Effect of seafloor depth on phytoplankton blooms in high-nitrate, low-chlorophyll (HNLC) regions

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[1] We calculated correlations between seafloor depth and phytoplankton blooms in all three main high-nitrate, low-chlorophyll (HNLC) regions, but with a particular focus on the subarctic North Pacific area. It has long been known that the central parts of the east and west subarctic North Pacific are HNLC regions. The deep western basin of the Bering Sea is also HNLC, whereas the wide continental shelf of the eastern Bering Sea is not. We carried out a statistical comparison of spatial maps of (1) seafloor depth and (2) chlorophyll *a* concentration from satellite data. This comparison reveals that shallow waters have, on average, higher peak chlorophyll *a* concentrations (more intense phytoplankton blooms) than deep waters (p ≪ 0.01). Possible artifacts of the satellite data are considered but it is concluded that the signal is genuine, in part because the same patterns are found in in situ data. There are several possible explanations for the observed correlation; the most probable, we suggest, is that iron diffusing out of the seafloor causes alleviation of iron limitation in shallow waters.

1. Introduction

1.1. High-Nitrate, Low-Chlorophyll Phenomenon and Mesoscale Iron Fertilization Experiments

[2] Macronutrients such as nitrate are either perennially or seasonally depleted in most surface oceans of the world. Three exceptions are the eastern equatorial Pacific Ocean, the subarctic North Pacific Ocean, and the Southern Ocean, together accounting for about 30% of global ocean surface area. Nitrate concentrations are high throughout the year in these regions, yet there is a surprising absence of phytoplankton blooms, leading to the term high-nitrate, low-chlorophyll (HNLC) regions. The cause of these anomalous areas has long been debated, with three hypotheses most actively considered: (1) a growth-limiting scarcity of the micronutrient iron [*Martin*, 1990a], (2) top-down grazing control [e.g., *Frost*, 1991; *Fasham*, 1995], and (3) low light levels [*Mitchell and Holm-Hansen*, 1991b]. The most parsimonious explanation would involve the same cause for all three HNLC regions, but the reality could of course be more complex. The low-light explanation has been put forward mainly for the Southern Ocean; mixed layer depths are rather shallow year round in the subarctic North Pacific (15–30 m in summer, maximum ~120 m in winter) and in

the eastern equatorial Pacific (typically 25–40 m), and the surface layers in these latter two areas should therefore be adequately illuminated.

[3] During the last decade the first of these hypotheses has been tested by multiple mesoscale iron fertilization experiments: two in the eastern equatorial Pacific [*Martin et al.*, 1994; *Coale et al.*, 1996], four in the Southern Ocean [*Boyd et al.*, 2000; *Gervais et al.*, 2002; *Coale et al.*, 2004] and most recently two in the subarctic North Pacific (one on the western side closer to Japan [*Tsuda et al.*, 2003], one on the eastern side in the Gulf of Alaska [*Boyd et al.*, 2004]). (A fifth Southern Ocean iron enrichment experiment (EIFEX) was carried out in February 2004 and a second western subarctic Pacific experiment (SEEDS II) in July and August 2004, but their results have not yet been reported.) The results of all the published experiments have been synthesized by *de Baar et al.* [2005]. Dramatic proliferations of phytoplankton were seen in response to all the iron enrichments, together with strong drawdowns of nitrate and carbon. IronEx-1 was a partial exception in that the water mass was subducted beneath the surface several days after fertilization, bringing an end to the increase in chlorophyll [*Martin et al.*, 1994]. Diatoms increased in number in response to the added iron and came to dominate the phytoplankton community by the ends of the experiments. In the SOFeX experiment, iron was added to two patches, a southern patch (in polar waters) high in both nitrate and silicate, and a northern patch (in subantarctic waters) high in nitrate but low in silicate: Diatoms came to dominate following the iron fertilization of the southern patch, but silicate limitation led to eventual co-dominance between diatoms and flagellated algae in the northern patch [*Coale et al.*, 2004]. During all in situ fertilizations the small picophytoplankton (<2 μm) which were numerically dominant

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prior to seeding underwent only a small increase in numbers as a result of the added iron, leading to the suggestion that the picophytoplankton are grazer controlled even if diatoms and some others are not [*Price et al.*, 1994; *Landry et al.*, 1995]. The eventually dominant diatoms, by weight, have been middle-sized or relatively large species such as *Pseudo-nitzschia sp.*, *Chaetoceros debilis* or *Fragilariopsis kerguelensis* [*de Baar et al.*, 2005]. From these experiments it seems likely that parts of the phytoplankton community are top-down controlled by grazers, and hence unable to increase in number in response to the added iron, whereas other parts of the community (particularly large diatoms) are able to proliferate when their bottom-up limitation is removed, even when simultaneously being heavily grazed [*Strom et al.*, 2001; *Banse*, 2002].

[4] From a biogeochemical perspective it may make little difference if part of the community is kept under control by grazers. Even if only one species is free to proliferate in response to additions of the most limiting nutrient, then total community export will still end up being limited by the supply rate of that nutrient. The explanation of HNLC areas may thus be twofold [*Cullen et al.*, 1992; *Price et al.*, 1994; *de Baar et al.*, 2005]: (1) that the proliferation of picophytoplankton is capped by microzooplankton grazing, and (2) that the proliferation of large diatoms and other phytoplankton is held back by lack of iron. Both classes of phytoplankton, but for different reasons, are prevented from consuming the excess nitrate.

[5] In recent years, increasing attention has been paid to the higher dissolved iron concentrations in shallow waters, perhaps deriving from the sediments (see section 4.3 for further discussion). This has led to the suggestion that "iron is not likely to be biolimiting over a continental shelf" [*Bucciarelli et al.*, 2001]. If we ignore occasional exceptions to this generalization (section 4.3), and if HNLC is caused by iron scarcity, then this statement leads to the expectation that HNLC conditions should not occur in shallow waters, because iron limitation is alleviated.

1.2. Island Effects

[6] When considered across the globe, phytoplankton primary production [*Muller-Karger et al.*, 2005] and organic carbon burial [*Berner*, 1992] tend to be disproportionately high in shallow water compared to deep water. In the Southern Ocean, in particular, it has been recognized for decades that elevated levels of chlorophyll and phytoplankton production are occasionally found close to islands and over continental shelves [e.g., *de Baar and de Jong*, 2001; *Watson*, 2001; *Banse*, 1996], in contrast to generally lower levels in deep waters. Higher chlorophyll concentrations have also been detected between the Galapagos Islands, compared to the values in the surrounding eastern equatorial Pacific [*Martin et al.*, 1994; *Chavez et al.*, 1991]; some instances of higher values near to the coast were also noted for the North Pacific by *Banse and English* [1999] in their wide-ranging review.

[7] *Banse and English* [1999] made use of data from the Coastal Zone Color Scanner (CZCS) satellite sensor, which ceased operation in 1986. Since September 1997 improved ocean color data have been available from a new range of sensors such as SeaWiFS, MODIS and MERIS. Modern digital data sets of seafloor bathymetry have been produced

by the amalgamation of: (1) seafloor data determined along cruise tracks by depth soundings, and (2) estimates of seafloor depth from satellite altimeter data [*Smith and Sandwell*, 1997]. The combination of high-resolution, global-coverage data sets for both seafloor topography and for sea-surface chlorophyll *a* allows comparison of the two to look for correlations. *Moore and Abbott* [2000] carried out such a cross-comparison in the Southern Ocean from Antarctica north to 30°S. They found (in agreement with an earlier CZCS study by *Comiso et al.* [1993]) that, on average, surface chlorophyll concentrations were higher in areas of shallow water depth (<500 m) than in areas where the seafloor was deeper, and that this correlation between bathymetry and chlorophyll was stronger than that between chlorophyll and any of the other variables that they examined. Their choice of latitudes (northern limit of 30°S), however, allows inclusion of waters outside the HNLC region. Nutrient data sets, such as the World Ocean Atlas [*Levitus et al.*, 1993] and the World Ocean Circulation Experiment (WOCE), show that the boundary between nitrate-poor and nitrate-rich waters, which varies with longitude and season, is in some places as far south as 40°S (see also auxiliary material supplfig02[1]). Here we restrict our area of investigation to include only latitudes containing HNLC waters.

[8] In this study we carried out a systematic comparison of bathymetric and chlorophyll *a* data sets. This analysis was carried out in all three HNLC areas but focused in particular on the North Pacific area because: (1) a systematic analysis has not previously been attempted there, and (2) there has been intense in situ sampling of chlorophyll and nutrients during recent years in the subarctic North Pacific and adjacent seas, including about 4000 stations on board the commercial cargo carrier M/V *Skaugran* during numerous transects across the North Pacific between January 1995 and January 2001 [*Wong et al.*, 2002]. These in situ data are useful because they enable validation of the results of the satellite analyses. In addition, whereas there is relatively little shelf area in the eastern equatorial Pacific, the great extent of the eastern Bering Sea shelf (large number of shallow water pixels in the satellite images) considerably improves the quality of the statistical comparison.

2. Methods

[9] Our analysis of satellite-derived chlorophyll *a* concentrations used data from the Sea-viewing Wide Field-of-View (SeaWiFS) sensor. Chlorophyll *a* concentrations were estimated from remote-sensed radiances using the OC4v4 algorithm [*O'Reilly et al.*, 2000], developed for "Case 1" waters low in colored dissolved organic matter and suspended particulate material. The chlorophyll *a* maps shown in this paper are annual composite images generated from many overpasses of the satellite; they are calculated by NASA using a weighted average of all valid values during the composite period. Annual composites are used for the figures, whereas monthly composites are used for the statistical calculations, for reasons outlined below. Annual composite images as well as monthly chlorophyll-*a* values

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[1]Auxiliary material is available at ftp://ftp.agu.org/apend/jg/ 2005JG000041.

used in the statistical calculations were taken from SeaWiFS Global Area Coverage (GAC) level 3 Standard Mapped Image data from the NASA-GSFC DAAC: http://oceancolor. gsfc.nasa.gov/cgi/level3.pl.

[10] One characteristic of HNLC waters is a low and rather constant chlorophyll concentration through the year (hence the LC in HNLC), as exemplified by data collected over many years at Ocean Weather Station Papa in the subarctic North Pacific where chlorophyll concentrations are almost always <1 mg chl-*a* m^{-3}. This is in contrast to most temperate latitudes, which typically experience intense spring blooms (although these could be missed by the satellite in any one year because of cloud cover) but lower values through the rest of the year (occasionally a smaller fall bloom is also observed). Because of our interest in discriminating between HNLC areas (no blooms) and non-HNLC areas (blooms), we worked with peak rather than average chlorophyll-a concentrations. These were calculated as the maximum out of 58 (September 1997 through to June 2002) monthly composite (i.e., average) values for each $0.5° × 0.5°$ grid cell.

[11] We worked with monthly rather than annual average chlorophyll *a* values in order to obtain an estimate of peak bloom concentrations. However, phytoplankton blooms persist typically for only a week or so and it is therefore likely that our peak chlorophyll *a* concentrations are under-estimates. We would expect analyses using weekly or daily chlorophyll *a* values to yield higher peak chlorophyll *a* concentrations. Maximum monthly chlorophyll *a* values greater than 30 mg m^{-3} were omitted from the analysis to exclude undue influence of outliers.

[12] Seafloor depth for each $0.5° × 0.5°$ grid cell was calculated as the shallowest depth in that cell, according to the GTOPO30 bathymetry data set [*Smith and Sandwell*, 1997]. This data set combines information from depth soundings taken from ships together with anomalies in the marine gravity field as determined from satellites; the latter are caused primarily by variations in height of the seafloor and are derived from satellite altimeter measurements of the sea surface [*Smith and Sandwell*, 1997].

3. Results

[13] Chlorophyll *a* and bathymetry maps for several different areas are presented side-by-side to allow comparison (Figure 1 and auxiliary material supplfig01). Visual inspection shows that most high phytoplankton concentrations (yellows and reds) occur in shallow water. It also shows that the connection between bathymetry and chlorophyll-a concentrations is not absolute. In particular it can be seen that some deep waters close to continental shelves contain high rather than low phytoplankton concentrations (for instance along the northern edge of the western basin of the Bering Sea, or east of the Kamchatka peninsula, particularly in 2002). This may be a result of eddies advecting off shelves, taking iron-rich coastal water with them out into the adjacent open ocean [*Johnson et al.*, 2005; *Whitney and Robert*, 2002]; chlorophyll concentrations are high in such eddies [*Crawford et al.*, 2005] and nutrient drawdown continues until either nitrate or silicate [*Peterson et al.*, 2005; *Whitney et al.*, 2005] become biolimiting. In other locations, where prevailing ocean currents sweep water rapidly across shallow topography, high chlorophyll *a* concentrations occur in large part downstream of islands and submerged banks. This is seen particularly in the Southern Ocean (bottom half of Figure 1). The Antarctic Circumpolar Current (ACC) sweeps around Antarctica in a predominantly eastward direction, but its path is deflected northward at South Georgia [*Korb et al.*, 2004] and Crozet [*Pollard et al.*, 2002], which lie in its path, and flows eastward north of Kerguelen Island [*Blain et al.*, 2001]. High chlorophyll *a* plumes are seen downstream of all these islands, and of the Antarctic peninsula (Figure 1).

[14] We carried out a systematic analysis to examine whether the visually apparent correlation is supported statistically; that is to say, we checked whether the pattern seen by eye, of higher chlorophyll *a* concentrations in shelf waters compared to deep waters, is borne out by statistical analysis of the data. The bar charts in the right-hand column of Figure 1 were obtained by binning chlorophyll *a* concentrations (maximum monthly values between September 1997 and June 2002) according to seafloor depth. The height of the first bar therefore represents the average of the maximum chlorophyll *a* concentrations in all grid cells containing seafloor shallower than 100 m. Bars are only shown for depth intervals where N > 10, and for this reason there are only a few bars for shallow ocean in the equatorial Pacific (where the Galapagos Islands are surrounded by only a narrow continental shelf).

[15] The suggestion that peak chlorophyll *a* concentrations are higher in shallow water is supported by the statistical analysis (Table 1). Average peak concentrations were higher in shallow water in every HNLC area that we examined, and the difference was statistically significant in each case (Table 1). A similar on-shelf/off-shelf distinction was also found in non-HNLC waters, for instance when we

Figure 1. Comparison of bathymetry and chlorophyll *a* in HNLC systems. Each row corresponds to a different HNLC system (rows numbered from top to bottom): (1) Bering Sea, (2) subarctic North Pacific, (3) eastern Equatorial Pacific, (4) Southern Ocean (Indian Ocean sector) encompassing the islands of Kerguelen and Crozet, (5) Southern Ocean (Atlantic Sector) encompassing South Georgia, the South Orkney and the South Sandwich Islands, and (6) Southern Ocean around the Antarctic Peninsula. Column 1 shows seafloor bathymetry from the ETOPO2 ($2' × 2'$) data set plotted using the OCEANMAP package. The second shows corresponding chlorophyll *a* maps (SeaWiFS, OC4v4 algorithm, 2001 annual composite). The 200-m- and 500-m-depth contours are overlaid in white. The third column shows a bar chart of average maximum monthly chlorophyll *a* for each seafloor depth bin (see section 2 of main text). Standard deviations are shown in red. The color scale for the bathymetric maps is chosen to emphasize the distinction between shelves and deeper waters. The color scale for the chlorophyll *a* maps (annual composites for 2001 shown here, for 1998–2001 shown in auxiliary material supplfig01) is the standard NASA color scale. Pixels with no valid chlorophyll-a values during 2001 (for instance because of ice or cloud throughout) are colored black, as is land.
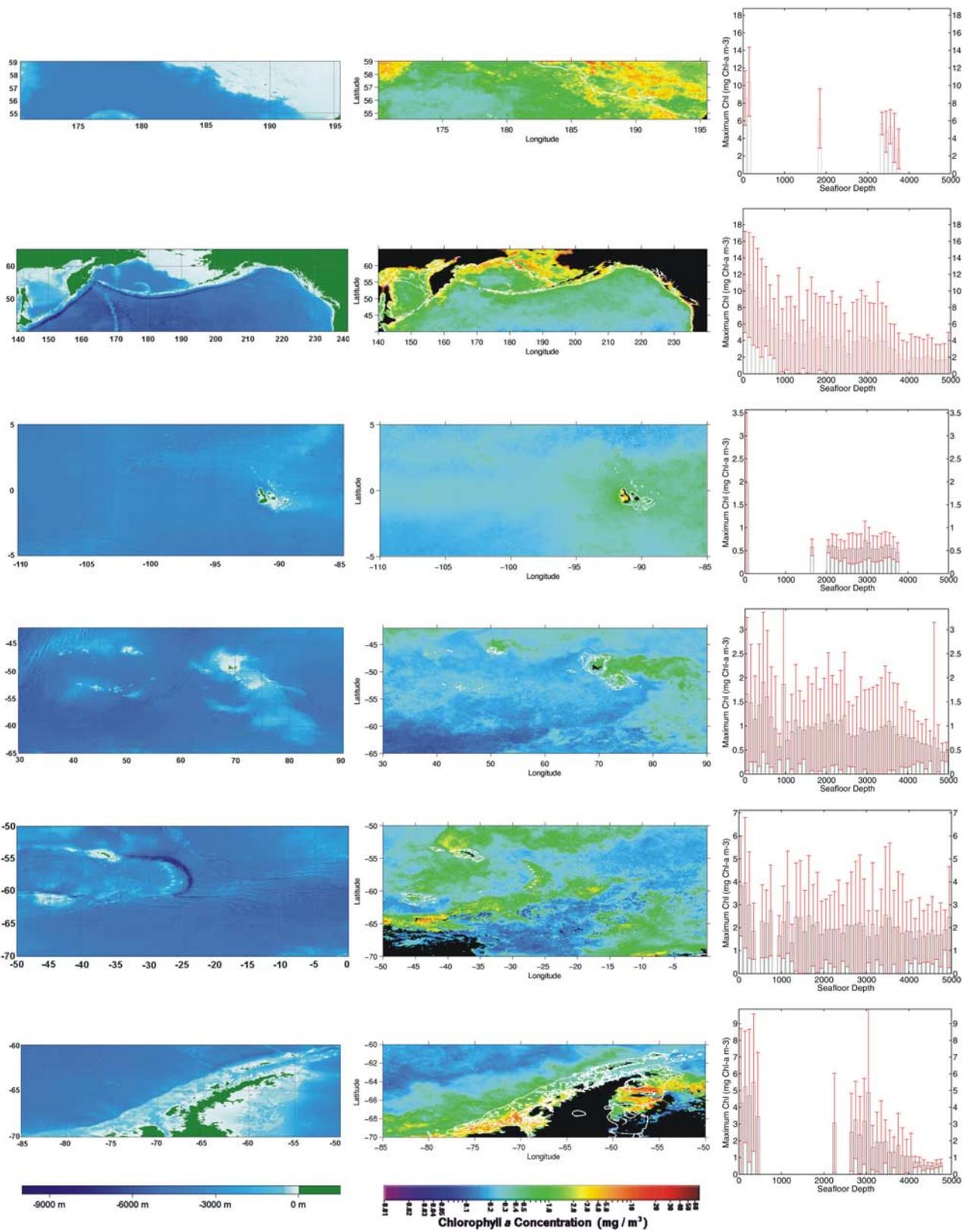
Figure 1

Table 1. Analysis of Influence of Seafloor Depth on Maximum Chlorophyll a Concentration ([chl-a])[a]

HNLC Area	Coordinates (Longitude, Latitude)	Chl-a (≤200 m)	Chl-a (≥2000 m)	σ (≤200 m)	σ (≥2000 m)	N (≤200 m)	N (≥2000 m)	Chl-$a_{(\leq 200\ m)}$/ Chl-$a_{(>2000\ m)}$	P
Subarctic North Pacific	(140°E–120°W, 40°N–65°N)	11.0	2.3	6.1	3.3	1905	4993	4.7	≫99%
Bering Sea	(170°E–164.5°W, 54.5°N–59°N)	8.9	4.1	3.3	2.7	118	261	2.2	≫99%
Equatorial Pacific	(110°W–85°W,5°S–5°N)	1.8	0.6	1.9	0.3	19	885	3.1	99%
Southern Ocean									
Crozet and Kerguelen	(30°E–90°E,65°S–42°S)	1.6	0.8	1.5	0.9	158	4669	2.1	≫99%
South Georgia and South Sandwich	(50°W–0°W,70°S–50°S)	3.8	1.9	2.3	1.8	99	3232	2.0	≫99%
Antarctic Peninsula	(100°W–30°W,72°S–60°S)	4.5	1.5	4.3	1.9	263	597	3.0	≫99%

[a]Seafloor depth (sz) and chlorophyll a concentration for each $0.5° \times 0.5°$ grid cell are calculated as described in section 2. Columns are ocean area, co-ordinates of box analyzed, average maximum monthly [chl-a] in all the grid cells where sz ≤ 200 m (shelf), average [chl-a] in all the grid cells where sz ≥ 2000 m (deep), standard deviation of [chl-a] values where sz ≤ 200 m (note that this is the standard deviation of the population, not of the mean), standard deviation of [chl-a] values where sz ≥ 2000 m, number of [chl-a] values where sz ≤ 200 m (sample size), number of [chl-a] values where sz ≥ 2000 m, ratio of maximum [chl-a] value for shelf waters to maximum [chl-a] value for deep waters, and probability of a genuine difference between the two means (shelf and deep [chl-a]'s), using a Student's t-test in which the two variances are not assumed identical [*Press et al.*, 1991].

compared chlorophyll a concentrations over the Grand Banks to those in adjacent deeper waters (results of analysis not shown). In these cases, however, the difference can be understood as the result of intensive remineralization of macronutrients in the shallow sediments and their subsequent resupply to the surface waters. Because macronutrients are always present in excess in HNLC waters, the higher chlorophyll a concentrations in adjacent shallow waters cannot be due to supply of additional macronutrients.

[16] Our results are in agreement with previous observations of high satellite chlorophyll a concentrations around and downstream of the Galapagos [*Palacios*, 2002], South Georgia [*Korb et al.*, 2004], Kerguelen [*Blain et al.*, 2001] and Crozet Islands [*Pollard et al.*, 2002]. A study of levels of phytoplankton chlorophyll along the Polar Front in the Southern Ocean found highest levels where it impinges on relatively shallow seafloor [*Moore and Abbott*, 2002]. An association between phytoplankton blooms and shallow waters/continental masses was previously suggested for the Southern Ocean, from CZCS data by *Sullivan et al.* [1993] and, from single years of SeaWiFS data, by *Moore and Abbott* [2000] and by *Watson* [2001]. In 4 years (1998–2001) of SeaWiFS imagery (Figure 1 and auxiliary material supplfig01) we found that blooms are also seen around and downstream of other islands in the Southern Ocean, such as Marion/Prince Edward and the South Sandwich Islands. These features repeat in all or most years in SeaWiFS data (auxiliary material supplfig01).

[17] If our hypothesis is correct (blooms in shallow waters, lack of blooms in deep waters), then the effects should also be manifest in nutrient data. The phytoplankton blooms in shallow waters would take up nutrients and, assuming the blooms are accompanied by export, lead to seasonal nutrient depletion. We took advantage of intense sampling during recent years in the subarctic North Pacific and adjacent seas. Nitrate data were collated from several areas within and adjacent to the HNLC subarctic North Pacific. These data show that low summer nitrate concentrations are also related to bathymetry (Figure 2) and that rates of nitrate drawdown are more rapid over shelves than over deep water (Table 2).

4. Discussion

4.1. Limitations to Satellite Data Over Shelves

[18] The OC4v4 algorithm is designed for "Case 1" waters, that is to say waters whose optical properties are dominated by phytoplankton and derivative products. Many coastal waters, on the other hand, are "Case 2"; their optical properties are affected by the presence of colored dissolved organic matter (CDOM) and suspended particulate material (SPM). It is therefore necessary to consider the extent to which detected on-shelf/off-shelf differences in [chl-a] could be due to artifacts associated with using OC4v4 in Case 2 waters for which it was not designed. The accuracy of OC4v4 is likely to be low in areas of high CDOM (for example where the absorption of light by CDOM is greater than about 0.1 m^{-1} at 380 nm) or high SPM (for example where the concentration is greater than about 0.5 g m^{-3}) [*Mueller et al.*, 2002]. SeaWiFS OC4v4 chlorophyll a values should therefore be treated with caution within estuaries and near river mouths. Comparisons of SeaWiFS OC4v4 versus in situ chlorophyll a measurements in such areas [*Gohin et al.*, 2002; *Richardson et al.*, 2004; *Darecki and Stramski*, 2004] show large statistical errors, for instance root-mean square differences between algorithm and in situ of >200% [*Darecki and Stramski*, 2004]. Away from river mouths, the prediction of in situ chlorophyll a by

Figure 2. Seasonal chlorophyll and nitrate concentrations in the subarctic North Pacific and adjacent waters (surface layer). (a, b) Data collected over 25 years (1970–1995) at the Ocean Weather Station Papa (OWSP) site (50°N, 145°W) in the eastern side of the subarctic North Pacific. The small number of high chlorophyll a and low nitrate values could be due to occasional dust events [*Boyd et al.*, 1998] or advection of coastal-derived eddies across the site [*Johnson et al.*, 2005]; (c–f) data from the western side of the subarctic North Pacific (160°E–180°E, 45°N–50°N) and from the western side of the Bering Sea (175°E–175°W, 53°N–57°N), collected on board the commercial cargo carrier M/V *Skaugran* between January 1995 and January 2001 [*Wong et al.*, 2002]; (g, h) data from the southeastern Bering Sea (middle shelf), assembled [*Merico et al.*, 2005] from cruises of the T/V *Oshoro Maru* and from the World Ocean Database; (i, j) data from the shelf south of Alaska (~154°W–144°W, 58°N–61°N) from the World Ocean Database; (k, l) data from the CYPRIS sampling station (4°50′W, 54°05′N), Irish Sea, for comparison.

OC4v4 is much more accurate; a recent study in Case 1 coastal waters of the northeast New Zealand shelf calculated a root-mean square difference between algorithm and in situ of only 8% [Pinkerton et al., 2005]. The possibility of Case 2 overestimations needs to be kept in mind when interpreting SeaWiFS chlorophyll data, and may account for some of the trends that we observe.

[19] Although ocean color estimates are accurate when averaged across the globe (mean ratio of SeaWiFS OC4v4 chl-a to in situ chl-a of 1.0056 [Eplee et al., 2001]), there is evidence that they are not so accurate in particular regions [Claustre and Maritorena, 2003]. In particular, several studies have found that satellite algorithms tend to underestimate high (peak) chlorophyll a concentrations
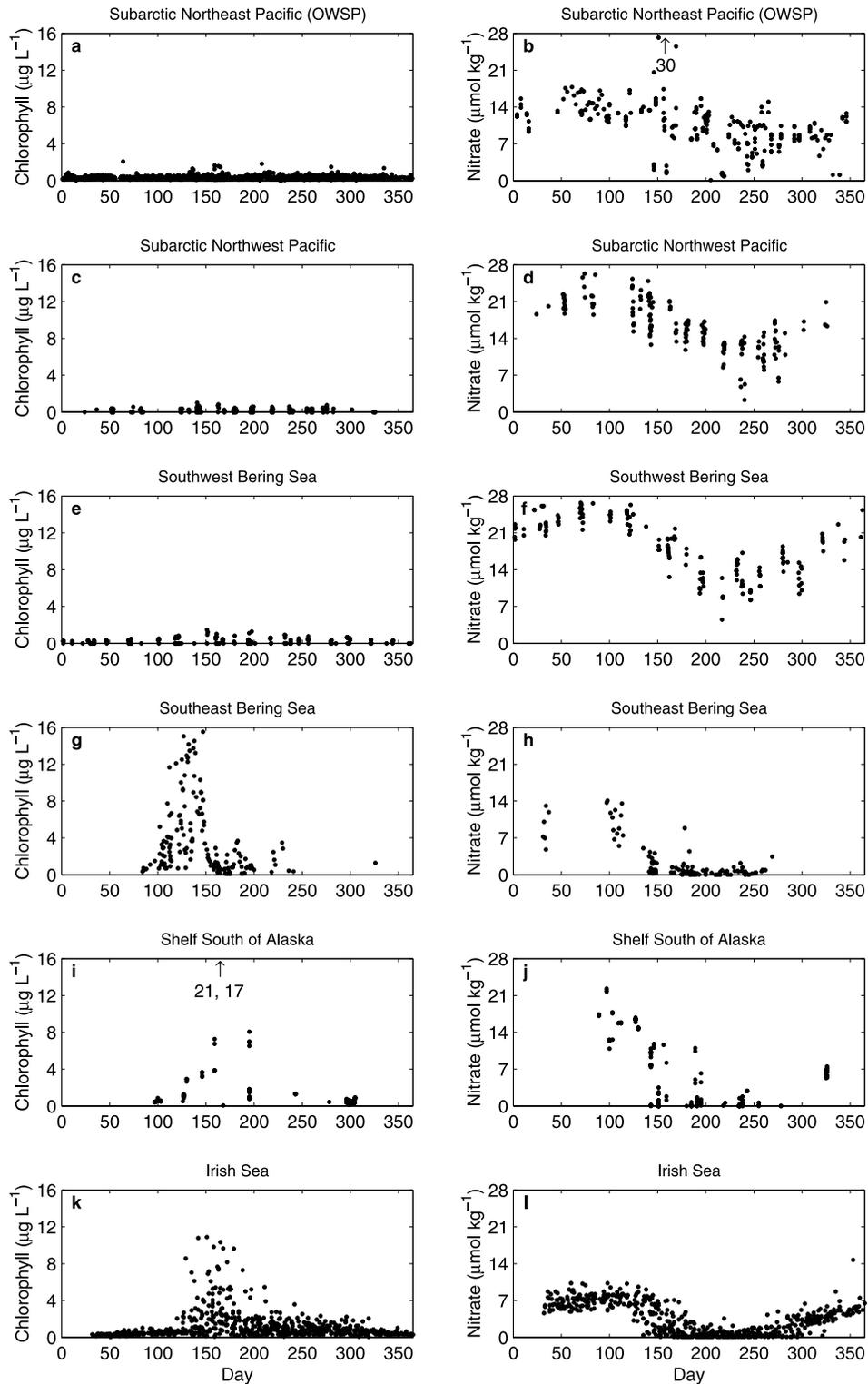

Figure 2

Table 2. Seasonal Nitrate Characteristics[a]

Area	Shallow/Deep	Spring Blooms	Winter $[NO_3]$, $\mu mol\ kg^{-1}$	Summer $[NO_3]$, $\mu mol\ kg^{-1}$	$\Delta[NO3]$ Winter−Summer, $\mu mol\ kg^{-1}$	Average Rate of $[NO3]$ Decline, $\mu mol\ NO_3\ kg^{-1}\ d^{-1}$	Reference
Subarctic North Pacific							
OWS Papa (Station 'P') (49°N–51°N, 146°W–144°W)	deep	no	14[b]	8[b]	6	0.03	*Whitney and Freeland* [1999]; *Wong et al.* [2002]; Figure 2b
Western side (45°N–50°N, 160°E–180°E)	deep	no	22	12	10	0.06	*Wong et al.* [2002]; Figure 2d
Bering Sea							
Western (deep basin) (53°N–57°N, 175°E–175°W)	deep	no	24 (22–27)	12 (8–15)	12	0.07	*Wong et al.* [2002]; Figure 2f
Eastern (middle shelf) (56°N–58°N, 170°W–160°W)	shallow	yes	12 (5–15)	1 (0–1)	11	0.4	*Merico et al.* [2005]; *Whitledge and Luchin* [1999]; Figure 2h
Edges of Subarctic North Pacific							
Shelf south of Alaska	shallow	yes	10–15	<1	10–15	n/a	*Childers et al.* [2005]; *Whitney and Welch* [2002]; Figure 2j
British Columbia shelf (El Niño years: 1997–1998)	shallow	yes	10–15	<1	10–15	n/a	*Whitney and Welch* [2002]
British Columbia shelf (La Niña year: 1999)	shallow	yes	10–15	0–15	variable	n/a	*Whitney and Welch* [2002]
Irish Sea (for comparison)	shallow	yes	8[c]	<1	7	0.2	Figure 2l

[a]Data show rate and amount of nitrate removal in the different areas. The penultimate column gives an indication of the approximate rapidity with which nitrate is consumed during the spring/early summer. This number cannot be calculated accurately from multiyear data sets, because of interannual differences in spring bloom timings at the same location (for instance, calculations using data from individual years suggest an average nitrate uptake rate of about 0.75 $\mu mol\ NO_3\ kg^{-1}\ d^{-1}$ during spring blooms in the eastern Bering Sea [*Whitledge et al.*, 1986], about twice the value calculated here from multiannual data). The values in this column should therefore be considered only in relative terms. The important point here is that nitrate utilization proceeds more rapidly (and until nitrate is exhausted) in shallow waters. At first glance, the shelf off British Columbia appears to be an exception to this rule. However, high summer nitrate levels there are a consequence of coastal upwelling during summer; widespread nitrate depletion was observed along the shelf when this upwelling was suppressed during the 1997–1998 El Niño [*Whitney and Welch*, 2002]. Here n/a means number not available.

[b]This is the approximate average 1969–1997, during which time there has been a long-term trend toward lower nitrate concentrations in more recent years: summer and winter averages are approximately 9 and 15 $\mu mol\ kg^{-1}$ during 1969–1981 and approximately 7 and 13 $\mu mol\ kg^{-1}$ during 1992–1997 [*Whitney and Freeland*, 1999].

[c]This is the approximate average 1960–2003, during which time there has been a long-term trend toward higher nitrate concentrations in more recent years: winter average is approximately 6 $\mu mol\ kg^{-1}$ during the 1960s and approximately 10 $\mu mol\ kg^{-1}$ during the 1990s; summer average is always 0–1 $\mu mol\ kg^{-1}$ (K. Kennington et al., Biogeochemical signature of recent climate variability in the Irish Sea, submitted to *Limnology and Oceanography*, 2004).

(>1 mg chl-a m^{-3}) by a factor of 2 or more in the Southern Ocean [*Mitchell and Holm-Hansen*, 1991a; *Sullivan et al.*, 1993; *Korb et al.*, 2004]. The lower on-shelf/off-shelf chlorophyll a ratios calculated here in the Southern Ocean (Table 1, column 9), compared to elsewhere, are probably related to this underestimation of the highest phytoplankton concentrations.

4.2. Multiple Lines of Evidence Show That HNLC is Alleviated Over Shelves

[20] CDOM and SPM are not, however, responsible for a large part of the observed correlation. There is a significant difference both where the shelf is relatively narrow, and also over the extensive continental shelf of the eastern Bering Sea, some parts of which are more than a hundred kilometers from any land. The on-shelf/off-shelf difference in chlorophyll a concentrations is also apparent in seasonal cycles of [chl-a] which have been compiled from data collected from ships (left-hand side of Figure 2). Occasional very high phytoplankton concentrations have historically been observed at many locations around the world where

shallow seafloor intrudes into HNLC waters (Table 3). Where the spatial patterns of both satellite data and in-situ data can be compared, there seems to be broad agreement (auxiliary material supplfig02).

[21] A second characteristic of HNLC waters is the year-round persistence of high concentrations of macronutrients (hence the HN in HNLC), even in spring and summer. Spring blooms in temperate non-HNLC waters such as the northern North Atlantic and the North Sea deplete nitrate and other macronutrients, giving rise to nitrate exhaustion (low concentrations, generally <1 $\mu mol\ kg^{-1}$) through the summer. This does not happen in HNLC areas. The in-situ nutrient data are also consistent with the pattern seen in satellite [chl-a]. Nitrate utilization is more rapid in shallow seas (Table 2). Although there is some seasonal drawdown of nitrate in the deep HNLC areas such as the east and west subarctic North Pacific, the rate of drawdown is not sufficient to exhaust nitrate by the end of the summer (Figure 2). Nutrients are depleted much more rapidly over shelf areas such as the eastern Bering Sea, leading in most cases to nutrient exhaustion over summer (Figure 2). Exceptions

Table 3. In Situ Measurements Confirming Very High Chlorophyll a Concentrations Over and Near to Shelves[a]

Area	Maximum Chlorophyll a Concentration, mg m^{-3}	Reference
Eastern Bering Sea	20	*Whitledge et al.* [1986]; Figure 2g
Shelf south of Alaska	21	*Childers et al.* [2005]; Figure 2i
British Columbia shelf	8	F. A. Whitney, unpublished data
Galapagos Islands	13	*Martin et al.* [1994]
Ross Sea Shelf	15	*Smith et al.* [2000]
Anvers Island, west of the Antarctic Peninsula	30	*Holm-Hansen et al.* [1989]
Gerlache Strait, west of the Antarctic Peninsula	25	*Holm-Hansen and Mitchell* [1991]
King George Island, north of the Antarctic Peninsula	19	*Heywood and Priddle* [1987]
Bransfield Strait, north of the Antarctic Peninsula	14	*von Bodungen* [1986]
Signy Island (South Orkneys)[b]	39	*Clarke and Leakey* [1996]
South Georgia	22	*Korb et al.* [2004]
Bouvet and South Sandwich Islands	7	*Perissinotto et al.* [1992]
Kerguelen	17	N. Metzl unpublished data; auxiliary material supplfig02
Crozet	4	N. Metzl unpublished data; supplfig02
Prydz Bay, East Antarctica	23	*Gibson and Trull* [1999]

[a]By comparison, in situ measurements in deep HNLC waters average about 0.5 mg m^{-3} and rarely exceed 1.0 mg m^{-3} (Figure 2).

[b]Data are from sampling every week over 6 years.

occur, however, in locations where there is a continuous influx of nutrients throughout the year, such as: (1) the Anadyr Stream, which flows from the deep basin onto the northern part of the Bering Sea shelf [*Springer and McRoy*, 1993], and (2) the coast of British Columbia during the upwelling season in non-El Niño years [*Whitney and Welch*, 2002]. Despite a lack of nutrient exhaustion, these waters are also not HNLC; in the Anadyr Stream, high concentrations of phytoplankton persist during a summer-long eutrophic bloom, but do not exhaust the nutrients because of ongoing resupply [*Springer and McRoy*, 1993]. In both these cases, high nutrients co-exist with high [chl-a] [*Springer and McRoy*, 1993; *Whitney and Welch*, 2002]. In summary, the on-shelf/off-shelf difference seen in satellite [chl-a] data is corroborated by in situ chlorophyll a and nitrate data.

4.3. Contribution to Understanding of the HNLC Phenomenon

[22] How does this pattern relate to the various hypotheses as to the cause of the HNLC phenomenon? Three hypotheses were listed in the introduction: top-down (grazing) control, light limitation and iron limitation.

[23] The on-shelf/off-shelf dichotomy in bloom tendency is not obviously explicable in terms of a grazing (top-down) hypothesis. It has previously been suggested that deep winter mixing (to ~500 m) in the North Atlantic (not an HNLC region) makes winter phytoplankton concentrations so dilute that zooplankton starve in winter and are not able to cap the spring blooms, whereas shallow winter mixed layers (~100 m) at Ocean Weather Station Papa (OWSP) allow overwintering zooplankton to keep a lid on phytoplankton in spring [*Fasham*, 1995]. It seems hard to reconcile this hypothesis with the picture revealed here of spring phytoplankton blooms in shallow waters, where winter mixing necessarily cannot be deep.

[24] Mixed layers tend to be shallower in coastal waters and in the lee of islands [*Mitchell and Holm-Hansen*, 1991b], consistent with alleviation of light limitation causing the pattern shown here. However, phytoplankton proliferation occurred universally in response to all Southern Ocean iron enrichments [*Martin et al.*, 1994; *Coale et al.*, 1996; *Boyd et al.*, 2000; *Gervais et al.*, 2002; *Tsuda et al.*, 2003; *Coale et al.*, 2004; *Boyd et al.*, 2004], whatever the mixed layer depth; this would seem to argue for iron scarcity as the overriding limitation, even though the rate of increase in [chl-a] is found to be negatively correlated with mixed layer depth [*de Baar et al.*, 2005], suggesting that underwater light climate is also an important influence on the development of blooms. Moreover, a light-limitation hypothesis cannot explain the HNLC phenomenon in the subarctic North Pacific, where mixed layer depths are rather shallow year-round (15–30 m in summer, maximum ~120 m in winter), or in the equatorial eastern Pacific Ocean, where mixed layer depths are even shallower.

[25] This pattern of shallow water blooms is consistent with iron scarcity as the cause of HNLC. Many studies concur in finding elevated concentrations of dissolved iron in shallow waters (Table 4). This association between shallow seafloor and higher iron could be due to one or more of several processes, including: iron-rich run-off from land, induced upwelling of iron-rich deep water, and release of iron from the seafloor. However, following *Bucciarelli et al.* [2001], *Johnson et al.* [1999], *Elrod et al.* [2004] and *Croot and Hunter* [1998], we assume that the sediments are an intense source of iron and therefore that most shallow waters are iron replete. Although most studies have found elevated concentrations of dissolved iron over shelves, *Hutchins and Bruland* [1998] found phytoplankton to be iron-limited in those parts of the California coastal upwelling region where the continental shelf is particularly narrow, suggesting an exception to shelf blooms (release from iron limitation) in those few regions where both: (1) upwelling is intense, and (2) the shelf is narrow.

Table 4. In Situ Evidence of Elevated Dissolved Iron Concentrations in Surface Waters Overlying Shallow Topography[a]

Area	Iron Off Shelf, nM	Iron On Shelf, nM	Reference
California Current System[b]	0.2	average 6, up to 20	*Johnson et al.* [1999]
Transect from central California to Hawaii[b]	0.2	0.8−1.4	*Elrod et al.* [2004]
Northwest Atlantic[c]	≤1.0	0.5−6.0[d]	*Wu and Luther* [1996]
Northeast Atlantic[c]	0.7	1−2	*Boye et al.* [2003]
Eastern tropical Pacific, up-stream and between Galapagos[b]	0.06	3	*Martin et al.* [1994]
Kerguelen archipelago and vicinity[e]	0.46−0.71[f]	5.3−12.6	*Bucciarelli et al.* [2001]
Gulf of Alaska onto shelf south of Alaska[e]	0.1	0.1[g]	*Martin et al.* [1989]
Ross Sea[e]	≤0.10	0.22	*Fitzwater et al.* [2000]
Drake Passage/Gerlache Strait[e]	0.16	7.4	*Martin* [1990b]

[a]Although the large majority of shelf waters appear to be Fe-replete, exceptions in regions of upwelling have been noted [*Hutchins et al.*, 1998; *Hutchins and Bruland*, 1998].

[b]"Dissolvable" Fe fraction was measured, determined in unfiltered sampling following a period of acidification. It includes Fe(II+III) in the dissolved, colloidal and labile particulate phases.

[c]"Dissolved" Fe fraction was measured, following filtration using 0.2-μm pore size filters. It includes Fe(II+III) in the dissolved and possibly colloidal phases.

[d]Sampling was conducted close to the mouth of the Delaware River. Stations most affected (lowest salinities) were excluded.

[e]"Dissolved" Fe fraction was measured, following filtration using 0.4-μm pore size filters. It includes Fe(II+III) in the dissolved and possibly colloidal phases.

[f]These offshore values are higher than elsewhere in the open Southern Ocean and are thought to be affected by advection from the continental shelf.

[g]Measured subsurface (e.g., about 200 m) concentrations were much greater near the shelf (1−2 nM) than offshore (0.2 nM).

[26] While blooms in shallow waters bordering HNLC regions are easily reconciled with the iron limitation hypothesis, it is also possible to conceive of alternative explanations. For instance, the life cycles of some diatom species involve resting spores which sink out of the surface, and the timing and strength of spring blooms could potentially be influenced by the presence or absence of shallow sediments acting as a source of spores [*Eilertsen et al.*, 1995]. Other putative explanations might involve an effect of seafloor depth on zooplankton life cycles. The on-shelf/off-shelf difference in bloom propensity is fully compatible with lifting of iron limitation due to a seafloor source, but clearly does not constitute proof that iron limitation is the cause of the HNLC phenomenon. The supposition that the distribution of phytoplankton is driven by that of iron can be tested by more detailed studies of iron, phytoplankton and macro-nutrients dynamics where HNLC water meets shallow sediments, and the results of recent studies around the Crozet (CROZEX project) and Kerguelen (KEOPS project) islands are therefore awaited with interest.

4.4. Cause of High Productivity in the Eastern Bering Sea

[27] We consider the Bering Sea to be an interesting natural laboratory demonstrating the difference that iron from shallow sediments makes to the HNLC condition. The Bering Sea is split up into a deep western basin (HNLC) and a shallow eastern side consisting of an extensive continental shelf (not HNLC) (Figures 1 and 2). Nitrate is drawn down to limiting concentrations in summer (Figure 2) by spring blooms which remove 15 or more μmol NO_3 kg^{-1} [*Whitledge et al.*, 1986; *Whitledge and Luchin*, 1999; *Merico et al.*, 2005]. The bulk of this nitrate must be exported to below the surface mixed layer and/or to the sediments (there are low stocks in summertime of phytoplankton (Figure 2) and ammonium [*Whitledge and Luchin*, 1999]).

[28] The eastern Bering Sea is exceptionally productive and supplies over half of the United States demand for fish and shellfish [*Macklin*, 1999]. It supports populations of king crabs, salmon, and the world's largest single-species fishery: the walleye pollock *Theregra chalcogramma* [*Napp and Hunt*, 2001]. The region is also a feeding ground for many resident and migratory seabird and mammal species [*Springer et al.*, 1996]. The data shown here are compatible with the "Iron Curtain" hypothesis [*McRoy et al.*, 2001], which suggests that this high productivity is due in large part to the position of the eastern Bering Sea as an iron oasis adjoining an iron desert. When iron-poor, nitrate-rich waters of the western Bering Sea are supplied with iron as they flow onto the shelf, then phytoplankton proliferation becomes freed from all nutrient limitations. This hypothesis could be tested in future by integrated studies of iron and macronutrient cycling in the North Pacific margins, including across the Bering Sea shelf break.

4.5. Effects of Ice Ages and Global Warming on High-Latitude Shallow Seas

[29] This shelf effect also has implications for our understanding of past and future ocean biogeochemistry. For instance, our analysis implies that the subarctic North Pacific HNLC area may have had higher macronutrient concentrations and may have covered a much larger area during glacial times, because the eastern Bering Sea was then a land bridge between Alaska and Siberia rather than, as at present, an enormous hot spot for nutrient removal from seawater (Figures 2g and 2h). We speculate that the absence in glacial times of such a large sink for macronutrients may have forced an expansion of the HNLC area to lower latitudes in the North Pacific.

[30] Much of the continental shelf around Antarctica is presently covered by ice year round and is thereby rendered biologically quiescent. Where the shelf is presently ice-free in summer, large blooms occur, for instance in the Ross Sea [*Smith et al.*, 2000], the Weddell Sea (Figure 1) and in Prydz Bay [*Gibson and Trull*, 1999]. The data reviewed here suggest that the seas around Antarctica could become an increasingly large sink for CO_2 as global warming melts back this ice and releases intense biological and biogeo-

chemical activity around the continent. The iron limitation that experiments suggest is prevalent in the surrounding Southern Ocean appears not to apply near to the continent, and hence incipient phytoplankton blooms are unlikely to be held back by iron limitation. This shelf iron fertilization effect is not included in most existing models; addition of this effect would probably reverse the current model predictions of reduced chlorophyll close to Antarctica under global warming [*Sarmiento et al.*, 2004].

[31] The Arctic Ocean is on average shallower than other oceans, and a third or more of its area consists of continental shelf. The annual extent of sea ice is decreasing significantly under global warming [http://earthobservatory.nasa.gov/Study/ArcticIce]. As sea ice continues to diminish, this work suggests that phytoplankton blooms will occur in the Arctic Ocean, or at least that potential blooms are unlikely to be prevented by lack of iron [*Moore et al.*, 2004].

[32] The contribution of the sedimentary iron source to total global primary production (TPP) may well be relatively small, however. This has been estimated for the first time by *Moore et al.* [2004] in a model which includes iron cycling, macronutrient cycling and phytoplankton in a $100 \times 116 \times 25$ grid cell physical framework. *Moore et al.* [2004] estimated a minor (<1%) effect of sedimentary iron on global TPP, by comparing runs in which their seafloor iron source is switched on to those in which it is switched off. There are significant uncertainties associated with any such estimate, however, related to paucity of our current understanding of iron chemistry and the bioavailability of different iron fractions. In addition, their number may be an underestimate due to setting iron scavenging too high, preventing the influence of seafloor iron spreading away from the shelves. In reality currents and eddies transport iron away from the shelves [*Blain et al.*, 2001; *Johnson et al.*, 2005] and lead to plumes of high chlorophyll *a* concentration downstream of islands and shelves in the Southern Ocean and elsewhere (section 3). For instance, there is some evidence to suggest that the shelves of South Georgia and the North Scotia Ridge may be responsible for elevated iron [*de Baar et al.*, 1995] and chlorophyll concentrations as much as 2000 km or more downstream [*Korb et al.*, 2004]. The greater the persistence of sediment-derived iron in the water column, the more its influence will be felt over an area much larger than that of just the shelves themselves, an effect which appears to be underestimated in *Moore et al.*'s [2004] model. For instance, the model produces low chlorophyll *a* concentrations in the eastern Bering Sea downstream of Kerguelen, in contrast to observations (Figure 1, auxiliary material supplfig01). A further difficulty inherent in even such high-resolution models is that of accurately representing effects of islands and shelves when they may be smaller than the size of an individual grid box. *Moore et al.* [2004] may well be correct that it is a relatively small effect, but, given the possible shortcomings of the model, we suggest that more work remains to be done in calculating the quantitative significance to global TPP of fertilization by shelf-derived iron.

5. Conclusions

[33] The question addressed in this study was whether HNLC conditions (1) extend into and are unaffected by shallow waters or (2) are alleviated there. This question was tested using a combination of satellite [chl-*a*] data and in situ [NO_3] and [chl-*a*] data. We analyzed data from all three HNLC areas but with a focus on the North Pacific. Peak chlorophyll *a* concentrations were seen to be higher over the shelves. Summer nitrate levels were found to be generally lower (and limiting to phytoplankton growth) over the shelves. The data indicate that HNLC conditions are usually alleviated above shallow seafloor. The on-shelf/off-shelf difference is most notable in the dichotomies between the subarctic NE Pacific and the shelf south of Alaska, and between the deep western and the shallow eastern Bering Sea.

[34] HNLC waters are important globally (accounting for ~30% of total ocean area) and offer a contrast to the more typical phytoplankton-nutrient dynamics that operate elsewhere. Our data reveal an interesting feature of the natural dynamics: that a shallow seafloor appears to be antagonistic to the HNLC condition. The seafloor is a known source of dissolved iron and so this is consistent with scarcity of iron as the overriding cause of the HNLC phenomenon. According to this understanding, global warming–induced melt-back of ice in coastal or shallow polar regions will probably stimulate increased phytoplankton production and carbon dioxide drawdown, even though these regions generally receive low atmospheric dust inputs.

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