High Nutrient Low Chlorophyll Ecosystems
In ~1/3 of the ocean, excess nutrients are perennially available yet phytoplankton biomass is relatively low. Such regions are termed High Nitrate Low Chlorophyll (HNLC) waters.
Whatever factors limit complete utilization of nutrients in HNLC regions have important consequences on the functioning of the biological pump such processes limit new production and thus ultimately export of carbon to the deep sea.
North Atlantic Spring Bloom

(b) Chlorophyll a (µg L⁻¹)
Silicate (µM)

Nitrate
Silicate
Chl a

47°N

20 April 30 April 10 May 20 May 30 May
110 120 130 140 150
Julian Days 1989

Nitrates (µM)
Subarctic North Pacific

Fig. 7. Interannual variation in NO₃ concentration as seen during three spring and summer cruises.
What limits the accumulation of phytoplankton in large regions of the oceans?

- H1: Phytoplankton growth is limited by light (due to deep mixing)
- H2: Plankton biomass is kept low by vigorous predation
- H3: Nitrate uptake is inhibited by uptake of ammonium
- H4: Phytoplankton growth is limited by availability of specific nutrients
H1: Deep mixing results in light limited growth

Remember the Critical Depth?
Cold temperatures and high winds often results in very deep mixing in Southern Ocean; however, the Subarctic North Pacific and Equatorial Pacific typically do not mix as deep (<120 m) as other systems that experience regular nutrient drawdown.

Conclusion: although light limitation may be important in some HNLC systems, light alone is insufficient to explain lack of seasonal nitrate drawdown.

Fig. 1.4  Data for 1949 from Weathership “M” (66°N, 2°E) showing the relationship between the approximate critical depth (shading between approximate $k$ values of 0.075 and 0.10) and mixing depth. Phytoplankton counts increased in April–May, when critical depth exceeded the mixing depth. While these data are crude, the observation set has never been duplicated. (After Sverdrup 1953.)
Three possible scenarios of factors limiting the accumulation of phytoplankton biomass

- **Nutrients**
- **Grazing**
- **Grazing + nutrients**

- **Control**
- **Grazers removed**
- **Nutrients (+)**
- **Grazers removed & Nutrients (+)**
H2: Food web control of plankton biomass--grazers keep biomass cropped to low levels, allow nutrients to accumulate

Fig. 4. Diagram of principal food-web connections in the subarctic Pacific. Black arrows—consumption; white arrows—regeneration processes; stippled arrows—transfers to dissolved organic pool.
In the subarctic North Pacific and Eastern Equatorial Pacific, strong evidence supporting micrograzer control of algal biomass.
Remember:

Production = growth rate * biomass

\[ P = \mu B \]

If grazers reduce biomass, production decreases (unless growth rates increase). Thus, grazing can directly limit production.
The case for Iron

• Iron is essential for life: required for synthesis of chlorophyll, component of cytochromes (electron transport chain), needed for nitrate utilization (nitrate reductase), essential for N\textsubscript{2} fixation (nitrogenase).
• Iron is highly insoluble in oxygenated seawater; readily precipitates.
• In regions far removed from continental shelves primary Fe input occurs via atmospheric deposition and upwelling.
• In areas of active upwelling, demand for Fe is elevated; however, many of these regions are also far removed from terrestrial Fe sources.
Various metals essential to life demonstrate nutrient like distributions in the oceans

Surface depletion due to algal uptake; increasing concentrations increase through remineralization

In many HNLC regions, upper ocean concentrations of Fe <0.1 nM

From Morel and Price [2003]
Obtaining accurate measurements of Fe concentrations in the open ocean have plagued oceanographers for many years.
A little bit of Fe goes a long way...

Phytoplankton biomass:
106C : 16N : 1P : 0.005Fe
There is evidence suggesting that changes in Fe supply influence atmospheric CO$_2$

Glacial-interglacial variations in CO$_2$ demonstrate inverse relationships to the availability of iron in seawater
The “Iron Hypothesis”, John Martin, MLML
Dust source regions and transport routes

Pye (1987)
Dust flux overlaid on the NO$_3$ distribution (µM) in the upper ocean

NOAA world ocean atlas, 1994

Atmospheric Fe flux (mg m$^2$ yr$^{-1}$)
Duce et al. 1991
Experiments done in carboys and bottles confirmed that phytoplankton growth was limited by Fe.

Fig. 7. A comparison of doubling rates from the Antarctic, Gulf of Alaska, and equatorial Pacific with and without added Fe (data from Table 2); theoretical maxima for various temperatures are also shown.

Martin et al. (1990)
Bottle experiments demonstrated increases in Chl by the addition of iron; however, there were concerns about what might have been missed...exclusion of large grazers, sinking, mixing, etc.

The case for iron

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Does iron really limit phytoplankton production in the offshore subarctic Pacific? Karl Banse

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Yes, it does: A reply to the comment by Banse
• Bottle experiments indicated that the addition of iron shifted the phytoplankton assemblage from small cells (subject to tight grazing) to large cells (diatoms) that grow rapidly, consume nutrients, and sink.

• But was this due to a bottle effect? Exclusion of grazers....

No iron controls

+Fe

Synechococcus
Solution: Mesoscale (100s of km) enrichment experiments to examine community level responses to iron.

Iron added as acidic iron sulfate. The inert tracer $\text{SF}_6$ is added along with iron.

Cartesian coordinate system

Lagrangian system following drogues
IronEX I: 1993, Equatorial Pacific near Galapagos Islands. 443 kg of Fe into a 64 km² patch. Initial Fe concentrations ~0.1 nM, final target Fe concentration was 4 nM. Added 17,500 L of 0.5 M Fe solution (pH 2.0). A separate batch of 2000 L of SF6 was mixed into the iron solution.

Coale et al. (1994)
IronEX I: Chl concentrations enriched in the patch and downstream of natural Fe source (Galapagos Islands). However, only weak drawdown of nitrate observed over course of experiment...perhaps Fe is not the only limiting nutrient? Grazing? After day 4, the patch subducted beneath a low salinity front.

Coale et al. (1998)

Fe concentrations downstream of the Galapagos Islands (in the island plume) were ~1 nM.
June 1995, Equatorial Pacific; 225 kg Fe in 72 km²; Day 1 Fe concentrations ~2 nM. Fe added again on days 3 and 7 (to bring surface water concentrations to ~1 nM)

Coale et al. (1996)
IRONEX II: Equatorial Pacific June 1995; a shift from cyanobacteria to diatoms

The increase in Chl within the Fe seeded patch appear largely driven by growth of diatoms (85-fold increase in abundance).

Landry et al. (2000)
12 mesoscale Fe experiments in > 10 years

Boyd et al. (2007)
Thanks Dr. Jim Gower of IOS and NASA SOIREE (Southern Ocean) SERIES (Subarctic North Pacific)

The resulting blooms are large enough to be viewed from space.
One of the major findings from these open ocean Fe enrichment experiments was that specific components of the phytoplankton community increased in biomass following the addition of Fe.
Diatoms grow rapidly, then disappear?
Iron supply impacts many aspects of phytoplankton processes and ocean biogeochemistry.
A wide range in bloom signatures

De Baar et al. 2005
The HNLC condition-lessons learned from large scale manipulation experiments

- HNLC conditions are maintained by low Fe supply which suppresses phytoplankton growth and biomass production.
- Low concentrations of Fe appear to favor smaller cells (picoplankton).
- Growth of dominant picoplankton also suppressed by Fe supply but to a lesser extent than larger, rarer cells.
- Active microzooplankton grazing keeps picoplankton biomass low and relatively invariant, providing a highly regenerative upper ocean (rapid NH$_4^+$ cycling).
HNLC Regions of the Ocean

SUMMARY

HNLC waters – 30% OF OPEN OCEAN
IRON SUPPLY causes the HNLC condition
But some regions are also influenced by light,
Grazing or silicic acid supply
Biomass levels in HNLC waters are set by
Grazing pressure – which in turn resupplies iron

Seeding a bloom and studying its development has provided
important information on plankton control of biogeochemistry