GLACIAL-INTERGLACIAL CO_2 CHANGE:
THE IRON HYPOTHESIS

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Abstract. Several explanations for the 200 to 280 ppm glacial/interglacial change in atmospheric CO_2 concentrations deal with variations in southern ocean phytoplankton productivity and the related use or nonuse of major plant nutrients. An hypothesis is presented herein in which arguments are made that new productivity in today's southern ocean (7.4×10^{13} g yr^{-1}) is limited by iron deficiency, and hence the phytoplankton are unable to take advantage of the excess surface nitrate/phosphate that, if used, could result in total southern ocean new production of $2-3 \times 10^{15}$ g C yr^{-1}. As a consequence of Fe-limited new productivity, Holocene interglacial CO_2 levels (preindustrial) are as high as they were during the last interglacial ($\approx$ 280 ppm). In contrast, atmospheric dust Fe supplies were 50 times higher during the last glacial maximum (LGM). Because of this Fe enrichment, phytoplankton growth may have been greatly enhanced, larger amounts of upwelled nutrients may have been used, and the resulting stimulation of new productivity may have contributed to the LGM drawdown of atmospheric CO_2 to levels of less than 200 ppm. Background information and arguments in support of this hypothesis are presented.

INTRODUCTION

One of the great advances of the 1980s was the development of the capability to measure the CO_2 content of ancient air trapped in ice [Berner et al., 1980; Delmas et al., 1980; Neftel et al., 1982; Barnola et al., 1987]. As a result, we now know that global atmospheric CO_2 levels were highest ($\approx$ 280 ppm) during the present (preindustrial) and last interglacial periods and lowest during the glacials (e.g., $\approx$ 200 ppm during the last glacial maximum 18,000 years B.P. [Barnola et al., 1987]). This change in CO_2 concentration from 200 to 280 ppm represents about 170 Gt (gigatons) (billion tons) of C for the Earth's atmosphere. What factor or factors were responsible for these changes?

There is general agreement that oceanic processes were primarily involved, since the oceanic reservoir of CO_2 is about 60 times greater than that for the atmosphere [e.g., Berger and Keir, 1984; Duplessy, 1986]. Several ocean/atmosphere models have been developed. For example, Broecker [1981, 1982a, b] has observed that surface ocean CO_2 and atmospheric CO_2 amounts are lower than expected in comparison to alkalinity and oceanic CO_2 content. This disequilibrium is caused by

the photosynthetic uptake of CO_2 and
removal to the deep ocean when the remains
of the phytoplankton sink away from the
surface. This mechanism of CO_2 removal is
referred to as the "biological pump."
When it is functioning efficiently, atmos-
pheric CO_2 levels are low, and vice versa.

Berger and Keir [1984] have summarized
several models offered in explanation of
CO_2 variation. These involve either phos-
phate extraction, denitrification, coral
reef buildup, and/or changes in ratios of
C:P and/or the organic/inorganic C ratio.
Another group of models deals with changes
in high-latitude circulation and/or pro-
ductivity [Sarmiento and Toggweiler, 1984;
Knox and McElroy, 1984; Siegenthaler and
Wenk, 1984; Toggweiler and Sarmiento,
1985; Keir, 1988]. Broecker and Peng
[1990] recently presented an hypothesis
which calls for CO_2 change in response
to variations in polar surface water
alkalinity.

In general, there appears to be agree-
ment that changes in southern ocean phyto-
plankton productivity could very well have
resulted in the observed rapid glacial-
interglacial changes in atmospheric CO_2
content; however, why productivity rates
changed, if they did, is unknown. For
example, Keir [1988] poses the question of
how a factor of 2-3 increase in Antarctic
production could have occurred. Toggweiler
and Sarmiento [1985] also wonder how high-
latitude productivity could have changed
and note that it is hard to imagine how a
500% increase in high-latitude glacial-
period production could result from a
10-15% increase in insolation alone.

The iron hypothesis deals specifically
with this issue. Arguments are presented
herein that productivity in today's south-
ern ocean is limited by iron deficiency,
and hence the phytoplankton are unable to
take advantage of the excess surface
nitrate/phosphate (Table 1), the use of
which could result in total southern ocean
new production as high as 2-3 Gt C yr^{-1}.
As a consequence of limited new produc-
tivity, Holocene interglacial CO_2 levels
(preindustrial) are as high as they were
during the last interglacial ($\approx$ 280 ppm).

In contrast, atmospheric dust Fe sup-
plies were 50 times higher during the last
glacial maximum [De Angelis et al., 1987].
As a result of this Fe enrichment, phyto-
plankton growth may have been greatly
enhanced, larger amounts of upwelled
nutrients may have been used up, and this
stimulation of new productivity may have
contributed to the drawdown of atmospheric

CO_2 concentrations to less than 200 ppm
during glacial periods. In the sections
that follow, background information and
arguments in support of this hypothesis
are presented.

IRON BACKGROUND INFORMATION

Iron is essential for all life on Earth
and is especially important in oceanic
plant nutrition because chlorophyll cannot
be synthesized, nor can nitrate be re-
duced, nor atmospheric N fixed, without
it [e.g., Rueter and Ades, 1987; Glover,
1977]. However, unlike major building
block elements such as C, N, and P that
have Redfield ratios of 6.6 C:N and 106
C:P, very small amounts of Fe are needed;
that is, the molar ratios of C to Fe are
of the order of 10,000 (Fe replete [Morel
and Hudson, 1985]) to 100,000:1.0 (Fe
deficient [Anderson and Morel, 1982]).
In view of these small amounts, one would
think that plant requirements would be
easily met, especially since iron is the
fourth most abundant element in the
Earth's crust (5.63% [Taylor, 1964]).
However, Fe is very insoluble in oxygen-
ated seawater, since it is rapidly
oxidized from the soluble Fe(II) to the
highly insoluble Fe(III) state [e.g., Sung
and Morgan, 1980].

In spite of the fact that the physio-
logical importance of Fe in the ocean has
been recognized at least since the 1920s
[e.g., Hart, 1934], attempts to measure
the concentration of this element in the
water column have been frustrated by the
horrendous contamination problems associ-
ated with collection and analytical pro-
cedures. Nevertheless, we are beginning
to learn just how low open-ocean dissolved
Fe levels really are (maximum - < 1 nmol
kg^{-1} [Martin and Gordon, 1988; Martin et
al., 1989; Landing and Bruland, 1987]).
Furthermore, Fe depth profiles are similar
to those for other plant nutrients, that
is, depleted at the surface and enriched
at depth (Figure 1).

It also appears that the amounts of Fe
are so low, at least in the Pacific, that
the Fe mixed up into the euphotic zone via
advective/diffusive processes would be
exhausted long before the major nutrients
that were mixed up along with it; for
example, with 25 μmol of NO_3 carried up
into the photic zone, the phytoplankton
could produce 160 to 170 μmol of C, assum-
ing the Redfield ratio of 6.6 C:1 N. The
Fe transported along with the 25 μmol NO_3
(0.00028 μmol Fe; based on nmol Fe kg^{-1} =

TABLE 1. Examples of Southern Ocean High-Surface Nutrient Concentrations From the
Pacific, Atlantic, and Indian Ocean Sectors Poleward and Equatorward of 56°S

Station	Latitude °S	Longitude °W/E	Depth m	Temperature °C	Salinity	NO₃ μmol kg⁻¹	PO₄ μmol kg⁻¹
South of 56°S							
Pacific 285	61.48	169.97E	9	2.24	33.963	25.9	1.65
Atlantic 78	61.05	62.97W	6	1.35	33.833	25.1	1.69
Indian 430	59.98	60.97E	8	1.80	33.841	27.4	1.87
North of 56°S							
Pacific 322	43.0	129.56W	2	12.80	34.202	7.3	0.67
Atlantic 64	39.05	48.33W	12	14.11	34.374	3.7	0.49
92	46.11	14.36E	2	7.38	33.824	17.4	1.20
93	41.46	18.27E	11	13.67	34.853	4.2	0.47
Indian 429	47.40	57.51E	4	6.49	33.726	20.2	1.48
434	45.38	107.15E	4	11.76	34.641	8.6	0.76
435	39.57	109.58E	5	15.49	34.840	3.6	0.44

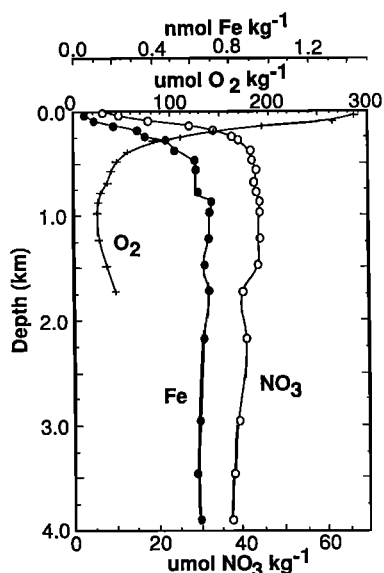Data from GEOSECS (Pacific, Broecker et al. [1982]; Atlantic, Bainbridge [1981]; Indian, Weiss et al. [1983]).

Fig. 1. Vertical distribution of dissolved iron, oxygen, and nitrate at Gulf of Alaska Ocean Station PAPA (50°N;145°W). Figure from Martin et al. [1989].

0.0137 [μmol NO₃ kg⁻¹] - 0.0619 [from Martin et al., 1989]) would support at most 30 μmol C of new growth (Figure 2). This means that about 80% of the NO₃ would be left unused following the cessation of new growth because of Fe depletion. This creates a classic marine example of Liebig's law of the minimum: growth stops
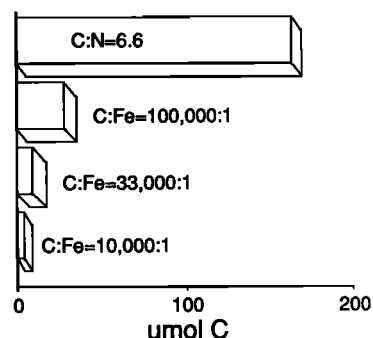

Fig. 2. Amounts of phytoplankton carbon that could be produced with 25 μmol NO₃ and the dissolved Fe that would mix up into the euphotic zone with the NO₃; that is, 0.00028 μmol Fe (from NO₃:Fe relationship of Martin et al. [1989]), assuming Redfield 6.6 C:N ratio and various C:Fe ratios (100,000:1 [Anderson and Morel, 1982], 33,000:1 [Martin et al., 1989], and 10,000:1 [Morel and Hudson, 1985]).

when the minimum requirements for an essential element are not met [Liebig, 1847]. Basically, then, offshore Pacific water is infertile and capable of supporting very little plant growth without supplemental Fe from sources other than conventional advective-diffusive input processes.

Meeting biological Fe requirements is relatively easy in neritic waters, where resuspended bottom sediments and associated Fe-rich oxides, colloids, etc., occur

together with elevated concentrations of
dissolved Fe (e.g., see Figures 6 and 7 of
Martin and Gordon [1988]). Hence excess
NO_3 is never observed in coastal upwelling
environments such as those off the west
coasts of Africa and North and South
America.

Although fulfilling the phytoplankton's
offshore demand for this element is more
of a problem, it appears that adequate Fe
amounts are supplied to the oligotrophic
gyres via long-range transport and fallout
of Fe-rich atmospheric dust originally
derived from terrestrial arid regions.
Surprisingly, 95% of the North Pacific
gyre phytoplankton's Fe requirement
appears to be met via this mechanism
[Duce, 1986; Martin and Gordon, 1988],
an observation that is very important in
the development of this hypothesis.
Apparently, then, the problem of excess
major plant nutrients occurs only in
oceanic regions where the amounts of Fe
falling down upon the surface are not
sufficient to meet the demand created by
the increased major nutrient input result-
ing from enhanced offshore upwelling
(e.g., the Gulf of Alaska, the equatorial
Pacific, and the southern ocean; see
Figure 13 of Martin et al. [1989]).

THE POTENTIAL

The possibility of iron limitation is
especially important in these environments
because of the potential productivity the
upwelling of major nutrients represents.
For example, Chavez and Barber [1987]
describe an area in the eastern equatorial
Pacific of 1.1×10^{13} m^2 with an upwelling
rate of 0.39 m d^{-1}. Using their low NO_3
estimate of 10 mmol m^{-3}, the potential new
(not total) productivity would be $\approx$ 26
mmol C m^{-2} d^{-1} (0.39 m d^{-1} X 10 mmol N m^{-3}
X 6.6 C:N) or 9.5 mol C m^{-2} yr^{-1}, or about
1.2 Gt C yr^{-1} for the entire area. This
is a conservative estimate, since GEOSECS
data [Broecker et al., 1982] show the
equatorial high-nutrient region extending
5°-6° farther south than the 5°S bound
used by Chavez and Barber [1987]. Evi-
dence that this potential is not being
realized is provided by the recent studies
of Murray et al. [1989]. Estimates of new
productivity via four different methods at
two eastern equatorial Pacific stations
with excess nutrients (surface NO_3 = 8.1,
10.8 μmol kg^{-1}) were in the range of 3-10
mmol C m^{-2} d^{-1}; that is, 12-38% of the
potential productivity based on the above

estimated (26 mmol C m^{-2} d^{-1}) upwelling of
NO_3.

It is also apparent that the present
biological working strength of the south-
ern or Antarctic Ocean is very low, at
least judging by the excess of unused
major nutrients in seasonally well-lit
surface waters (Table 1). Here, the
potential maximum productivity is even
greater than that for the equatorial
Pacific; that is, the southern ocean
upwelling rate is 60 Sv (1 Sv - 10^6 m^3
s^{-1}) during the six summer months in the
area from 56°S to the Antarctic continent
(2×10^{13} m^2 [Gordon, 1971]). This repre-
sents an upwelling of $\approx$ 0.25 m d^{-1}. This
rate times the NO_3 concentration times the
Redfield ratio of 6.6 C:N results in a
potential new productivity of $\approx$ 40 mmol C
m^{-2} d^{-1} or an annual rate of 7.3 mol C m^{-2}
yr^{-1} (assuming production during 6 summer
months only), or a total of 1.8 Gt yr^{-1}
for this area during the austral summer.

In addition, there is also excess NO_3
equatorward of 56°S to about 45°S (Table
1). This represents an additional high-
nutrient area, between 45° and 56°S, of
about 2.8×10^{13} m^2. If these waters have
an average of 15 mmol NO_3 m^{-3} and if a
bloom removed all of this excess NO_3 to a
depth of 30 m just once a year, the result
would be an additional gigaton of new pro-
ductivity C for this region. In summary,
the equatorial Pacific and southern
oceans, which represent only 18% of the
global ocean area, have a potential new
productivity of the order of 4 Gt C yr^{-1}.
This equals 50-100% of the new productiv-
ity currently estimated for the entire
ocean (e.g., Eppley and Peterson [1979]
give 3.4-4.7, and Martin et al. [1987]
give 7.4 Gt C yr^{-1}; also see Table 7 of
Sundquist [1985]).

SOUTHERN OCEAN PRODUCTIVITY IN FE-RICH
AND FE-POOR AREAS

There are no reliable water column Fe
measurements for the Antarctic Ocean and
hence no direct evidence that Fe defi-
ciency is limiting phytoplankton growth.
Nevertheless, there is abundant indirect
evidence supporting an Fe limitation
hypothesis. Suspicions of Fe deficiency
are not new. For example, in discussing
the extensive results of the 1925-27
Discovery expedition, Hardy [1967, p. 489]
talks about Gran's observation that the
greater abundance of phytoplankton ". . .
often observed in proximity to land--in

what are technically known as neritic conditions--may be because of the presence of certain beneficial substances derived from land drainage." In reporting phytoplankton abundance, Hart [1934] noted that the neritic influence was very strong around South Georgia (52°-55°S;33°-41°W) and that here phytoplankton concentrations were ten times higher than in other Antarctic oceanic regions. Hart [1934, p. 186] goes on to say that "Among the . . . chemical constituents of sea water . . . possibly limiting phytoplankton production, iron may be mentioned. . . . it may help to explain the observed richness of the neritic plankton . . . the land being regarded as a source of iron . . . ." Hart [1942, p. 339] says that "We are left with the hypothesis that extremely small amounts of organic compounds, iron, manganese . . . derived from the land, exert a strongly favourable influence on phytoplankton production. . . ." and [p. 330] "Only where these (neritic) influences are felt do the Antarctic seas retain their claim to be amongst the richest in the world."

Resuspended sediments with adsorbed oxides, etc., should provide an abundant source of Fe in the shallow waters around South Georgia. Resuspended Fe-rich sediments from the Antarctic peninsula may also be transported downstream to the Scotia Sea via the easterly flowing Antarctic Circumpolar Current [Whitworth, 1988]. Evidence of resuspended lithogenic material is provided by the Bransfield Strait sediment trap studies of Wefer et al. [1988]. They reported lithogenic fluxes of 471 and 777 mg m^{-2} d^{-1} for depths of 494 and 1588 m, respectively, during the month of January. In contrast, the total maximum particle flux in the Weddell Sea under ice-free conditions was ≈ 10 mg m^{-2} d^{-1} for a trap set at a depth of 863 m during the month of March [Fischer et al., 1988]. Fischer et al. [1988] also show that the annual lithogenic flux in the semienclosed Bransfield Strait (53.5 g m^{-2} yr^{-1}) is more than 10,000 times greater than that in the open Weddell Sea (0.004 g m^{-2} yr^{-1}).

In a recent discussion, El-Sayed [1988] notes that diatom blooms are rather common near the coastal regions and in the vicinity of islands. He goes on to say that productivity rates as high as 3.2 and 3.6 g m^{-2} d^{-1} have been reported in the Gerlache Strait and near Deception Island, respectively, during the austral summer.

Such high rates ". . . have no doubt perpetuated the belief in the proverbial richness of the Antarctic waters" [El-Sayed, 1988, p. 491]. However, El-Sayed estimates the mean productivity rate for the open southern ocean at only 0.1 g C m^{-2} d^{-1}, a value in agreement with the 0.1 g C m^{-2} d^{-1} rate of M. Tilzer and B. von Bodungen quoted by Wefer et al. [1982]. El-Sayed and Taguchi [1981] also report mean primary productivity rates of 0.104 g C m^{-2} d^{-1} for the deep northern central Weddell Sea area in comparison to the 0.41 g C m^{-2} d^{-1} rate measured in the shallow southern Weddell Sea shelf region.

Direct evidence that Fe is abundant in the highly productive Gerlache Strait was obtained in a particle trap study in cooperation with D. Karl of the University of Hawaii. A refractory Fe flux of 650 μmol Fe m^{-2} d^{-1} was measured at a depth of 100 m. This was an order of magnitude higher than the Fe flux measured in the Bransfield Strait and 2 orders of magnitude higher than a flux measured in the Drake Passage (Table 2). The latter serves as an example of the Fe-poor conditions in offshore southern ocean waters. Although it is located less than 50 km from the Antarctic peninsula, the Fe flux measured here is the same as that 1600 km offshore in the northeast Pacific (33°N;139°W; 2.0 μmol Fe m^{-2} d^{-1} [Martin and Gordon, 1988]). In summary, southern ocean productivity rates are high in neritic areas, where it is logical to assume that resuspended-sediment-associated dissolved and particulate Fe is abundant, and are low in deep, offshore waters, where Fe supplies are severely limited.

IRON IN ICE

In addition to high rates of primary productivity in neritic areas, there are numerous reports of enhanced phytoplankton productivity along retreating ice edges [e.g., Hart, 1934, 1942; Marra and Boardman, 1984; Smith and Nelson, 1985a, b]. For example, Hart [1942, p. 339] states "One important feature of the work . . . is the great importance of the pack-ice in maintaining the flora within the Antarctic zone and in giving rise to . . . pseudo-coastal conditions at vast distances from land . . . ." The greater productivity is related to the increased stability of the water column; that is, as the ice melts, the warmer, less salty water forms a stable layer in which phy-

TABLE 2.   Refractory (RE) and Leachable (LE; 25% Acetic Acid) Fe Fluxes Measured in
Inshore (Gerlache Strait), Nearshore (Bransfield Strait), and Semioffshore
(Drake Passage) Waters Using VERTEX-Type Particle Traps Set at 100 m
for 24 Hours in January 1987

Location	Fluxes, m^{-2} d^{-1}			Ratios[a]	Ef
	Organic C mmol	RE Fe μmol	LE Fe μmol	C:Fe	Fe/Al
Gerlache Strait (64°17'S;61°17'W)	31	650	4.0	450	0.61
Bransfield Strait (63°14'S;60°55'W)	21	65	0.16	3,200	0.91
Drake Passage (61°55'S;62°00'W)	8.1	2.4	0.046	28,000	0.85

Carbon data courtesy of David Karl, University of Hawaii.   Enrichment factors (Ef)
were calculated using crustal abundance data of Taylor [1964].
[a] Fe = LE + 10% of RE.

toplankton can maintain themselves in the light and grow.   The melting ice also facilitates growth by contributing a "seed" population of diatoms.   Nevertheless, other factors are involved.   Nelson et al. [1989] report phytoplankton biomass distributions with little correlation with the meltwater field.   In considering various reasons for the lack of growth in stable, well-lit, major-nutrient-rich waters, they mention the possibility of Fe deficiency.   The low chlorophyll levels they observed in relation to high carbon biomass also suggest "chlorosis," a condition resulting from Fe deficiency.

It has been suggested that atmospheric dust iron that accumulates over the winter is released with the summer ice meltback, and this may also stimulate growth [Martin et al., 1989; Martin and Gordon, 1988]. Although there are no Fe estimates for modern annual sea ice, it is assumed that there is about as much as that in present-day dome C snow ($\approx$ 0.02 nmol Fe g^{-1} [Petit et al., 1981]) or as much as that contained in Holocene ice from the Vostok ice cores; that is, about 0.03 nmol Fe g^{-1} [De Angelis et al., 1987].   The amount of sea ice melting and freezing each year has been estimated by Munk [1966] at 2.3 X 10^{19} g.   Assuming that each gram of ice has $\approx$ 0.03 total nmol of Fe and that 10% becomes available to the phytoplankton [see Duce, 1986], the annual release would be about 7 X 10^{16} nmol or 7 X 10^7 mol of Fe.   Assuming a 33,000 C:1.0 Fe

ratio [Martin et al., 1989], the total new phytoplankton production from annual ice-meltback-released Fe would be 2.3 X 10^{12} mol C.   Dividing by the winter-summer sea ice area estimate of Cooke and Hays [1982] (1.5 X 10^{13} m^2) results in a new productivity rate of 150 mmol C m^{-2} yr^{-1}.

This is a very low rate when expressed on an annual basis; however, it occurs over a period of a few days as the ice melts back.   For example, if all of the productivity takes place in a week, the daily rate would be around 20 mmol C m^{-2}. In the oligotrophic north Pacific, estimated daily new primary productivities are of the order of 4 mmol m^{-2} d^{-1} [Martin et al., 1987]; this occurs over a whole year, for a total of 1.5 mol C m^{-2} yr^{-1} instead of the 0.13 mol C m^{-2} yr^{-1} estimated here.

CURRENT SOUTHERN OCEAN NEW PRODUCTIVITY

In addition to the new productivity resulting from ice meltback, Fe would also be provided via upwelling and summer dust fallout on open water.   Based on the NO_3-Fe relationship of Martin et al. [1989], the amount of Fe supplied via upwelling would be 6.25 mmol NO_3 m^{-2} d^{-1} X 0.0137 (NO_3) - 0.0619 = 0.024 μmol Fe m^{-2} d^{-1}. This would be enough Fe (X 33,000) to produce 800 μmol C m^{-2} d^{-1}, or 2% of the potential capacity based on the upwelling of NO_3 (see above).   Although estimates for summer dust Fe input are not available, it

is assumed that the Fe input would be about the same as that estimated for ice meltback. Thus, if, indeed, the Antarctic is Fe limited, the total new productivity today may be as low as 1.6 mmol m^{-2} d^{-1} (Table 3). This is about 4% of the estimated potential productivity based on NO_3 upwelling. Using the average total productivity rate of El-Sayed [1985] ($\approx$ 11 mmol C m^{-2} d^{-1}) for the 120- to 150-day austral light regime or M. Tilzer and B. von Bodungen (as cited by Wefer et al. [1982]) ($\approx$ 8.3 mmol C m^{-2} d^{-1}), the ratio of new/total productivity (the f value) would be 0.14-0.19. These values are similar to those for the oligotrophic ocean [Eppley and Peterson, 1979].

PRODUCTIVITY DURING THE LAST GLACIAL MAXIMUM

There is evidence that paleoproductivity rates may have been higher during glacial periods than in previous and present interglacial stages, perhaps by a factor of three [Sarnthein et al., 1987]. With the onset of the present interglacial, Sarnthein et al. [1988] estimate, new productivity rates in low- and mid-latitude upwelling regions decreased by 2-4 Gt C yr^{-1}. Sarnthein et al. [1988] attribute these decreases in productivity to decreased meridional wind strength and the lowering of upwelling rates. Sarnthein et al. [1987, p. 311] also note that eastern Atlantic productivity began ". . . to decrease slightly prior to or simultaneously with global ice melting, synchronously with a drastic increase in atmospheric CO_2 . . . ."

As noted above, the equatorial Pacific has excess nutrients that are not used up by the resident phytoplankton. Pedersen et al. [1988] present evidence that eastern equatorial Pacific productivity rates were markedly higher during the LGM than at present. These higher rates may have resulted not only from intensified upwelling of major nutrients but also from greater availability of Fe. In addition to the wind strength studies of Sarnthein et al. [1987], Petit et al. [1981] also note that in general, glacial period tropical arid areas were 5 times greater, wind speeds 1.3-1.6 times higher, and Fe-rich atmospheric dust loads 10-20 times greater. Dramatic evidence of these increased winds and arid conditions is provided by the dune studies of Sarnthein [1978]. In comparison to present conditions and those during the climatic optimum (6000 years B.P.), active dune fields were plentiful in the southern as well as the northern hemisphere 18,000 years B.P. during the LGM. It is obvious that these climatic conditions also resulted in the transport of large amounts of dust down into the Antarctic. For example, the dust load in the Vostok ice core was 50 times higher during the LGM (Figure 3). If the Fe-limited new productivity estimates based on ice meltback and summer atmospheric dust input (0.16 mol C m^{-2} yr^{-1}; Table 2) are multiplied by this factor of 50, an estimated glacial southern ocean new productivity of 8 mol C m^{-2} yr^{-1} results. This value is about equal to the potential productivity based on the upwelling of nitrate (7.2 mol m^{-2} yr^{-1}; see above) and indicates that surface nutrients could have been used up instead of sinking away unused as preformed nutrients, as is the case in the present-day ocean.

TABLE 3.   Summary of Estimated Fe-Limited New Productivity Rates in Southern Ocean

Process	Daily Rate mmol m^{-2} d^{-1}	Annual Rate mol m^{-2} yr^{-1}	Total Grams of C
Upwelling	0.78	0.14	3.4 X 10^{13}
Ice meltback	12.0[a]	0.082	2.0 X 10^{13}
Summer atmospheric fallout	0.45	0.082	2.0 X 10^{13}
Total new production	1.6[b]	0.30	7.4 X 10^{13}
Potential new production	40.0[c]	7.2	1.7 X 10^{15}

[a] For a few days while ice is melting back.

[b] El-Sayed [1985] average total primary production = 11 mmol C m^{-2} d^{-1} for 120- to 150-day austral light regime; new/total = f = 0.15.

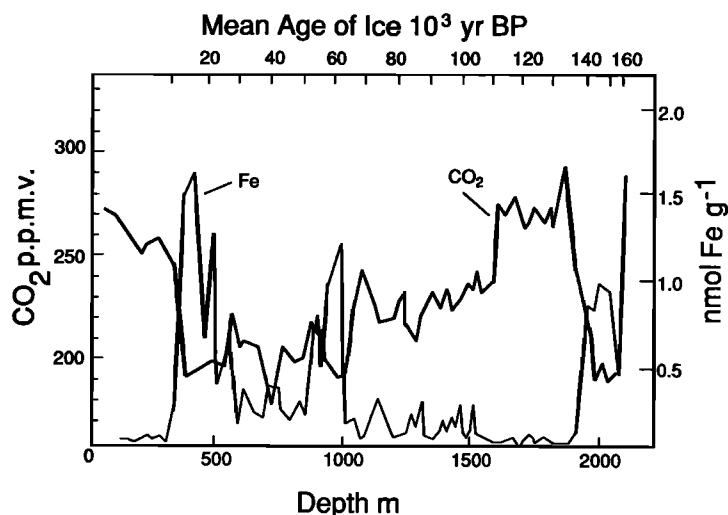[c] Six summer months only.

Mean Age of Ice 10^3 yr BP

Fig. 3. Fe concentration as a function of real depth in Antarctic
Vostok ice core, together with mean CO_2 concentrations in air trapped
in ice, versus mean age of air. Original figure taken from De Angelis
et al. [1987]. Their Al data were converted to Fe estimates using
Taylor's [1964] crustal abundance values. Age data are from Lorius
et al. [1985]; CO_2 concentrations are from Barnola et al. [1987].
Air age was used for the CO_2 plot because of the 2000- to 4000-year
difference between ice and air ages [see Barnola et al., 1987].

Although the Vostok ice core clearly
shows that Fe was readily available, were
LGM southern ocean productivity rates
really 50 times higher? Keir [1988]
points out that there is little direct
evidence of increased Antarctic produc-
tivity during the LGM other than the $\delta^{13}C$
findings of Curry et al. [1988]; that is,
the isotopic records from two cores demon-
strate that the glacial-interglacial
change in $\delta^{13}C$ of the southern ocean is
the largest observed, $0.8^\circ/oo$. More sig-
nificantly, the southern ocean cores have
the lowest $\delta^{13}C$ observed in the glacial
ocean: -0.46. Curry et al. [1988,
p. 328] also note that late Holocene $\delta^{13}C$
values for the southern ocean fall between
the values of the North Atlantic Deep
Water (NADW) and recirculated Pacific deep
water, showing the effects of mixing ^{13}C-
enriched NADW into the southern ocean.
They argue that the lowest observed
glacial $\delta^{13}C$ values from the southern
ocean demonstrate the reduced glacial
production of NADW.

Obviously, it is argued here that
these very low glacial $\delta^{13}C$ values may
also have resulted from the remineral-
ization of organic C that was originally
produced at the surface when enhanced Fe

input facilitated the greater utilization
of major nutrients upwelling to the
surface in the southern ocean during the
summer months.

Evidence of increased productivity is
also provided by the non-seasalt sulphate
data of Legrand et al. [1988]; that is,
sulphate amounts in the Vostok core from
phytoplankton production during the LGM
are approximately 3 times higher than
those in the present interglacial. None-
theless, evidence of increased southern
ocean productivity in the way of ocean
sediment skeletal remains is difficult to
find. The situation is complicated by the
nonpreservation of $CaCO_3$ phases in these
waters and the shifts in annual sea ice
coverage during the glacials [e.g., Cooke
and Hays, 1982]. On the other hand,
favorable conditions for diatom growth
do exist in the Antarctic, and siliceous
frustules are found in the sedimentary
record. Indeed, Holocene siliceous oozes
do occur of such purity that, when dried,
they give the appearance of glass wool
[e.g., Cooke and Hays, 1982].

One of the more abundant species in the
southern ocean is *Phaeocystis pouchetti*
[El-Sayed, 1985], a plant that has no
$CaCO_3$ or siliceous hard parts. If it were

the dominant species during the ice ages, no skeletal remains would have been left behind for paleoceanographers to ponder over. It is also observed that diatoms, when growing rapidly, may not lay down thick frustules. For example, in Fe limitation experiments at Ocean Station PAPA, the diatom *Nitzschia* sp. took up scarcely any SiO_3 in a 6-day experiment [Martin et al., 1989]. Hart [1934, p. 186] also observed that although the diatom *Coscinodiscus* sp. was dominant in Antarctic bottom sediments, it rarely exceeded 1-2% of the surface phytoplankton species composition. Furthermore, dominant surface forms such as *Chaetoceros*, *Corethron*, and *Rhizosolenia* ". . . are but rarely represented in the bottom samples." Hence it is very possible that the phytoplankton that were growing during the LGM left little evidence of high productivity in the way of skeletal remains. Nevertheless, in spite of these arguments, the lack of clear evidence for increased glacial Antarctic productivity is a weak point of this hypothesis.

Another argument against high productivity during glacial periods is that widespread anoxia would have resulted, and no evidence of low oxygen conditions can be found. Again, it must be remembered that conditions in the southern ocean are different; that is, assuming that krill were the dominant grazers, as they are today, the large fecal pellets produced by these euphausiids would sink at a rate of the order of hundreds of meters each day [Small and Fowler, 1972]. Perhaps, then, these rapidly sinking packages, falling through very cold water, would use up relatively little oxygen in the upper water column; most would be consumed in the more oxygen-rich deep water. This would also provide the mechanism whereby intermediate-depth nutrients would be transferred to deeper waters [Boyle, 1988]. Pedersen et al. [1988] also present several strong arguments that eastern equatorial deep water remained oxygen replete in spite of the higher productivity occurring in this region during the LGM. Rapid sinking of particulate matter could also be facilitated if Fe-stimulated blooms occurred sporadically, as is the case with the northeast Atlantic spring bloom [Billett et al., 1983; Lampitt, 1985].

Others point out [e.g., Roger and Wilson, 1988] that glacial-interglacial changes in nutrients ($\approx$ 20% [Boyle, 1986a, b]) were not large enough to account for the observed CO_2 change. The record laid down via analog-Cd in benthic foraminifera shells fails to distinguish between preformed and regenerated Cd/nutrients. If southern-ocean-krill-rapid-sinking-fecal-pellet regeneration was largely in deep waters, not near the surface as it is in today's low-latitude ocean [e.g., Martin et al., 1987], the deep-water regenerated nutrients could be of similar concentration to the preformed nutrients occurring in modern deep water. For example, using depth-dependent elemental $-O_2$:C:N:P ratios, Martin et al. [1987] estimate that about three-fourths of the NO_3 and PO_4 at GEOSECS 246 (0°0';178°59'E [Broecker et al., 1982]) is preformed and only one-fourth regenerated at depths of $\approx$ 5000 m. If all southern ocean surface major nutrients were used up during the austral summer (that is, half of the preformed nutrients annually), the deep Pacific (GEOSECS 246) proportions would change to 63% regenerated, 37% preformed (e.g., 0.82 preformed; 1.39 regenerated; total = 2.21 μmol PO_4 kg^{-1} at 5497 m). The increase in regenerated PO_4 would have an accompanying C increase of 134 μmol kg^{-1} using the VERTEX depth-dependent C:P ratio of 164 C:1 P for a depth of 5000 m. It is also apparent that the use of the VERTEX O_2:P ratio for 5000 m (-259 O_2:1 P) would result in the complete utilization of the available oxygen (5497 m = 196 μmol kg^{-1}; 259 X 0.82 μmol PO_4 kg^{-1} = 212 μmol O_2). On the other hand, the use of the -183 O_2:1 P ratio of Broecker et al. [1985] would result in leftover deep oxygen of 46 μmol O_2. Be that as it may, the point here is that the forams recording these events via Cd would be showing 2.12 μmol PO_4 in spite of large changes in amounts of CO_2, oxygen, and portions of regenerated versus preformed nutrients.

CONCLUSION

This hypothesis, concerned with glacial-interglacial CO_2 change, deals with ". . . the concentration of preformed nutrients as the master variable controlling both atmospheric pCO_2 and deep-sea oxygen" [Ennever and McElroy, 1985, p. 157]. In accordance with ice core records, it provides a mechanism whereby changes in atmospheric CO_2 could have taken place rapidly, in hundreds, not thousands, of years [Keir, 1988; Sarnthein et al., 1987, 1988]. It also supports the suggested sequence of primary productivity

TABLE 4. Glacial-Interglacial Atmospheric C Rates of Change

Description	Mean Age of Air Years B.P.	CO_2 Concentration ppm	Total Gt C	Average Rates of Change Gt C yr^{-1}
End of penultimate glacial to beginning of last interglacial	146,340 to 134,170	191.0 to 296.5	222	+0.018
End of last interglacial to beginning of last glacial	115,290 to 112,700	276.0 to 240.0	76	-0.030
Beginning of last glacial to end of last glacial	112,700 to 16,250	240.0 to 193.0	99	-0.001
End of glacial to beginning of present interglacial	16,250 to 12,930	193.0 to 245.0	110	+0.033

Data from Barnola et al. [1987].

change --> CO_2 change --> climate change [Shafter, 1989]. Potential Fe-stimulated changes in new productivity rates are large (2-4 Gt C yr^{-1}) in relation to changes in the Vostok record (e.g., 0.03 Gt C yr^{-1}; Table 4). The Vostok record (Figure 3) clearly shows that atmospheric dust Fe was abundant when CO_2 was low, and vice versa.

This hypothesis can be tested in two ways. In addition to looking for evidence of increased glacial southern ocean productivity, we can seek proof that, indeed, productivity is limited by Fe deficiency in the present southern ocean and equatorial Pacific. Assuming we find evidence, as was the case in the Gulf of Alaska [Martin and Fitzwater, 1988; Martin et al., 1989], it then becomes feasible to perform realistic large-scale Fe enrichment experiments in which phytoplankton species composition, elemental ratios of C:N:P and Si, $\delta^{13}C$ ratios, etc., can be determined, as well as the effects of grazing and associated fecal pellet production, sinking rate, and oxygen consumption processes. One can even contemplate the ultimate enrichment experiment: the fertilization of the whole southern ocean with 430,000 tons of Fe, the amount required to support the removal of 3 Gt C yr^{-1}. Clearly, the reasons for glacial-interglacial CO_2 change are complex. Iron availability appears to have been a player; however, whether it had a lead role or a bit part remains to be determined.

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