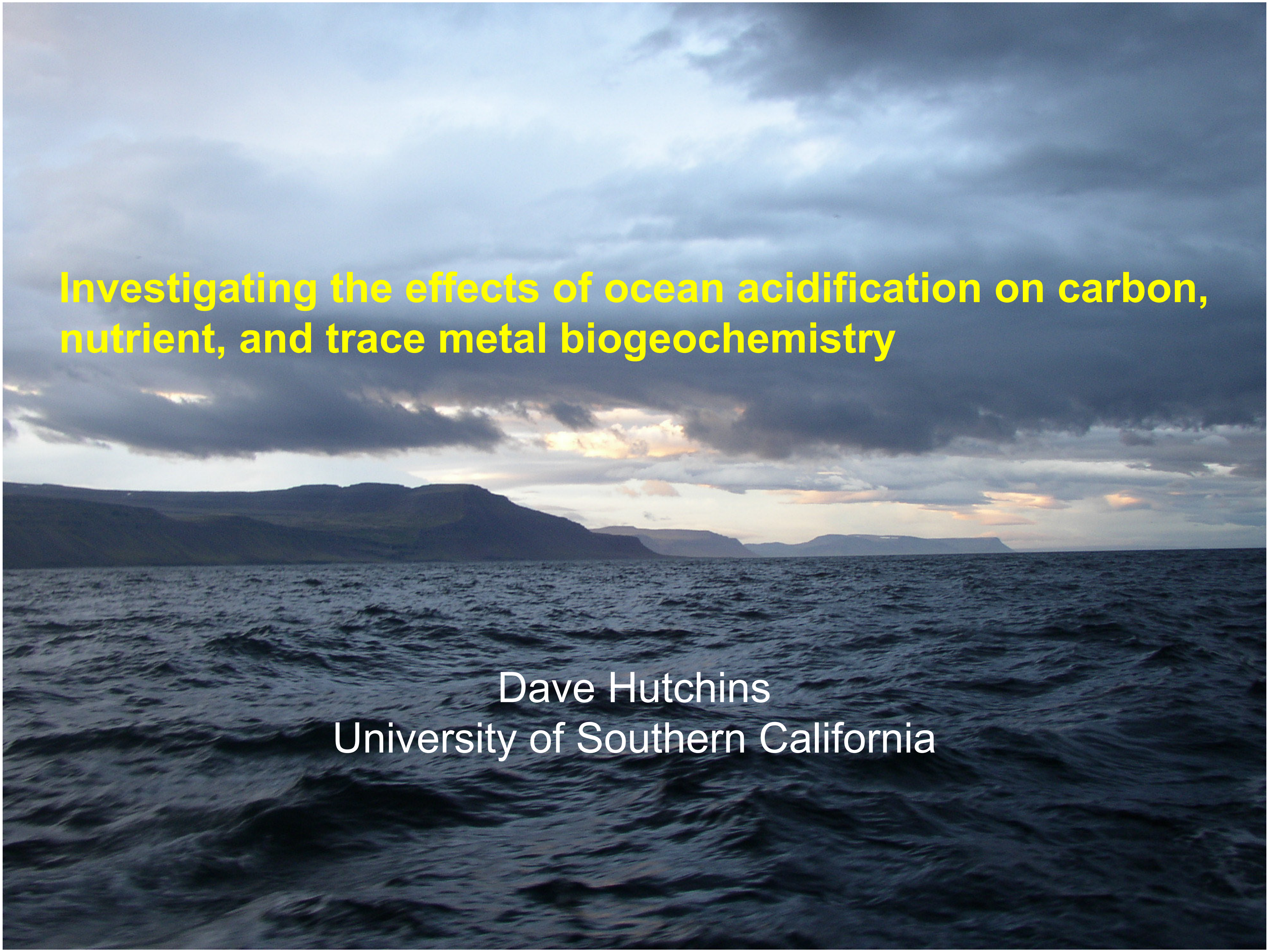
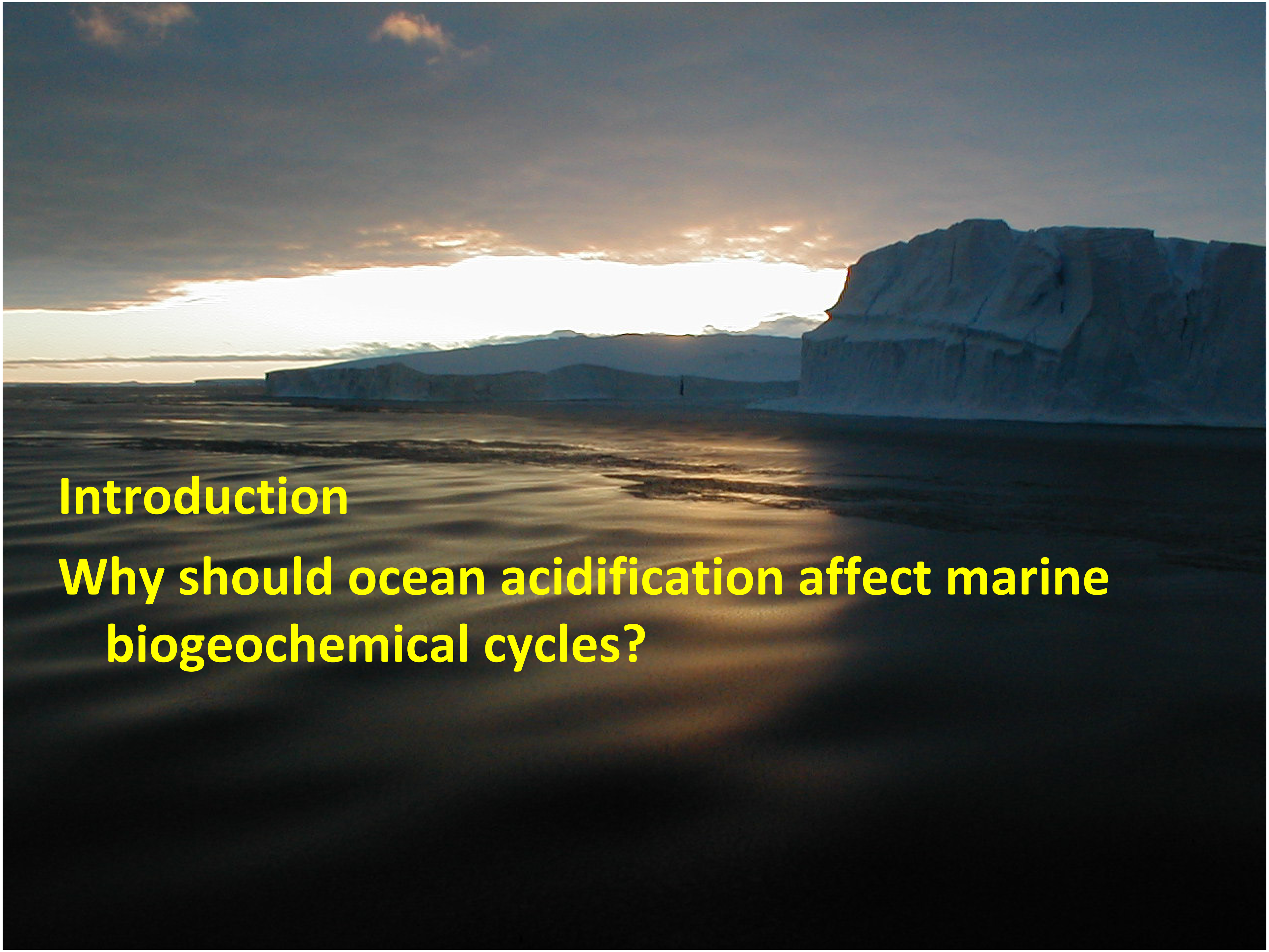
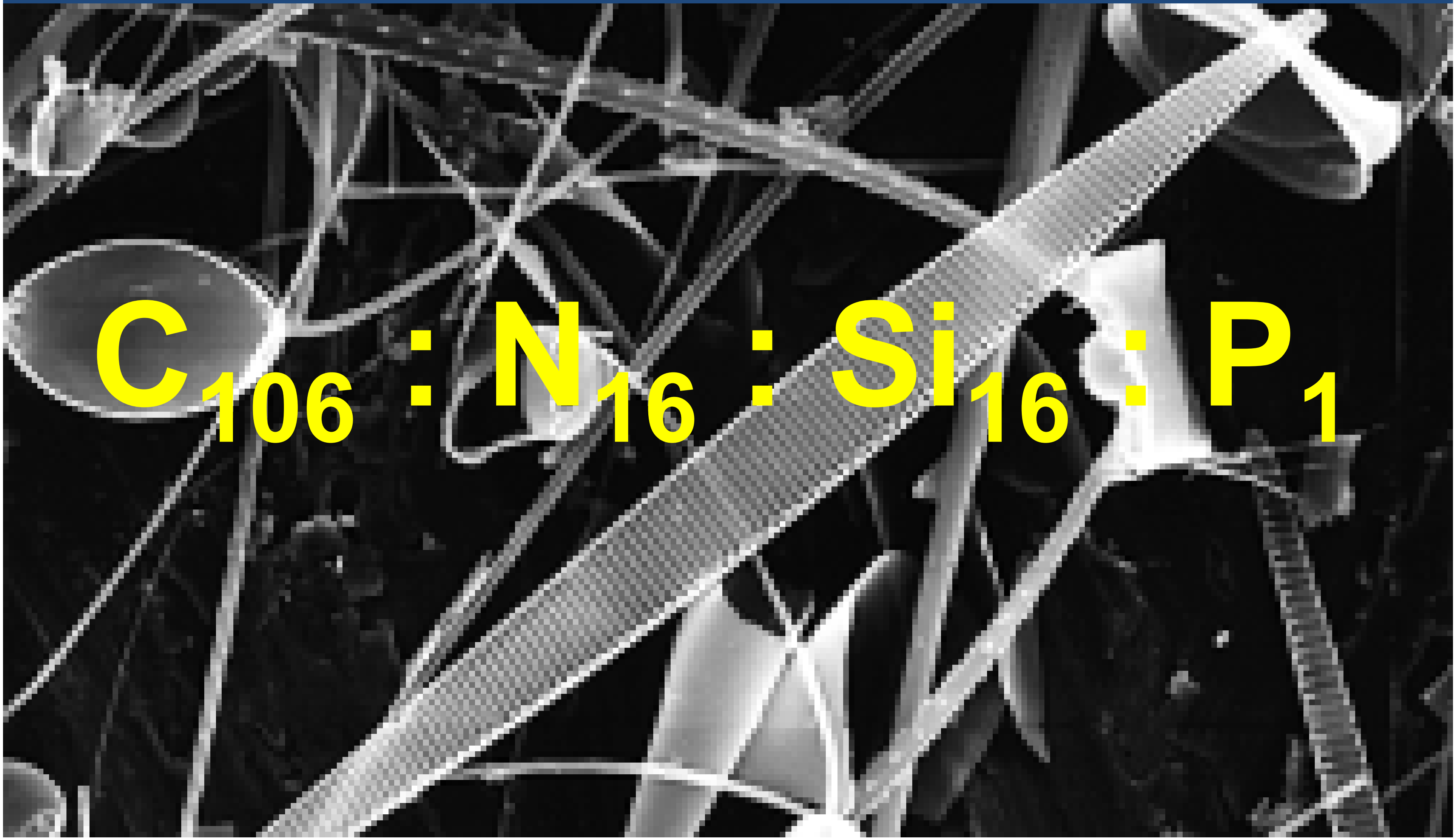


Investigating the effects of ocean acidification on carbon, nutrient, and trace metal biogeochemistry

Dave Hutchins
University of Southern California


Introduction
Why should ocean acidification affect marine biogeochemical cycles?

How will nutrient biogeochemistry change in an acidified ocean?



Phytoplankton Elemental Ratios

- Redfield: 106C:16N:16Si:1P
- Ho et al. 2003: $(C_{124}N_{16}P_{1}S_{1.3}K_{1.7}Mg_{0.56}Ca_{0.5})_{(1000)}Fe_{7.5}$
- Price 2005:

  $C_{97}:N_{14}:Si:_{4.7}:P_{1}:Fe_{0.029}$ (Fe-replete)

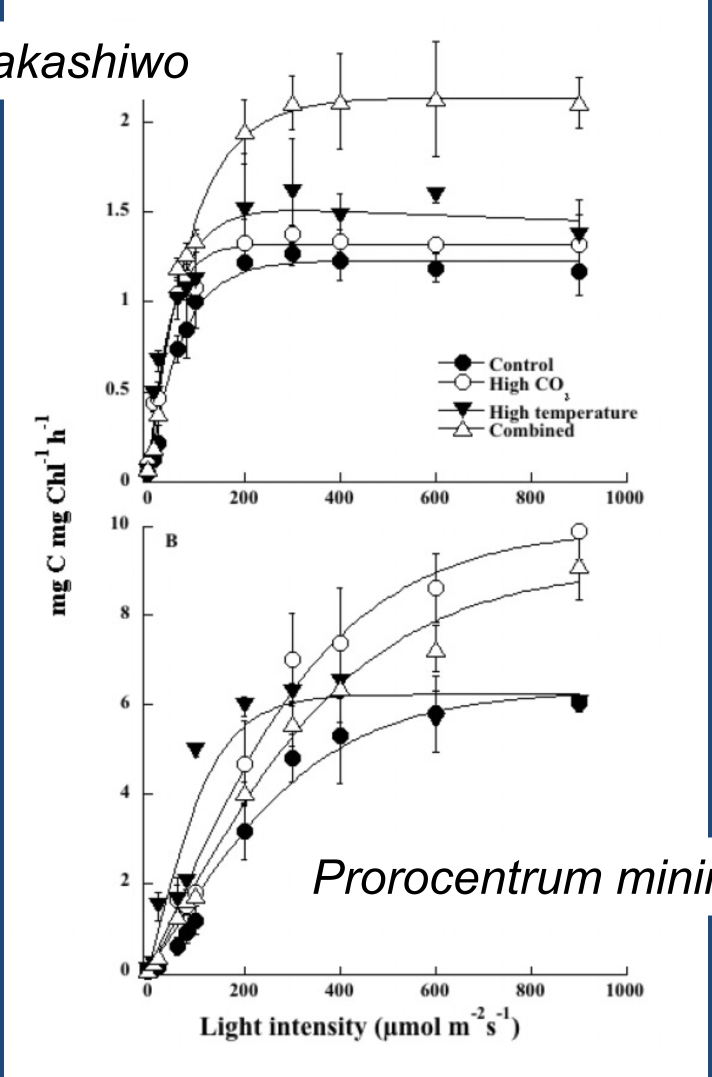
  $C_{70}:N_{10}:Si:_{5.9}:P_{1}:Fe_{0.00074}$ (Fe-limited)

Carbon

- CO_2 enrichment can potentially promote the photosynthesis and growth of autotrophs such as phytoplankton and chemoautotrophic bacteria.
- Responses to changing pCO_2 depend partly on the efficiency of carbon-concentrating mechanisms (CCMs), like various carbonic anhydrases. Autotrophic groups with less efficient CCMs may benefit the most from increasing pCO_2.
- For calcifying autotrophs (coccolithophorids), it is perfectly possible for higher pCO_2 to increase photosynthetic carbon fixation, while at the same time calcification is reduced.
- For both CO_2 fixation and calcification, interactions with other global change variables like temperature or light can be as important (or more so) as the effects of elevated CO_2 alone.

Effects of CO_2 and temperature increases on photosynthesis versus irradiance (PE) curves of two harmful bloom flagellates

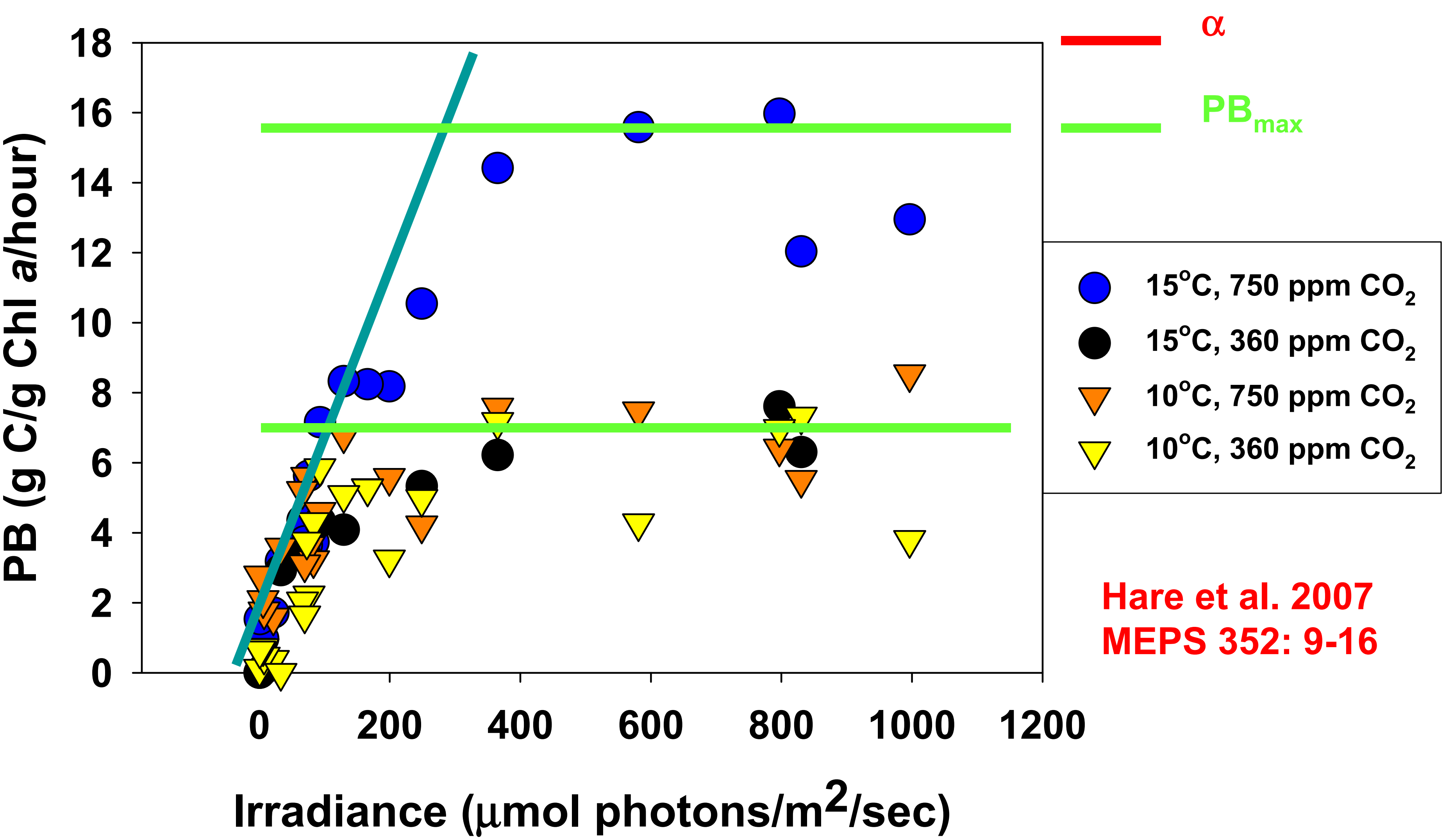
Heterosigma akashiwo



Prorocentrum minimum

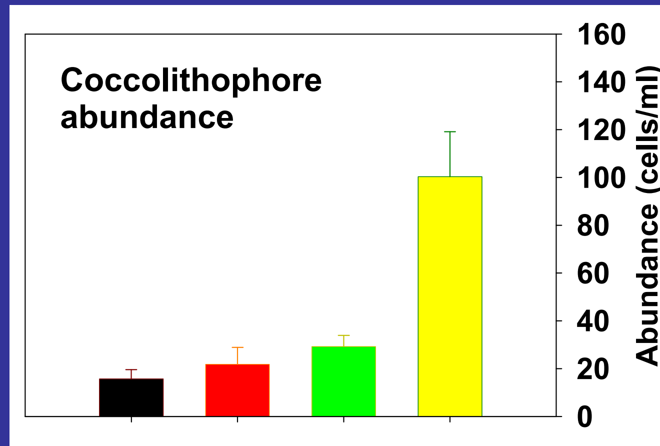
Fu et al. 2008.
Harmful Algae 7:
doi:10.1016/j.hal.2007.05.006.

Bering Sea temperature/pCO_2 matrix: Photosynthesis vs. Irradiance Curve

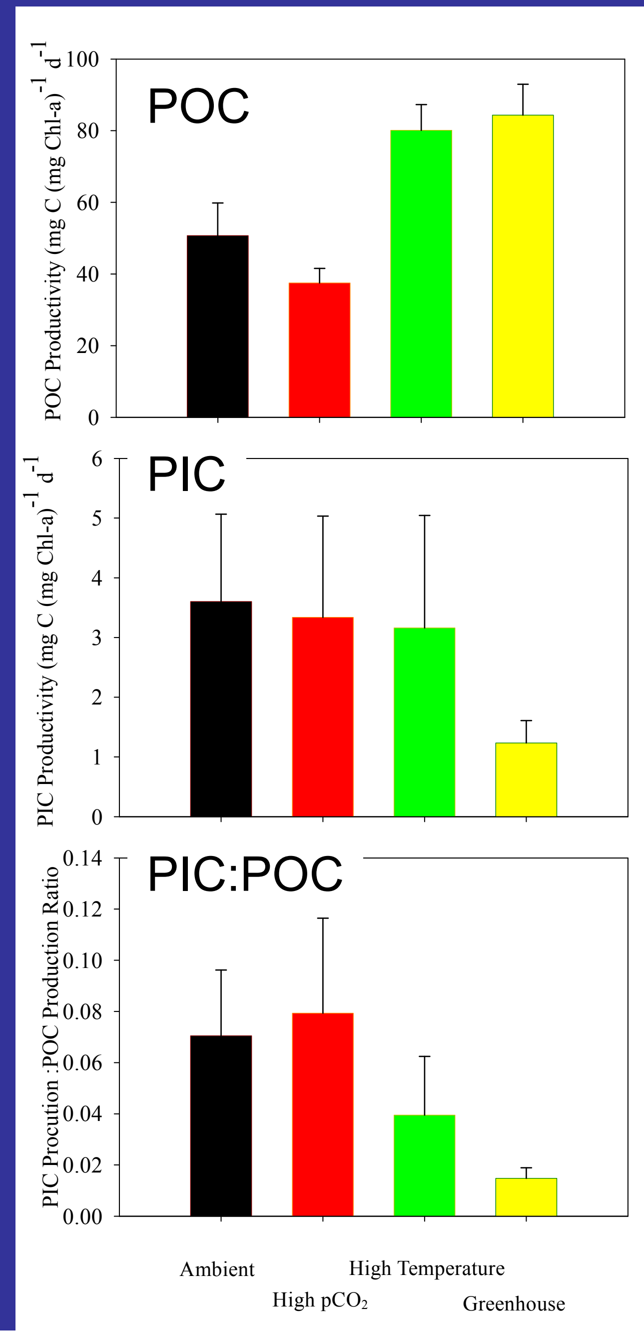


Hare et al. 2007
MEPS 352: 9-16

North Atlantic Bloom CO_2/ temperature experiment: coccolithophore abundance, POC and PIC production

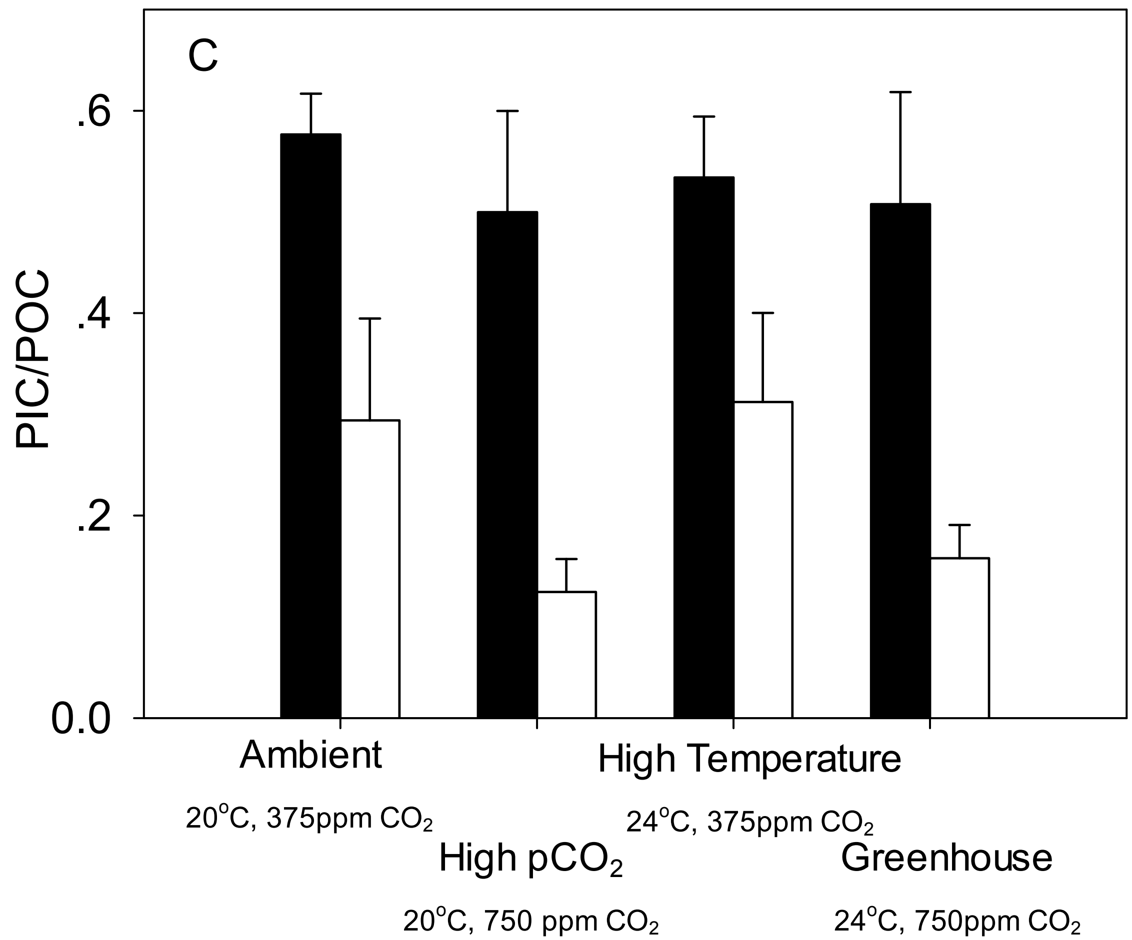


Black: Ambient control
Red: High pCO_2
Green: High temp
Yellow: High pCO_2 and high temp



Feng et al. 2009. Effects of increased pCO_2 and temperature on the North Atlantic spring bloom. I. The phytoplankton community and biogeochemical response. MEPS 388: 13-25

Interactive effects of light, temperature and pCO_2 on calcification by a Sargasso Sea *E. hux.* isolate

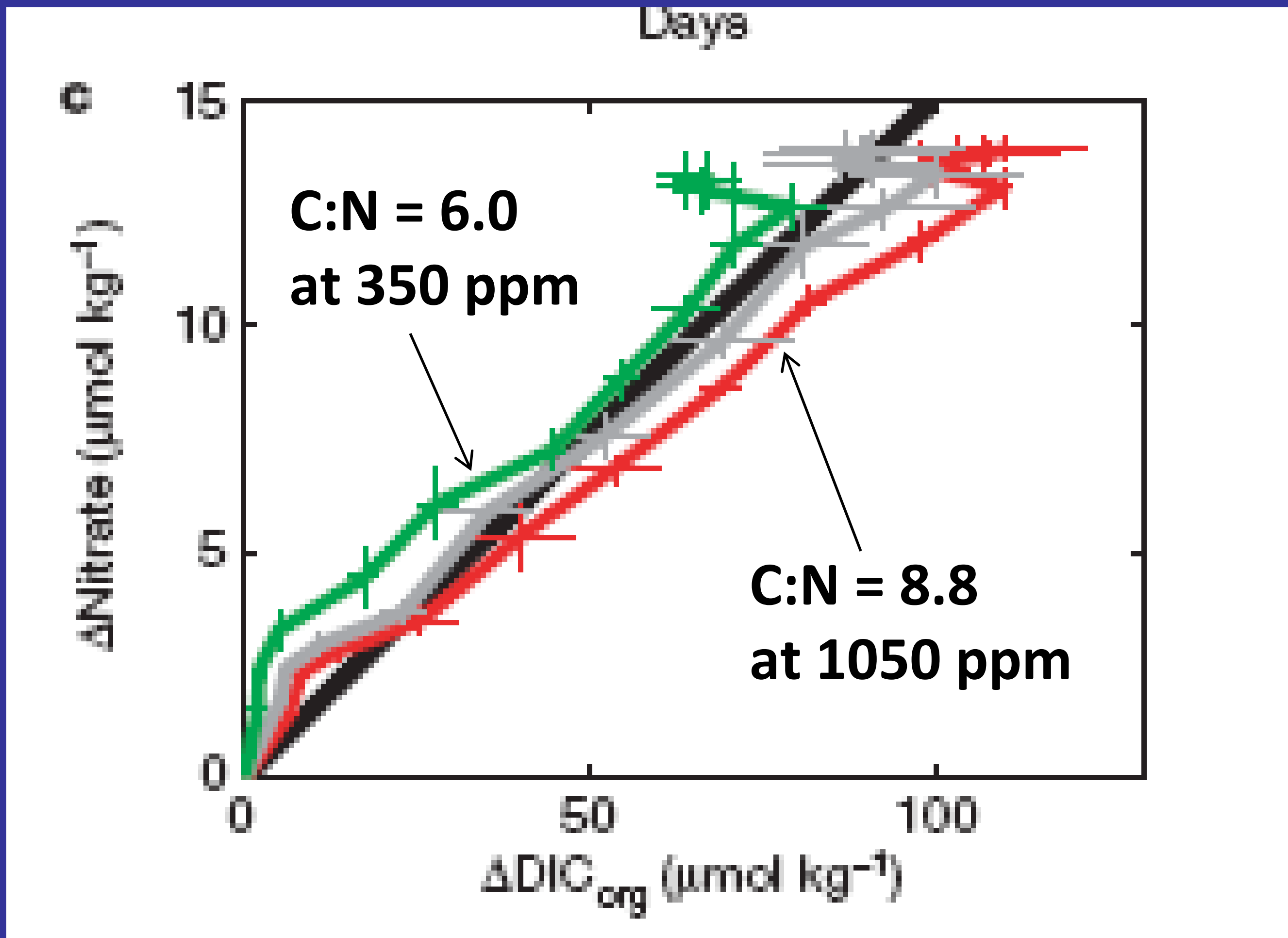


Open bars = high light (400 μEinsteins)
Filled bars = low light (50 μEinsteins)

Feng et al. 2008, European Journal of Phycology 43: 87-98

The primary control on calcification in this strain is light intensity-
pCO_2 exerts a secondary effect, but only under saturating light conditions

Carbon "overconsumption" at high pCO_2?

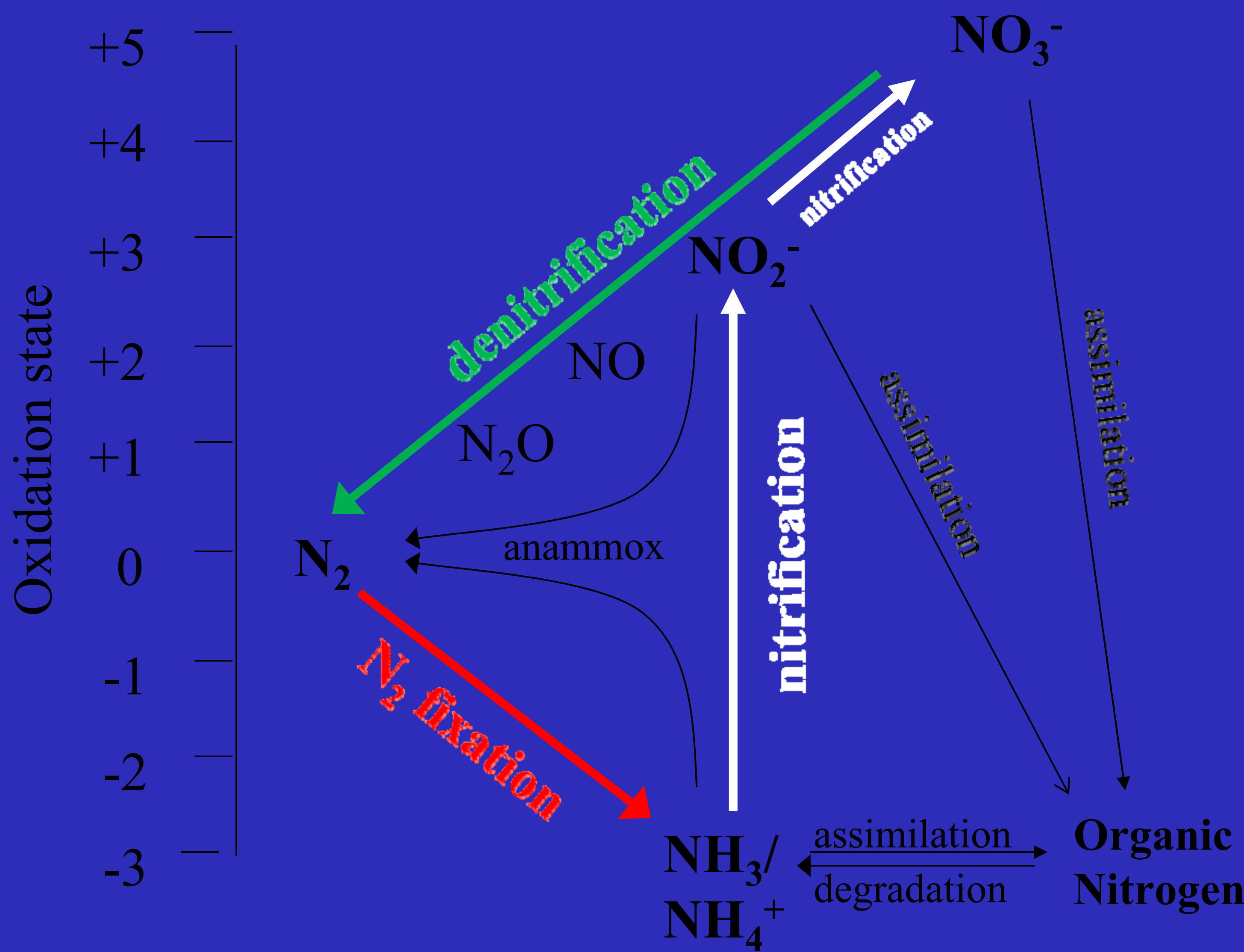


Riebesell et al. 2007, Nature 450: 545-548

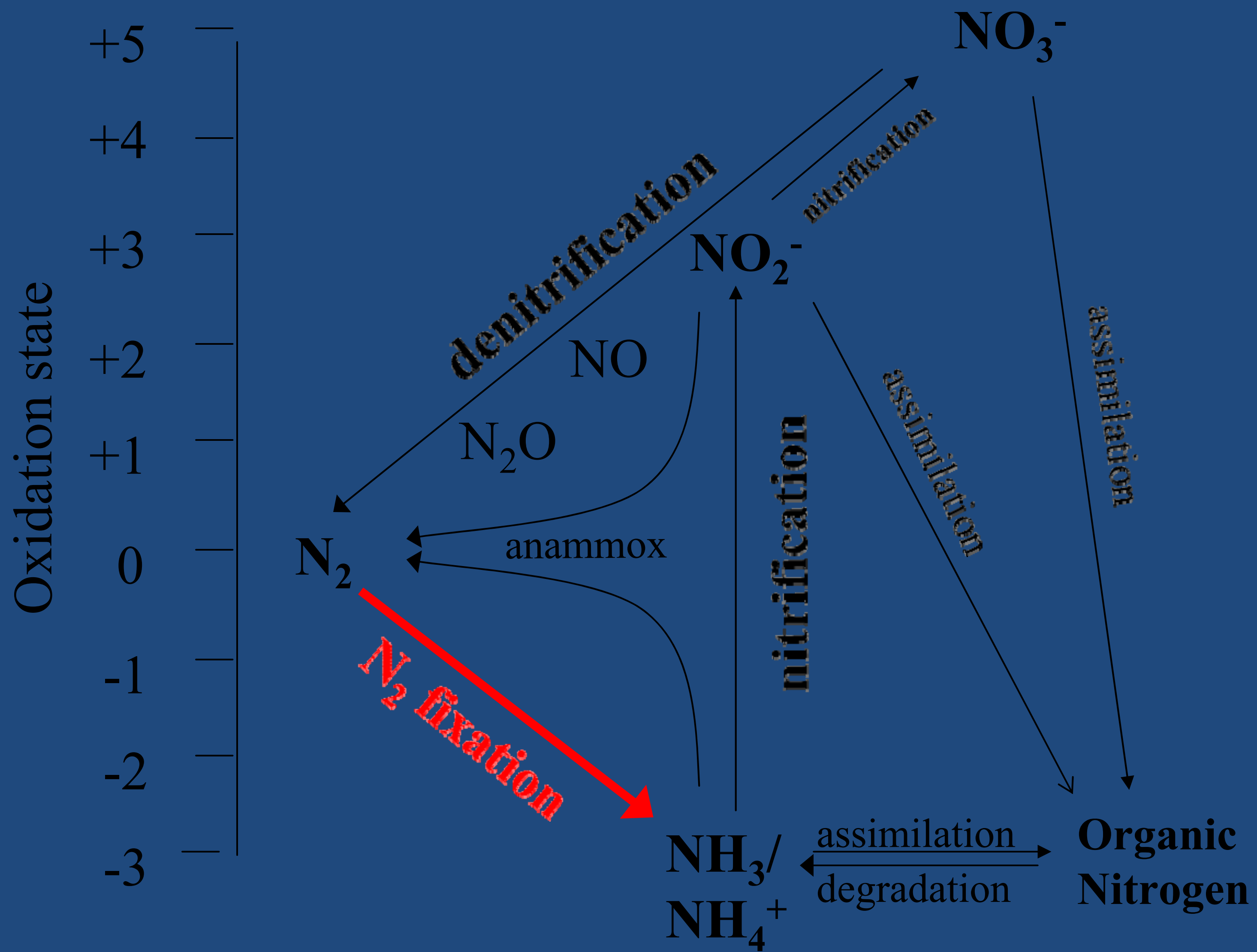
Carbon measurement methods

1. Covered elsewhere in the course:
   – DIC drawdown
   – Calcification and organic carbon fixation using ^{14}C
2. CHN analysis: Simple gas chromatography method to measure particulate organic (and inorganic) carbon and nitrogen (Sharp 1974. Limnol. Oceanogr. 19: 984-989.), or use a mass spectrometer.
3. P/E curves: Requires a photosynthetron which produces a wide range of light levels; samples are incubated briefly with ^{14}C (van Hilst and Smith 2002 MEPS 226: 1-12; Feng et al. 2009 MEPS 388: 13–25)

The marine nitrogen cycle



Nitrogen fixation



Nitrogen fixation

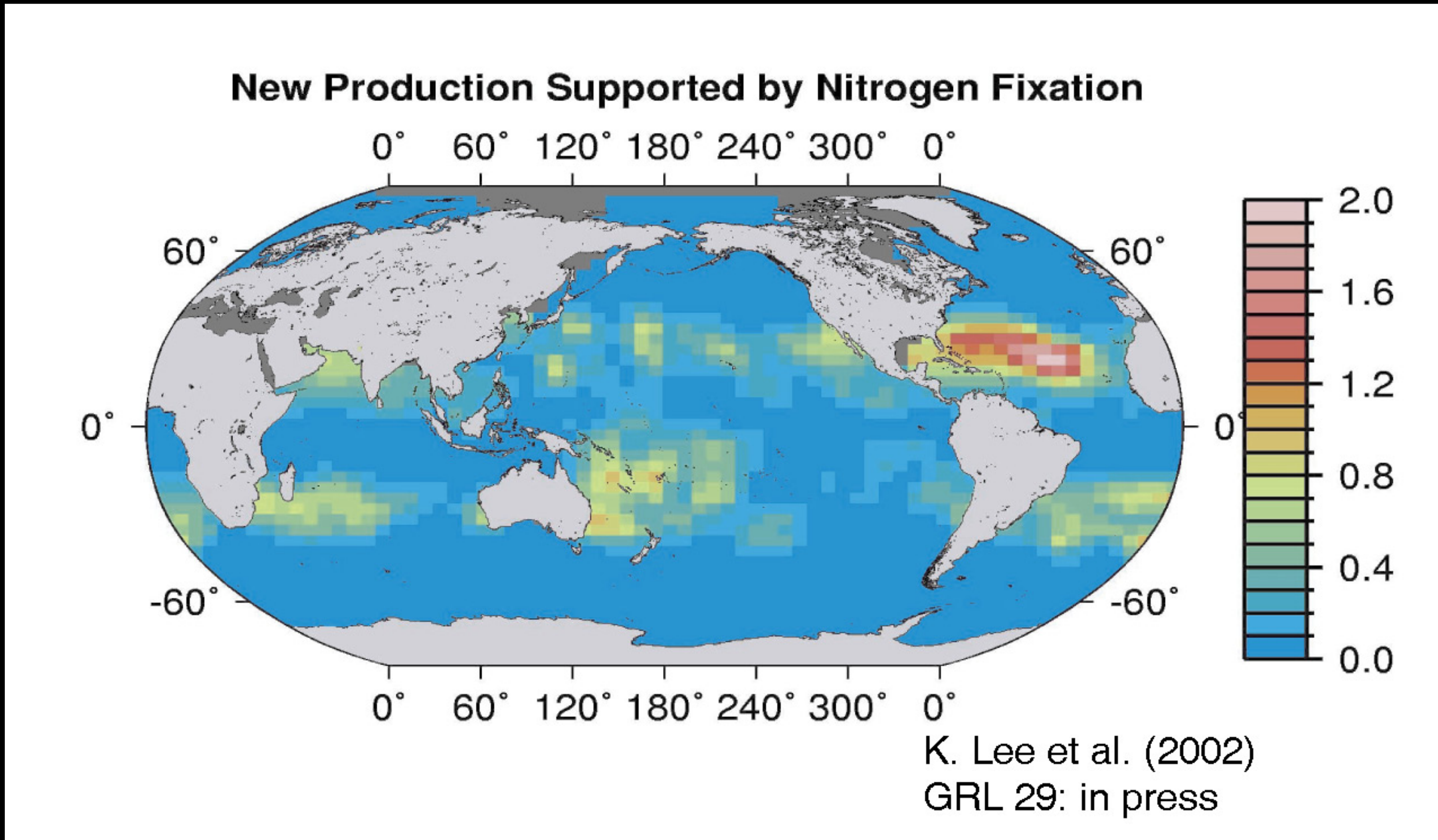
1. **Biological nitrogen fixation is the primary natural source of fixed nitrogen in the ocean.**

2. **Major groups include cyanobacteria (*Trichodesmium*, *Crocosphaera*) along with diatom/diazotroph and zooplankton/diazotroph symbioses, N_2-fixing heterotrophic eubacteria and archaea.**

3. **Most prominent in sub-tropical and tropical regimes, but now being found in other marine environments as well.**

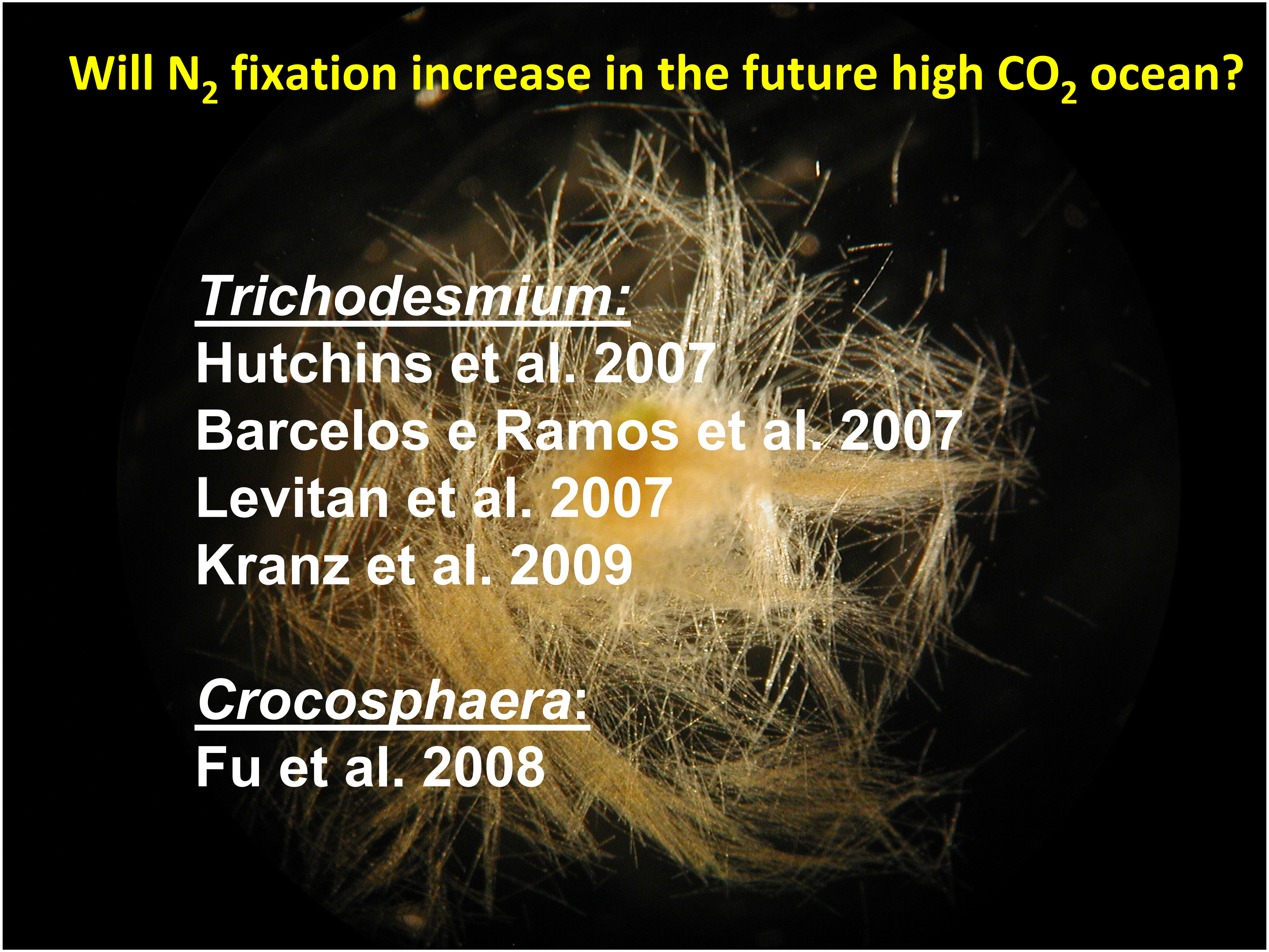
4. **Thought to be often limited by the availability of P or Fe.**

Hutchins and Fu 2008. Linking the oceanic biogeochemistry of iron and phosphorus with the marine nitrogen cycle.
pp. 1627-1653, Nitrogen in the Marine Environment, 2nd edition. Elsevier Press



Global estimate of new production based on N_2 fixation. DIC drawdown in NO_3-depleted warm waters is equivalent to 0.8 ±0.3 Pg C yr^{-1}

Will N_2 fixation increase in the future high CO_2 ocean?



Trichodesmium:

Hutchins et al. 2007

Barcelos e Ramos et al. 2007

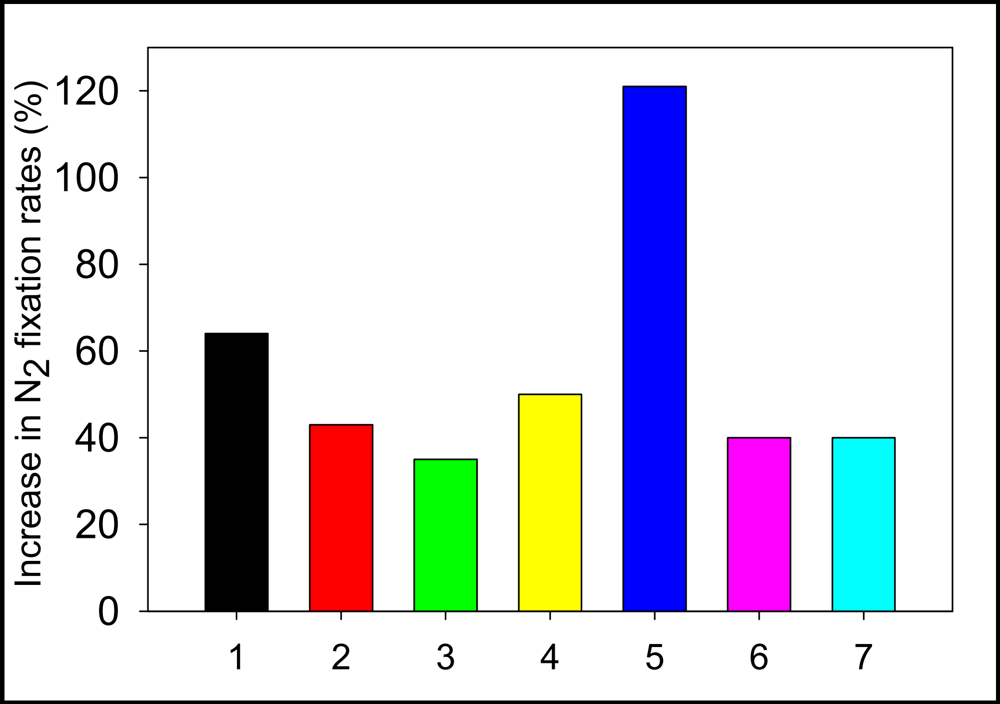
Levitan et al. 2007

Kranz et al. 2009

***Crocosphaera*:**

Fu et al. 2008

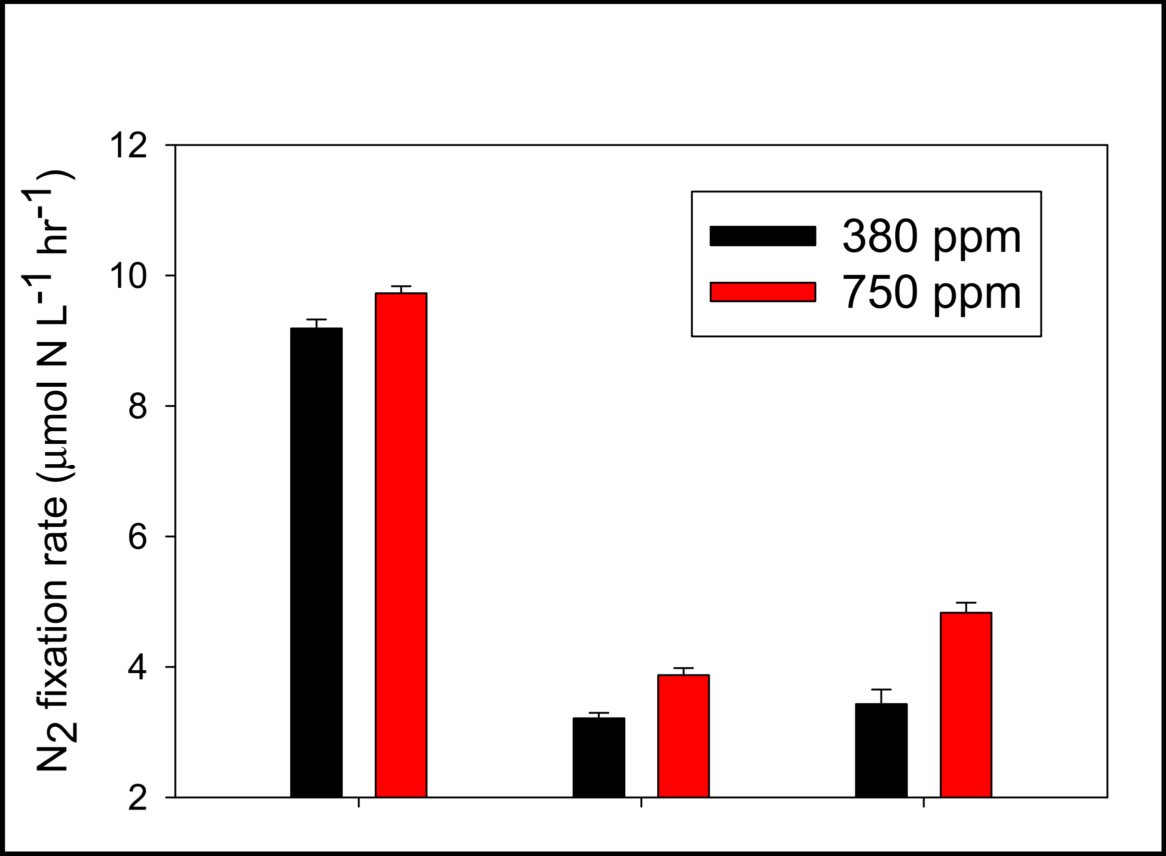
Elevated N_2 fixation rates at high pCO_2 in cultured cyanobacteria



1) ***Trichodesmium erythraeum*** **strain GBR at 29°C, 380-750 ppm CO_2 (Hutchins et al. 2007)**
2) ***T. erythraeum*** **strain GBR at 25°C, 380-750 ppm CO_2 (Hutchins et al. 2007)**
3) ***T. erythraeum*** **strain IMS 101 at both 25°C and 29°C, 380-750 ppm CO_2 (Hutchins et al. 2007)**
4) ***T. erythraeum*** **strain IMS 101 at 25°C, 380-750 ppm CO_2 (Barcelos e Ramos et al. 2007)**
5) ***T. erythraeum*** **strain IMS 101 at 25°C, 400-900 ppm CO_2 (Levitan et al. 2007)**
6) ***T. erythraeum*** **strain IMS 101 at 25°C, 370-1000 ppm CO_2(Kranz et al. 2009)**
7) ***Crocosphaera watsonii*** **strain WH8501 at 28°C, 380-750 ppm CO_2 (Fu et al. 2008)**

Hutchins et al. in review, Oceanography

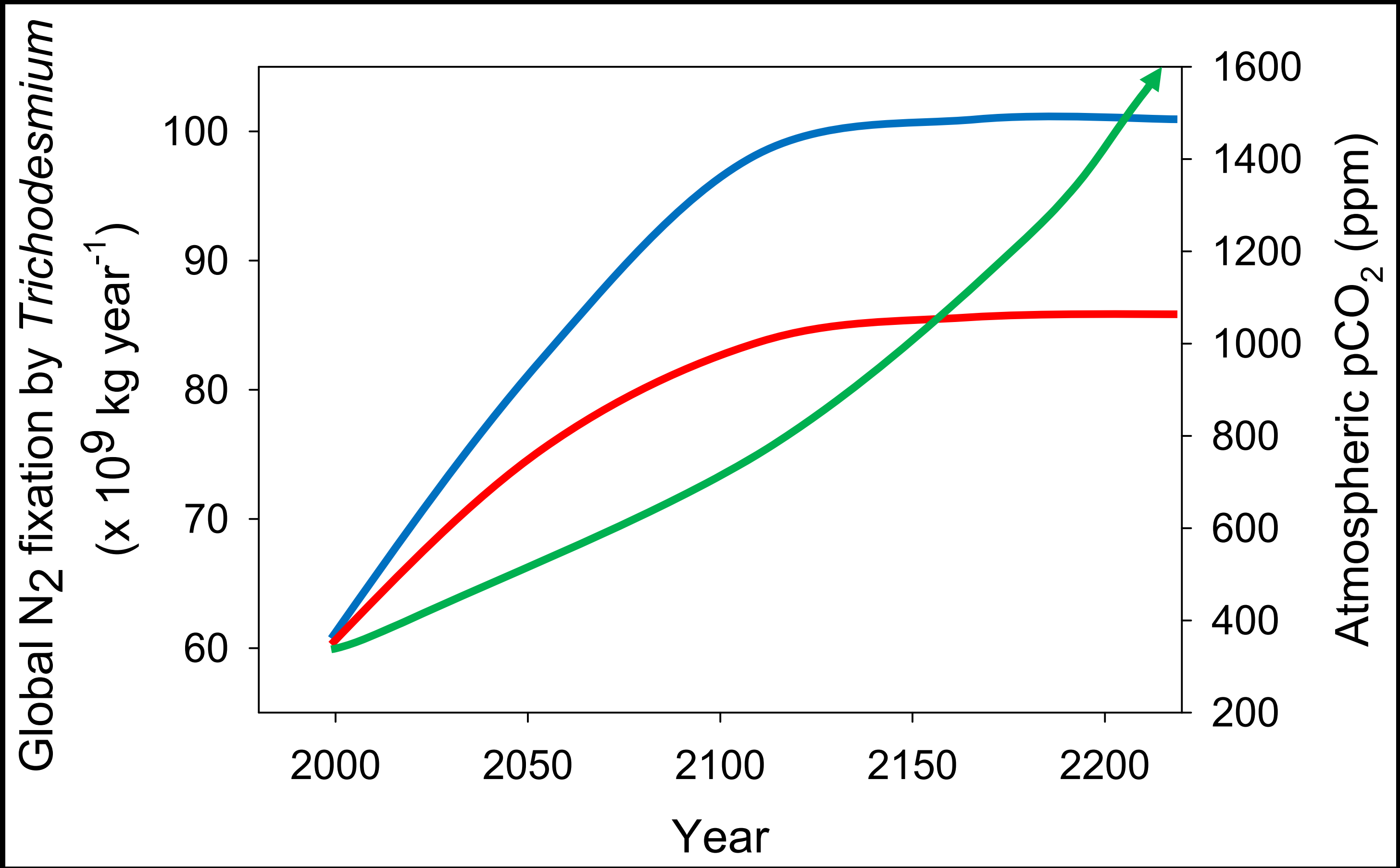
Short-term CO_2 enrichments using natural *Trichodesmium* colonies from the Gulf of Mexico



N_2 fixation rates increased 6- 41% within a few hours of elevating pCO_2 to 750 ppm

Hutchins et al. in review, Oceanography

Future trends in global N_2 fixation by *Trichodesmium*?

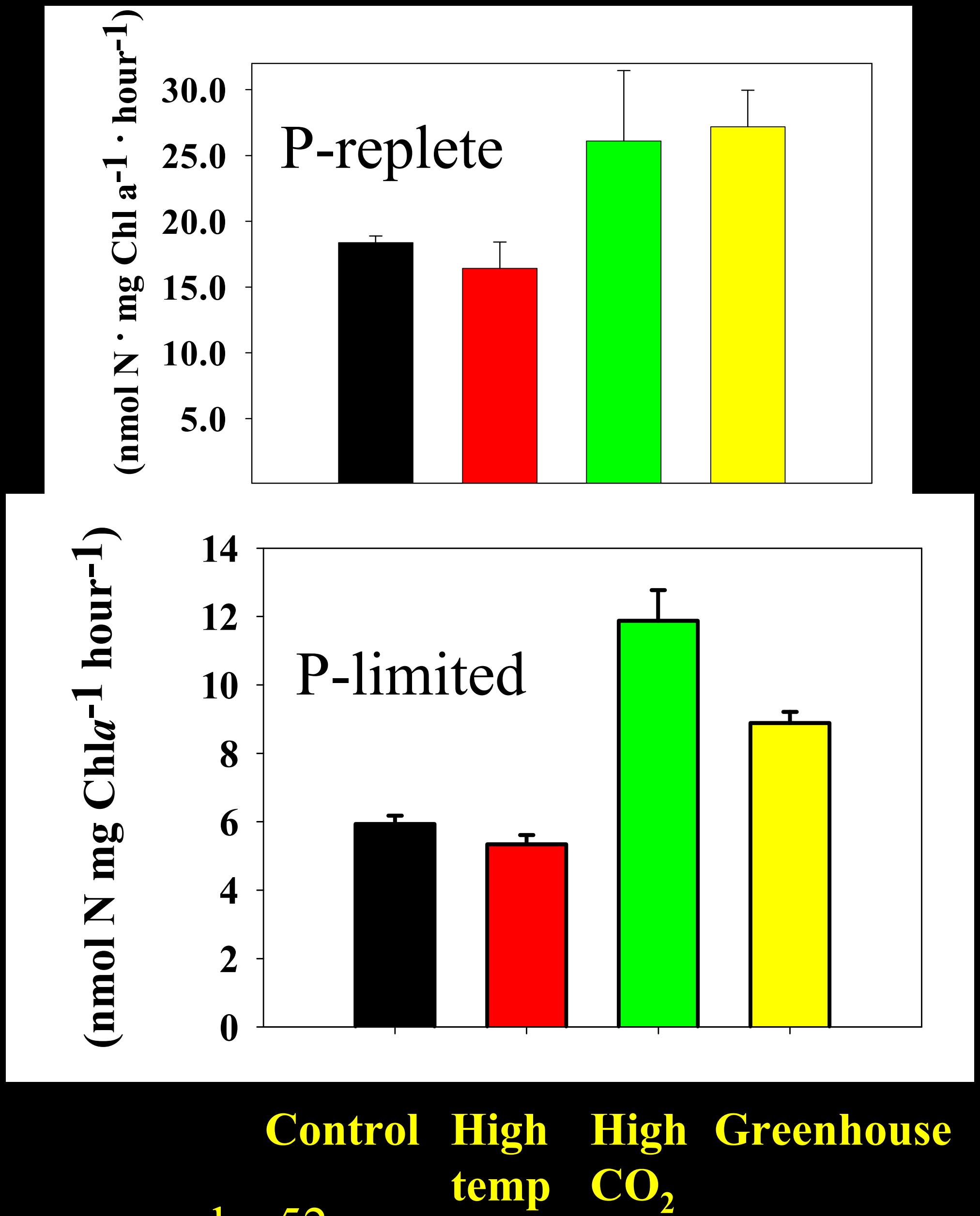


Maximum (blue) and minimum (red) projected annual global N_2 fixation increases versus pCO_2 (green)

Hutchins et al. in review, Oceanography

pCO_2 and P co-limitation of *Trichodesmium* N_2 fixation

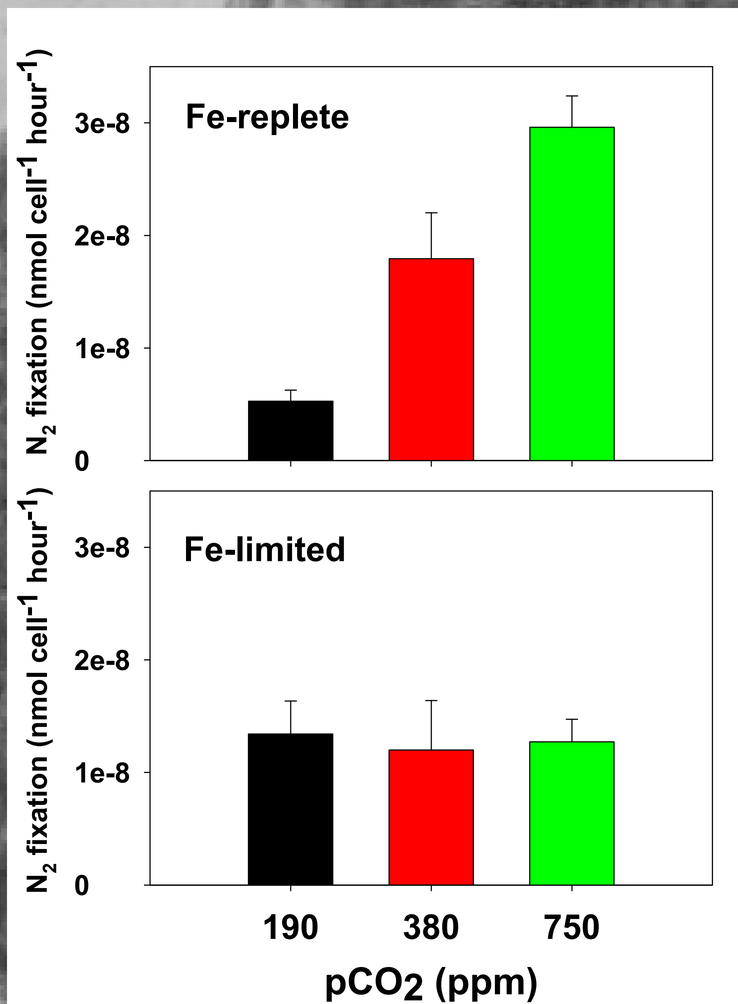
Adding <u>either</u> P or CO_2 will increase N_2 fixation and growth rates of P-limited cultures at present day pCO_2



Hutchins et al. 2007, Limnology & Oceanography 52

Crocosphaera: N_2 fixation rates as a function of pCO_2 and Fe

N_2 fixation rates



Fu et al. 2008. Interactions between changing pCO_2, N_2 fixation, and Fe limitation in the marine unicellular cyanobacterium *Crocosphaera.* L&O 53: 2472- 2484

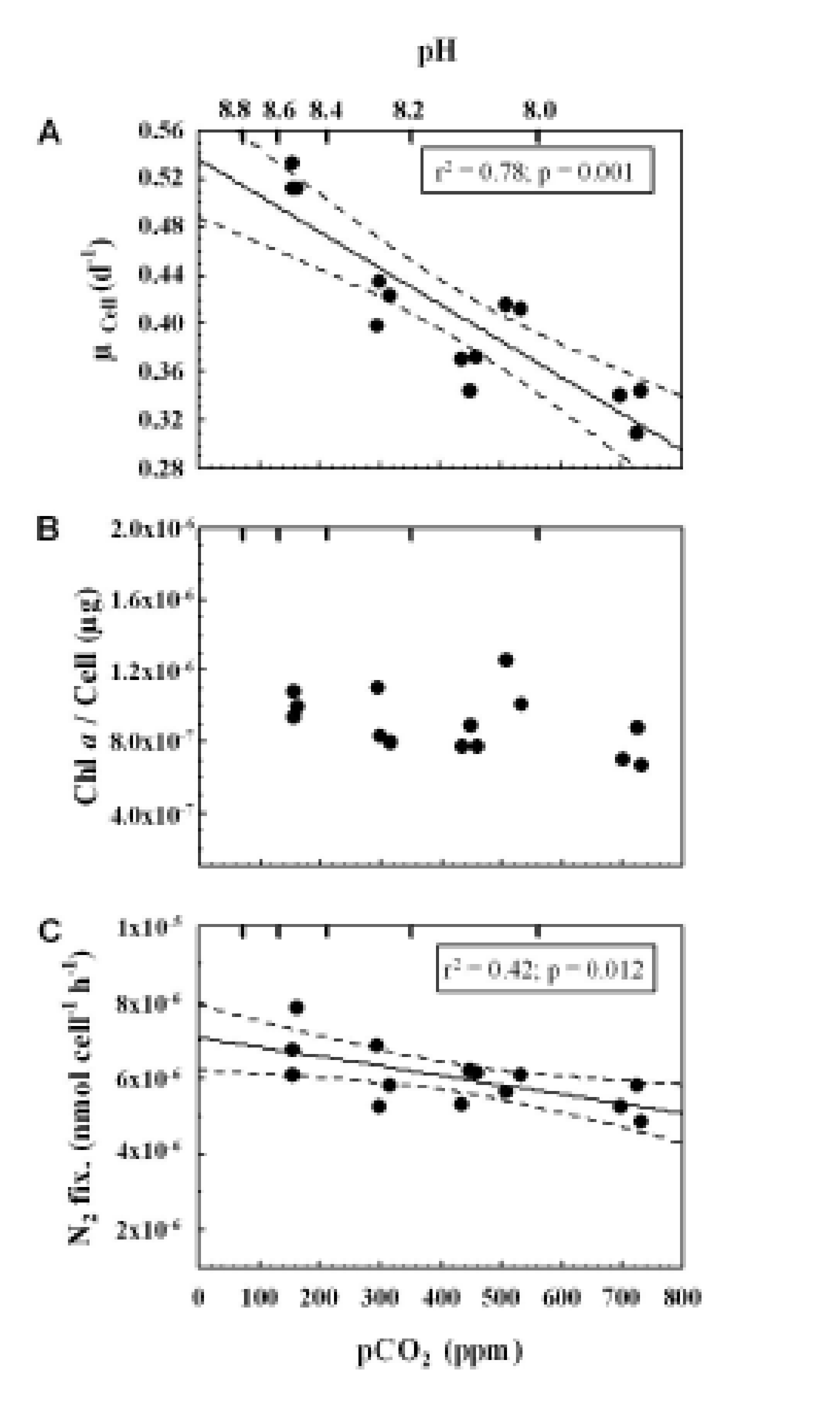
The two nutrients Fe and P interact very differently with changing pCO_2 in N_2-fixing cyanobacteria

- Severe Fe limitation essentially cancels out the stimulatory effect of increased pCO_2
- Severe P limitation however does not- effectively, the cells are co-limited by both P and CO_2

Not all N_2-fixing cyanobacteria will necessarily benefit from high pCO_2:

The harmful bloom species *Nodularia spumigena* from the brackish Baltic Sea

Czerny et al. 2009,
Biogeosciences Discussions 6: 4279-4304



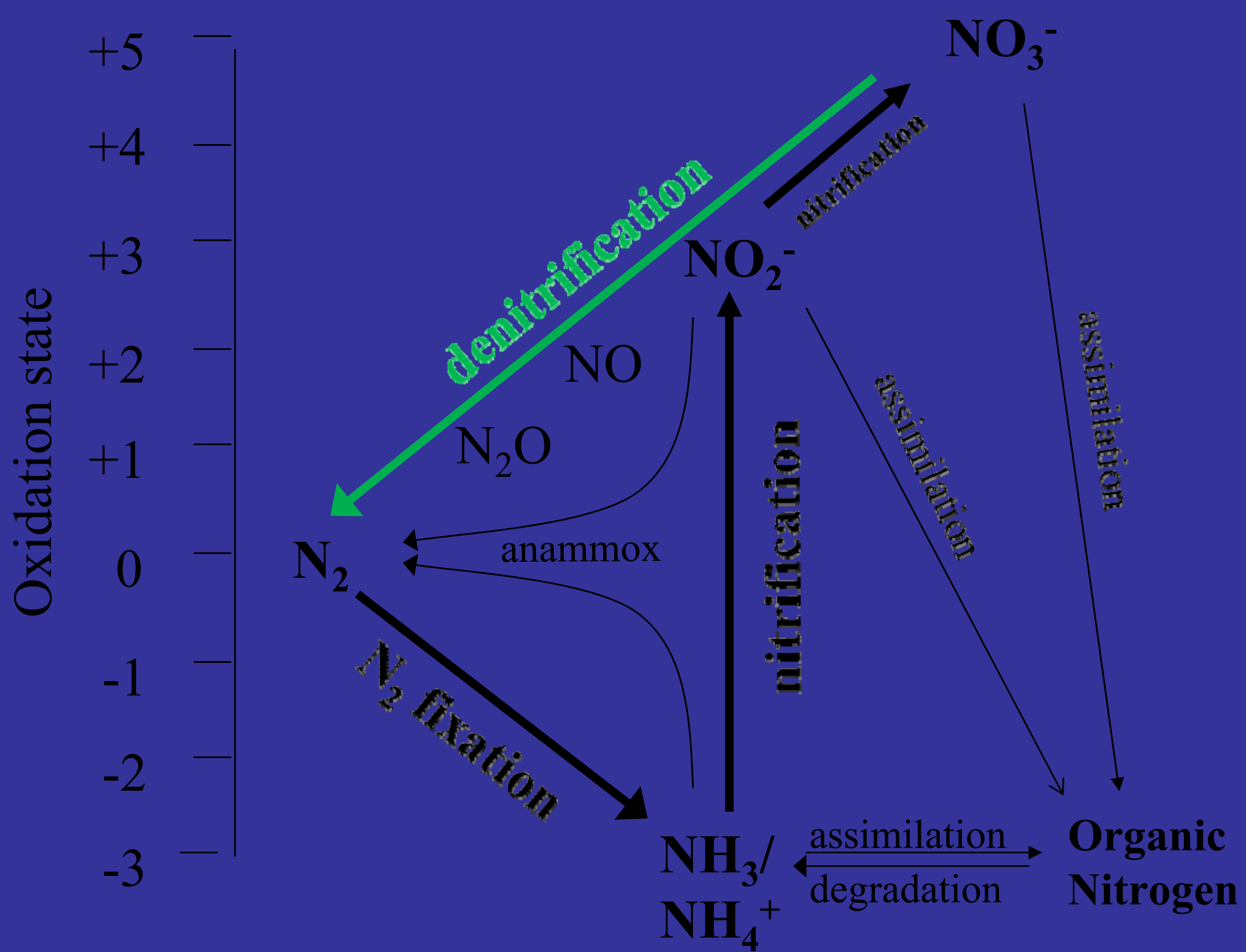
Nitrogen fixation measurements

1. **Measurements of acetylene reduction to ethylene using gas chromatography**

(Capone 1993. Determination of nitrogenase activity in aquatic samples using the acetylene reduction procedure. Handbook of methods in aquatic microbial ecology, pp. 621-631, Lewis Publishers).

2. **$^{15}N_2$ incorporation measured by mass spectrometry**
   (Mulholland and Bernhardt, 2005. The effect of growth rate, phosphorus concentration, and temperature on N_2 fixation, carbon fixation, and nitrogen release in continuous cultures of *Trichodesmium* IMS101. Limnol. Oceanogr. 50: 839–849).

Denitrification



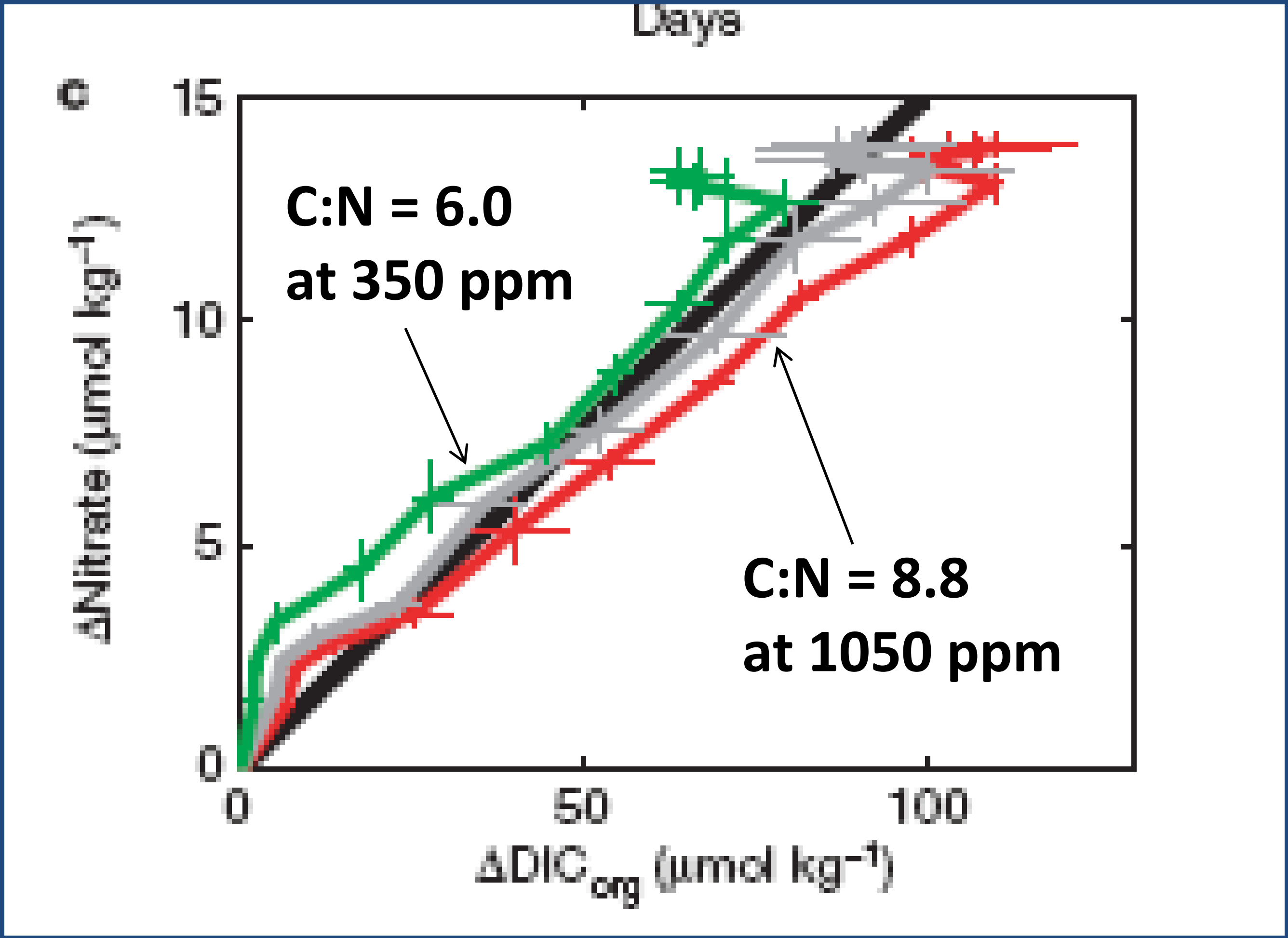
Denitrification

1. Heterotrophic, largely facultative anaerobic micro-organisms (eubacteria, archaea, and fungi) use oxidized NO_3^- as a respiratory terminal electron acceptor, reducing it through a series of intermediates to N_2.

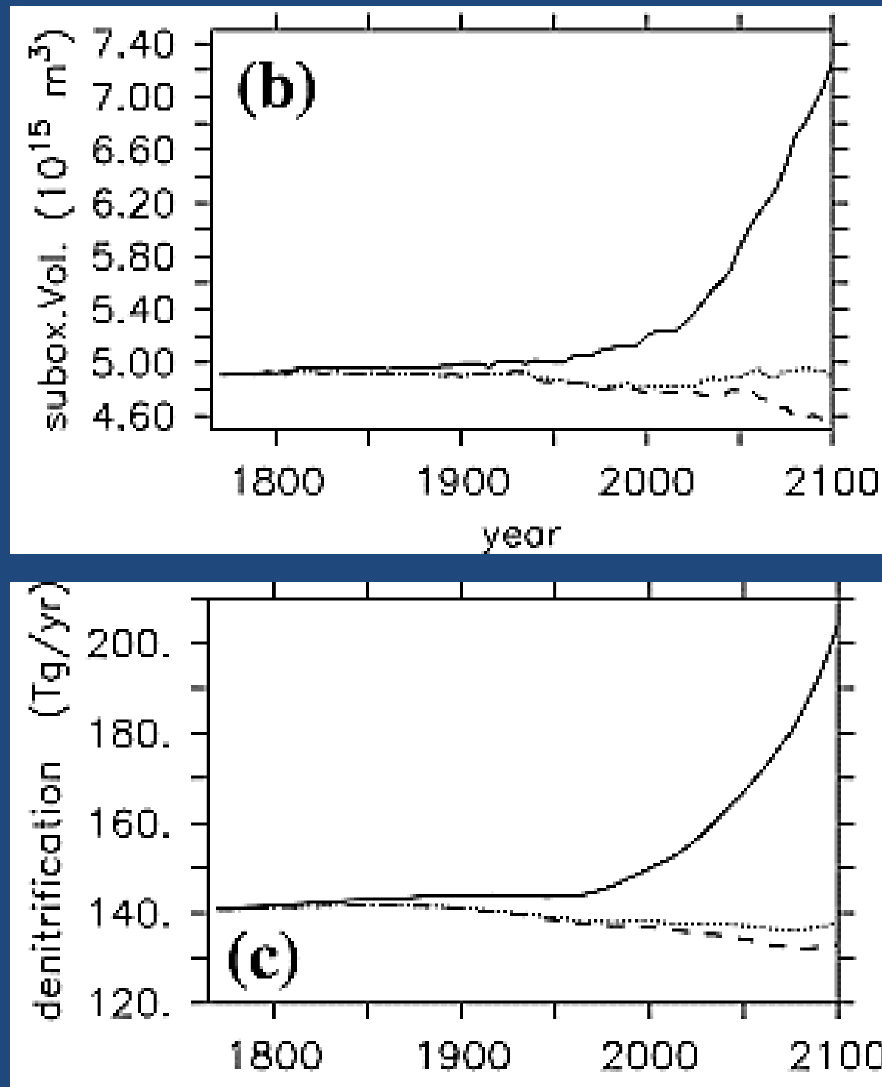
2. Denitrification occurs in the large water column suboxic regions (tropical North and South Pacific, Arabian Sea), and in suboxic sediments worldwide.

3. Along with annamox, denitrification represents the principle loss term for fixed nitrogen in the ocean.

Carbon "overconsumption" at high pCO_2?



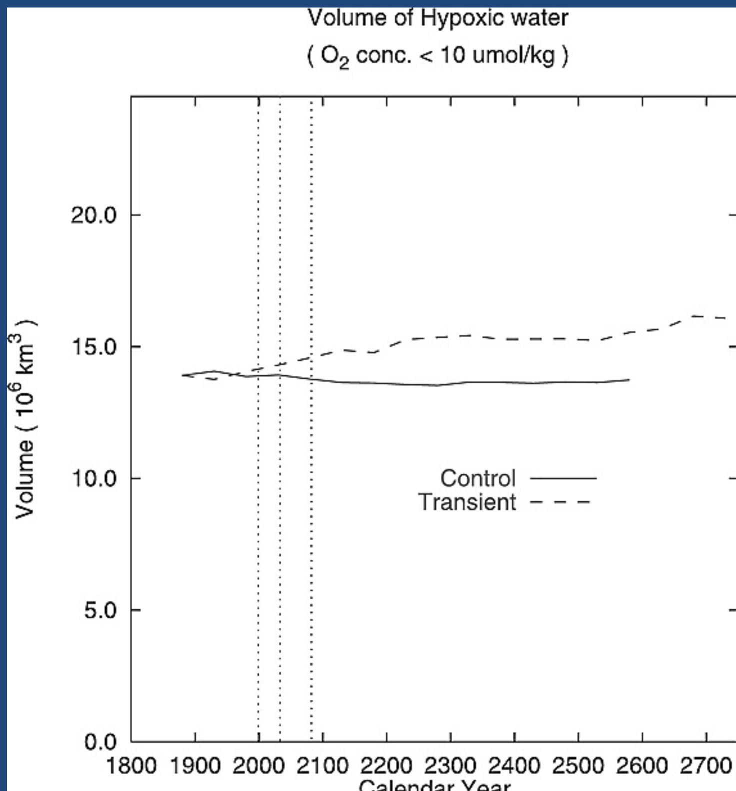
Riebesell et al. 2007, Nature 450: 545-548

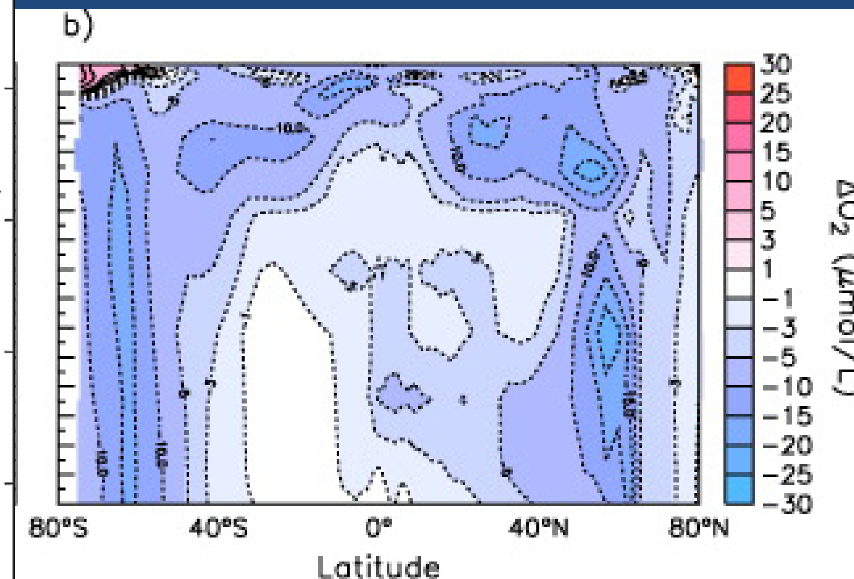


Oschlies et al. 2008, Global Biogeochemical Cycles 22

"Simulated 21st century's increase in oceanic suboxia by CO_2-enhanced biotic carbon export"

Simulated effects of warming and stratification on global suboxic water volume





Future increases in the global volume of hypoxic water

Matear and Hirst 2003, Global Biogeochemical Cycles 17

Differences in zonal mean of ocean dissolved O_2 between 2080–2100 and 1980–2000

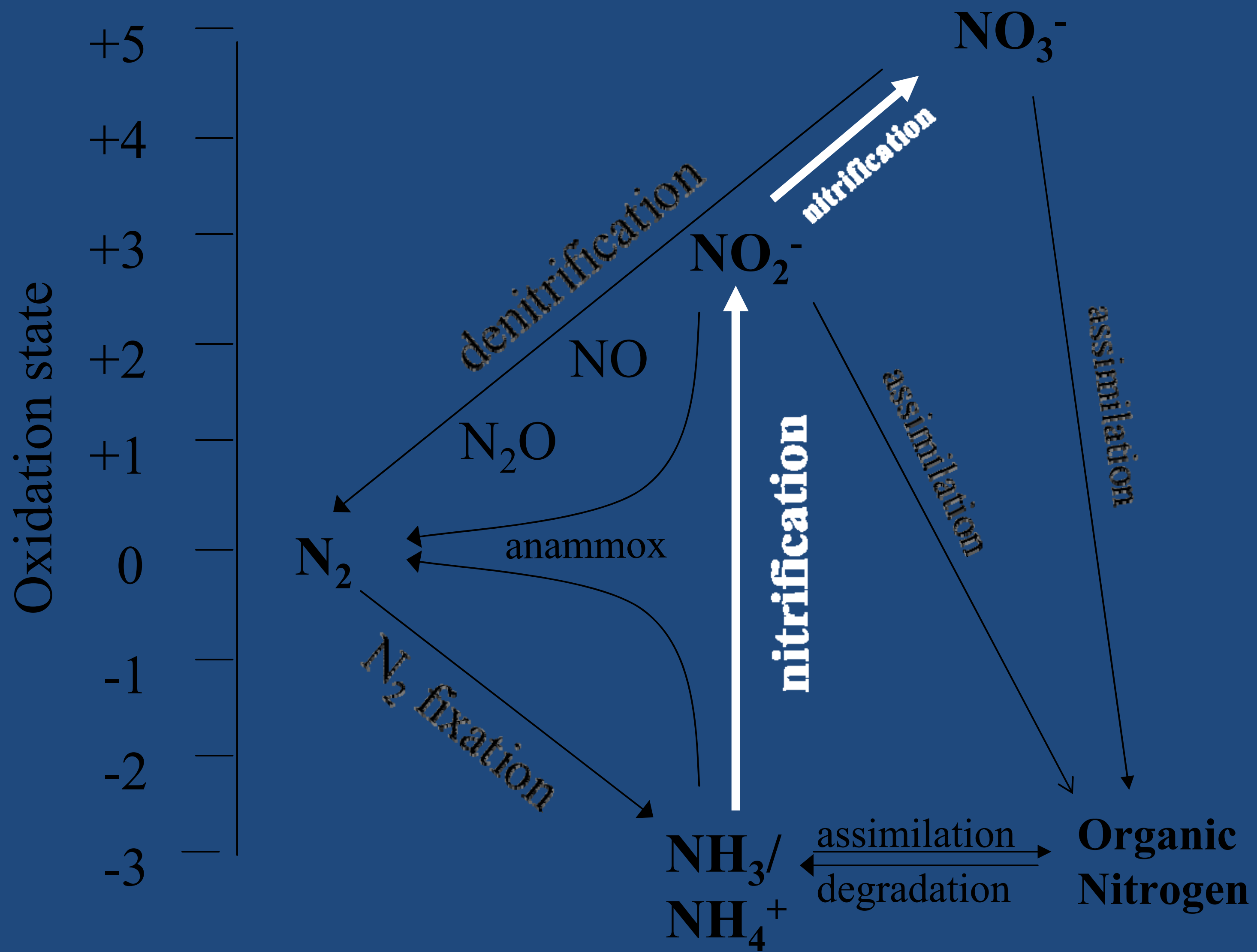
Bopp et al. 2002, Global Biogeochemical Cycles 16

Denitrification measurements

1. Stoichiometric calculations- NO_3^- deficit (negative N*, Deutsch et al. 2001, Gruber and Sarmiento 1997, 2002)
2. Enzymatic activity of electron transport systems measured colorimetrically using the artificial electron acceptor tetrazolium (Devol, 1975, Codispoti and Packard, 1980, Naqvi and Shailaja, 1993)
3. $^{15}NO_3^-$ incubation experiments measuring the production of $^{29}N_2$ by mass spectrometry (Devol et al. 2006)

Devol, A.H. 2008. Denitrification including anammox. pp. 263-302, In: Nitrogen in the Marine Environment, 2nd edition. Capone, D.G., Bronk, D.A., Mulholland, M.R. and Carpenter, E.J. [Eds.], Elsevier Press,

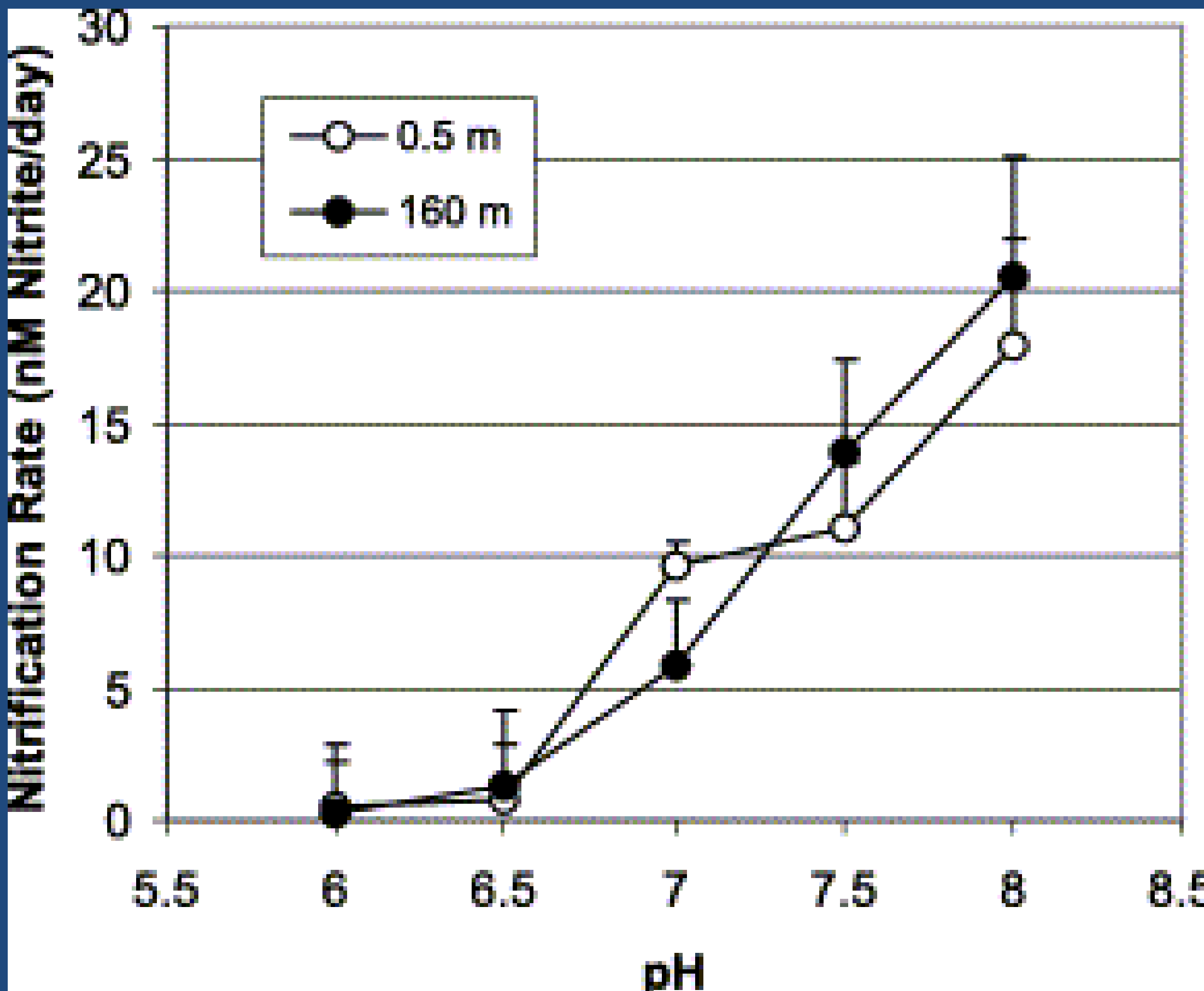
Nitrification



Nitrification

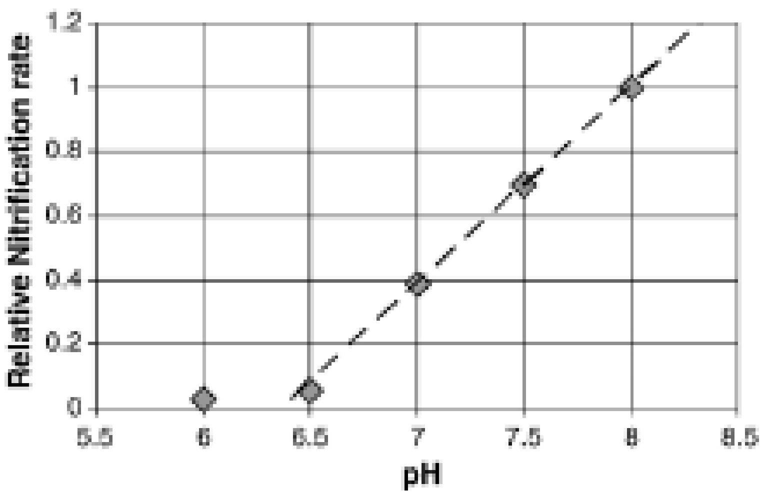
- **Oxidation of ammonia/ammonium first to nitrite, then to nitrate**
- **Aerobic, chemoautotrophic eubacteria and archaea obtain electrons from these reduced nitrogen compounds to fix CO_2**
- **A large fraction occurs just below the euphotic zone (Yool et al. 2007), where it is vulnerable to near-term ocean acidification**
- **NH_3-oxidizing genus *Nitrosomonas* and the NO_2^--oxidizing genus *Nitrobacter* fix carbon using the Calvin cycle**
- **Seawater ammonia/ammonium (NH_3/NH_4^+) buffer system pKa ~9.19; over the next century the fraction of NH_3 will decrease by nearly 50%, from ~6% to ~3%.**
- **NH_3 appears to be the chemical species actually oxidized by *Nitrosomonas* (Suzuki et al. 1974, Ward 1987)**

Nitrification rates decrease with acidification

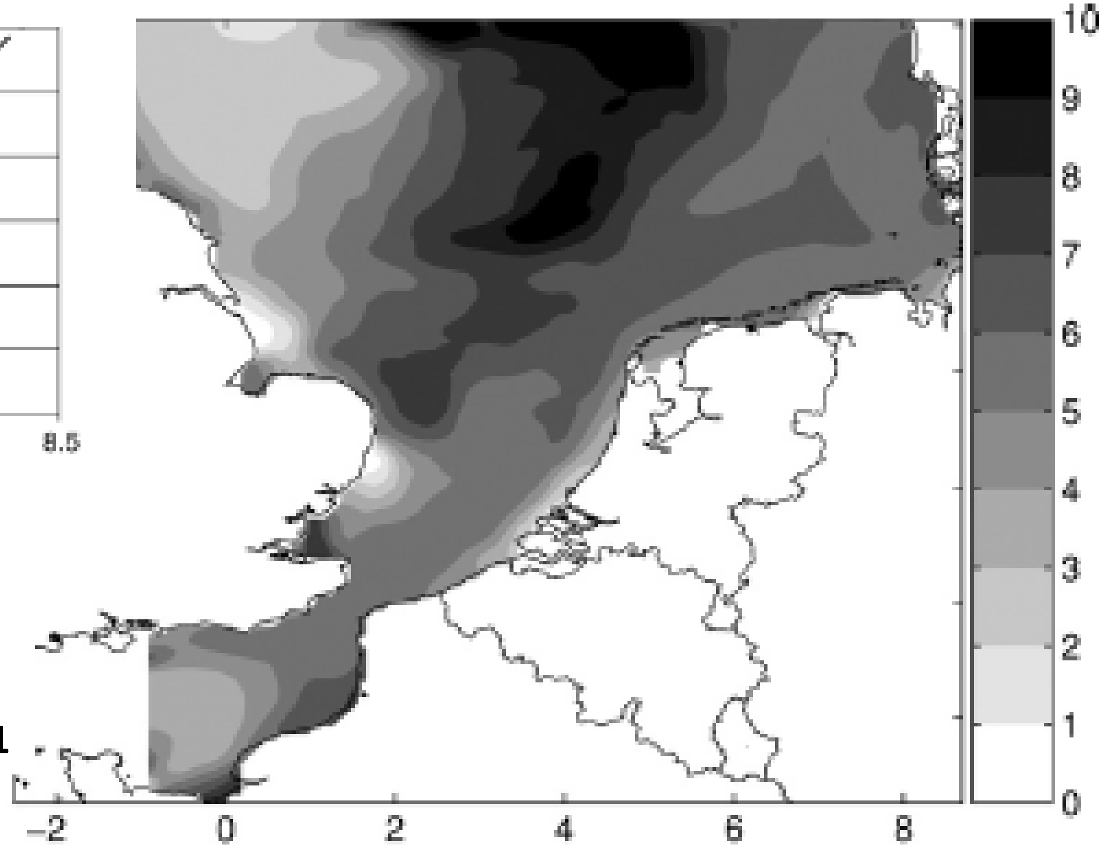


Huesemann et al. 2002, Marine Pollution Bulletin 44: 142-148

Modeled effects of a 20% reduction in North Sea nitrification rates at 1000 ppm CO_2



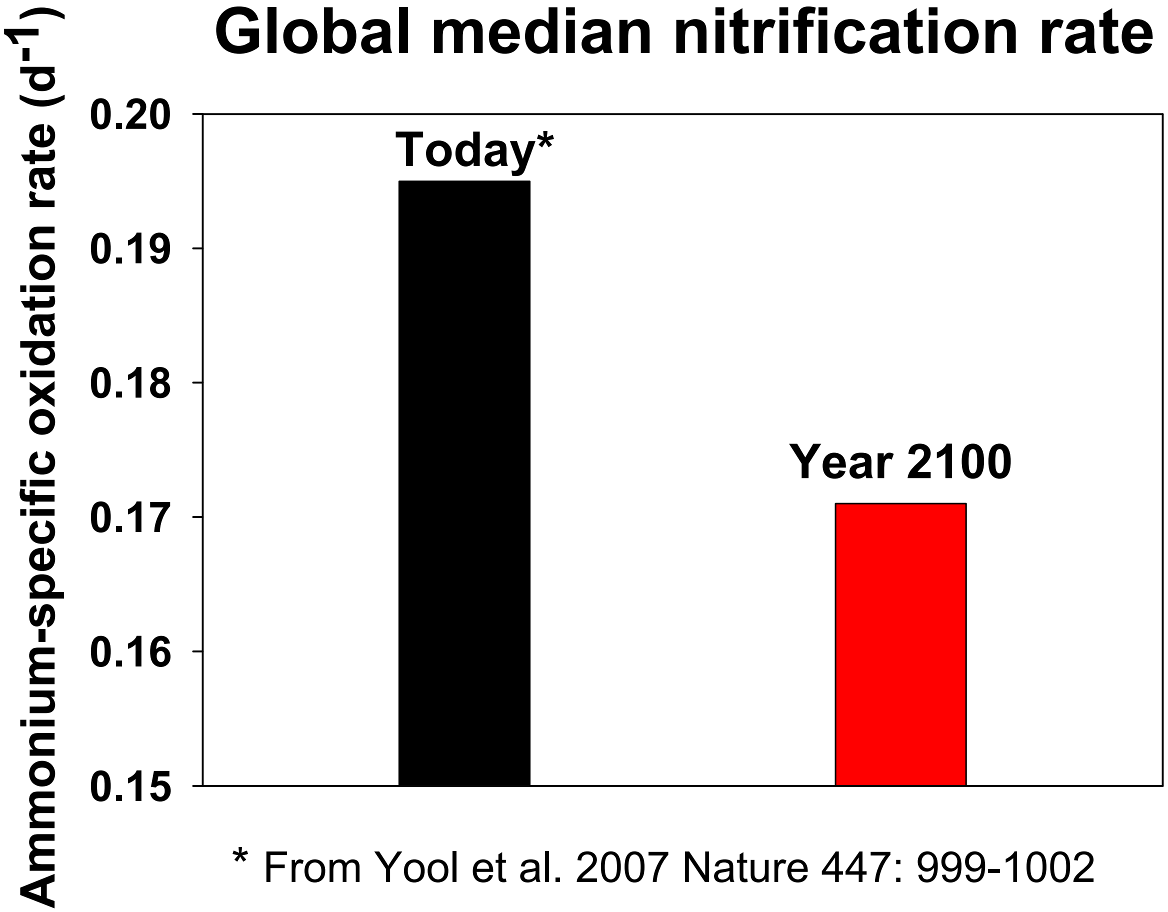
Change in the ratio of nitrate: total DIN (%)



Blackford and Gilbert 2007

Journal of Marine Systems 64: 229-241

Global median nitrification rate



* From Yool et al. 2007 Nature 447: 999-1002

Nitrification measurements

1. Simple mass balance nutrient measurements of changes in NO_2^- and NH_4^+ concentrations in seawater, sometimes coupled with specific inhibitors of NH_4^+ oxidation (acetylene, allylthiourea, methyl fluoride, N-serve) or NO_2^- oxidation (chlorate).

2. Inhibitors can also be coupled with $^{14}CO_2$ uptake measurements
Problems: inhibitor artifacts, long incubations

3. ^{15}N substrate tracer measurements using mass spectrometry
Problem: True tracer levels sometimes hard to achieve, though.

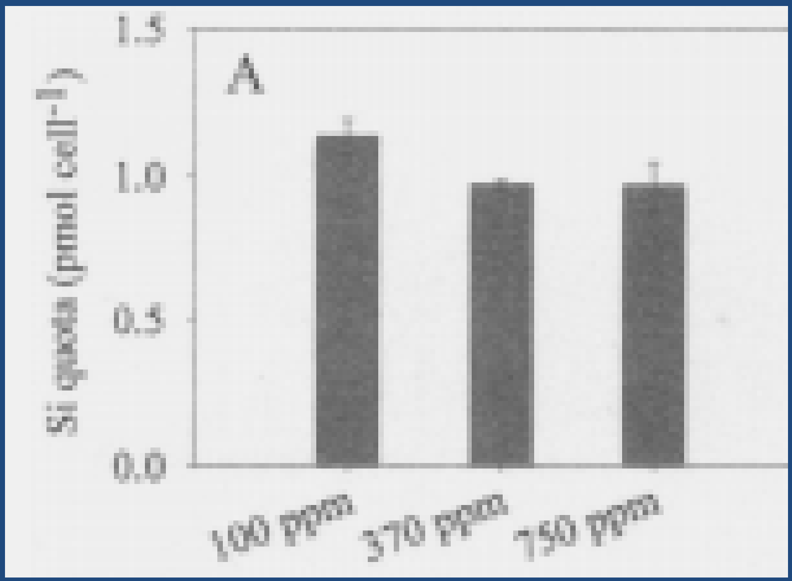
4. Isotopic enrichment factors: Ammonium oxidizers produce isotopically enriched NH_4^+ and isotopically depleted NO_2^-

Ward, B.B. 2008. Nitrification in marine systems. pp. 199-262. In: Nitrogen in the Marine Environment, 2nd edition, Elsevier Press.

The silicon cycle

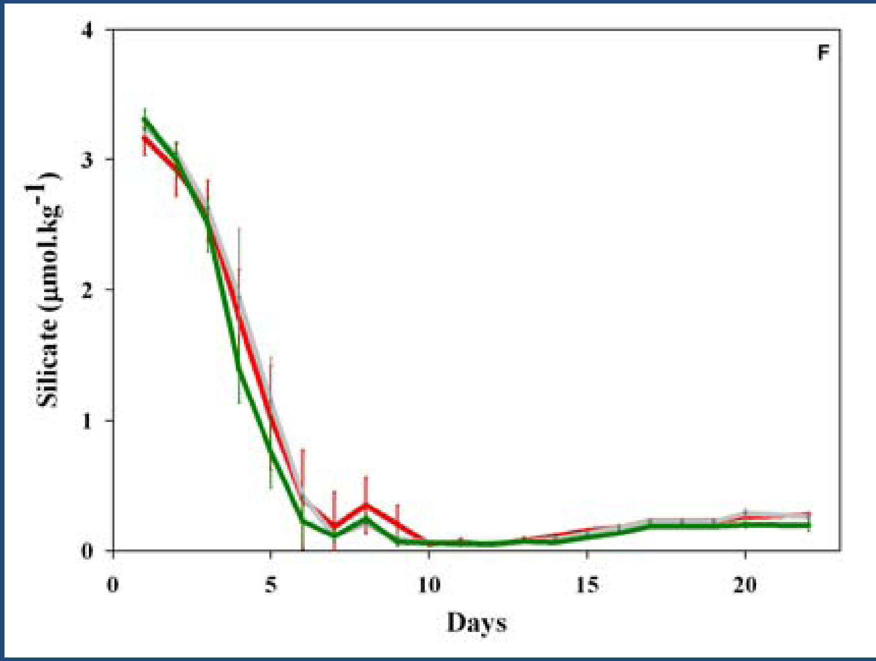
1. Si is a required element for the shells of diatoms and silicoflagellates (phytoplankton), as well as radiolarians (protozoa).
2. Principle dissolved form in seawater is silicic acid (H_4SiO_4); forms a buffer system in seawater (pK_{a1}=9.84, pK_{a2}=13.2)
3. Very simple cycle: no gas phase or organic forms.
4. How is the use of Si affected by ocean acidification?

Most studies have found little or no direct impact of changing pCO_2 on diatom Si utilization



Cellular Si quotas of a cultured diatom are unchanged between 370 and 750 ppm CO_2

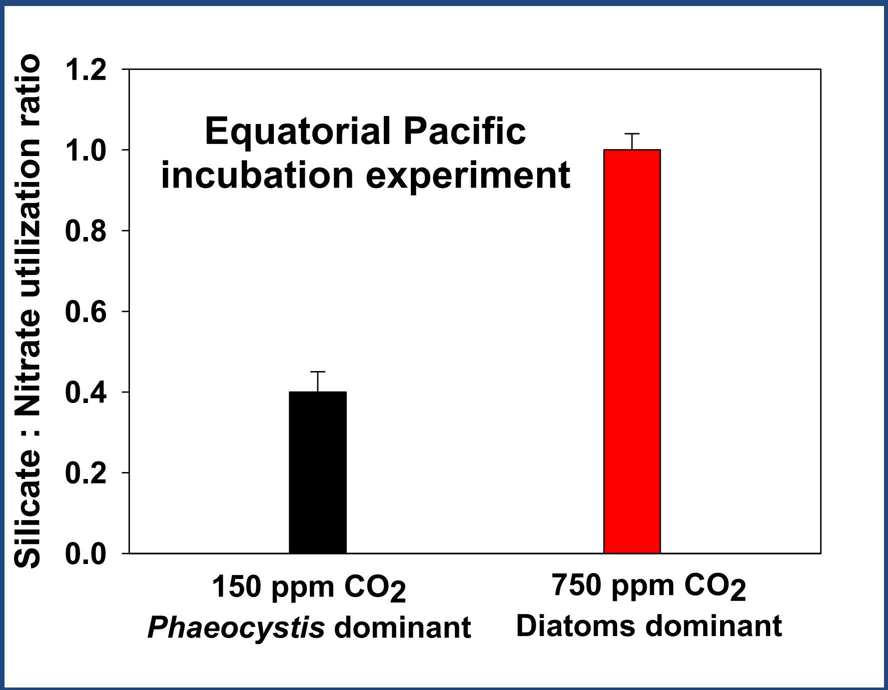
Milligan et al. 2004,
Limnology and Oceanography 42: 322-329



Silicate drawdown is identical at 350, 700 and 1050 ppm CO_2 in a Bergen mesocosm experiment

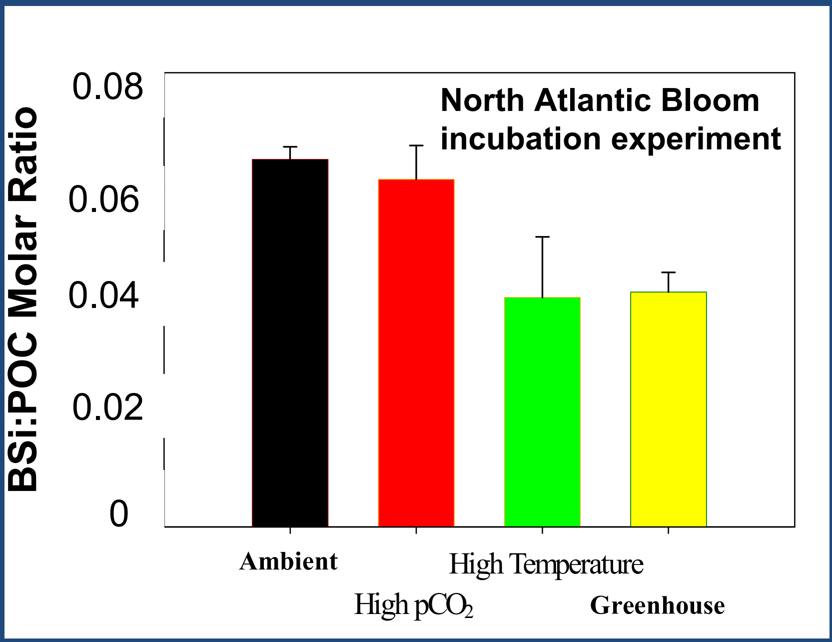
Bellerby et al. 2008,
Biogeosciences Discussions 4

pCO_2 and temperature indirectly change Si cycling due to phytoplankton community shifts



Changing Si:N utilization ratios due to a CO_2-driven community shift between diatoms and *Phaeocystis*

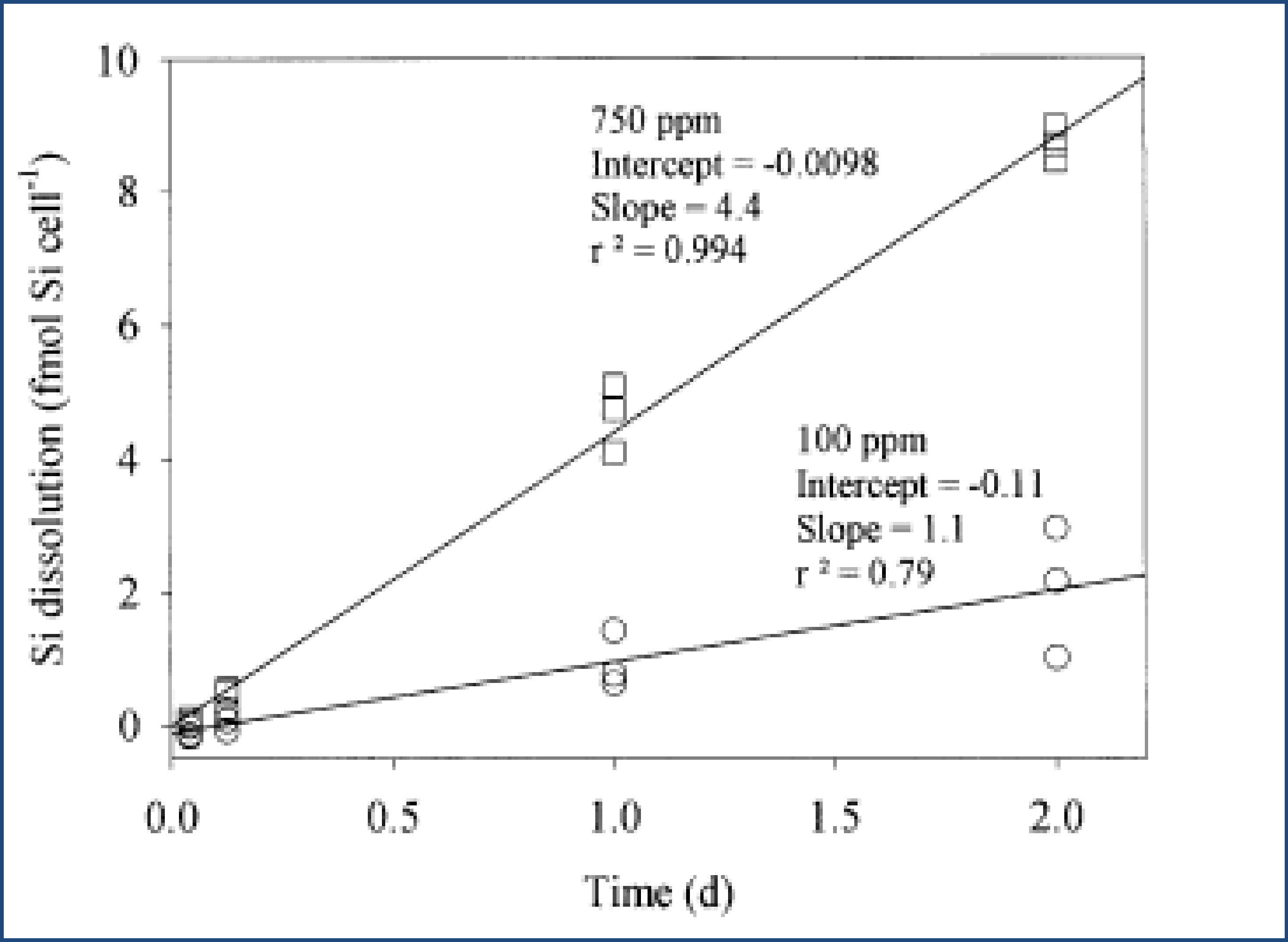
Adapted from Tortell et al. 2002, MEPS 236



Changing particulate Si: C ratios due to a temperature-driven community shift between diatoms and coccolithophores

Feng et al. 2009. MEPS 388: 13–25.

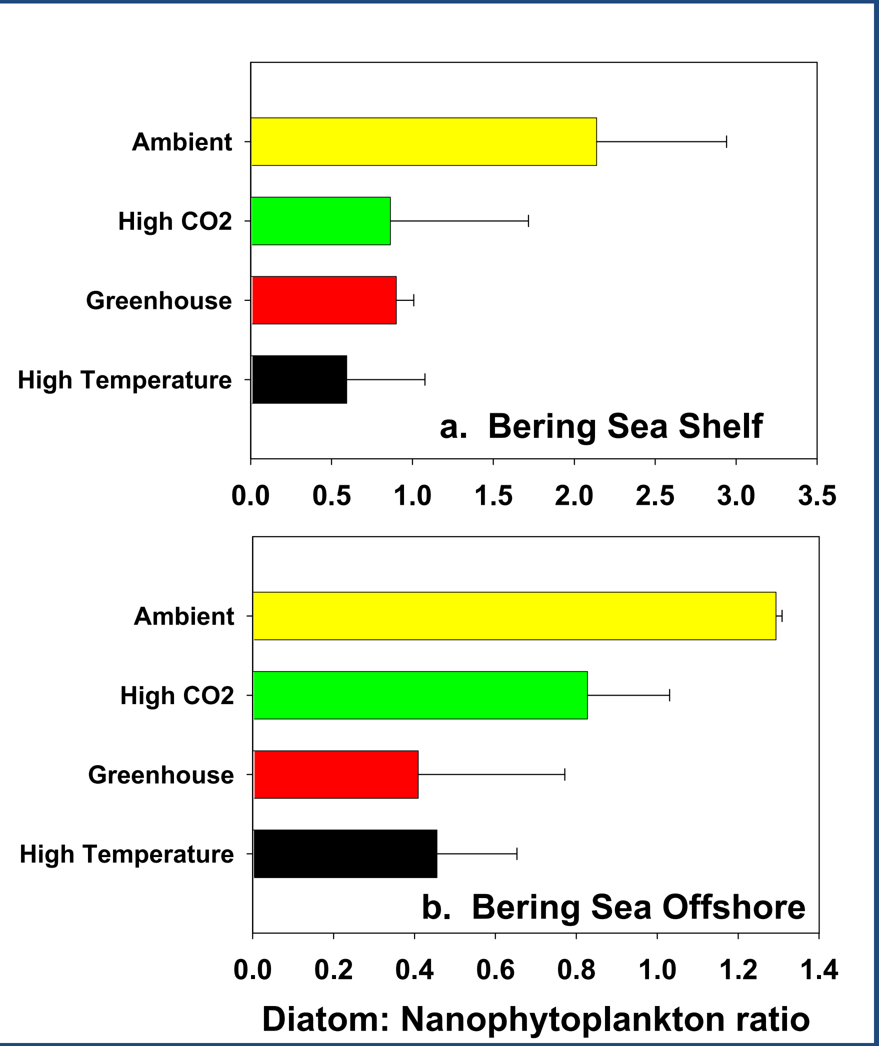
Ocean acidification enhances the silica dissolution rates of empty diatom frustules



Milligan et al. 2004, Limnology and Oceanography 42: 322-329

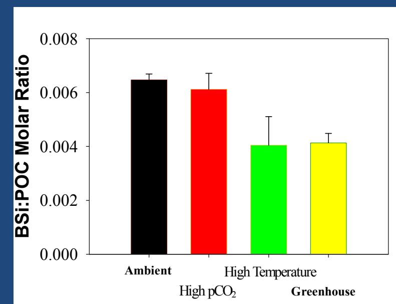
Rising temperature and pCO_2 drive shifts from diatom to nanophytoplankton dominance in the Bering Sea

(Hare et al. 2007, Marine Ecology Progress Series 352: 9-16.)

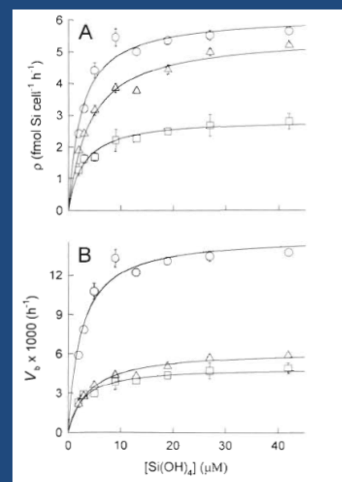


Silicon measurements

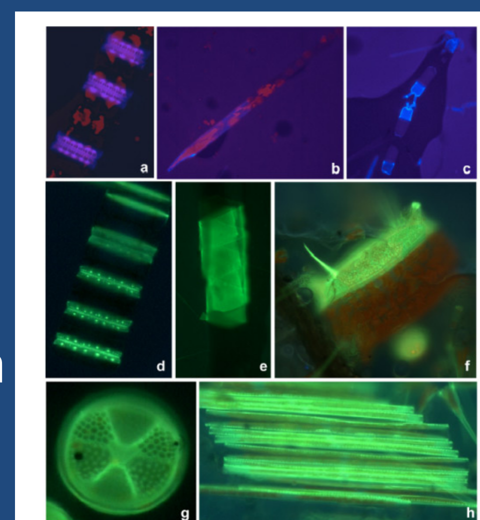
Biogenic silica measurements: Simple spectrophotometric method, after alkaline digestion of BSi on filter samples to form silicic acid. (Brzezinski and Nelson 1986, Marine Chemistry 19: 139-151; Feng et al. 2009. MEPS 388: 13-25)



^{32}Si radioisotope tracer uptake: (Brzezinski. 1997. L&O 42 : 856; De la Rocha et al. 2000. MEPS195: 71- 79).



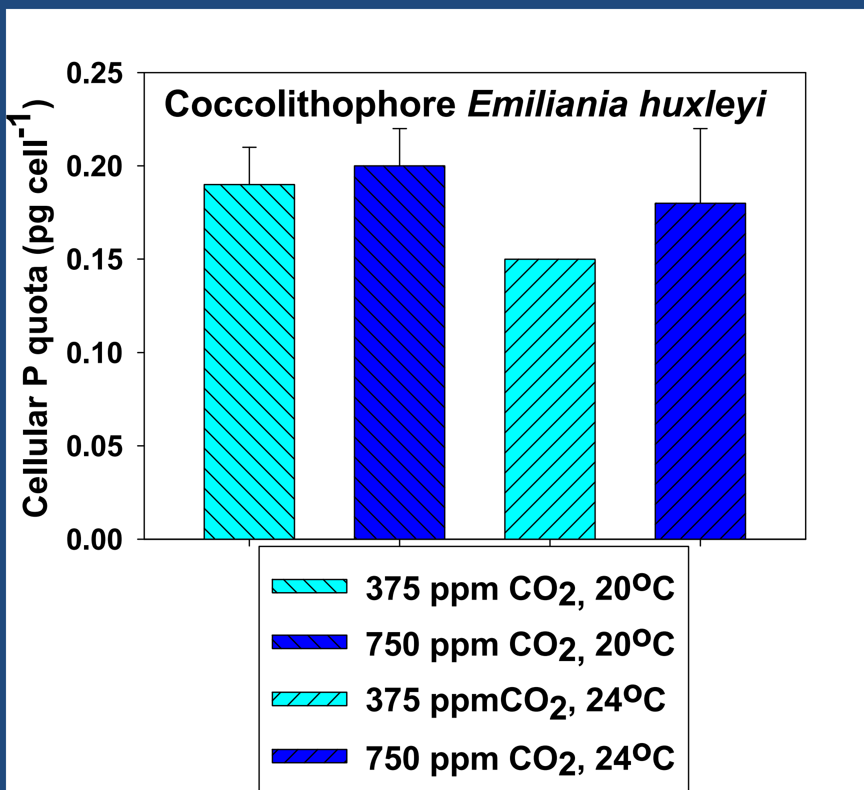
PDMPO: A fluorophore to trace new Si deposition in diatoms (Leblanc and Hutchins 2005, L&O Methods 3: 462- 476.)



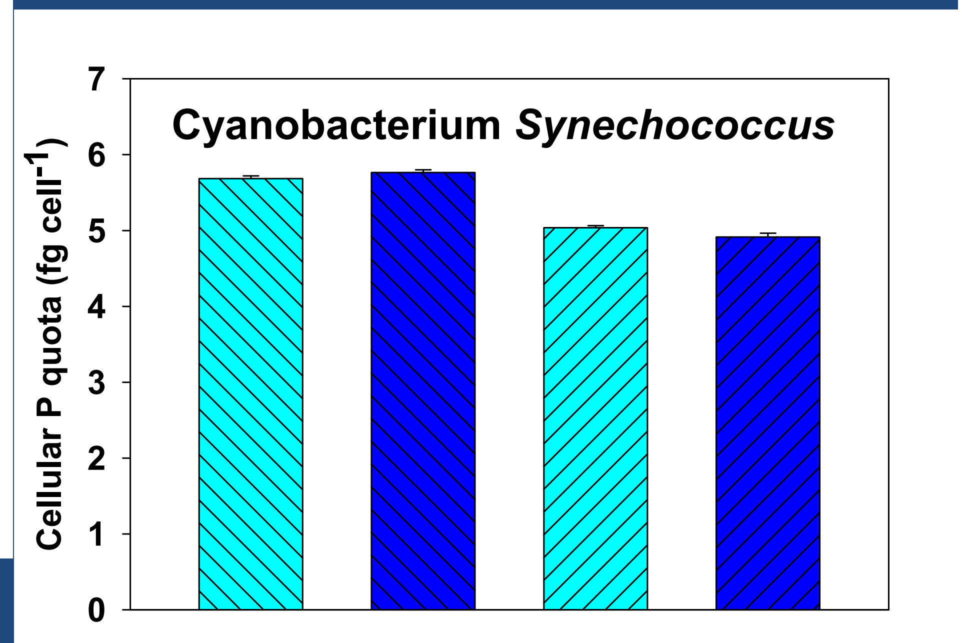
The phosphorus cycle

1. P is required by all cells for nucleotides and nucleic acids, and for some phosphorylated proteins; required by most cells for phospholipid cell membranes
2. Principle form in seawater is as orthophosphate or dissolved organic phosphorus; dominant form of inorganic phosphorus at pH 8 is HPO_4^{2-} (~87%), but the fraction of $H_2PO_4^-$ will increase with future acidification.
3. Simple cycle: No gas phase.
4. Will P requirements change with ocean acidification?

Phytoplankton P requirements: Usually, little or no response to pCO_2 increases



Feng et al. 2008
European Journal of Phycology 43: 87-98



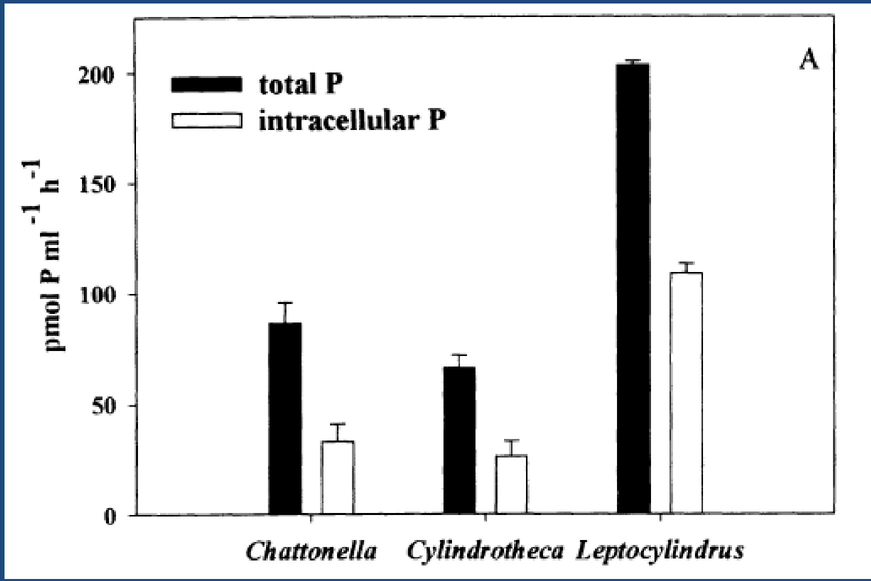
Fu et al. 2007
Journal of Phycology 43: 485-496

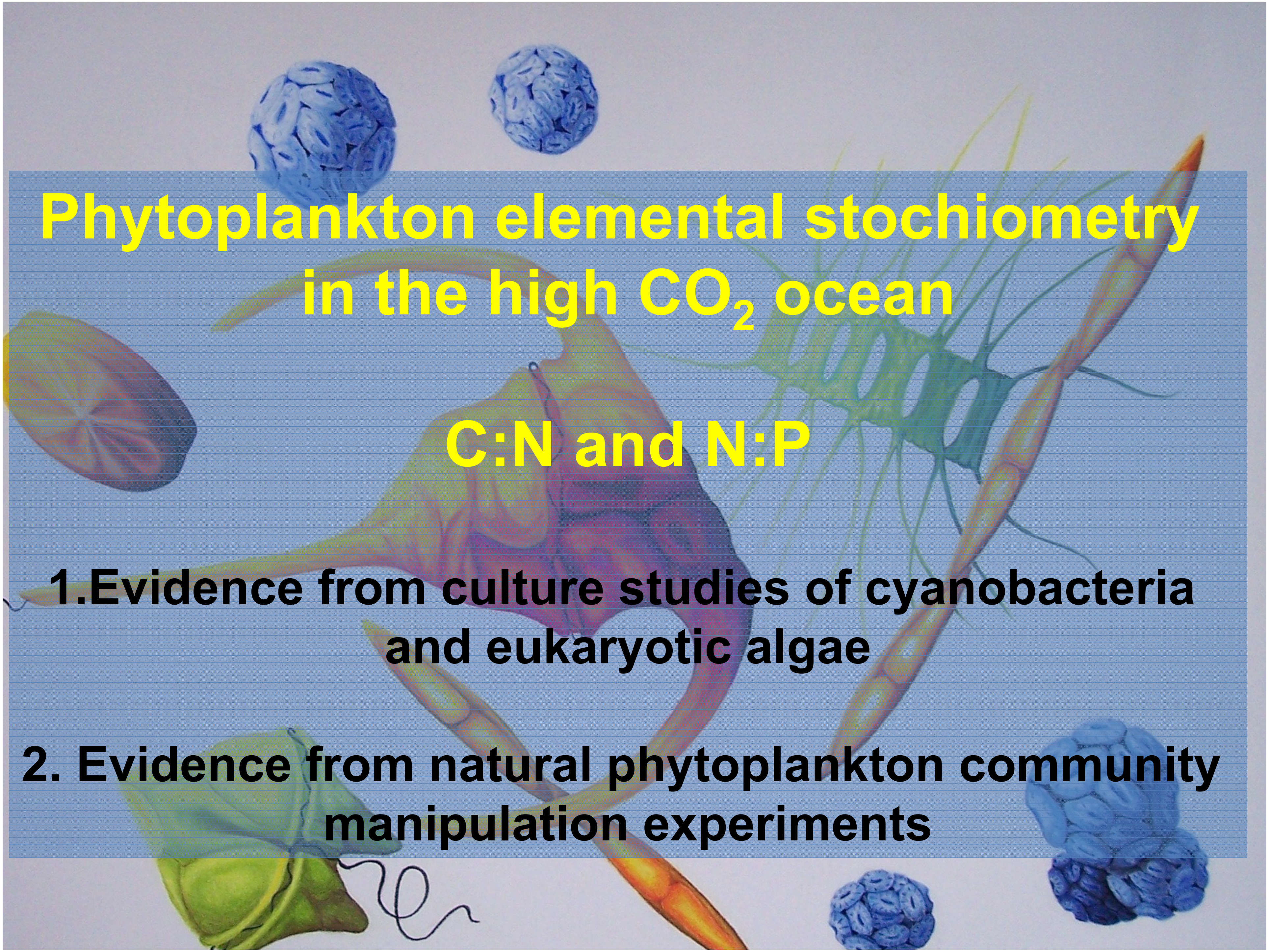
Phosphorus measurements

Particulate organic phosphorus measurements: Simple spectrophotometric method, after digestion of POP on filter samples to form phosphate. (Fu et al 2005, L&O 50: 1459-1472; Fu et al 2007, Journal of Phycology 43: 485- 496.)

^{33}P radioisotope tracer uptake: Commercially available ^{33}P-labeled phosphate, ATP, etc. (Fu et al. 2006, European Journal of Phycology 41: 15-28)

Cell surface scavenging of P: A cell surface wash can be used to remove adsorbed phosphate from cells, giving a better estimate of true cellular P quotas (Sanudo-Wilhelmy et al. 2004, Nature 432: 897- 901; Fu et al. 2005, Limnology and Oceanography 50: 1459- 1472.)



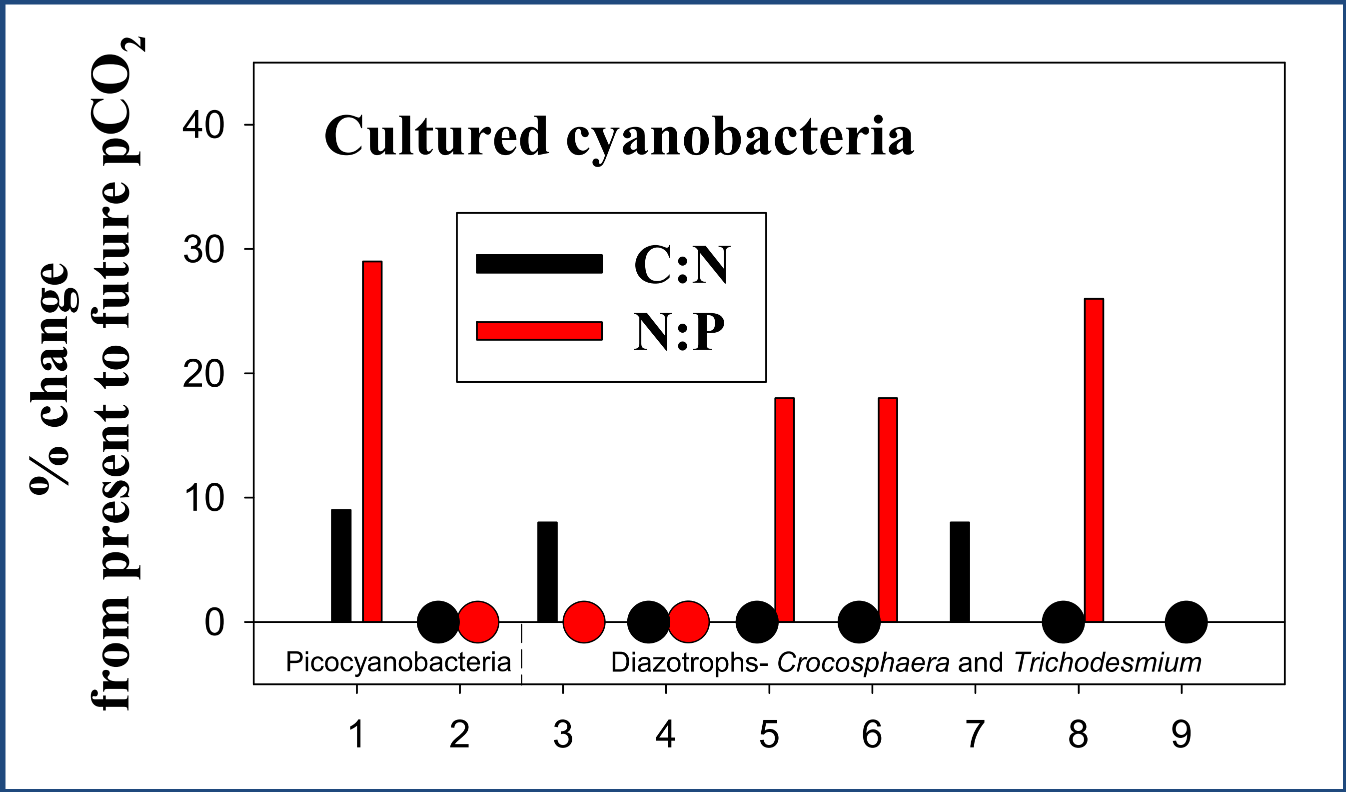


Phytoplankton elemental stochiometry in the high CO_2 ocean

C:N and N:P

1.Evidence from culture studies of cyanobacteria and eukaryotic algae

2. Evidence from natural phytoplankton community manipulation experiments



1 &**2**, *Synechococcus* and *Prochlorococcus* at 380 and 750 ppm CO_2 (Fu et al. 2007)

3 &**4**, Fe-replete and Fe-limited *Crocosphaera* at 380 grown aand 750 ppm CO_2 (Fu et al. 2008)

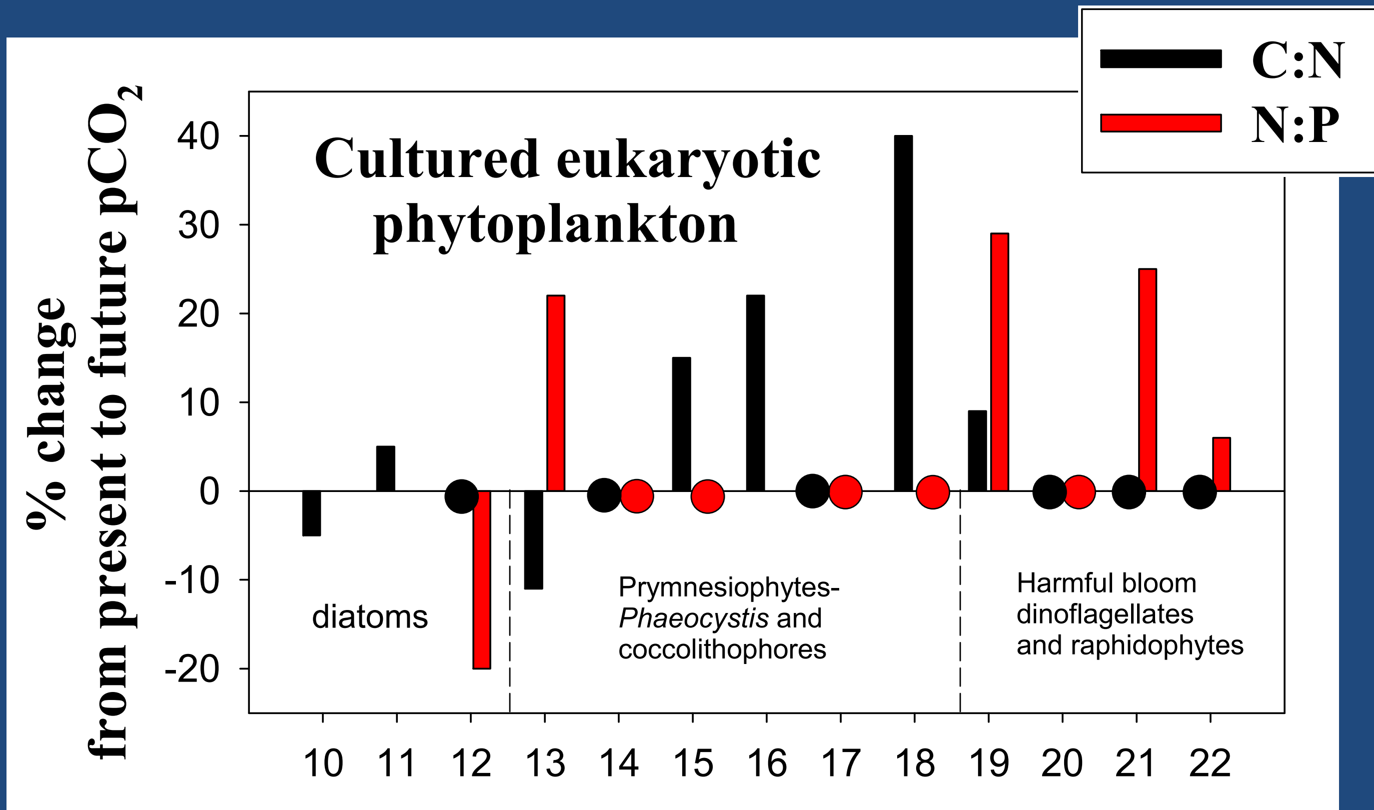
5&6 P-replete and P-limited *Trichodesmium* at 380 and 750 ppm CO_2 (Hutchins et al. 2007)

7 *Trichodesmium* at 400 and 900 ppm CO_2 (Levitan et al. 2007)

8 *Trichodesmium* at 380 and 750 ppm CO_2 (Barcelos e Ramos et al. 2007)

9 *Trichodesmium* at 370 and 1000 ppm CO_2 (Kranz et al. 2009)

Hutchins et al. in review, Oceanography



10 &11 Diatoms *Asterionella* at 430 and 820 ppm CO_2 and *Skeletonema* at 400 and 720 pCO_2 (Burkhardt et al. 1999)

12 &13 Antarctic diatom *Chaetoceros* and prymnesiophyte *Phaeocystis* at 430 and 820 ppm CO_2 (Fu et al. unpubl results)

14&15 Coccolithophorid *Emiliania huxleyi* under low and high light at 375 and 750 ppm pCO_2 (Feng et al. 2008)

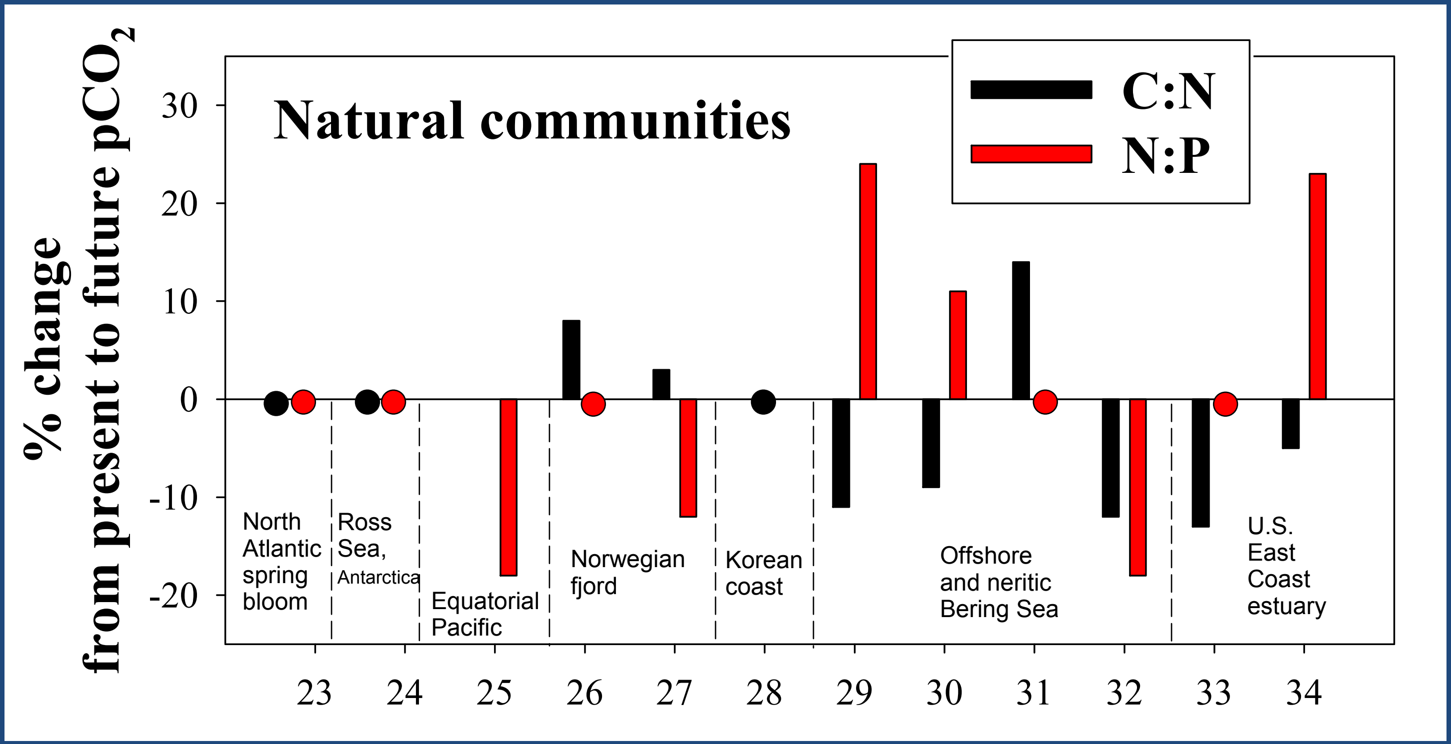
16 Coccolithophorid *Emiliania huxleyi* at 490 and 750 ppm pCO_2 (Iglesias-Rodriguez et al. 2008)

17&18 Non-calcifying *Emiliania huxleyi* gunder low and high light at 360 and 2000 ppm CO_2 (Leonardos and Geider 2005)

19 &20 Toxic raphidophyte *Heterosigma* and the dinoflagellate *Prorocentrum* at 375 and 750 ppm pCO_2 (Fu et al. 2008)

21 &22 P-replete and P-limited dinoflagellate *Karlodinium* at 430 and 745 ppm CO_2 (Fu et al. in review)

Hutchins et al. in review, Oceanography



23. North Atlantic spring bloom, 390 and 690 ppm CO_2 (Feng et al. 2009)
24. Ross Sea, Antarctica, 380 and 750 ppm CO_2 (Feng et al. in review)
25. Equatorial Pacific, 150 and 750 ppm CO_2 (Tortell et al. 2002)
26. Norwegian fjord, 350 and 700 ppm CO_2 (Riebesell et al. 2007)
27. Norwegian fjord, 410 and 710 ppm pCO_2 (Engel et al. 2005)
28. Korean coastal waters, 400 and 750 ppm CO_2 (Kim et al. 2006)

29 &30. Bering Sea shelf at 10°C and 15°C, 370 and 750 ppm pCO_2 (Hare et al. 2007)

31 &32. Bering Sea offshore at 10°C and 15°C, 370 and 750 ppm pCO_2 (Hare et al. 2007)

33 &34. U.S. East Coast estuary, 380 and 750 ppm pCO_2 (Fu et al. unpubl.results)

Hutchins et al. in review, Oceanography

Generalizations

- C:N and N:P ratios of individual phytoplankton species often increase at high pCO_2, but the trends in whole community stoichiometry are much more variable
- Be cautious when extrapolating from any particular experiment or regime to the whole future ocean…
- More work is needed to draw firm conclusions about the effects of OA on major elemental stoichiometry.

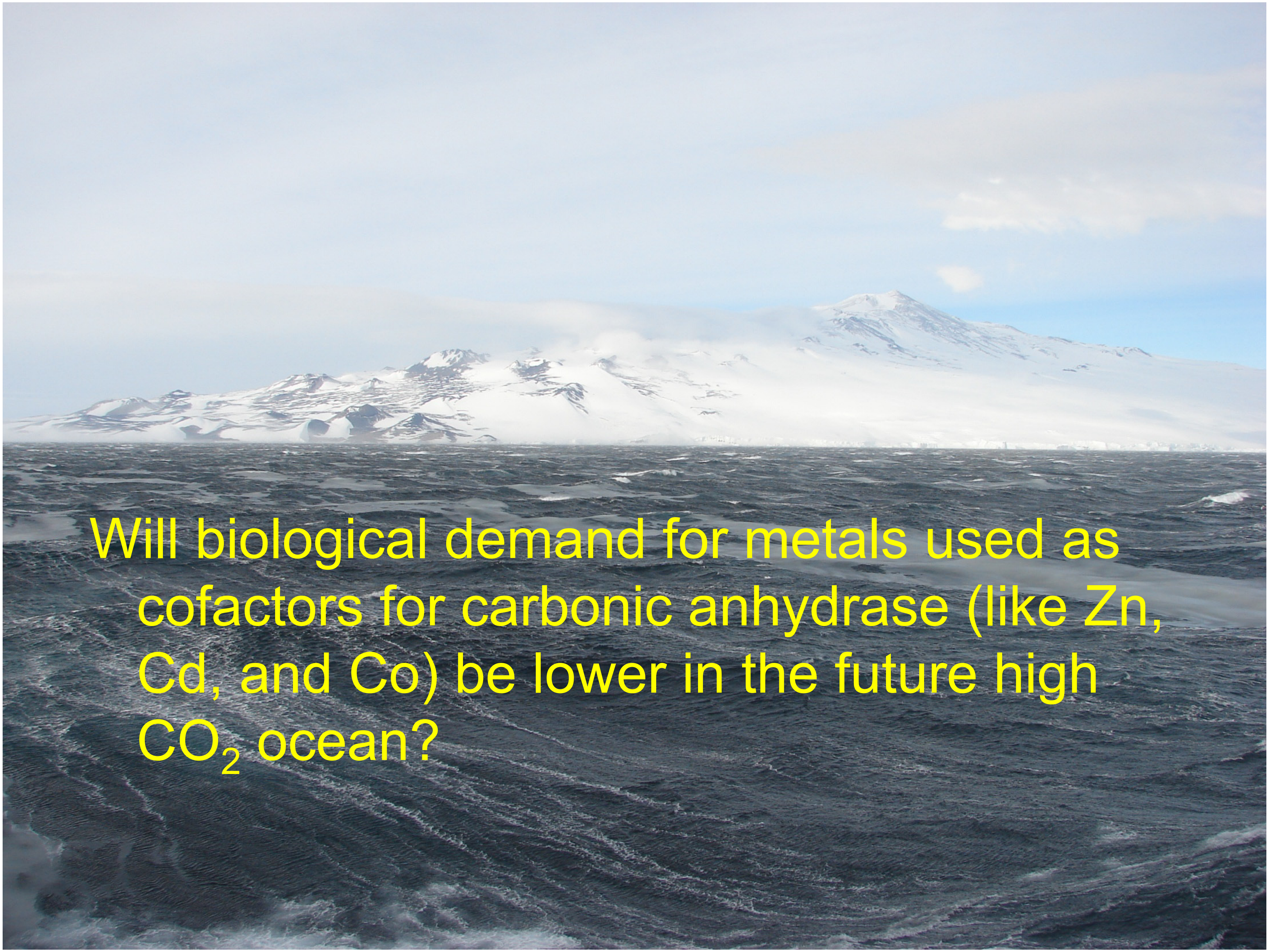
Trace metals

1. Iron (Fe) is the trace metal with by far the best documented biogeochemical impacts. Phytoplankton production is limited or co-limited by this micronutrient over a large fraction of the ocean surface.

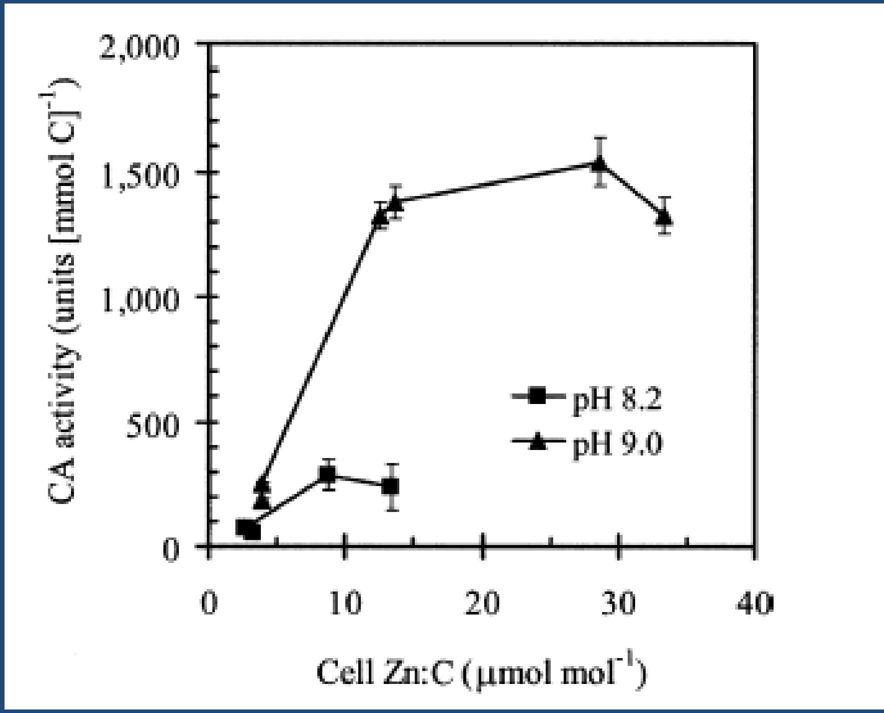
1. Iron is heavily involved in photosynthesis, respiration, nitrate uptake, and nitrogen fixation , making Fe/CO_2 interactions very likely.

1. Other bioactive trace elements whose cycles may potentially be affected by ocean acidification include Mo (required for nitrogen fixation), as well as Zn, Cd, and Co (all co-factors for various forms of carbonic anhydrase).

1. Effects of acidification on trace metal cycling may include changes in biological requirements; shifts in their inorganic chemical speciation (e.g., many are affected by carbonato complexation); and possible pH effects on the metal-binding functional groups of organic ligands.

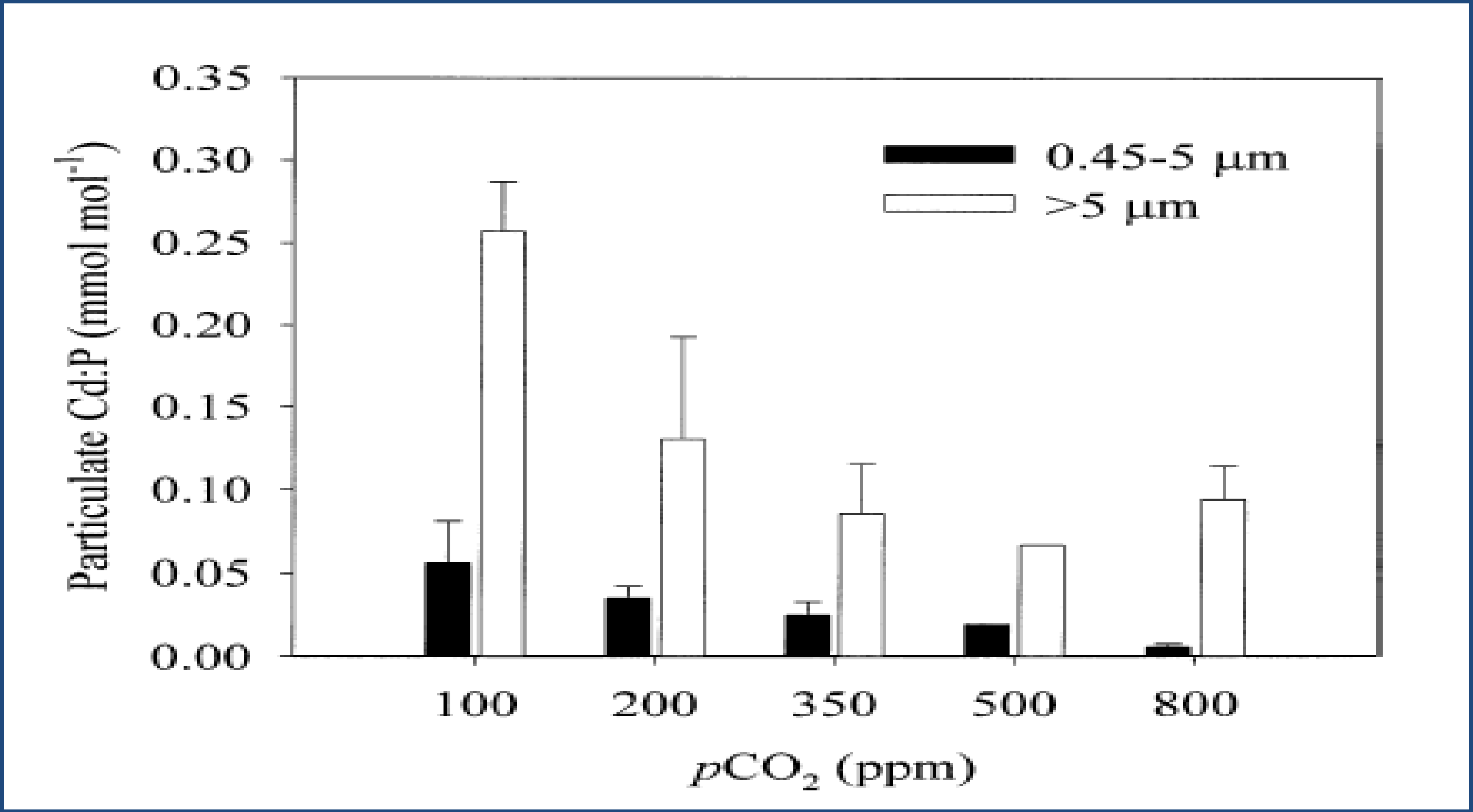

Will biological demand for metals used as cofactors for carbonic anhydrase (like Zn, Cd, and Co) be lower in the future high CO_2 ocean?

pCO_2, carbonic anhydrase activity, and cellular Zn:C (Sunda and Huntsman 2005)



At higher pCO_2 (lower pH), phytoplankton have much lower levels of CA activity, and require much less cellular Zn

Changes in natural community Cd:P with varying pCO_2 (Cullen and Sherrell 2005)



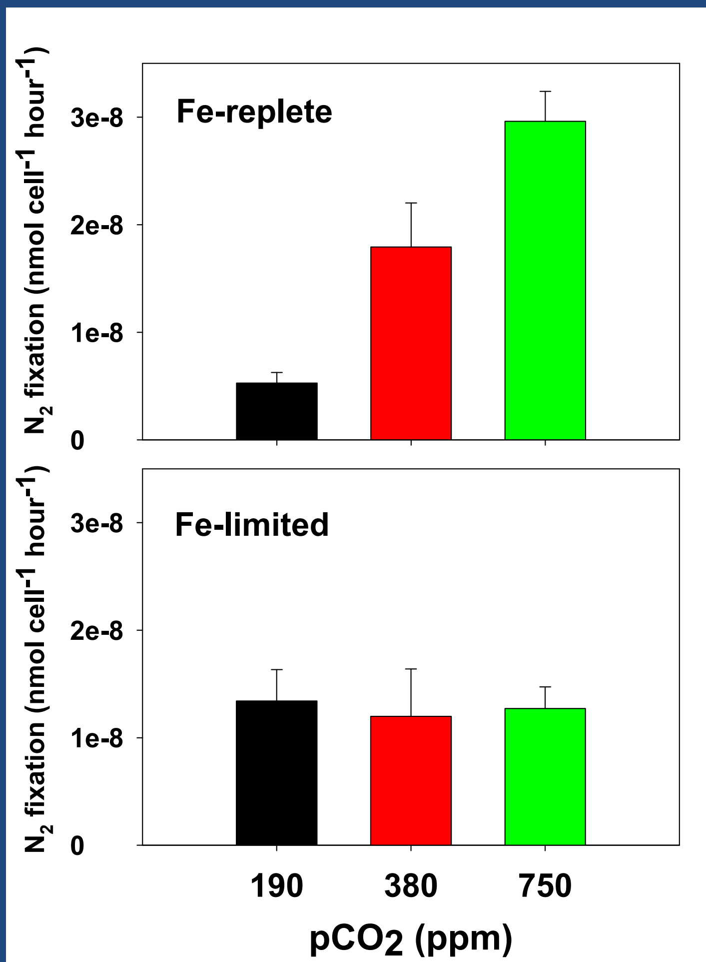
Trace metal quotas (mmol metal: mol P) of a natural *Phaeocystis* bloom in the Ross Sea, incubated at 380 ppm and 750 ppm CO_2.

CO_2 levels	Cd:P	Co:P	Zn:P	Fe:P	Mn:P
380 ppm	0.20	0.012	8.7	10.7	0.28
750 ppm	0.095	0.002	0.34	5.1	0.12

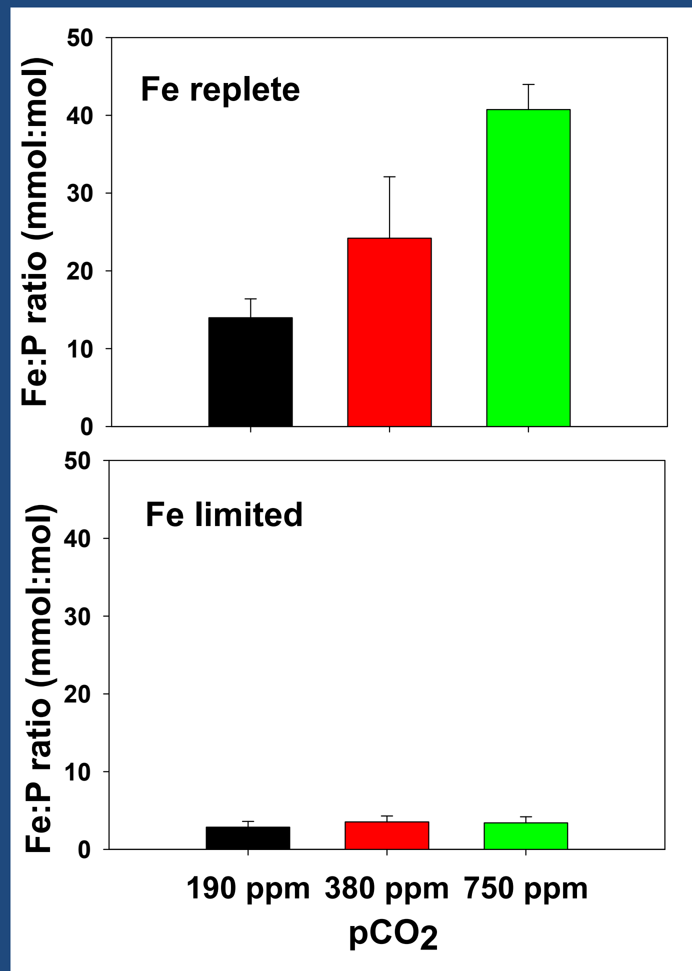
Hutchins et al. in preparation

Crocosphaera: N_2 *fixation rates as a function of* pCO_2 and Fe

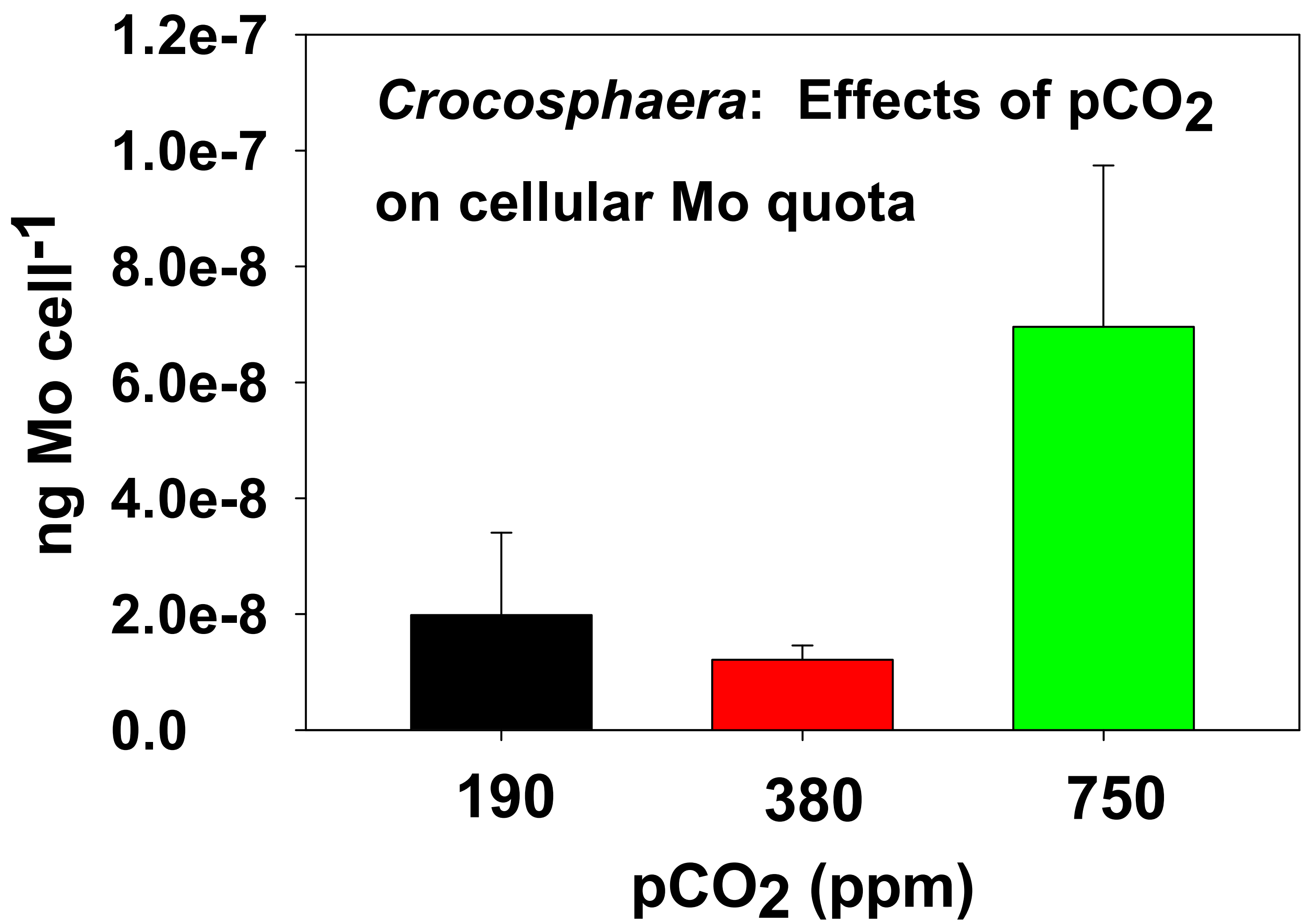
N_2 fixation rates



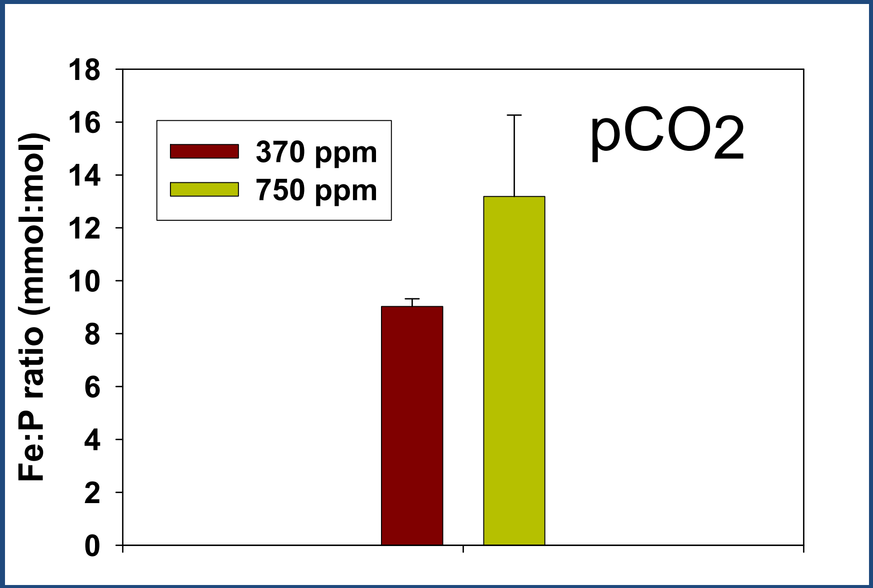
Cellular Fe quota



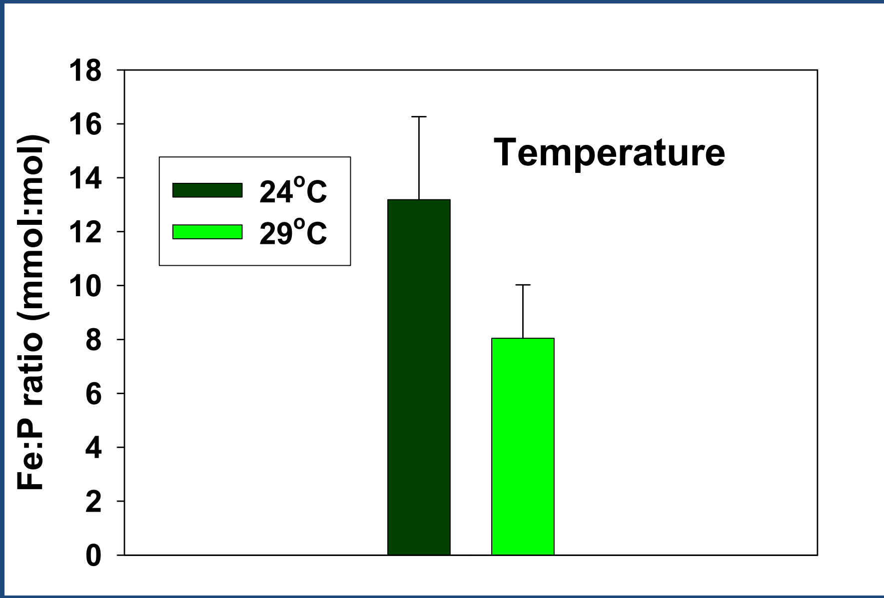
Fu et al. 2008 L&O 53: 2472- 2484



Sanudo-Wilhelmy, Fu and Hutchins unpublished



Trichodesmium
Fe:P ratios increase
~40% between
370 and
750 ppm CO_2



But decrease by about the same amount with a 5°C temperature increase…

Sanudo-Wilhelmy, Fu and Hutchins unpublished

Trace metal biogeochemical methods

Approaches:

-Laboratory culture studies

-Field incubations and measurements

-Both require combining OA methods with scrupulous trace metal clean techniques (see Bruland et al. 1991, L&O 36: 1555-1577).

Analytical methods:

-Radiotracer techniques- ^{55}Fe, ^{59}Fe, ^{65}Zn, ^{109}Cd, etc. (Hutchins et al. 1999 AME 19: 129-138)

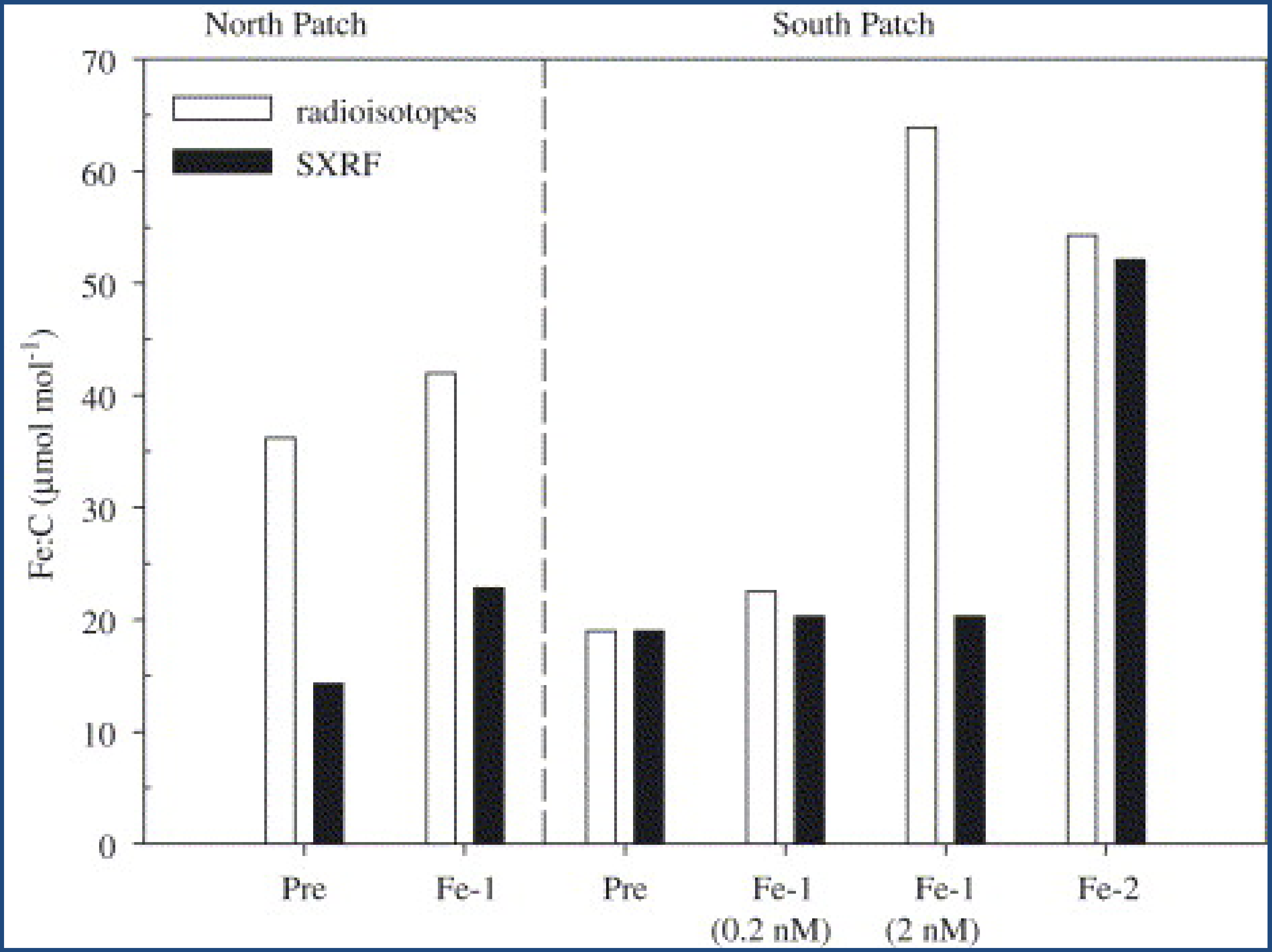
-Titanium and oxalate wash methods to remove cell surface-scavenged metals (Hudson and Morel 1989 L&O 34: 1113–1120; Tovar-Sanchez et al. 2003 Marine Chemistry 82: 91-99)

-Graphite Furnace Atomic Absorption Spectrometry (GFAAS, Bruland et al. 1985 Mar. Chem 17: 285-300).

-Inductively Coupled Plasma Mass Spectrometry (ICP-MS) Bulk measurements and now metal speciation (coupled with HPLC) and trace metal stable isotopes (Multi-Collector ICP-MS). (Wells and Bruland 1998 Mar. Chem. 63: 145-153; Bergquist and Boyle 2006, Earth and Plan Sci Let 248: 54-68; Dauphas and Rouxel 2006. Mass Spec Rev 25: 515-550;).

-Synchrotron X-Ray Fluorescence (SXRF), Measurements and localization of trace metals in individual cells and particles (Twining et al. 2004, L&O 49: 2115; Lamborg et al. 2008. DSR II 55: 1564).

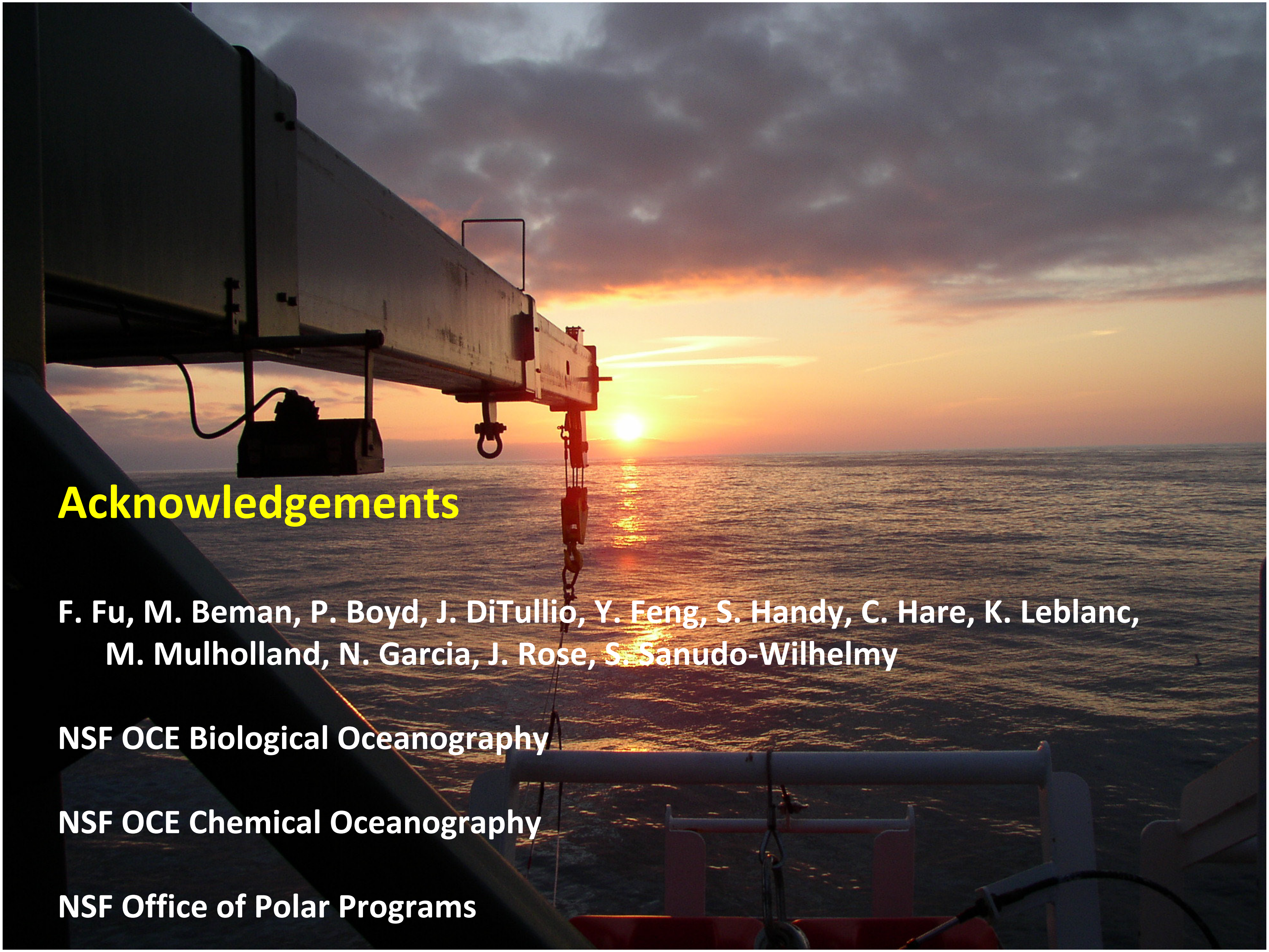
Radioisotope versus SXRF comparison



Twining et al. 2004, DSR I 51

Conclusions

1. Changes in ocean pCO_2 and acidification will fundamentally change the present-day ocean biogeochemistry of carbon and nitrogen. Changes in the phosphorus and silicon cycles may be indirect and less dramatic. Trace metal biogeochemical responses are just now beginning to be investigated.
2. Interactions of other global change variables like temperature, stratification, and major and micronutrients with pCO_2 are at least as important to consider as OA effects in isolation. Reductionist, "CO_2-centric" experiments can often give incomplete or misleading results.
3. A new generation of experimental, observational, and modeling work is needed to address issues of long-term biogeochemical changes, including the effects of biological acclimation and adaptation.
4. The responses of numerous key ocean biogeochemical processes to ocean acidification have been tested only in very preliminary studies, or not at all. There is a lot of room for new investigators in this field…



Acknowledgements

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The marine nitrogen cycle