided higher resolution images than previously available (Moore et al. 1999). At the start of 2000, a new approach to study the environmental control of phytoplankton processes has been adopted in the Southern Ocean (Watson et al. 1991, Coale et al. 1996), that of *in situ* perturbation experiments (iron enrichments; Boyd et al. 2000, Smetacek 2001).

The aim of this review is to synthesize the developments over the last decade in understanding the factors controlling phytoplankton processes. For completeness earlier research is addressed briefly, and the reader is encouraged to obtain more detailed perspectives from reviews conducted during the 1970s (Holm-Hansen et al. 1977), the 1980s (Smith and Sakshaug 1990, Smith and Harrison 1991), and on biogeochemical studies (Priddle et al. 1992, Trèquer and Jacques 1992, Bathmann et al. 2000). Here, the Southern Ocean is defined as the waters south of the Subtropical Front (Fig. 1). There is insufficient space to detail the effects of top-down control on phytoplankton processes or to look at the coastal ocean (see grazing studies such as Conover and Huntley [1991] or Verity and Smetacek [1996] and coastal research by Agusti and Duarte [2000], Nichol et al. [2000], or Smith et al. [1998]).

DISTRIBUTION OF PHYTOPLANKTON STOCKS IN THE SOUTHERN OCEAN

Before establishing the environmental mode(s) of control on phytoplankton in these waters, information was required first on the spatial and temporal distribution of algal stocks. However, the geographical isolation of the Southern Ocean was a major barrier to such data collection. Although relatively comprehensive suites of stations were sampled in the Weddell Sea and around the Peninsula as early as 1930 (see Fig. 1 in Hendey 1937), they had insufficient temporal or spatial resolution to provide comprehensive maps of phytoplankton stocks. It was not until the

1970s with the launch of the CZCS that detailed maps were made (Comiso et al. 1990, 1993, Sullivan et al. 1993). Indeed, striking images of blooms in the Ross Sea (Arrigo and McClain 1994) and open ocean (Sullivan et al. 1993), where blooms were interspersed with low chl waters, provided the first indications of the "variegated nature" of the Southern Ocean. This view differed somewhat from that referred to by Hart (1934) in his description of the "Southern Ocean paradox." The observed wide range of chl concentrations offered a means to investigate the environmental forcing causing such patterns (Comiso et al. 1993). Moreover, such spatial and temporal trends in algal stocks could be compared with the location of different water masses, each with distinct oceanic properties (Trèquer and Jacques 1992). These developments led to an assessment of the seasonality of algal stocks in polar (Comiso et al. 1993) and subpolar (Comiso et al. 1993, Banse 1996, Banse and English 1997) waters and for the first time to view time scales of bloom evolution both in the SIZ (Comiso et al. 1990, Arrigo and McClain 1994) and POOZ (Sullivan et al. 1993).

Shipboard surveys also played a key role in such analysis via the provision of concurrent information on properties such as density, macronutrient concentrations (Nelson et al. 1987), and floristics (Wilson et al. 1986, Laubscher et al. 1993) and provided a platform to conduct physiological experiments (Smith and Sakshaug 1990). In particular, the recent JGOFS program has given us a much needed temporal resolution on algal stocks and associated properties (Fig. 1).

Two important recent developments in investigating phytoplankton spatial and temporal distributions have been the launch of SeaWiFS and the establishment of ocean observatories. SeaWiFS has provided much needed high resolution maps of chl, enabling particular features of interest to be followed such as the iron-rich high chl Kerguelen plume (Blain et al. 2001). Observatories include both land-based platforms that support oceanic time-series stations such as KERFIX (Jeandel 1997, Blain et al. 2001) and the deployment of long time-series (months) multiple arrays of bio-optical moorings (Abbott et al. 2000). Such observatories provide suitable data sets for model validation (Pondaven et al. 2000) and highly resolved temporal data sets (not possible with SeaWiFS due to the need to composite images in this cloudy region) on bloom evolution near the polar front (PF).

OCEANOGRAPHIC PROPERTIES AND DISTRIBUTIONS OF PHYTOPLANKTON STOCKS

The existence of marked gradients in physical and chemical properties and the separation of water masses by pronounced and persistent circumpolar features (Rintoul and Bullister 1999) provided a powerful, albeit indirect, tool to interpret observed distributions of phytoplankton stocks. For example, there are marked meridional gradients in the magnitude of geostrophic flows/currents (Comiso et al. 1993) and in silicic acid concentrations (Zentara and Kamykowski

1981). During the 1970s and 1980s an unprecedented number of satellites, carrying environmental sensors, were launched (Shuchman and Onstott 1990). These provided highly resolved data sets on properties such as sea surface temperature and sea ice extent.

The climatologies of many remotely sensed data sets were related to trends in the distributions of algal stocks from the 8-year CZCS archive by Comiso et al. (1993). They used these data sets in conjunction with regression analysis to determine what factors influence phytoplankton spatial and temporal distributions. Comiso et al. reported that the most significant relationship was a negative one between pigment levels and bathymetry. They interpreted this trend as indirect evidence for upwelling induced by topographical features that resulted in nutrient resupply to surface waters and/or the resuspension of iron (and algal cells) in shallow waters. A similar approach was used by Banse (1996) and Banse and English (1997) for subpolar waters southeast of New Zealand. They occasionally observed episodic relatively small-scale "bloom" levels of chl in these waters and speculated that the causal mechanism was iron-rich dust inputs from Australia. Recently, SeaWiFS archives have provided new data sets to correlate spatial and temporal trends in algal stocks with oceanographic features. Moore et al. (1999) compared the location of features such as the Sub-Antarctic front and the PF with marked increased in phytoplankton stocks at these frontal regions.

Analysis of macronutrient data derived from shipboard surveys in the Pacific sector enabled Zentara and Kamykowski (1981) to identify that water masses had distinct nutrient imbalances, such that in subpolar waters (45°S) up to 15 μM of nitrate remained when silicic acid was depleted. In contrast, there was a potential excess of silicic acid, relative to nitrate, in Ross Sea waters. These imbalances—which may have marked effects on diatom abundances—were due to both physical (conditions of water mass formation) and biological (different rates of nutrient uptake and remineralization) effects. The influence of trace element distributions on algal stocks was explored by de Baar et al. (1995), who reported a pronounced coincidence between elevated chl and high dissolved iron levels near the PF (Atlantic sector) that was in contrast to the surrounding HNLC waters characterized by low dissolved iron levels. Such natural laboratories, where marked gradients in environmental properties exist may be related to distributions of algal stocks, have subsequently been exploited.

Such a laboratory was present in the waters downstream from Kerguelen (Blain et al. 2001, Bucciarelli et al. 2001) (Fig. 1). Blain et al. reported on the presence of contrasting water masses in this region. Despite all three water masses being iron rich (>0.5 nM), two of the regions (coastal, Antarctic water tongue) exhibited low chl levels, whereas only offshore waters had high chl. These trends in algal stocks were interpreted as being due to herbivory (coastal waters), an unfavorable light-mixing regime (Antarctic water tongue), with high chl recorded in iron-rich waters where the light-mixing regime was favorable (Blain et al. 2001). Another natural laboratory, a pronounced silicic acid front in the vicinity of the PF (Pacific sector), has been observed during vessel surveys, with concentrations decreasing 20-fold over 300 km from south to north (Franck et al. 2000, Daly et al. 2001).

In all these observational studies, important contributions were made indirectly to understanding the control of phytoplankton processes. However, the reported trends had to be confirmed or further interpreted using data from laboratory or field studies (e.g. Martin et al. 1990a,b, 1991) or the hypotheses put forward validated in the future via carefully designed field experiments (Banse and English 1997). Indeed Comiso et al. (1993) stated "Simple linear regression analysis undoubtedly does not provide complete information about the relationships of variables in such a complex system."

PHYSIOLOGY OF SOUTHERN OCEAN PHYTOPLANKTON: EXPERIMENTAL APPROACHES

The other key approach to understanding the environmental control of algal stocks was laboratory and shipboard experiments on phytoplankton processes. As early as the 1930s, Gran (1931) and Hart (1934) had speculated on the possibility of trace element limitation in the Southern Ocean and of silica limitation in "the Northern parts of the Antarctic Zone." Hart (1934) suggested the possibility of nitrate or phosphate limitation of phytoplankton in open ocean waters could not "be regarded at any time as a factor limiting phytoplankton growth or controlling periodicity" due to the persistently high concentrations even in subpolar waters.

Since 1930, candidate mechanisms for environmental control have included temperature (Neori and Holm-Hansen 1982, Tilzer and Dubinsky 1987), irradiance (El-Sayed et al. 1964, 1970), suppression of nitrate uptake capacity due to ammonium accumulation (Dugdale and Wilkerson 1991), "organics" (Carlucci and Cuehel 1967), silicic acid (Hart 1934, Jacques 1983, Sommer 1986, 1991), and iron (Hart 1934, Martin 1990). In brief, as early as 1977 Holm-Hansen et al. concluded that there was "considerable variation in phytoplankton growth rates in Antarctic waters under fairly comparable conditions of temperature, inorganic nutrients, and light," and that they could not account for such variations in growth. Therefore, other factors—organics, conditioning agents (ligands) from depth, or microelements—might be implicated (Holm-Hansen et al. 1977). Smith and Sakshaug (1990) summarized the role of temperature as setting an upper limit on growth rates that are subsequently modified by other environmental factors.

Three aspects of light limitation of phytoplankton processes have been investigated in polar waters: the photosynthesis–irradiance relationship, such as photosynthetic capacity, quantum yield (Tilzer et al. 1985), photoadaptation, and incident light (Sakshaug and

Holm-Hansen 1986); the impact on the accumulation of algal stocks of deep surface mixed layers (Mitchell et al. 1991, Nelson and Smith 1991, Sakshaug and Slagstad 1991); and, due to increasing awareness of the evolution of the ozone hole, the UV inhibition of photosynthesis (Cullen and Lesser 1991, Cullen et al. 1992, Neale et al. 1998).

Why N-specific uptake rates of nitrate were so low in Southern Ocean HNLC waters was also debated (Dugdale and Wilkerson 1991). The potential for ammonium accumulation to suppress nitrate uptake capacity was considered (Wheeler and Kokkinakis 1990). This puzzle of low N-specific nitrate uptake rates has subsequently been resolved. Increased iron supply elevates significantly both nitrate uptake (Martin et al. 1990b) and N-specific nitrate uptake rate (Price et al. 1994, Boyd et al. 1996).

Detailed perspectives on the role of temperature, irradiance, and ammonium in controlling phytoplankton processes are provided by Holm-Hansen et al. (1977), Smith and Sakshaug (1990), and Dortch (1990), respectively. The review by Cullen (1991) on environmental control of phytoplankton processes in HNLC regions is recommended, and for a review of UV inhibition on photosynthesis see De Mora et al. (2000). Here we focus on the role of irradiance (mixed layer depth), silicic acid, iron supply, and the potential for simultaneous limitation of algal processes by several mechanisms as they represent the major recent advances in this field.

Irradiance: mixed layer depth and light attenuation. A synthesis of our understanding of the role of irradiance on phytoplankton processes, via a mathematical model, indicated that mixed layer depth and light attenuation were the key determinants (Sakshaug et al. 1991). The potential influence of deep surface mixed layers on phytoplankton growth has mainly been explored indirectly using a combination of models and observational data, such as wind stress climatologies (Mitchell et al. 1991), incident irradiance (Mitchell et al. 1991), density sections (Nelson and Smith 1991), calculated algal loss terms (Nelson and Smith 1991), and the site-specific relationships between chl levels and mixed layer depth (Mitchell and Holm-Hansen 1991). A common factor in these approaches was the use of Sverdrup's (1953) critical depth theory, which was sometimes reformulated (Smetacek and Passow 1990).

In general, this suite of studies emphasized the importance of the magnitude of algal loss terms and mixed layer depth in setting the maximum sustainable chl levels (Fig. 4 in Mitchell et al. 1991) in both the coastal and open ocean. Sakshaug and Holm-Hansen (1986) proposed that blooms would only develop in a mixed layer of less than 40 m. In the POOZ, Nelson and Smith (1991) predicted that chl higher than 1 mg·m^{-3} was unsustainable due to the combination of relatively weak vertical stability and strong winds. These models did an admirable job of exploring a key determinant of the functioning of phytoplankton in both the Southern Ocean. However, because these studies took place before research on the effect of iron on phytoplankton processes, the models were incomplete. Nevertheless, Sverdrup's 1953 formulation of Z_c/Z_m (critical depth/mixed layer depth) remains a powerful tool in interpreting trends in phytoplankton processes. Sambrotto and Mace (2000) measured the rate of new production ($^{15}NO_3^-$) along the 170°W meridian (Fig. 1) and reported that Z_c/Z_m explained more than 50% of the variance in new production.

Silicic acid. There is a pronounced meridional gradient in silicic acid concentrations from 4 μM (winter reserve) in Sub-Antarctic waters to more than 60 μM (winter reserve) in the Ross Sea (Zentara and Kamykowski 1981, Levitus et al. 1993). Based on observations of low silicic acid concentrations in the Northern parts of the Antarctic Zone, Hart (1934) suggested that silicic acid might limit algal growth, particularly in subpolar waters. Because diatoms are the major contributors to bio-silicification (Martin-Jèzèquel et al. 2000), they are the main group potentially affected by low silicic acid concentrations. However, the influence of ambient silicic acid concentrations on diatoms may be confounded by the silica requirements (degree of silicification) of diatom species that can vary by up to 4-fold (reviewed by Martin-Jèzèquel et al. 2000). The key determinants of silicification are cell division and growth rate, and under silica-limiting conditions the degree of silicification varies directly with growth rate (Brzezinski et al. 1990). Moreover, silicification rate is also influenced, to a lesser extent, by irradiance, temperature, macronutrients (N, P), and micronutrients (Zn, Fe) (Martin-Jèzèquel et al. 2000; see below). (Note: as a result of such variations in the degree of silicification, diatoms are able to maintain high growth rates despite limiting concentrations of silicic acid for uptake [i.e. $K_s \gg K_\mu$] [Nelson et al. 2001].) Thus, kinetic evidence for silicic acid limitation, as derived from the relationship between K_s and ambient silicic acid concentrations, usually refers to limitation of uptake rather than growth (see Fig. 8 in Nelson et al. 2001).

Two main approaches have been used to assess whether silicic acid concentrations are limiting to diatoms and hence if silicic acid levels exert environmental control: laboratory culture or field experiments to measure the silicic acid uptake kinetics of species (e.g. Jacques 1983) or of the resident diatom assemblage (Nelson and Trèguer 1992), respectively, and shipboard perturbation experiments on the resident diatoms (Franck et al. 2000, Hutchins et al. 2001).

There was evidence from culture studies of silicic acid limitation of some polar diatom species (Jacques 1983). Jacques reported particularly high K_s for silicic acid (i.e. low affinity for Si) of up to 89 μM, whereas subsequent studies—near the SIZ in the Ross Sea—recorded considerably lower values comparable with those from other oceanic regions (K_s 0.5–5 μM Si; Nelson and Trèguer 1992). Thus, it was unclear whether diatoms were limited by low silicic acid concentrations in

these waters (Nelson et al. 2001). Nelson et al. (2001) exploited the natural laboratory provided by the silicic acid front near the PF (0.25–0.65 μM Si·km^{-1}, Franck et al. 2000) to investigate silicic acid uptake kinetics during summer along 170°W (Fig. 1). This study of silicic acid uptake kinetics is the most comprehensive so far in polar waters and merits attention. Nelson et al. observed a diatom bloom during this period—propagating southward—and reported a wide range of K_s values (0.7–10 μM; 35% were in the 0- to 5-μM range). Despite a two orders of magnitude range in K_s during this study, there was little evidence of relationships between K_s and latitude or ambient silicic acid concentrations, with the strongest relationship being temporal (increasing K_s with season, but with concurrent increases in the variability of K_s). Nelson et al. reported that K_s exceeded more than 20 μM (i.e. a particularly low affinity for silicic acid) in 15% of their experiments, with higher values being recorded later in the season, but there was no evidence of such higher values being associated with particular taxa. High values of K_s (31 μM) for resident diatoms were evident from other kinetic studies near the northern PF zone, south of Australia (Fig. 1) by Quèguiner (2001).

Several approaches were used by Nelson et al. (2001) to investigate whether there was silicic acid limitation of uptake (ratio of v_a:v_{max}; E, the uptake enhancement ratio) and/or and growth rate (ratio of μ_a:μ_{max}) of resident diatoms in the western Pacific. From kinetic evidence during spring and summer, they concluded that diatom growth rates were silica limited at the north end of the silicic acid front, whereas the limitation of silicic acid uptake rates was more widespread. Thus, the observed southward progression of the bloom (59–62°S from November to January, Franck et al. 2000) was probably driven by silicic acid limitation at the north end of the silicic acid front (Nelson et al. 2001).

Perturbation experiments, in which seawater is supplemented with silicic acid (and sometimes trace elements; see below) were conducted in subpolar and polar waters. Experiments were conducted in subpolar waters in spring (Boyd et al. 1999) and summer when silicic acid levels less than 1 μM were recorded (Sedwick et al. 1999, Hutchins et al. 2001, Sedwick et al. 2002). Despite the few experiments carried out so far, an underlying trend of a seasonal change in the role of silicic acid supply in controlling phytoplankton processes is evident in subpolar waters in the Pacific and Indian Ocean sectors. Boyd et al. (1999) observed no effects of silicic acid enrichment on the assemblage in spring (ambient concentrations 4 μM Si) in the waters east of New Zealand. In contrast, during summer in subpolar waters, Hutchins et al. (2001) recorded evidence of silicic acid limitation of algal processes; however, it was in conjunction with limitation by iron supply (simultaneous limitation; see later). Interestingly, they also reported that lightly silicified chrysophytes (type 4 haptophytes), rather than diatoms, responded to silica enrichment. In the sub-

polar waters of the Crozet Basin (Fig. 1) during summer, Sedwick et al. (in press) also reported limitation of phytoplankton processes by silicic acid but again reported that it was in conjunction with iron limitation of the assemblage.

The trends reported for silicic acid in subpolar waters differed to those south of the PF, whereas a similar seasonal progression was evident for waters near the PF. South of the silicic acid front (>40 μM Si), Franck et al. (2000) observed no increase in silicic acid uptake rates upon silicic acid enrichment in either spring or summer. However, in the vicinity of the PF they recorded silicic acid limitation of diatoms in both spring (ambient levels 15 μM) and to a greater extent in summer (ambient levels 5 μM), with uptake rates increasing, after a lag time of days, by up to 16-fold during experiments. Franck et al. (2000) also added iron or zinc to samples from these waters and noted a complex pattern of results, discussed later.

Iron. The potential role of iron in controlling algal processes was alluded to in the 1930s (Hart 1934) but was first addressed experimentally by Martin et al. (1990a). By both developing trace metal "clean" sampling techniques and markedly improved precision and accuracy in dissolved iron measurements, Martin et al. were able to conduct iron perturbation experiments in the Ross Sea. Their findings strongly suggested iron limitation of phytoplankton processes and were closely followed by others in the Atlantic sector and Weddell-Scotia Confluence (de Baar et al. 1990, Buma et al. 1991, Helbling et al. 1992). Several common trends emerged, including iron-mediated chl accumulation, elevated growth rates, nitrate uptake, and floristic shifts (see below), and pointed to the fundamental role of iron supply in controlling many aspects of algal processes. However, the interpretation of the iron enrichment experiments was contentious due to the difficulties in overcoming the confounding evidence from bottle effects such as under-representation of grazers (Banse 1990, Martin et al. 1991).

Alternative approaches to overcome such bottle artifacts included shipboard surveys of regions characterized by a wide range of both dissolved iron and chl concentrations (Blain et al. 2001). Indirect evidence of the role of iron in controlling algal stocks was presented by de Baar et al. (1995), who reported a link between the magnitude of algal stocks and dissolved iron concentrations in the vicinity of the PF. Other approaches to study the influence of iron included the use of intrinsic measurements of algal physiology such as active fluorescence (Boyd et al. 1999, Olson et al. 2000) and molecular markers of iron stress (Timmermans et al. 1998, Boyd et al. 1999). However, such approaches could not overcome the potentially confounding effects of simultaneous limitation of algal growth by iron/light and/or silicic acid (see section on simultaneous limitation) and the influence of grazers such as krill (Banse 1991). Thus, algal iron limitation could only be unequivocally investigated using a mesoscale *in situ* fertilization approach.

In austral summer of 1999, an *in situ* fertilization experiment, SOIREE (Southern Ocean Iron RElease Experiment), was performed in the waters south of the PF (Fig. 1) (Boyd et al. 2000, Boyd and Law 2001). This site was selected because it was representative of a large body of polar waters in summer with respect to light climate (mixed layer depth) and silicic acid levels (Boyd et al. 2000). Over 13 days SOIREE clearly demonstrated that iron supply elevated algal photosynthetic competence (Boyd and Abraham 2001), quantum yield (Gall et al. 2001b), growth rate, chl levels, nitrate uptake (Boyd et al. 2000), silicic acid uptake (Gall et al. 2001b), and altered algal community structure toward a diatom-dominated community (Boyd et al. 2000, Gall et al. 2001a). There were also iron-mediated increases in prymnesiophyte abundances resulting in DMSP production and subsequent grazer-mediated increases in DMS levels (Boyd et al. 2000). Changes in diatom iron stress were also recorded using the following proxies: sinking rates, flavodoxin levels, and iron uptake kinetics of both inorganically and organically bound iron (Maldonado et al. 2001). Another mesoscale experiment, EISENEX, took place in the Atlantic in spring 2000 (Fig. 1), and although few details are yet available, a similar suite of iron-mediated changes (such as photosynthetic competence) were observed (Smetacek 2001).

Thus, polar *in situ* studies have confirmed the main findings of shipboard iron enrichments (reviewed by de Baar and Boyd 2000) but have also enabled other key processes to be studied such as mesozooplankton grazing on iron-mediated blooms (Zeldis 2001), altered iron chemistry on algal physiology (Croot et al. 2001, Maldonado et al. 2001), and provided a platform to address questions such as the fate of these iron-stimulated blooms (Nodder et al. 2001). Moreover, they have provided an unprecedented level of concurrent detailed measurements that enable the construction of pelagic iron budgets (Bowie et al. 2001), validation of ecosystem models that have incorporated iron (Hannon et al. 2001), and a comparison of the effects of iron supply on a wide range of physiological parameters (Maldonado et al. 2001).

Simultaneous limitation of algal processes. The application of physiological definitions of the limitation of phytoplankton processes, such as Liebig limitation of standing stocks, to the ocean have been problematic (reviewed by Cullen 1991). It is now recognized that the interplay of environmental factors—as a combination of bottom-up and top-down processes (Cullen 1991, Lehman 1991) and also by multiple (bottom-up) environmental factors (Cullen 1991)—is a key determinant of phytoplankton processes. The interaction of environmental controls, that is, the limitation of processes by more than one factor such as iron and silicic acid (De La Rocha et al. 2000, Franck et al. 2000) or iron and irradiance (Raven 1990, Boyd et al. 1999, 2001), has become evident in recent years, particularly in the Southern Ocean. Limitation by more than one factor is referred to as simultaneous limitation and may

alter a range of processes including growth and/or nutrient uptake rate. In the case of limitation by iron supply and irradiance, low irradiance levels may exacerbate iron limitation of algal growth rates (Sunda and Huntsman 1997). For limitation by iron and silicic acid, iron availability may alter silicic acid uptake rates (degree of silicification) and hence change the elemental ratios of the phytoplankton (Hutchins and Bruland 1998, De La Rocha et al. 2000).

Raven (1990) in a theoretical study proposed an antagonistic relationship between light climate and iron supply, such that at low irradiances—where the light-harvesting requirements of phytoplankton increase—the cellular requirements for iron could increase by up to 50-fold. This assertion was validated in laboratory cultures by Sunda and Huntsman (1997), who suggested that iron–light co-limitation might be particularly relevant to the deep mixed layers of the Southern Ocean. Several field studies investigated aspects of iron–light co-limitation in polar waters. Van Leeuwe (1996) investigated the effects of both iron and light limitation on laboratory cultures of the Antarctic flagellate *Pyraminomonas* sp. from waters south of the PF. Van Leeuwe observed a complex set of trends: a decline in cellular pigment content due to Fe limitation, whereas light limitation elevated cellular pigment content.

Recently, experiments have been designed to investigate simultaneous limitation of phytoplankton processes using oceanographic data sets to define environmentally relevant upper and lower bounds for treatments (Figs. 2 and 3). During the SOIREE, a shipboard experiment was conducted in which iron-enriched samples were subjected to different light climates mimicking mixed layer depths of 45, 65 (that *in situ*), and 100 m (Boyd et al. 2000). In the 45- and 65-m treatments there were more than 10-fold increases in chl, whereas in the latter there was little change in algal growth rate indicative of simultaneous limitation by iron and irradiance (Fig. 3). Such results subsequently may be cautiously related to the Southern Ocean (Fig. 2). Boyd et al. (2001) conducted a similar experiment in subpolar waters south of Australia. At a site with a 45-m mixed layer they observed only iron limitation of phytoplankton growth rates, whereas at a subpolar site with a 90-m mixed layer they reported evidence of simultaneous limitation of growth by irradiance and iron levels.

The uptake rate of silicic acid can be altered by zinc or iron availability (De La Rocha et al. 2000); indeed, Reuter and Morel (1981) reported that zinc-deficient diatom cultures exhibited reduced uptake of silicic acid and proposed that zinc was involved in an uptake site for silicic acid. In HNLC waters, both coastal (Hutchins and Bruland 1998) and open ocean (Takeda 1998), there has been widespread evidence that iron supply mediates a decrease in the uptake stoichiometry of $Si:NO_3$ by a factor of 2 or more. Laboratory studies using *Thalassosira weissflogii* suggest that the supply of iron influences silicic acid uptake by
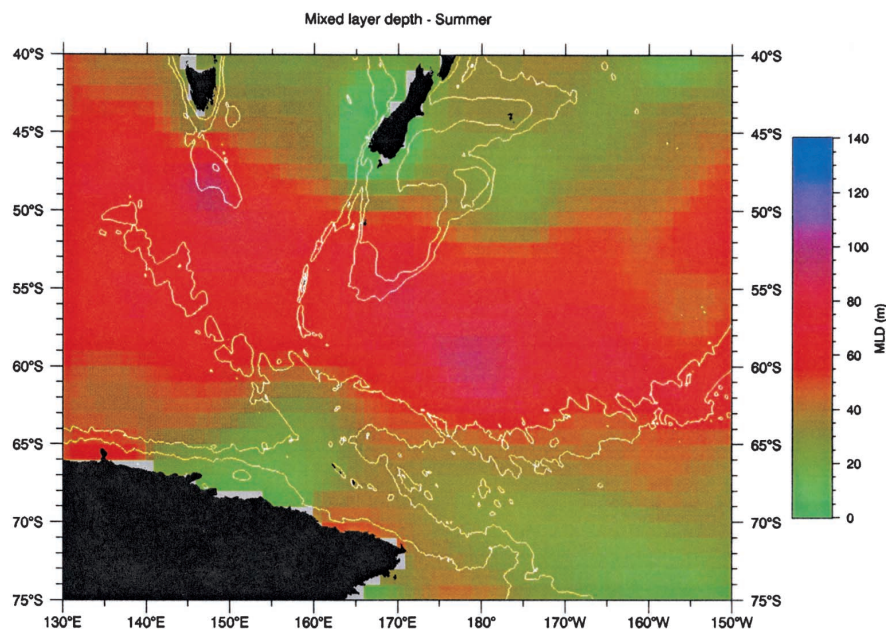
Mixed layer depth - Summer

Fig. 2. An example of the use of observational data in the design of perturbation experiments to examine simultaneous limitation of phytoplankton processes by several factors. A map of summer mean mixed layer depth for the Australasian-Pacific sector derived from the World Ocean Atlas (redrawn from Boyd et al. 2001).

diatoms in two ways: by the reduction in the degree of silicification and, paradoxically, by stimulation of growth rate (De La Rocha et al. 2000).

The presence of a marked meridional gradient in silicic acid (Zentara and Kamykowski 1981, Daly et al. 2001) and elevated iron levels at circumpolar features
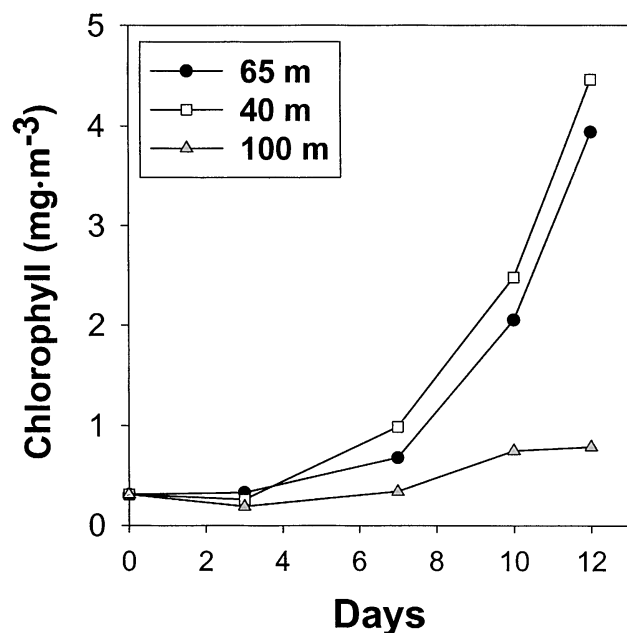

Fig. 3. Results from shipboard perturbation experiments to mimic iron supply at a range of mixed layer depths (100 m, deepest; 65 m, mean; and 40 m, shallowest) derived from Figure 2 (data redrawn from Gall et al. 2001a). These results may be applied cautiously to waters of the region represented in Figure 2.

(de Baar et al. 1995, 1999) led to studies of both iron and silicic acid supply on phytoplankton processes in polar (Franck et al. 2000) and subpolar (Hutchins et al. 2001, Sedwick et al. in press) waters. In the Pacific sector, Franck et al. (2000) reported that iron enrichment had little or no effect on silicic acid uptake rates in the low silicic acid waters north of the silicic acid front (59°S in November and 62°S in January) but resulted in elevated uptake rates in the high silicic acid waters to the south of this front (62°S in October and 68°S in January). Furthermore, iron supply resulted in a 2- to 5-fold decrease in the $Si:NO_3$ uptake rates in the experiments of Franck et al. (2000) and also during the mesoscale SOIREE (2-fold decrease, Watson et al. 2000). In the vicinity of the PF in the Pacific sector there was evidence of simultaneous limitation of the diatom assemblage in summer by iron and silicic acid, such that upon alleviation of silica limitation, iron limitation would prevent the attainment of maximal silicic acid uptake rates (Franck et al. 2000). In subpolar waters Hutchins et al. (2001) (Pacific sector) and Sedwick et al. (in press) (Indian sector) also reported evidence of simultaneous limitation of growth rates and altered floristics by silicic acid and iron, such that treatments which received both iron and silicic acid had elevated growth rates.

The interactive effects of silicic acid and light on phytoplankton processes are less well understood (see Ragueneau et al. 2000), yet clearly there are interactive effects between iron supply and irradiance (Raven 1990) and silicic acid and iron supply on algal processes (Hutchins and Bruland 1998, De La Rocha et al. 2000). Moreover, laboratory studies by Lippemeier et al. (1999) on *T. weissflogii* suggest that silicic acid availability may be a possible determinant of photosynthetic efficiency in diatoms. Although studies on

the effects of both light climate and iron supply on silicic acid uptake rates have been advocated (Boyd et al. 1999, Franck et al. 2000), there are presently no published data from such experiments in polar waters.

The influence of Zn supply on silicic acid uptake has long been established (Reuter and Morel 1981), and recent laboratory experiments with *T. weissflogii* have suggested that Zn deficiency results in a decreased affinity for silicic acid (i.e. an increase in K_s) and a decrease in the maximum specific uptake rate (i.e. a reduced V_{max}) for silicic acid (De La Rocha et al. 2000). In polar waters (Pacific sector) both Gall et al. (2001a) and Franck et al. (2000) reported no significant increase in silicic acid uptake due to zinc enrichment. This was interpreted as being due to the relatively high levels of dissolved zinc that characterize polar waters (Franck et al. 2000, Fitzwater et al. 2000) and is an example of the need to use oceanographic data to design perturbation experiments. During SOIREE, Frew et al. (2001) noted a pronounced shift from dissolved to particulate cadmium, which they interpreted as due to algal utilization. They discuss why cadmium was taken up, rather than zinc (for synthesis of carbonic anhydrase), despite observed high zinc ambient concentrations. The addition of other trace metals, such as cobalt, resulted in no significant effect on algal processes (Scharek et al. 1997), whereas manganese enrichment resulted in interesting, if equivocal, results, including floristic shifts to diatoms comparable with those reported for iron enrichment (Buma et al. 1991).

FIG. 4. Putative seasonal progression of factor(s) limiting or simultaneously limiting phytoplankton processes. The upper part of the panel represents the scheme originally proposed for diatoms in subpolar waters by Boyd et al. (1999). This scheme can also be related to polar diatoms; however, the period of silicic acid limitation will be shorter or nonexistent (Franck et al. 2000, Nelson et al. 2001). Note that the period over which limitation by irradiance, iron, or silicic acid will vary with basin, latitude, and from year-to-year. In the lower part of the panel is a similar seasonal scheme for *P. antarctica* in the Ross Sea. Due to several uncertainties outlined in the text this scheme is more speculative, and it is possible that factors other than irradiance and iron may be exerting environmental control (e.g. Tortell et al. 2002).

Such evidence of simultaneous limitation points to a seasonal progression in the environmental control of phytoplankton, in particular of diatoms, commencing with irradiance in early spring followed by iron/light, then iron limitation by a single factor and then simultaneous limitation (iron, silicic acid, irradiance) by mid-summer (Boyd et al. 1999) (Fig. 4). There are presently conflicting evidence of what limits phytoplankton processes in summer, with iron/irradiance (Boyd et al. 2001), iron/silicic acid (Hutchins et al. 2001), and silicic acid (Nelson et al. 2001) being proposed from regional studies. Thus, such a seasonal progression in modes of control as presented in Figure 4 will probably vary with water mass and depend also on the dominant algal taxa. A seasonal progression in the factors controlling diatom bloom dynamics was evident, indirectly, from the bio-optical mooring study of Abbott et al. (2000). Their mooring array has provided the most highly resolved data sets so far on the evolution of a bloom in the POOZ. The ratio of fluorescence to chl, derived from bio-optical sensors, enabled them to propose mechanisms for the onset (shoaling of the mixed layer) and decline of the bloom (silicic acid followed by iron limitation).

CONTROLS ON THE DISTRIBUTION OF ALGAL FUNCTIONAL GROUPS IN THE SOUTHERN OCEAN

The distributions of key algal functional groups such as diatoms or *Phaeocystis antarctica* will determine the biogeochemical mediation of elemental cycles, including carbon, nitrogen, or sulfur (Boyd and Doney in press). Because of difficulties in assessing phytoplankton community structure from space (Ciotti et al. 1999), virtually all data on the distributions of algal groups have been derived from shipboard surveys. Early studies focused on obtaining an inventory of algal species (Hendey 1937), and this continues, with recent surveys reporting a greater diversity of pico- and nanophytoplankton than previously thought (Kang et al. 2001).

The two main bloom-forming groups are diatoms and *P. antarctica.* Diatom blooms have mainly been observed near the PF, other frontal regions such as the Sub-Antarctic front (Sakshaug et al. 1991, Laubscher et al. 1993, Smetacek et al. 1997), and during summer in certain regions of the Ross Sea (Arrigo et al. 1999). *Phaeocystis antarctica* has mainly been recorded blooming in spring, in particular in regions of the Ross Sea (DiTullio and Smith 1996, Arrigo et al. 1999). Occasional blooms of nanoflagellates in the vicinity of the SIZ have also been reported (Kang et al. 2001). In the HNLC waters between the circumpolar fronts, the assemblage is mainly dominated by pico- and nanophytoplankton that make important contributions to both biomass and production (Weber and El-Sayed 1986, Daly et al. 2001, Kang et al. 2001). The picophytoplankton that dominate in subpolar waters are prokaryotic with a marked decline in abundance from north to south (Marchant et al. 1987, Detmer

and Bathmann 1997) and a predominance of picoeukaryotes further south (Gall et al. 2001b).

Most insights into the environmental control of algal community structure have been obtained from perturbation experiments, both deckboard and *in situ*, and to a lesser extent from algal cultures (e.g. Moisan and Mitchell 1999). In many cases the experimental results have provided a mechanistic understanding of the spatial distribution of algal groups, in some cases retrospectively. Diatoms appear to be primarily limited by iron supply, because in virtually all iron enrichments there has been a floristic shift toward this algal group (de Baar and Boyd 2000). Furthermore, the use of molecular markers specific to iron stress in diatoms (LaRoche et al. 1996) has provided evidence of high flavodoxin levels in resident subpolar and polar populations (Timmermans et al. 1998, Boyd et al. 1999, 2000). These data, in tandem with reports of relatively high iron levels at frontal regions (de Baar et al. 1995, 1999), provide explanations for the presence of diatoms at such boundaries (Laubscher et al. 1993). In polar waters iron has stimulated floristic shifts to large diatom species such as *Fragilariopsis kerguelensis* (Gall et al. 2001a). However, there is evidence from subpolar waters in summer (i.e. submicromolar silicic acid) that lightly silicified diatom species thrive under these conditions (Daly et al. 2001, Hutchins et al. 2001). Thus, there is a suggestion of both spatial variations (polar v. subpolar) and a seasonal progression within water masses in the diatom species that respond to iron supply.

Phaeocystis antarctica blooms appear to only be observed south of the Antarctic divergence, and there have been no reported instances of blooms in the vicinity of the PF. Despite the importance of this group to biogeochemical cycling of sulfur (DiTullio and Smith 1996), carbon (*P. antarctica* fixes more C per unit N than diatoms, Arrigo et al. 1999), and its potential for rapid export to depth (DiTullio et al. 2000), uncertainties remain as to what factors control its distribution. Moisan and Mitchell (1999) successfully cultured *P. antarctica* and reported that its photophysiology was better adapted to low light conditions than that of diatoms, a trend supported by observations (incidences of *P. antarctica* blooms only in waters with deeper mixed layers) by Arrigo et al. (1999). However, Mitchell and Moisan (1999) also acknowledged that *P. antarctica* could tolerate high irradiances and acclimate rapidly to pronounced changes in irradiance (via xanthophyll cycling, Moisan et al. 1998). The observations of Smith and Asper (2001) in the Ross Sea in austral spring differ from those of Arrigo et al. (1999) in that they suggest that *P. antarctica* dominates in waters with shallow mixed layers, whereas diatoms dominated deeper mixed layers.
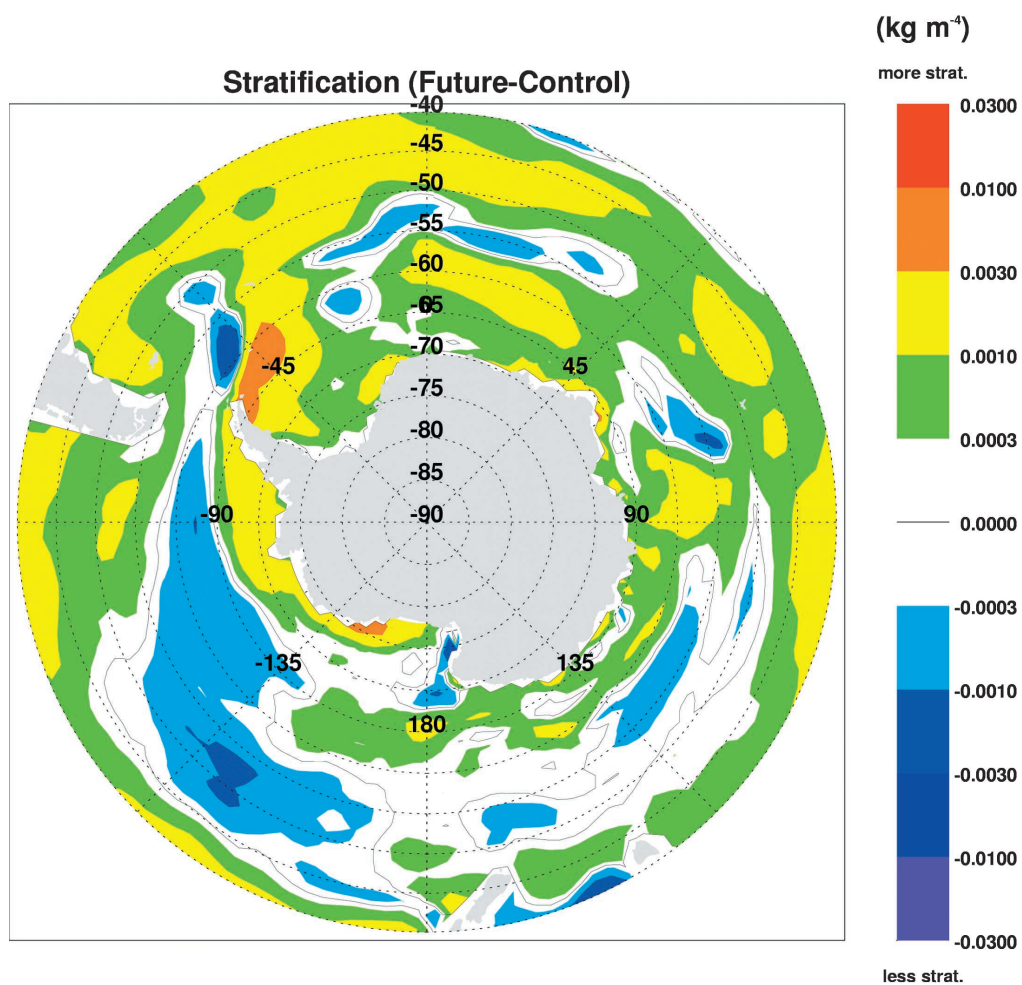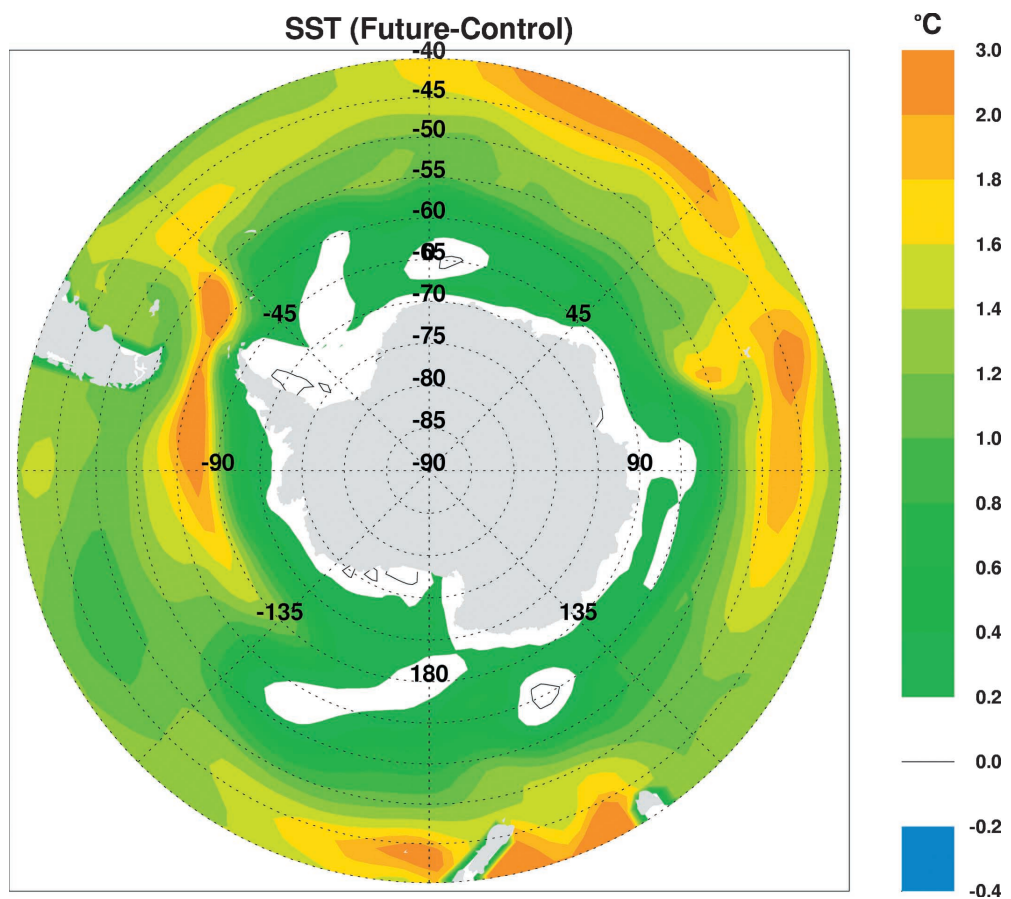
Little is known about the response of *P. antarctica* to iron supply, nor is there detailed information about the seasonal cycle of iron in the Ross Sea (Sedwick and DiTullio 1997, Fitzwater et al. 2000, Measures and Vink 2001). Olson et al. (2000) reported that by using pump-during-probe flow cytometry they could assess the response of *P. antarctica* to iron enrichment. Although the response of this taxon to iron supply was statistically significant, there were wide variations in F_v/F_m (0.2–0.6) by *P. antarctica* in both the control and Fe-enriched treatments (Olson et al. 2000). They concluded that a detailed study of the relationship between iron supply and photosynthetic efficiency is required for *P. antarctica*. There is also a need for observations from the Ross Sea in early spring on both iron levels and irradiance and for experiments on their interplay and subsequent effect on diatoms and *P. antarctica*.

Biogeography may also exert a control as to where different species are present. At the PF, diatoms bloom in spring under comparable environmental conditions that appear to promote spring *P. antarctica* blooms in the Ross Sea; *P. antarctica* blooms early in the season, in waters characterized by higher iron levels (Sedwick and DiTullio 1997), relatively deep mixed layers (Arrigo et al. 1999, but see also Smith and Asper 2001), and high silicic acid levels. Furthermore, in contrast to the PF, in the Ross Sea diatoms are reported to bloom later in the season and in waters characterized by shallower mixed layers (Arrigo et al. 1999, but see Smith and Asper 2001). Is it possible that some other factor in addition to iron, nutrients, and irradiance is responsible for these observed trends in the Ross Sea (Fig. 4)? Tortell et al. (2002) presented evidence, from shipboard experiments in the equatorial Pacific, that CO_2 levels influence species composition and macronutrient uptake stoichiometry. Such that low CO_2 concentrations prompted a floristic shift from diatoms to a *Phaeocystis*-dominated community in tropical waters.

What controls the distribution of other algal functional groups in these waters—in particular non-siliceous cells (referred to here as HNLC species) that dominate under conditions of low iron supply—such as nanoflagellates (Daly et al. 2001) and picoeukaryotes (Boyd et al. 1999, 2000)? Although such small cells are reported to better sequester trace elements such as iron (Sunda and Huntsman 1997), there is evidence that smaller cells are also slightly iron limited, with iron-mediated increases in F_v/F_m for cells less than 5 and less than 2 μm during shipboard (Olson et al. 2000) and *in situ* iron enrichments (Boyd and Abraham 2001). Iron-mediated increases in cell abundances have also been observed for both picoeukaryotes and prymnesiophytes (Gall et al. 2001b). Such increases in stocks are usually transient due to the usually tight coupling with microzooplankton grazers in HNLC waters (Frost 1991, Strom et al. 2000). However, during SOIREE, prymnesiophytes were thought to have been responsible for elevated DMSP levels and were not grazed down until 8 of 9 days of the experiment had elapsed, resulting in elevated DMS levels (Boyd et al. 2000).

In addition to iron supply and herbivory, other factors may influence the distribution of these HNLC species. There is evidence of decreased picoprokary-

SST (Future-Control)

°C
- 3.0
- 2.0
- 1.8
- 1.6
- 1.4
- 1.2
- 1.0
- 0.8
- 0.6
- 0.4
- 0.2
- 0.0
- -0.2
- -0.4

Stratification (Future-Control)

(kg m^{-4})

more strat.
- 0.0300
- 0.0100
- 0.0030
- 0.0010
- 0.0003
- 0.0000
- -0.0003
- -0.0010
- -0.0030
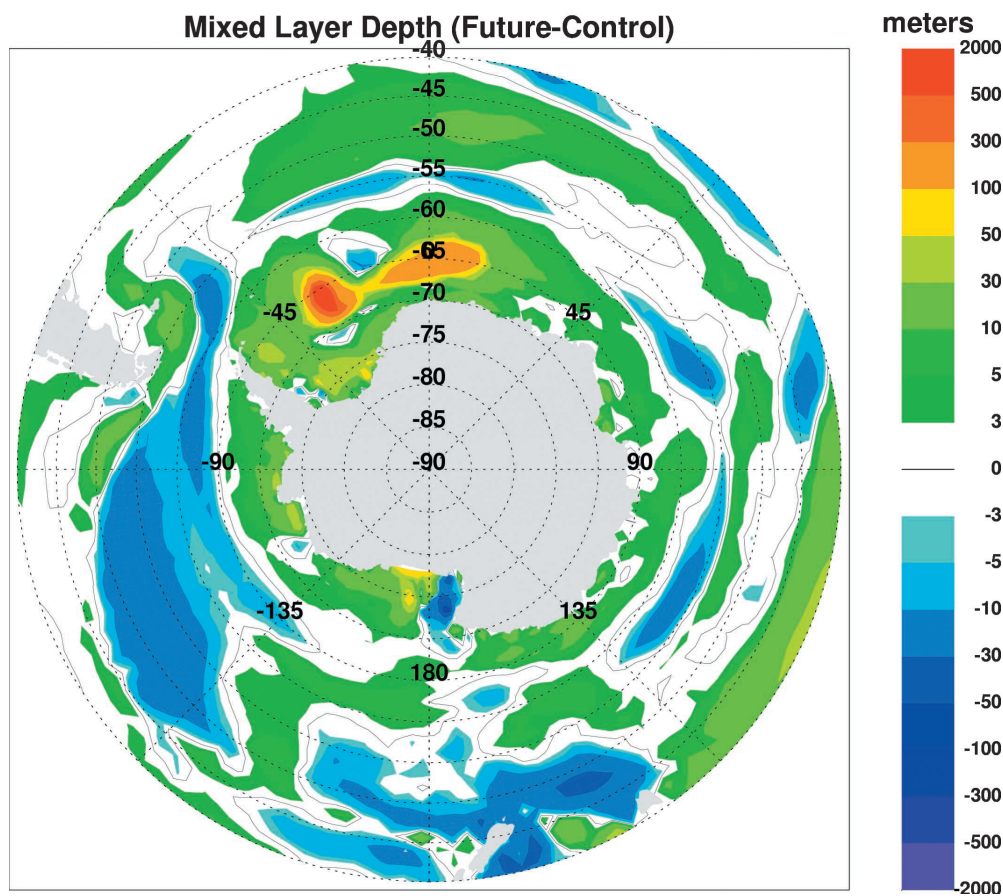- -0.0100
- -0.0300

less strat.

FIG. 5. Continued.

ote abundances with increasing latitude, which is thought to be linked to decreasing water temperature (Marchant et al. 1987, Detmer and Bathmann 1997), but recently Ellwood and van den Berg (2001) suggested a potential link to trace metal concentrations such as cobalt. Irradiance levels will also probably play a key role; Van Leeuwe (1996) is one of the few investigators to look at environmental control of an HNLC species, the flagellate *Pyraminomonas* sp. from waters south of the PF, and reported that both iron and light supply were important determinants of growth rate. Perhaps the best environment to investigate the mode(s) of control on HNLC species is during summer in subpolar waters when there is insufficient silicic acid (<1 μM) for diatom stocks to increase significantly. In recent shipboard iron enrichments, there was evidence of significant increases in nanoflagellate

(Sedwick et al. in press) or picophytoplankton abundances (Boyd et al. unpublished data) in the Indian and Pacific sectors, respectively.

Despite these advances in our understanding of the distribution of phytoplankton taxa in these waters, in the absence of satellite sensors to differentiate between taxa other approaches are needed. Sampling of the phytoplankton assemblage using time-series stations and/or upper ocean moorings with smart bio-optical and water sampling sensors are needed to define their seasonal and biogeographical distributions.

MODELING STUDIES: A TEST OF OUR PROGRESS

Our ability to understand the environmental control of phytoplankton processes can be gauged from how well current models are able to simulate observations or experimental results. Previous models sought

FIG. 5. Predicted changes in (A) sea surface temperature (SST), (B) stratification, and (C) mixed layer depth for the future minus control (2060–2070 minus present day) for polar waters south of 40°S and redrawn as a polar projection from Boyd and Doney (2002). Climate-induced changes in ocean physics are estimated from a coupled ocean-atmosphere-land simulation using the NCAR Community Climate System Model (Boville and Gent 1998). The CCSM model run for this scenario and the control simulation are available electronically (labeled b030.02, b030.03, and b030.04; see *www.cgd.ucar.edu/csm/experiments* for details). To account for inter-annual variability, 10-year average monthly climatologies are produced for temperature, mixed layer depth, upwelling velocity, stratification, irradiance, and other properties for the period 2060–2070 for both the Future and Control integrations.

to incorporate data from observations and experiments (on light and vertical mixing, Nelson and Smith 1991). Their findings, such as on the maximum chl levels for a POOZ bloom (1 mg·m^{-3}), did not always match other observations (4–5 mg·m^{-3}; Comiso et al. 1993, Turner and Owens 1995). Such mismatches reflected missing components from the models, for example, the effects of iron supply that tend to reduce the magnitude of algal loss terms, and hence increase the maximum sustainable chl levels, by selecting for species less prone to herbivory or sinking (Boyd et al. 2000).

The complexity of Southern Ocean waters where several modes of control on phytoplankton may be occurring concurrently is reflected in the recent development of multielement models (Hense et al. 2000, Lancelot et al. 2000). Furthermore, the performance of models may now be more readily validated via remote sensing (Moore et al. 1999) and time-series (Jeandel 1997) data sets. Examples include the validation of the one-dimensional coupled physical-biogeochemical model of Pondaven et al. (2000) using the 5-year KERFIX time series (Fig. 1). Pondaven et al. (2000) had considerable success in simulating the annual cycles of nutrients and plankton. Walsh et al. (2001) also used JGOFS and RACER (Fig. 1) data to validate their one-dimensional numerical model that focused on carbon dynamics with particular emphasis on herbivory. JGOFS data from the Atlantic sector were also used by Lancelot et al. (2000) to validate an ecological model (SWAMCO) of cycling of multiple elements (C, Fe, P, Si, and N) through the planktonic ecosystem. SWAMCO provided a relatively successful set of predictions, suggesting that our understanding of bloom evolution is improving.

Several recent modeling studies attempted to look at specific Southern Ocean systems in more detail. Hense et al. (2000) used a biogeochemical multielement multicompartment model to simulated plankton dynamics at the PF. Furthermore, such multielement models may also be used to simulate actual experiments, such as SOIREE, many aspects of which were simulated closely by Hannon et al. (2001) using a virtually unmodified form of SWAMCO. This suggests that some of the key aspects of the functioning of phytoplankton processes in polar waters have been further understood and assimilated into models. Indeed, Maldonado et al. (2001) compared data on kinetic coefficients for iron uptake from SOIREE with those from other oceanic regimes and reported an encouraging convergence in these estimates that will greatly assist biogeochemical modelers. A similar degree of convergence for kinetic coefficients for silicic acid has been noted for the Pacific (experiments, Nelson et al. 2001) and Indian (modeling, Pondaven et al. 2000) sectors by Nelson et al. (2001).

CLIMATE VARIABILITY AND CHANGE

At present, global circulation models predict that climate change will have a marked effect on the South-ern Ocean (Sarmiento et al. 1998, Bopp et al. 2001). Furthermore, there is growing evidence of warming (Gille 2002) and freshening (Wong et al. 1999) of intermediate Southern Ocean waters and of persistent warming trends on Sub-Antarctic islands (Smith 2002). Simulations from a coupled ocean atmosphere model indicate that the most likely scenario—in terms of altered environmental conditions—is a general increase in warming, stratification, and alteration of the depth of the surface mixed layer (Fig. 5). Model simulations point to 74% of the areal extent of the Southern Ocean experiencing an increase of at least 0.5°C, 57% will experience an increase in density stratification (at 50 m depth) of at least 0.003 kg·m^{-4}, and 18% a shoaling of more than 5 m in mixed layer depth (28% of polar waters will experience a deepening of >5 m) (S. Doney and J. Kleypas, personal communication). The simulations, at a regional scale, suggest a range of responses to climate change for mixed layer depth, with regions/basins characterized by either shallower or deeper mixed layers that are driven by changes in sea-ice cover and/or the physical oceanography (Fig. 5). However, caution is urged in interpreting these predicted changes at the basin-scale level because a recent Intergovernmental Panel on Climate Change review concluded that present climate model projections vary considerably at the regional scale, where coupled ocean atmosphere models are less well constrained (Houghton 2001). Thus, it is not advised to interpret these model simulations for the Southern Ocean over the next 70 years beyond that of the general trends of warming, increased stratification and alteration of mixed layer depth.

A major challenge will be to understand how such an altered environment will impact phytoplankton processes. Bopp et al. (2001) projected that increased stratification will reduce vertical nutrient and trace element fluxes by up to 10%, whereas a shoaling of the mixed layer will elevate mean underwater irradiances. Based on our present understanding of environmental control of phytoplankton processes, elevated mean underwater irradiances will reduce algal iron quotas (Raven 1990, Sunda and Huntsman 1997). However, such changes may be offset by a reduction in the vertical fluxes of iron, the main mechanism by which iron is supplied to these waters (de Baar et al. 1995, Measures and Vink 2001). The large inventory of unused nitrate and phosphate in surface waters (Levitus et al. 1993) suggests that any predicted reductions in vertical supply have little influence on the availability of these nutrients. However, alteration of winter reserve concentrations of silicic acid, which increase southward by more than 15-fold from Sub-Antarctic waters (Levitus et al. 1993), may have implications for diatom-dominated communities, particularly in subpolar waters. Nelson et al. (2001) reported pronounced changes in silicic acid uptake kinetics along a meridional silicic acid gradient. Although diatoms may alter the degree of silicification in responses to reduced silicic acid concentrations (Martin-Jèzèquel et al. 2000),

it is not known as to how the nutrient uptake kinetics of many species might alter in response to reduced nutrient supply (Boyd and Doney, in press b).

It has been proposed that the propagation of the Antarctic Circumpolar Wave around the Southern Ocean (White and Peterson 1996) and the associated changes to stratification and mixed layer depth might be used as a natural laboratory to study such climate-mediated effects (Le Quéré et al. 2002). On the basis of this review, it is also advocated that a new suite of perturbation experiments, in which both irradiance and nutrient supply are altered, must be designed using such model predictions to address these key issues.

CONCLUSIONS AND NEW GOALS

Data from two sources, observational and experimental, have provided a framework by which to better understand the modes of environmental control in the Southern Ocean. Over the last decade, consensus on the key modes of control (iron, irradiance, and silicic acid) is now emerging for different oceanic basins (note top-down control was not considered here). However, as the seasonal progression of controlling factors is region and taxon specific and in some cases the interplay of these factors (silicic acid and irradiance) is less clear, they will require further study. There is also a need to understand better the functioning and physiology of key algal species such as *P. antarctica*, and whether there is a species-specific relationship between diatoms, silicification, and silicic acid uptake kinetics. It is also recommended that the functioning of the species that dominate iron-poor HNLC waters (and that are under concurrent top-down control by grazers) require further investigation, perhaps using physiological/molecular markers and culture studies.

At present, global circulation models predict that climate change will have a marked effect on the waters of the Southern Ocean (Sarmiento et al. 1998). From such simulations, the most likely scenario—in terms of altered environmental conditions—is warming, increased stratification, and alteration of the mixed layer depth. A major challenge will be to understand how such an altered environment (and the interplay of projected changes in vertical nutrient/trace element fluxes and altered mean light levels) will impact phytoplankton processes.

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