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Bottom-up versus top-down control in phytoplankton of the Southern Ocean

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Abstract: Oceanic phytoplankton communities are a mixture of various algal functional groups, all of which are of different sizes, have variable physiologies, and interact differently with disparate herbivores. We suggest that polar plankton communities, and specifically the larger phytoplankton of Southern Ocean HNLC (high nutrient, low chlorophyll) systems, are controlled primarily by bottom-up processes, but that smaller (pico- and nanoplankton) reach an equilibrium that is set simultaneously by light, iron and grazing by microzooplankton. Thus Southern Ocean phytoplankton conforms to the "ecumenical iron hypothesis", albeit with the further addition of light as an environmental control. Examples of bottom-up controls include iron availability, irradiance regulation (either by the incident surface irradiance as controlled by season and sea ice cover, or by the effects of vertical turbulence and mixed layer depths), and macronutrient availability (silicic acid and nitrate). While the contribution of various phytoplankton taxa varies spatially and temporally within the Antarctic, we suggest that this is largely due to the specific responses of the important functional groups to the patterns of physical forcing and micronutrient inputs, rather than to changes in controls by small and large grazers. Examples of abiotic and biotic controls are examined from representative regions of the Antarctic, including continental shelf regions and open ocean HNLC systems. Results from models further support our contention that bottom-up control of large forms is paramount in the Southern Ocean, but top-down controls play an important part in regulating the equilibrium standing stocks of smaller taxa. If bottom-up control is indeed universal in the Antarctic, then it has profound implications for the understanding of interannual variability, food web structure, and population dynamics of higher trophic levels in both the present and past Southern Ocean.

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Introduction

In the past few decades ecologists and oceanographers have debated the importance of the two potential controls of phytoplankton biomass and growth. Specifically, phytoplankton standing stocks and production are considered to be under "bottom-up control" when irradiance levels and nutrient concentrations limit their increase, and under "top-down control" when herbivorous grazing limits algal stocks (e.g. Lehman 1991, Banse 1994, Verity & Smetacek 1996). This is similar and related to the trophic cascade concept, in which each trophic level within a food web is inversely and directly related to trophic levels above and below it (Carpenter *et al*. 1985, Brett & Goldman 1996). Trophic cascades have largely been studied in experimental mesocosms, ponds and lakes, but infrequently in marine systems, where immigration and emigration make such analyses difficult or impossible. The results from freshwater systems are controversial and remain open to interpretation (Brooks & Dodson 1965, DeMelo *et al*. 1991). A meta-analysis of 54 separate experiments suggested that the response of phytoplankton to the addition of an additional trophic level was highly skewed, with strong responses (i.e. clear changes in phytoplankton upon manipulation of a higher trophic level) in some cases, but relatively weak effects in others (Brett & Goldman 1996). The quantitative connection of zooplankton to higher trophic levels (such as fish) was shown to be far stronger than any feedback on primary producers.

Banse (1992, 1994) used a simple, one-dimensional model of *in situ* chlorophyll changes to estimate the losses due to grazing in a variety of locations. The equation was

$$\frac{d[Chl]}{dt} = [Chl](k - a - m - s - g \pm x) \quad (1)$$

where Chl = the chlorophyll a concentration in the surface layer, k the phytoplankton growth rate, a the vertical advection flux term (which may be positive or negative), m = changes due to vertical mixing, s = losses due to sinking, x is a horizontal movement term (can be either positive or negative), and g is the grazing loss term. Banse looked at regions where short-term (e.g. over days to a week) changes in chlorophyll are close to zero, and where zonal horizontal changes are minimal or zero. Therefore,

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$$g = k - m - s - a \quad (2)$$

Because phytoplankton growth rates are relatively well known, net grazing rates can be estimated by knowing the other (vertical) terms. His analysis suggested that grazing was an extremely important control on phytoplankton biomass, even in areas where nutrient inputs were substantial and phytoplankton growth rates were high.

Recent application of novel, *in situ* manipulations in oceanography has provided another tool to assess the controls of phytoplankton biomass and growth. This procedure adds the inert tracer sulphur hexafluoride to a defined patch of surface water and assesses the vertical and horizontal alterations by quantifying the changes in SF_6 (e.g. Coale *et al*. 1996, Boyd *et al*. 2000, Watson & Ledwell 2000). In conjunction with SF_6 additions, other nutrients (specifically the micronutrient iron) are added so that the diffusive losses of the specific nutrient can be measured as well. A number of these *in situ* enrichment experiments have been conducted in HNLC waters including the Southern Ocean (reviewed by Boyd 2002), and in nearly all cases have demonstrated that iron was controlling the growth of all phytoplankton, even though variations between the functional groups do occur. Similarly, certain taxa appear to be favoured by certain environmental conditions and nutrient ratios (e.g. diatoms are often found in regions with high nutrient fluxes; nitrogen fixers in areas of low N:P ratios). Thus, the relative quantity of the nutrients (i.e. the N:P:Si:Fe ratio) is also an important element structuring the phytoplankton community and the related plankton biomass and growth.

Within the ocean there are a number of large-scale gradients that exist between the tropics and polar oceans (Table I). For example, the effects of seasonality are much greater in polar regions than in the tropics, and hence phytoplankton growth, vertical fluxes from the surface layer, and food web processes are much more variable on seasonal than on daily or annual scales. Also, because tropical systems are much warmer, the temporal lags between growth and reproduction of phytoplankton and mesozooplankton are reduced, and coupling between the two is greater (Cushing 1981). Conversely, at the low temperatures found in the Antarctic, a large temporal lag often exists between phytoplankton and mesozooplankton, which has been suggested to allow the phytoplankton biomass to increase substantially (Cushing 1981). However, physical controls (e.g. limitation by available irradiance, either via seasonal variations in solar angle, vertical mixing by winds or convection driven by ice formation, or the simple presence of ice and snow as a significant attenuator) are at times and places critical in the Southern Ocean, and the initiation of the bloom in spring is largely under physical control (Lancelot *et al*. 1993). The termination of the bloom can be controlled by limitation by nutrients (most likely iron), self-shading and/or irradiance at elevated biomass, or removal *via* grazing, lysis, particle aggregation and/or sinking. Furthermore, since microzooplankton are ubiquitous and often similar in size to their phytoplankton prey, it remains possible that microzooplankton provide some top-down control of certain phytoplankton functional groups, at least at some time during the growing season (Lancelot *et al*. 1993).

Table I. Comparison between tropical and polar regions of various relative factors operative in each system.

Factor	Tropical regions	Polar regions
Temperature	High	Low
Seasonality	Low	High
Biological control of phytoplankton	High	Low
Maximum phytoplankton biomass	Low	High
Vertical export	Low	High
f-ratio	Low	High
Ambient macronutrient concentrations	Low	High
Abundance of diatoms	Low	Often High
Abundance of cyanobacteria and prochlorophytes	High	Low
Main source of iron	Atmospheric	Upwelling
Mean mesozooplankton abundance	Low	Low
Irradiance limitation	Rare	Frequent

Individual taxa also vary along a north-south gradient. For example, cyanobacteria (both small, single-celled forms and filamentous nitrogen fixers) and prochlorophytes are extremely important components of warm, oligotrophic regions, but are virtually absent in the polar regions. Coccolithophorids have traditionally been considered as warm water species, but recently large blooms of *Emiliana huxleyi* (Lohman) Hay & Mohler have been observed in the Bering Sea region (Olson & Strom 2002). Conversely, diatoms are often found in cool (temperate and polar), nutrient-rich regions, but this distribution may be due more to nutrient and irradiance requirements rather than to temperature *per se*. Some colonial prymnesiophytes such as *Phaeocystis* sp. are commonly found in colder regions (with elevated nitrate concentrations; Lancelot *et al*. 1998), but they are also found in temperate and warm waters (Schoemann *et al*. 2004). The Southern Ocean (particularly south of the Polar Front) is often dominated by heavily silicified diatoms, but locally and regionally large contributions of haptophytes, chrystophytes, and dinoflagellates have been observed. Gradients in taxa do occur, but understanding these patterns remains far from complete.

Our objective in this paper is to review published data describing both bottom-up and top-down controls on phytoplankton in order to test the hypothesis that phytoplankton assemblages in the Southern Ocean at all times are controlled by physical and chemical factors. Emphasis is placed on data collected from experimental mesocosms and *in situ* iron enrichment experiments in high nutrient, low chlorophyll (HNLC) regions of the Southern

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Ocean in order to directly compare regulation of phytoplankton here with that of other systems like the Equatorial Pacific. From these patterns we draw conclusions about the controls of phytoplankton functional groups throughout the Southern Ocean.

Bottom-up and top-down controls of Southern Ocean phytoplankton: case studies

Mesocosm experiments

Kuparinen & Bjørnsen (1992) reported the results of shipboard mesocosms (*c.* 25 L each) that were manipulated to assess the controls of phytoplankton growth and biomass accumulation. The two experiments were conducted in the Weddell Sea and Scotia-Weddell Confluence in late spring 1988. They sampled water from the mixed layer (elevated with macronutrients; no attempt was made to sample using trace metal clean conditions) and altered macronutrient concentration, irradiance (contrasting 90 vs 6 µmol photons m^{-2} s^{-1}), and community composition by filtering through 5, 20 and 200 µm screens to selectively remove the larger forms. The phytoplankton assemblage was initially dominated by cryptophytes, prymnesiophytes, prasinophytes and diatoms (Becqevort *et al*. 1992), and initial chlorophyll *a* concentrations were 0.4 and 2.8 µg L^{-1}, respectively. Growth of autotrophs was determined from changes in chlorophyll concentrations. Kuparinen & Bjørnsen (1992) suggested that their mesocosm manipulations implied "a strong top-down control by dinoflagellates on phytoplankton". However, their data may not warrant such a strong statement (Table II). In both experiments the range of estimates of growth rates for duplicates of controls or treatments was only 0.03 d^{-1}, which suggests that the difference between some treatments may not be significant (replicates were not available). For example, the difference between controls and macronutrient additions is small and can be taken as evidence that no macronutrient limitation occurs (as Kuparinen & Bjørnsen concluded). The difference between the growth of the control and < 20 µm fraction is also small (0.03 d^{-1}), and while Kuparinen & Bjørnsen (1992) suggested that this difference reflected "control by grazing in the size fraction 20–200 µm", we conclude that this difference is within the error of the chl *a*-based net growth rate determination and is not significantly different. We also believe that the > 20 µm phytoplankton (largely diatoms, colonial prymnesiophytes and autotrophic dinoflagellates) were not controlled by grazing but were growing at their maximum potential growth rate for the environmental conditions present. Net growth in the < 5 µm fraction was 0.23 d^{-1} (relative to the control net growth rate of 0.30 d^{-1}; Table II). Using Eq. (1) (the coefficients m, s and a are by definition zero in these experiments), the difference between the control and < 5 µm fraction's growth rate can be taken as a measure of grazing on the > 5 µm forms (in this case, 90% of the biomass). This also assumes that the growth rate of the larger sizes is equal to that of the control, which is reasonable given that they contributed most of the biomass to that fraction. The grazing rate would be 0.07 d^{-1}, or 23% of the growth of the > 5 µm phytoplankton. While this grazing rate is not insignificant, it does not suggest a strong coupling between micrograzers and the smallest phytoplankton cells, and in turn a strong top-down regulation. We also cannot exclude the presence of grazers in the fraction < 5 µm (Becquevort *et al*. 1992), and realize that mortality of delicate microherbivores can occur in containers, particularly when experiments last many days (Venrick *et al*. 1977). The growth observed by Kuparinen & Bjørnsen (1992) is less than the temperature-limited growth rate (Eppley 1972), but Eppley's equation predicts growth under optimal light and nutrient conditions, which may not have been present in the mesocosms (which were illuminated with artificial lights). Becquevort *et al*. (1992) suggested that the nanoplankton were closely coupled to their predators (predator:prey ratio of 0.4) and that their sizes were nearly the same, but they had no direct estimates of ingestion to support this. Based on these two studies, it is uncertain if the control was indeed significantly impacted by grazing-induced mortality or if the size fractionations did not adequately remove the active nanoplanktonic grazers.

Table II. Summary of net growth rates determined from changes in chlorophyll concentrations from the mesocosms of Kuparinen & Bjørnsen (1992). Reduced irradiance reflects a 93% decrease. nd = no data.

Location/Treatment	Weddell Sea	Weddell–Scotia Confluence
Control	0.235*	0.300*
< 20 µm	nd	0.33
< 5 µm	nd	0.23
+ Macronutrients	0.255*	0.28
Reduced irradiance	0.13*	0.15
Reduced irradiance, < 20 µm	nd	0.18

* Arithmetic mean of two independent measurements

A second study that involved *in situ* mesocosms was reported by Agusti & Duarte (2000). They enclosed large (35 m^3) volumes of water in the shallow waters of Livingston Island (62°39.6'S, 60°22.4'W) in summer and compared the changes in biological and chemical variables within and outside of the enclosures through time over 25 days. A large bloom of diatoms developed within the mesocosm, and this bloom did not occur outside the enclosure. The bloom clearly resulted from the improved irradiance environment inside the mesocosm, since the enclosure reduced turbulence and allowed the settling of glacial flour, thereby greatly decreasing attenuation of irradiance within the mesocosm. Thus the growth of the *in situ* assemblage in this embayment was largely limited by irradiance, but the site is far from typical of a coastal Antarctic site. Phytoplankton net growth rates in the mesocosm averaged 0.53 d^{-1}, and short-term growth rates

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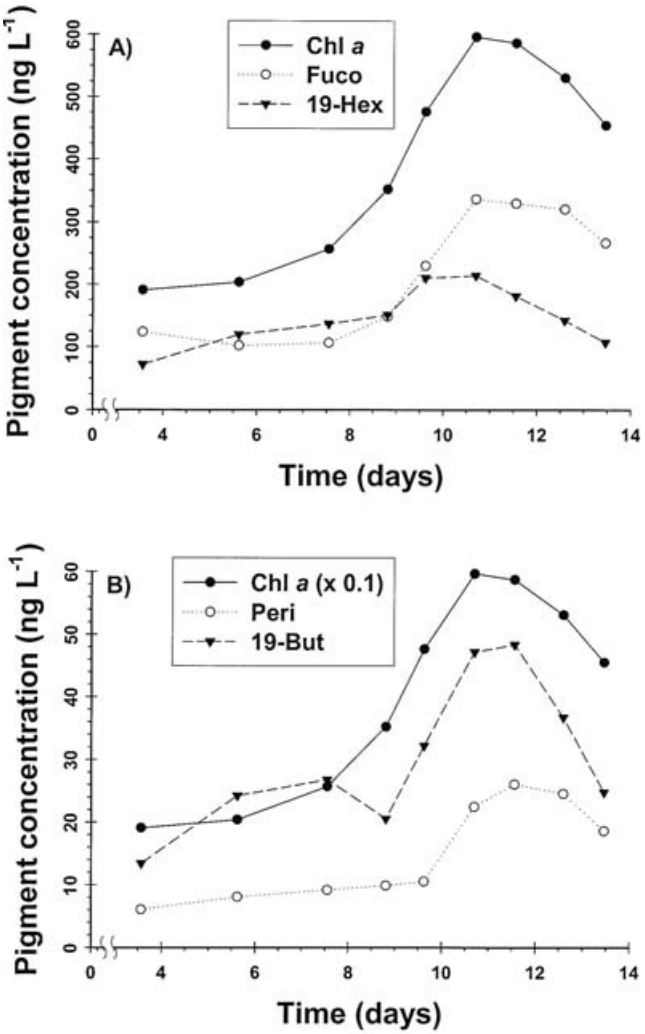

Fig. 1. The increases in pigment concentrations in an iron-enriched patch at 61°S, 139°E as part of the SOIREE experiment. a. The response of chlorophyll, fucoxanthin, and 19-hexanoyloxyfucoxanthin through time to iron enrichment, and b. the response of chlorophyll, peridinin and 19-butanoyloxyfucoxanthin through time to iron enrichment.

were even greater. Even though the experiment did not directly investigate the effects of top-down control, in the coastal waters near Livingston Island it is apparent that phytoplankton production and accumulation is controlled by physical and chemical factors.

A large-volume (25 L) experiment was conducted in the Ross Sea in summer on assemblages dominated by the prymnesiophyte *Phaeocystis antarctica* Karsten (Smith *et al*. 1998). *Phaeocystis antarctica* forms large colonies, and it has been suggested that this enables the species to escape grazing control by virtue of its size and nature of the colonial matrix (Lancelot *et al*. 1998, Hamm 2000). The investigation of Smith *et al*. (1998) did not directly address bottom-up and top-down controls, but simply grew large volumes of water at saturating irradiances and nutrient levels (nitrate concentrations were initially 25 µM or more). *Phaeocystis antarctica* grew at different rates in experiments that were initiated from different locations and times, but the net growth rate determined from chlorophyll changes was 0.35 d^{-1}. This rate is similar to the maximum rate of increase observed by Kuparinen & Bjørnsen (1992). Given the marked increases in biomass and rapid growth, we suggest that colonial *Phaeocystis* growth was under bottom-up control. Reductions in growth ultimately occurred after some 12 days, but these decreases resulted from nutrient limitation and not grazing losses.

Table III. Biomass accumulation (net growth) rates from the *in situ* iron enrichment experiment SOIREE. The rate calculated (µ) is the maximum rate of pigment increase measured over at least three successive days (apparent exponential growth phase). All growth rates were calculated assuming exponential growth.

Functional Group	Marker Pigment	µ (d^{-1})
All phytoplankton	Chlorophyll *a*	0.277
Diatoms	Fucoxanthin	0.421
Autotrophic dinoflagellates	Peridinin	0.453
Chrysophytes	19-butanoyloxyfucoxanthin	0.437
Type 4 Haptophytes	19'-hexanoyloxyfucoxanthin	0.216

In situ *iron enrichment experiments*

Southern Ocean Iron Enrichment Experiment: SOIREE

The first *in situ* iron enrichment experiment in the Southern Ocean was conducted south of the Polar Front at 61°S, 139°E, in austral summer 1999 when surface iron was less than 0.1 nM (Boyd *et al*. 2000). Like other Fe-addition experiments (Coale *et al*. 1996), inorganic iron was added along with SF_6 as a tracer to a patch of water, and the changes in phytoplankton biomass, production and composition were observed for 13 days. Iron additions clearly increased pigment-based phytoplankton growth rates of *all* taxa (Boyd *et al*. 2000) and altered the assemblage composition by favouring diatoms over other taxa (Gall *et al*. 2001). Thus the response was similar to that found in the equatorial Pacific and reinforced the ecumenical iron hypothesis: all forms respond to iron additions, but grazers quickly re-establish a new steady-state with the smaller forms, whereas larger groups (such as diatoms) rapidly increase in biomass and are unchecked by herbivorous removal. The specific responses of various taxonomic groups, as determined by HPLC data, reinforce that feature (Fig.1): diatoms increased in parallel to total chlorophyll and contributed significantly to that increase, but other taxa also responded positively and increased in abundance. For example, 19'-hexanoyloxyfucoxanthin, a marker for type 4 haptophytes (such as *Phaeocystis* sp.), doubled during the experiment, peridinin (autotrophic dinoflagellates) increased more than four-fold, and 19-butanoyloxyfucoxanthin (chrysophytes) increased by

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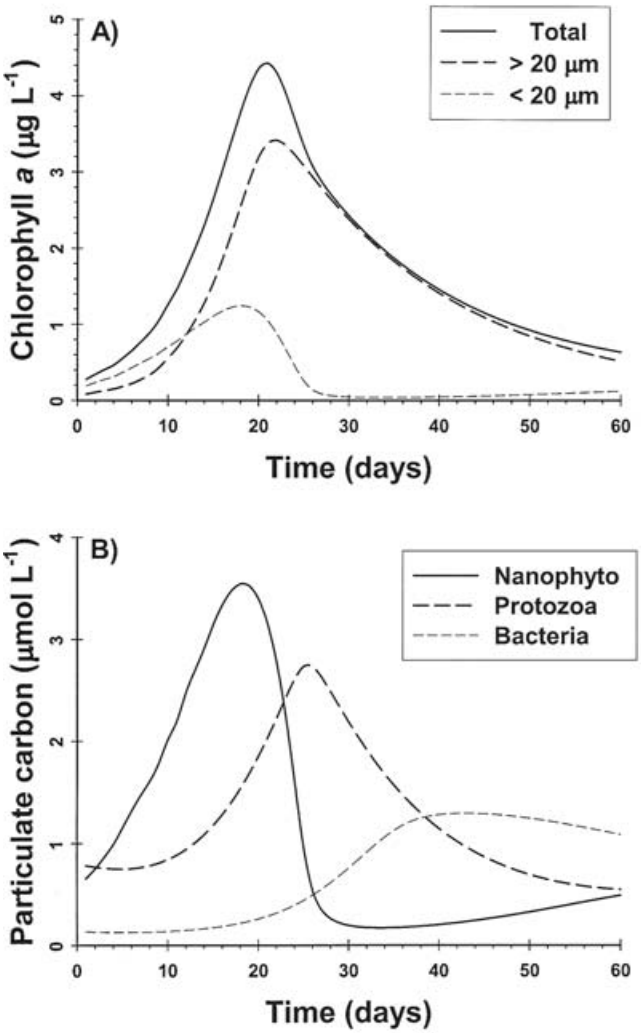

Fig. 2. The SWAMCO (Hannon *et al*. 2001) model of the response of **a.** different phytoplankton size classes and **b.** micrograzers to iron enrichment in SOIREE. The > 20 µm fraction increases and eventually is limited by iron concentrations, whereas the < 20 µm fraction increase, while noteworthy, is less and controlled quickly by grazer-induced losses.

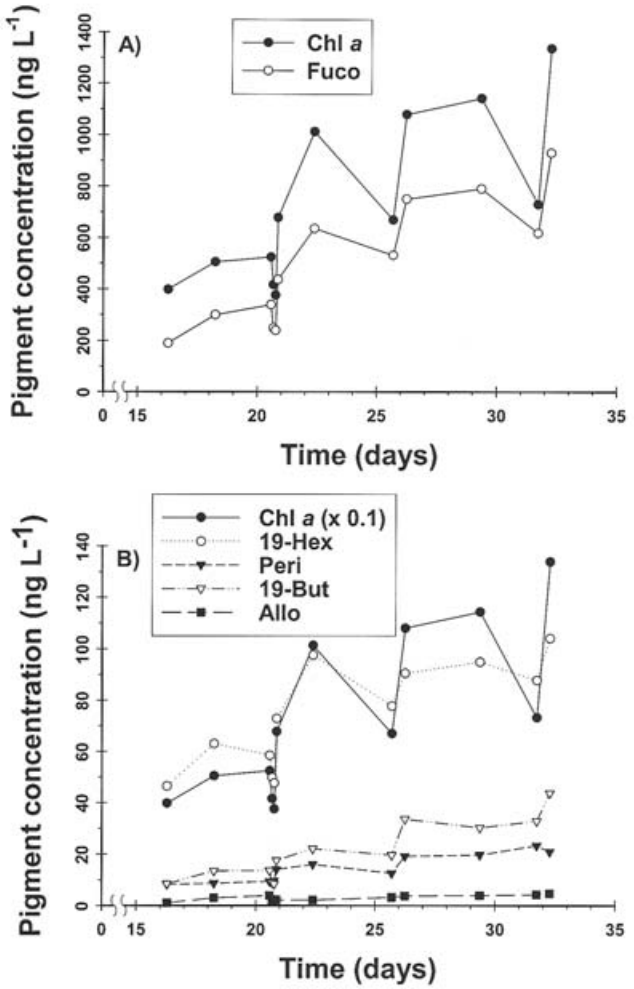

Fig. 3. The increases in pigment concentrations in an iron-enriched patch at 65°S, 170°W as part of the SOFeX experiment. **a.** The response of chlorophyll and fucoxanthin through time to a single iron addition, and **b.** the response of chlorophyll, peridinin, 19-hexanoyloxyfucoxanthin, alloxanthin and 19-butanoyloxyfucoxanthin through time to the same iron enrichment.

360%. Indeed, *all* functional groups responded positively to iron additions. Net growth rates calculated for these groups from changes in the pigment concentrations, both in the exponential phase and over the observation period, are summarized in Table III. Rates were quite high (up to 0.45 d^{-1}, or 0.66 doublings d^{-1}), although net growth of haptophytes was less due probably to control by small grazers. All groups appeared to respond positively to iron addition, which suggests that iron addition relieved growth limitation and allowed for the establishment of a new equilibrium condition. Indeed, the new equilibrium (as well as the initial steady-state) was set by both rates of iron inputs and grazer removal. Microzooplankton (dominated by ciliates) responded by increasing their biomass after the increase in phytoplankton growth and biomass (Hall & Safi 2001), which suggests that the small grazers responded to the increased prey biomass and re-established grazing control. Because larger cells are grazed by mesozooplankton, and because those grazers have a complex life history that takes much longer to respond to variations in food, grazing control of larger cells is not re-established within the duration of *in situ* enrichment studies. However, at least for the smaller phytoplankton groups, bottom-up and top-down controls appeared to be closely coupled in the generation of the steady-state biomass level.

A modelling study of the SOIREE results using the SWAMCO model (Lancelot *et al*. 2000) also suggested that control of nanoplankton by microzooplankton grazers could be quickly re-established (Fig. 2; Hannon *et al*. 2001). The model runs were conducted for the iron-fertilized waters using *in situ* iron concentrations and meteorological

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Table IV. Biomass accumulation rates from the *in situ* iron enrichment experiment SOFeX. Rates were calculated from the change of the marker pigment from the start to the maximum pigment concentration measured. All rates were calculated assuming exponential growth.

Functional Group	Marker Pigment	μ (d^{-1})
All phytoplankton	Chlorophyll *a*	0.076
Diatoms	Fucoxanthin	0.099
Autotrophic dinoflagellates	Peridinin	0.042
Chrysophytes	19-butanoyloxyfucoxanthin	0.043
Type 4 haptophytes	19'-hexanoyloxyfucoxanthin	0.050
Cryptophytes	Alloxanthin	0.009
Cyanobacteria/Prochlorophytes	Zeaxanthin	0.159

forcing. The model (run for 60 days after the initial Fe infusion) showed that nanoplankton-chlorophyll reached a maximum some 18 days after fertilization, whereas > 20 μm phytoplankton became maximal at *c.* 22 days (about 10 days after the observation period). The < 20 μm fraction decreased rapidly (by day 26) to background levels, coincident with an increase in protozoan biomass (Fig. 2b, whereas the larger size fraction decreased much more slowly due to growth limitation by iron and losses from the euphotic zone.

Southern Ocean Iron Experiment (SOFeX)

A similar analysis was completed using the pigment data collected as part of SOFeX (Southern Ocean Iron (Fe) Experiment). SOFeX was conducted at 66.45°S, 171.8°W in January–February 2002, and a total of four iron additions were made over 16 days. Mixed layers within the enriched patch averaged 45 m, slightly less than those encountered during SOIREE. All pigment concentrations increased within the enriched patch (Fig. 3), and diatoms (fucoxanthin) provided the greatest contribution to this increase. However, as in SOIREE, all other taxa also increased, including cryptophytes (delineated by the pigment alloxanthin) and cyanobacteria/prochlorophytes (zeaxanthin). The estimated net growth rates (Table IV) were much lower than those observed in SOIREE (Table V). The lower rates probably resulted from the fact that no iron additions were made after Day 16 of the experiment. Cyanobacteria/prochlorophytes actually had the most rapid growth during SOFeX, but it should be noted that the concentrations of zeaxanthin detected were at all times extremely low. Although net growth was modest for

Table V. Relative growth rates of functional groups observed in SOFeX and SOIREE. Note that the experimental design (e.g. frequency of iron enrichment) was different between the two experiments.

Functional group	Marker pigment	$\mu_{SOFEX}:\mu_{SOIREE}$
All phytoplankton	Chlorophyll *a*	0.472
Diatoms	Fucoxanthin	0.702
Autotrophic dinoflagellates	Peridinin	0.232
Chrysophytes	19-butanoyloxyfucoxanthin	0.056
Type 4 Haptophytes	19'-hexanoyloxyfucoxanthin	0.325

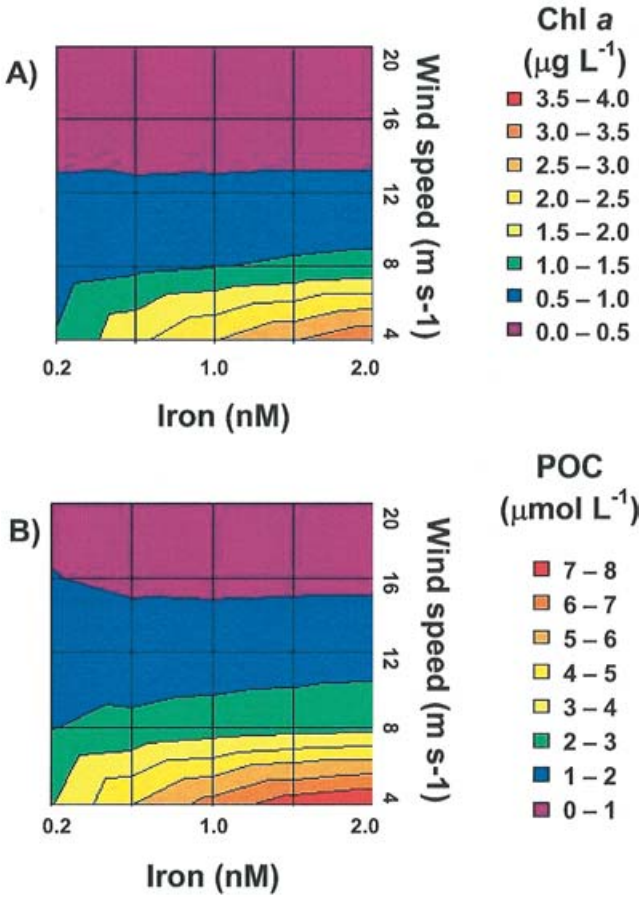

Fig. 4. SWAMCO model predictions of upper-mixed layer **a.** nanophytoplankton, and **b.** micrograzers biomass accumulation under different scenarios of iron and and wind stress. The latter determines the depth of the upper-mixed layer and hence light availability.

all taxa over the long time scales of these measurements (weeks), it was in all cases positive and suggests the importance of iron in controlling the steady-state phytoplankton biomass and growth. However, size fractionation experiments by Landry *et al*. (2002) showed no increase in the less than 5 μm fraction, and a modest increase in the 5–10 μm fraction. This suggests that the smaller forms were effectively controlled by microzooplankton activity over the duration of the experiment. Furthermore, since the sizes > 20 μm all showed substantial increases, this suggests that bottom-up control of larger forms was not re-established over the duration of the experiment (i.e. weeks), whereas the initial stimulation of even the smaller forms was effectively controlled by the activity of grazers.

Discussion

Experimental manipulations of the ocean have provided direct experimental evidence on the relative importance of bottom-up vs top-down controls in open ocean marine

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systems, particularly in HNLC systems. In nearly all cases the smaller forms (< 5 µm) initially responded positively, but not to the extent that the larger forms (> 20 µm) did. For example, in IRONEX-II (4ºS, 105ºW) the biomass of cyanobacteria more than doubled over three days, even though their contribution to the percentage of total chlorophyll decreased due to the greater response of the diatoms (Landry *et al*. 1997). Indeed, diatom contributions to chlorophyll in IRONEX-II increased dramatically (from 0.01–1.81 µg L^{-1}) and accounted for 81% of the total chlorophyll at the end (relative to 7.2% at the start of the experiment). As Landry *et al*. (1997) stated, "small phytoplankton grew at rapid, but usually less than physiological maximal, rates". This apparently occurs in the Southern Ocean as well, despite the fact that the taxonomic composition of the smaller forms is different and that the water temperatures are near zero and even below. That is, small forms of HNLC regions of the Southern Ocean are physiologically limited by iron, and when this limitation is removed, the standing stocks increase due to rapid growth, but the increase is quickly controlled by microzooplankton grazing, and a new equilibrium is established. Hence the control via top-down and bottom-up factors appears to be closely linked, and the addition of iron induces a transient biomass increase; however, the co-limitation is quickly re-established. This pattern is also corroborated by modelling studies with varying physical (ambient light) and iron conditions (Fig. 4). Model results show that both the maximum biomass reached by small phytoplankton and their grazers is determined by the iron concentrations and ambient irradiance.

Control of the larger forms by mesozooplankton grazing appears to be less effective. In both tropical and polar systems, diatoms bloomed in response to iron additions, and the increased growth rates were largely uncoupled from mesozooplankton reproduction and growth. Hence diatom chlorophyll increases until growth becomes limited by micro- or macronutrients (Fe, N; in the equatorial Pacific nitrate declined to undetectable levels upon repeated iron fertilization; Coale *et al*. 1996), implying that large phytoplankton in the ocean's HNLC regions are limited by bottom-up controls, rather than biological removal processes. Because different phytoplankton taxonomic groups (as well as within a single group like diatoms) have different iron requirements (de Baar *et al*. 1997, Timmermans *et al*. 2001), and because the photochemical response to iron addition varies by species and occurs at different rates (Peloquin unpublished), predicting the accumulation of single species or groups is difficult.

Given the large gradient in physical and chemical variables that exists between the tropics and polar systems (Table I), it is perhaps surprising that top-down controls are as effective as they appear to be. Indeed, when small forms exist or dominate the assemblages, it appears that throughout the ocean microzooplankton grazing effectively regulates their growth. Because of the similarity in size between microzooplankton and small phytoplankton, the time scales of their biological responses are similar. As a result, the top-down controls can be effective in the Southern Ocean (as in the rest of the ocean) and preclude the accumulation of large amounts of small forms *except* in very unusual conditions. For example, some small crysophytes bloom in areas strongly influenced by glacial run-off (e.g. Arrigo *et al*. 1999, Prézelin *et al*. 2000), and it is likely that the reduced salinities of these regions reduce the standing stocks of microherbivores and allow growth to proceed without top-down control. In tropical regions there have been only two published observations of substantial "blooms" (that is, relatively monospecific accumulations of chlorophyll that are above the long-term mean concentrations) of small forms: a bloom (> 1 µg L^{-1} chlorophyll) of *Synnechococcus* in the tropical Atlantic (Morel 1997) and a bloom of cyanobacteria observed in the Arabian Sea (Bidigare *et al*. 1997). The paucity of accumulations suggests that over most space and time scales in tropical waters, grazer control of picoplankton is extremely efficient.

The converse of the question of why don't small phytoplankton bloom in the ocean is why some species are so successful as bloom formers. Verity & Smetacek (1996) persuasively argued that marine biogeochemical fluxes are driven by key taxa "whose environmental adaptations, whether through behaviour, morphology, physiology or life history, are so strong that they direct trophic relations". Indeed, a number of polar phytoplankton were used to demonstrate the potential of evolutionary adaptations that would allow a taxon to escape predation. For example, they suggested that *Fragilariopsis kerguelensis* (O'Meara) Hustedt, a heavily-silicified diatom that is found near the polar front in large blooms, is "somehow selected for as a grazer deterrent in these waters" of the Southern Ocean. In fact, *F. kerguelensis* significantly increased its biomass during the SOIREE iron enrichment experiment. However, it remains unclear if the highly silicified frustule confers any inherent advantage to this species, or whether it is an intrinsic property that has evolved through time along with other species-specific features. *Fragilariopsis kerguelensis* also forms long chains, and effectively becomes a very large particle and one that is incapable of being ingested by microzooplankton and smaller herbivores.

Another species key example is the haptophyte *Phaeocystis antarctica*, which forms large, recurrent blooms in some areas of the Antarctic (e.g. Ross Sea, Prydz Bay; Lancelot *et al*. 1998). This species has a complex life cycle that involves both colonial forms (up to 1 mm in size) and solitary cells (and exchanges between the forms). Colonies are generally considered to be grazer resistant, whereas solitary cells are actively grazed by microzooplankton (Schoemann *et al*. 2004). However, it recently has been shown in the boreal *Phaeocystis* species

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(*P. pouchetii* (Hariot) Lagerheim) that grazing on solitary cells induces colony formation via a chemical signal (Tang 2003), so that an interaction between grazers and the functional form seems likely. It also is true that in areas where *P. antarctica* reaches very high concentrations that losses due to grazing appear to be extremely limited. While it is possible that the structure and chemical nature of the mucoid sheath inhibits grazing, it is more likely that the simple size of the colonies makes it unavailable to the dominant grazers. Unfortunately, few data are available to test this hypothesis directly. We therefore suggest that large size is perhaps the most effective means to escape grazing in polar systems where the response of the larger herbivores is delayed due to the colder temperatures. Other interactions (allelopathy, morphological adaptations like spines, extensive silicification, etc; Verity & Smetacek 1996) are possible, but increases in size (without a dramatic reduction in growth rate) may be the most effective way to escape grazing control in the Southern Ocean.

Understanding the controls of phytoplankton growth and accumulation is a central focus of biological oceanographers. While polar systems, and the Antarctic in particular, have unique physical constraints that impose structure on the biological regime, we suggest that the biological responses of micrograzers provides for effective top-down controls of small phytoplankton. Larger forms such as diatoms (often those that are important in vertical flux, carbon sequestration and food web dynamics) and *Phaeocystis* colonies are under bottom-up controls. It is essential that we treat "phytoplankton" not as a single, monophyletic group, but as functional groups, each with a different response to environmental and biological constraints. In some cases further differentiation is necessary, and the physical and biological influences on individual species is important to assess. Incorporation of this approach into ecosystem analyses and large-scale models of environmental change will greatly improve their power and predictive capability, and provide new, and perhaps unexpected, insights into the structure and function of the Southern Ocean.

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