

# Influence of phytoplankton-bacterial coupling on the export of biogenic carbon in the ocean: Insights from iron enrichment experiments...

“or the reverse”

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The logo for Memorial University, featuring a dark red banner with the text "MEMORIAL UNIVERSITY" in white and grey.

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The logo for the University of Portsmouth, featuring a stylized purple and blue circular graphic to the left of the text "University of Portsmouth".

University of  
**Portsmouth**



Thanks to many colleagues and students for stimulating, exciting and critical discussions and arguments... *that which does not kill us makes us stronger!*



# Order of Presentation

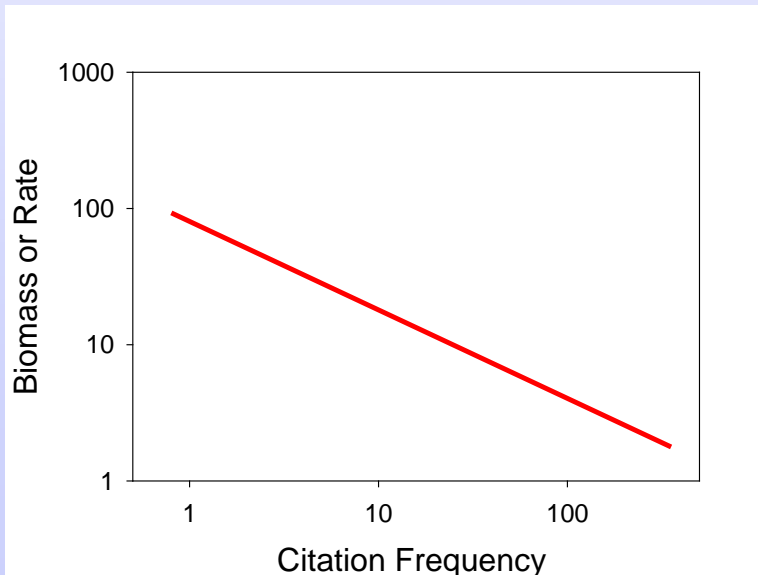
Why is it important to understand bacteria-phytoplankton interactions in the ocean?

Ocean iron fertilization experiments.

What can we learn and what are we missing?

Number of times a word is mentioned in the PICES book of abstracts...

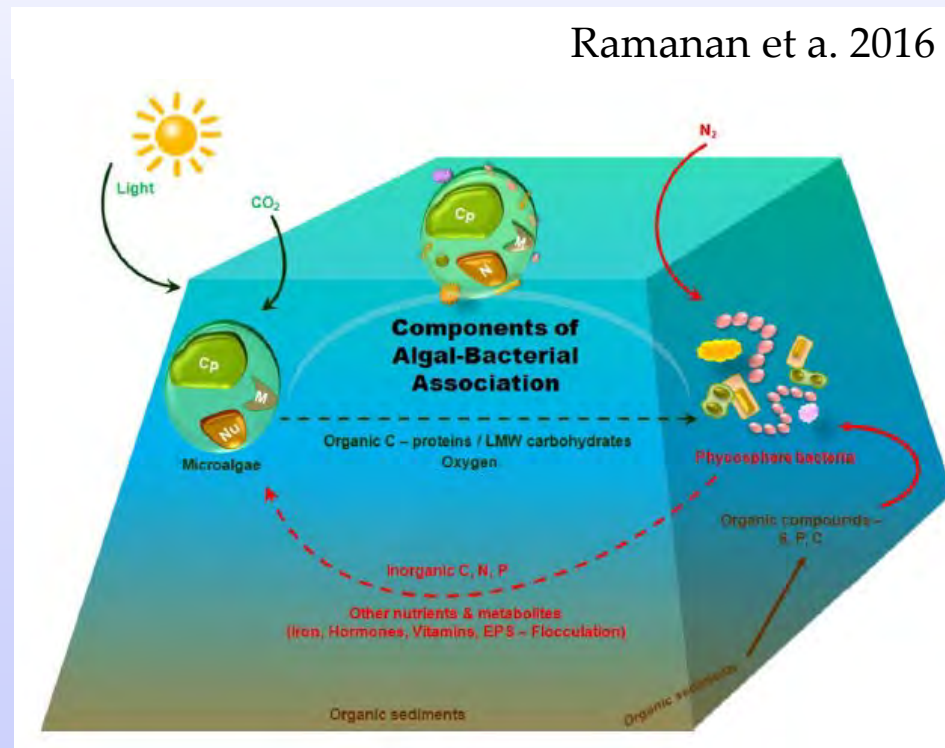
Dissolved Organic Carbon...	2	700 Pg C
Bacteria...	27	2.2 Pg C
<b>Export...</b>	<b>28</b>	<b><u>10 Pg C y<sup>-1</sup></u></b>
Phytoplankton...	131	1.8 Pg C
Zooplankton...	101	0.5 Pg C
Fish....	451	0.02 Pg C



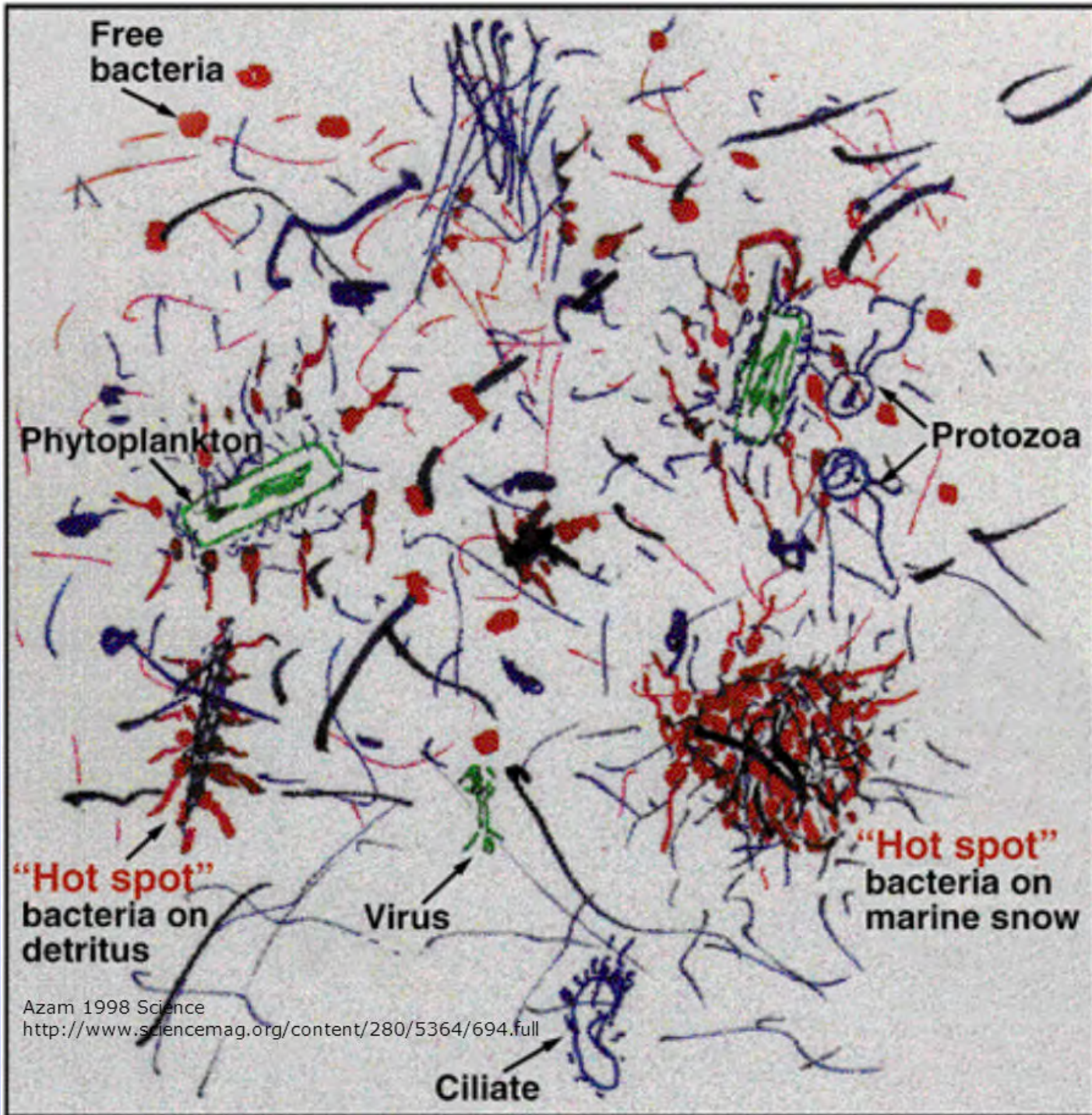
Inverse relationship between the word use frequency and biogeochemical relevance...

Marine microbes influence global ecosystem dynamics in fundamental ways by mediating the biogeochemical processes. Large-scale consequences result from interactions occurring at the level of the individual cells that propagate through ecosystems.

Algae and bacteria have coexisted since the early stages of evolution and their interactions influence earth systems and define many ecosystem processes including recycling, remineralization, aggregation and export of carbon and macro- and micro-nutrients in the ocean.

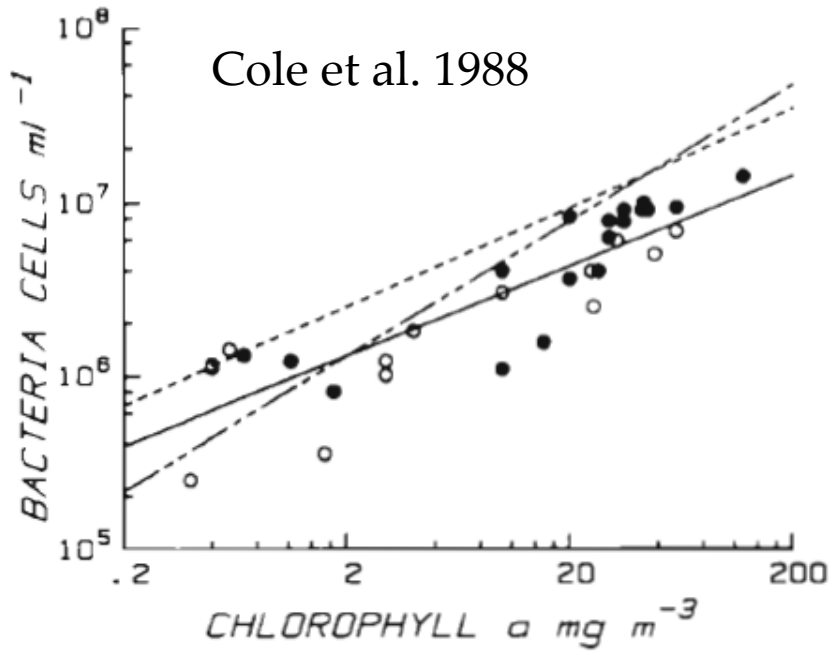






Azam 1998 Science  
<http://www.sciencemag.org/content/280/5364/694.full>

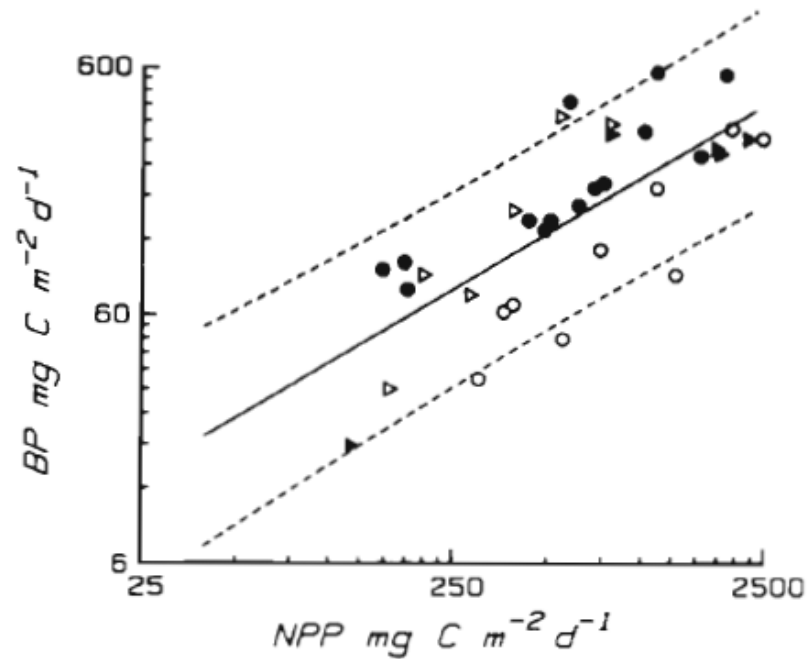
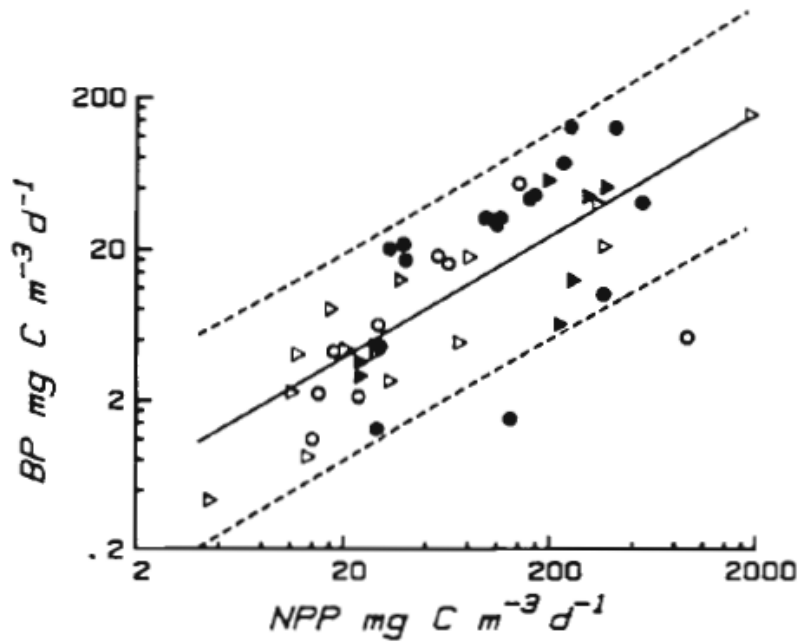
Cole et al. 1988



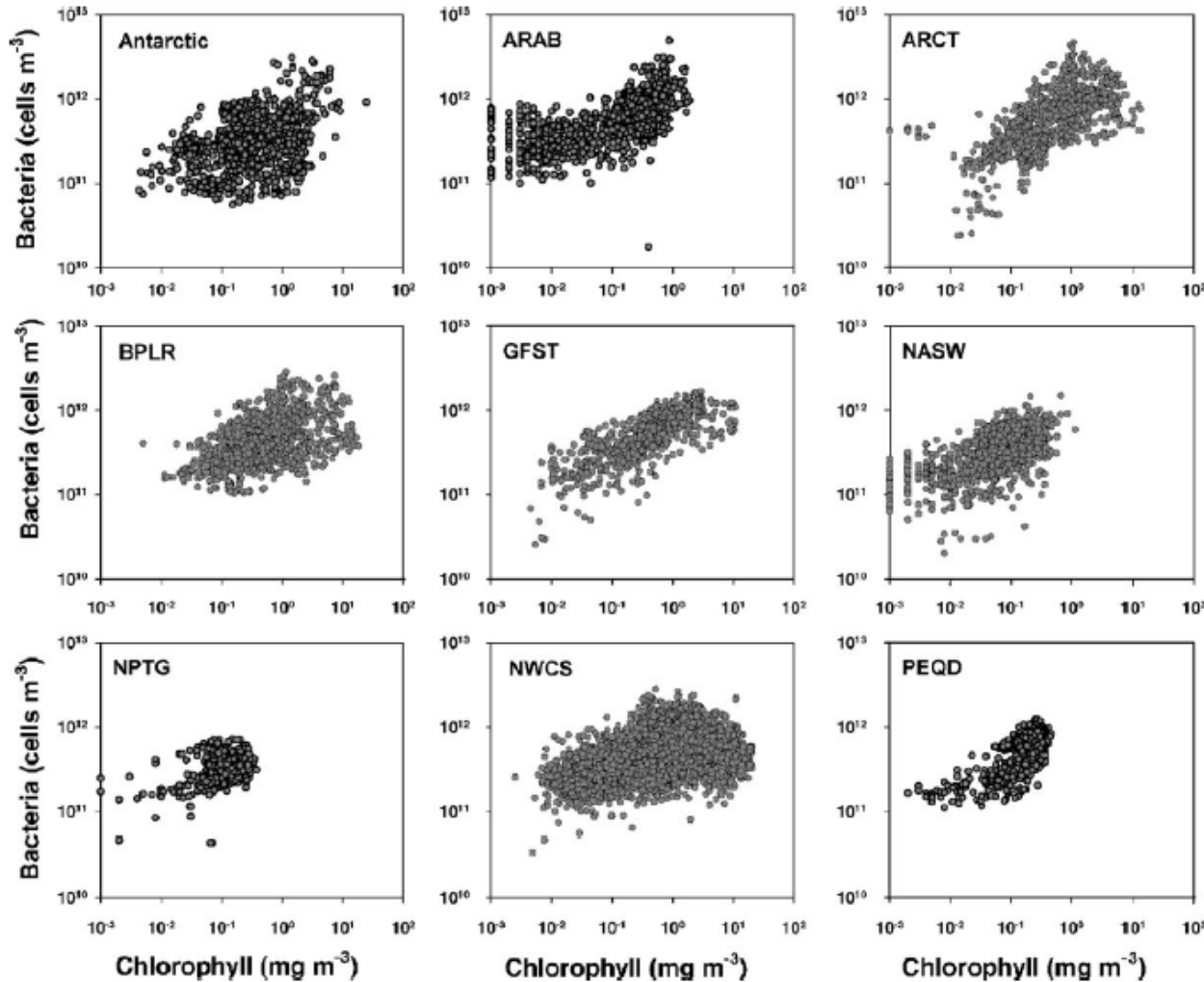
Significant linear and positive relationship between bacterial and phytoplankton biomass and production.

Relationship infers a causal link between the supply of resources by phytoplankton and use by bacteria.

Relationship is overly simplistic but is perhaps useful framework.



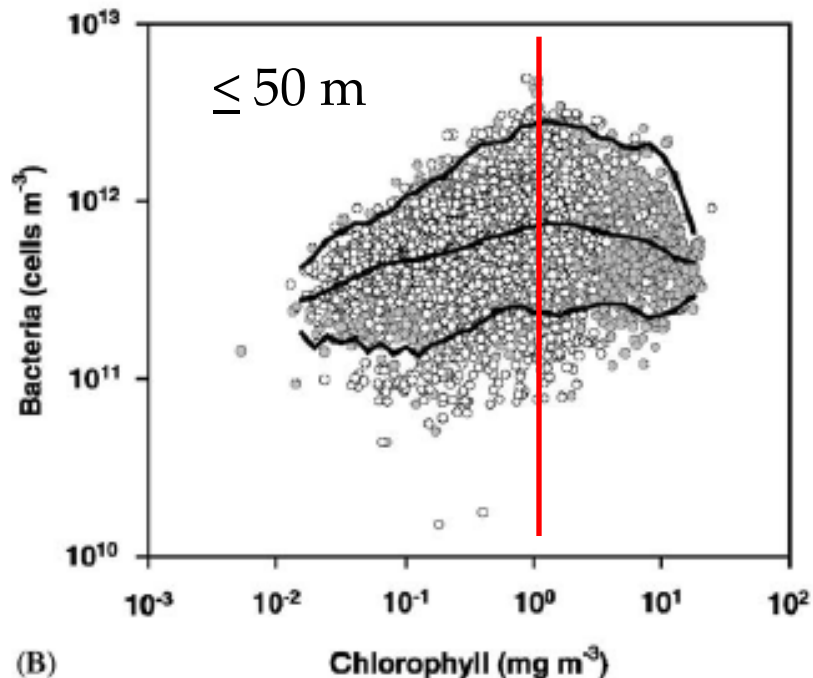
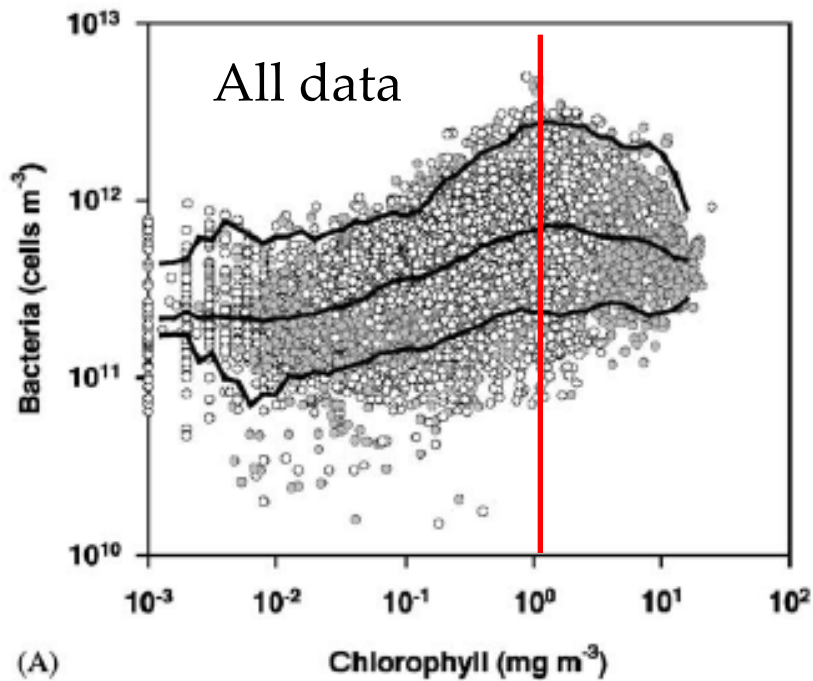
Li et al. 2004



For a wide range of ocean biogeochemical provinces the average slope = 0.46.

- Slope low and  $r^2$  high for coastal and upwelling regions.
- Slope high and  $r^2$  low for polar regions.
- Slope high and  $r^2$  high boundary current regions.
- Slope high and  $r^2$  variable for ocean gyres.



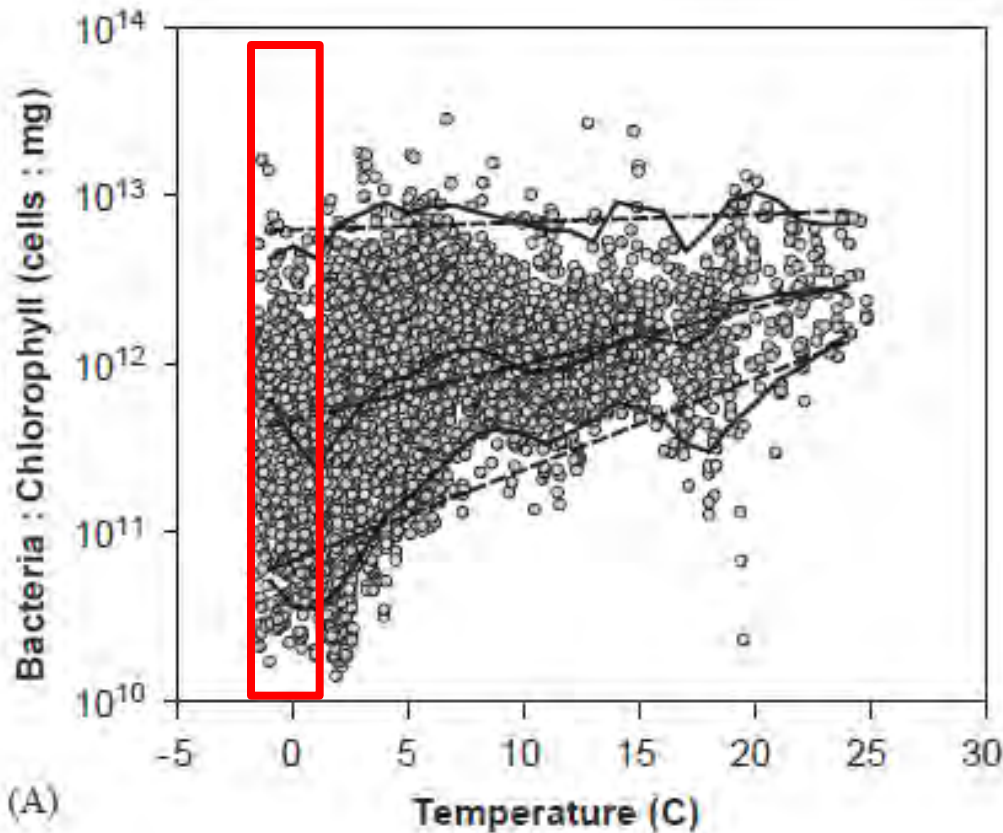


Macroecological (global rather than regional) perspective.

The slope of the bacteria-phytoplankton relationship is non-linear...

Shift from positive at low chlorophyll to negative and high chlorophyll concentrations.

Suggests a gradient from bottom up control (resource availability) at low chlorophyll a to top down (mortality) at high chlorophyll concentrations.

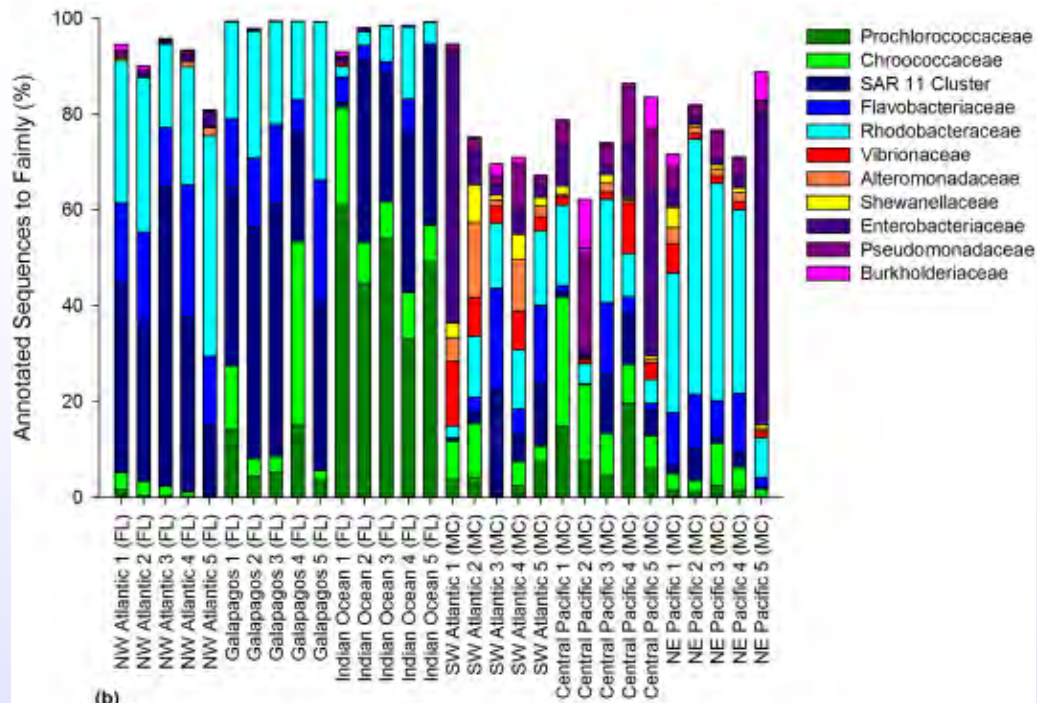


The bacteria : chlorophyll ratio is temperature dependent.

- Uncoupling of food webs.
- Alternate sources of substrate.
- Succession or change in nutritional diversity.

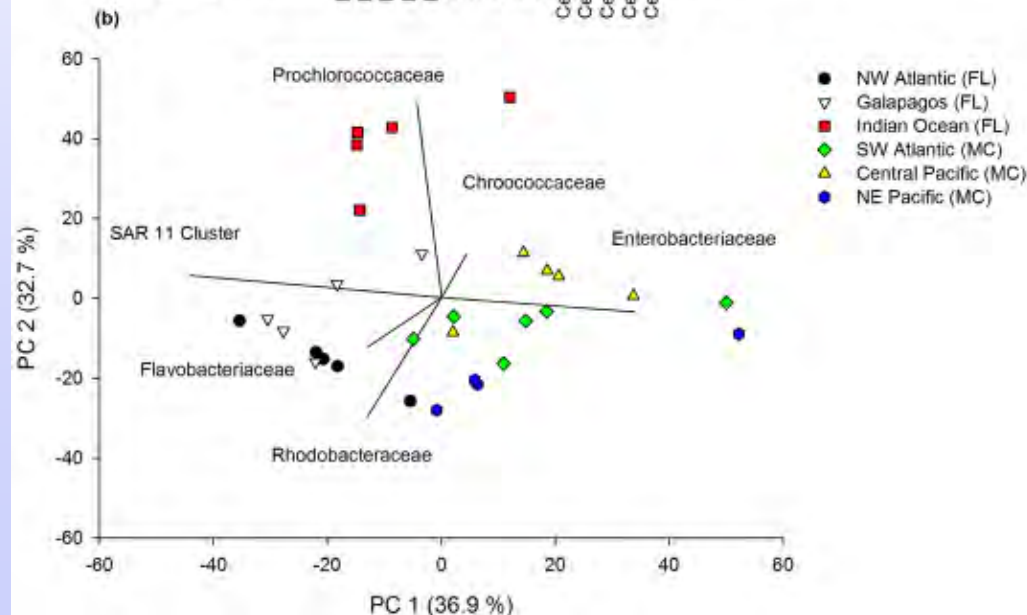
The greatest range and variability is at low temperatures, typical, of polar regions. What is the consequence of this characteristic?

# Haggerty & Dinsdale 2016

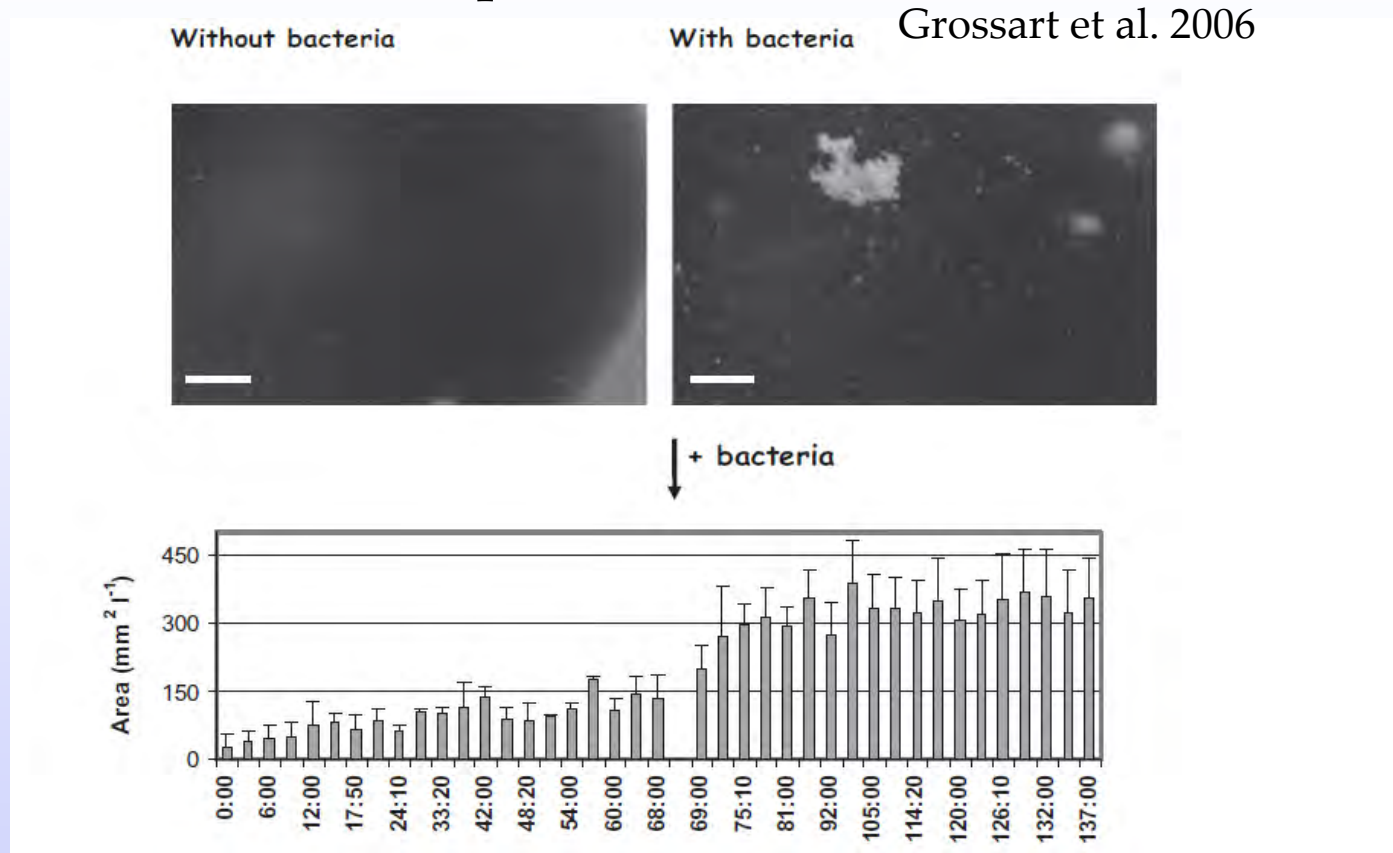


There are distinct biogeographical patterns of marine bacterial families and functional genes in the global ocean.

They show different proportional abundances among regions.



Bacteria and functional groups vary spatially and temporally and their interactions with phytoplankton have important biogeochemical consequences



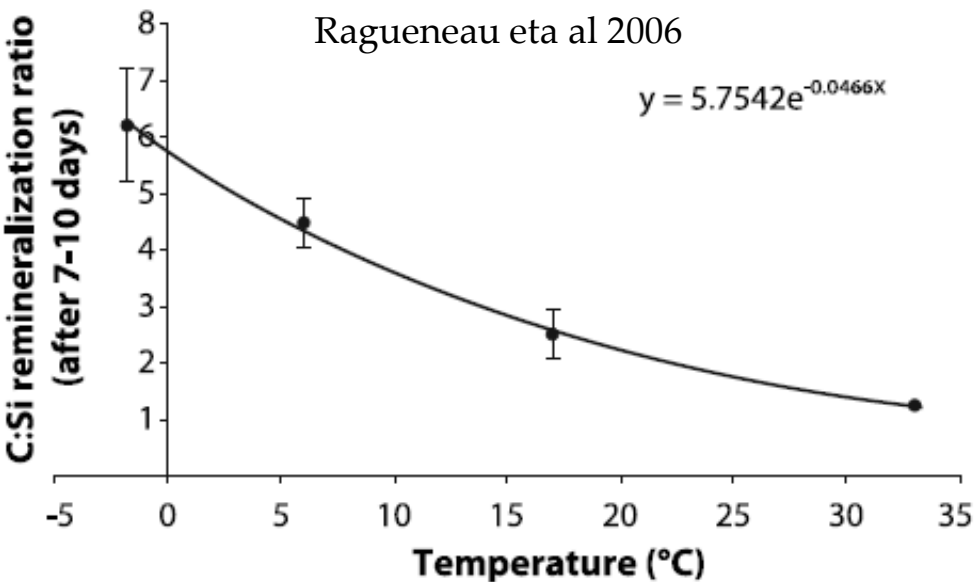
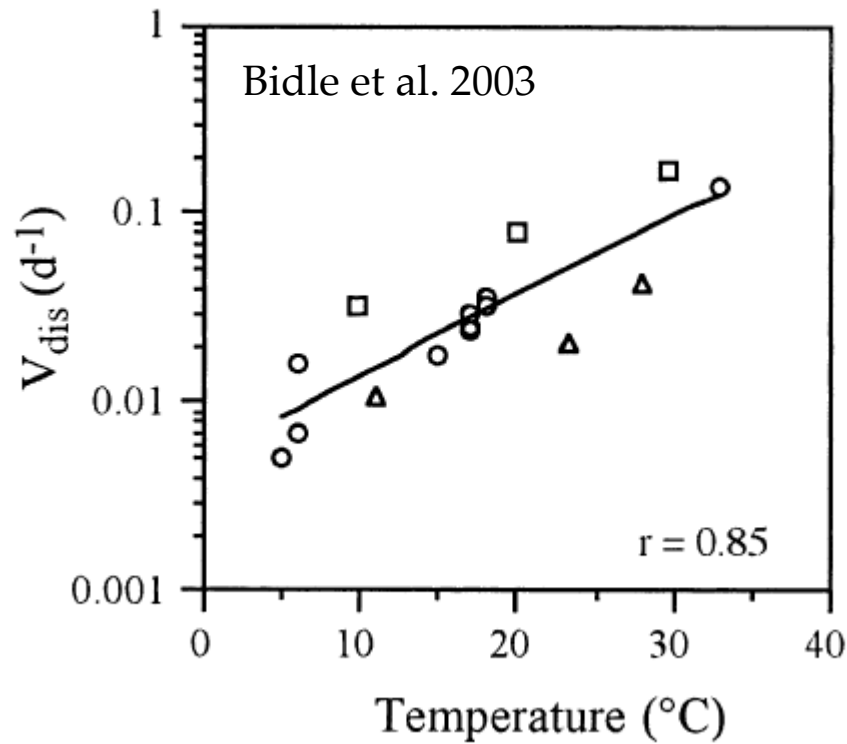
Axenic and non-axenic algae have different patterns of aggregate formation and the pattern and an magnitude of aggregate formation vary with phytoplankton taxa and bacterial phylotype.

Diatoms require silicic acid for cell division and the production of frustules. Seawater is under-saturated with respect to  $\text{bSiO}_2$ , so any exposed surface will undergo rapid chemical dissolution.

Living diatoms protect their frustules from dissolution with an organic matrix which stabilizes the  $\text{bSiO}_2$  dissolution rates.

The  $\text{bSiO}_2$  dissolution rates in "abiotic" sea water, was 0.2 to 0.9% per day, compared to 8-18 % per day when bacteria were present.





Temperature exerts a strong control on Si dissolution and C remineralization.

Bacterial mediation of bSiO<sub>2</sub> dissolution is temperature-dependent function.

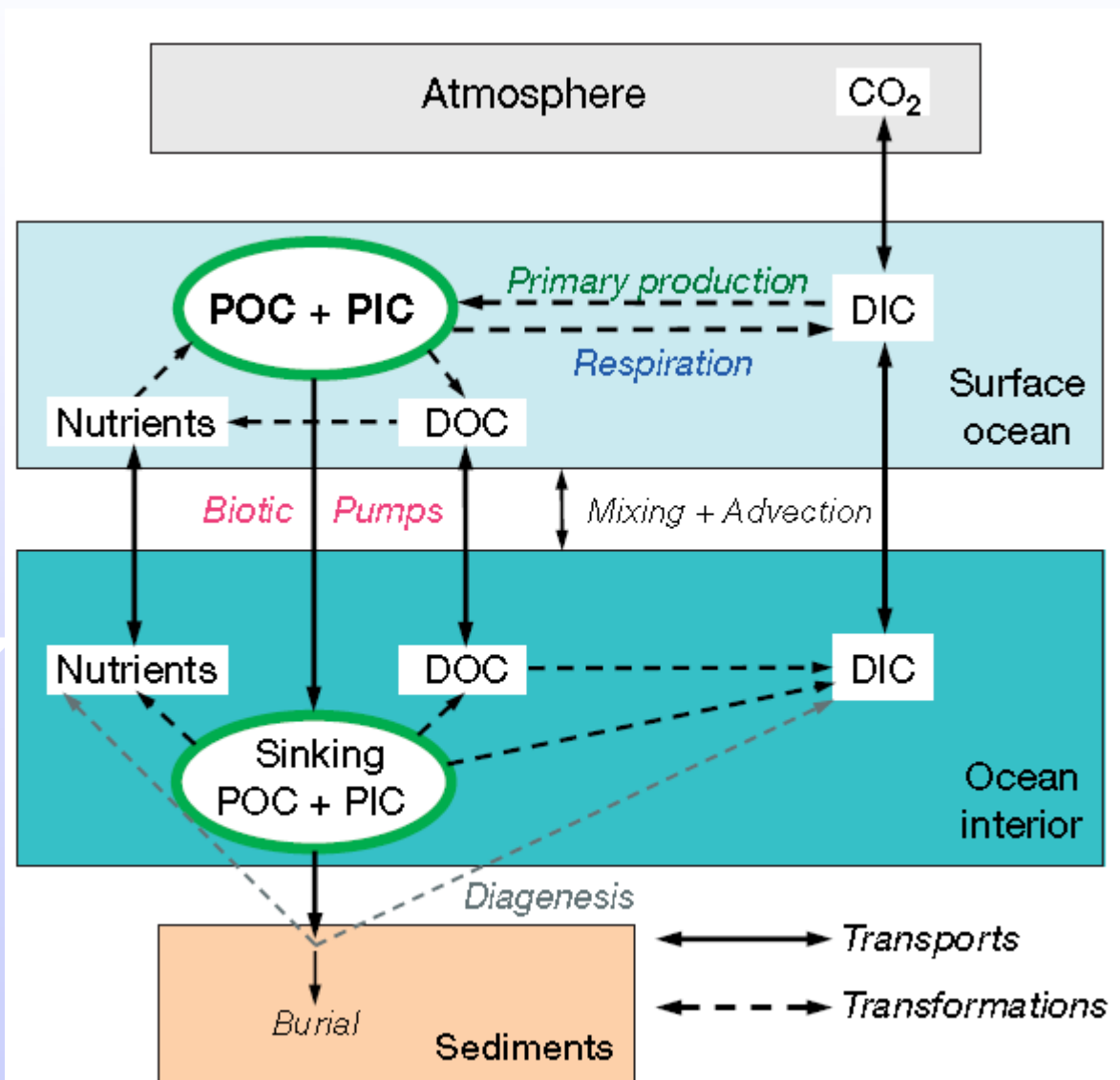
bSiO<sub>2</sub> remineralization is higher at high than low temperatures.

This temperature dependent pattern may influence the different remineralization length scales of bSiO<sub>3</sub> and CaCO<sub>3</sub> and contribute to the observed ballasting effect on carbon export.

Primary production (**PP**) which is exported (**E**) from the euphotic zone represents the fraction that escapes microbial-mediated solubilisation and remineralization (**R**).

$$E = P - R$$

Biologically mediated carbon pumps

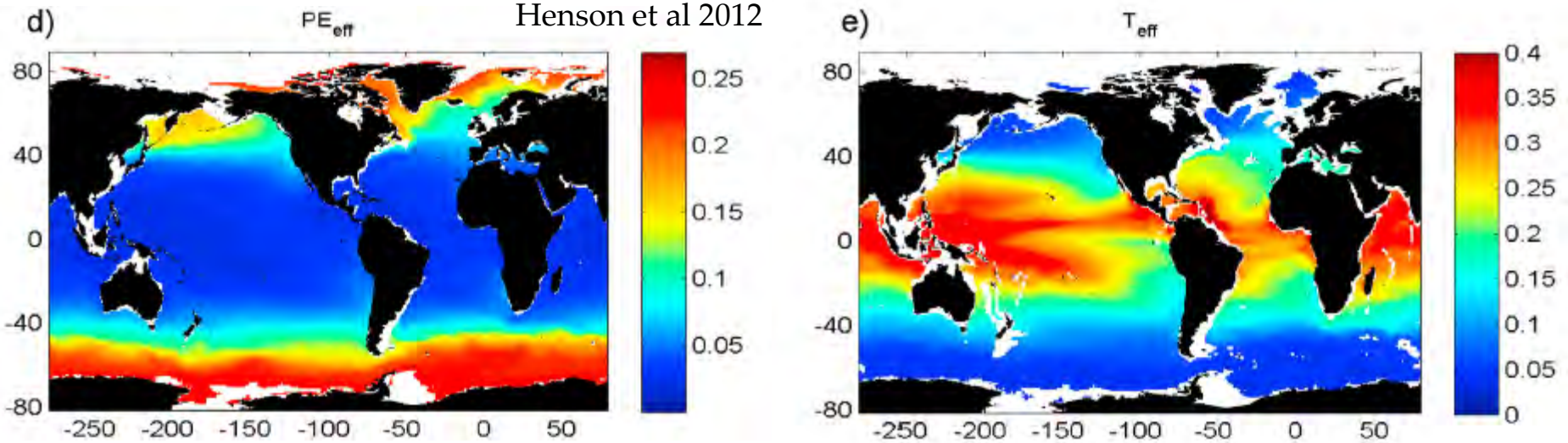


The biological pump is relatively inefficient. Most of the carbon fixed into phytoplankton is remineralized in the euphotic and the mesopelagic zones.

Two commonly used metrics to quantify export are:

Particle export efficiency ( $E_{\text{eff}}$ ), the proportion of **PP** that is exported from the surface ocean, i.e.,  $E/PP$  and,

Particle transfer efficiency ( $T_{\text{eff}}$ ), the fraction of exported organic matter that reaches the depth of sequestration (**S**) ~1000m, i.e.,  $S/E$



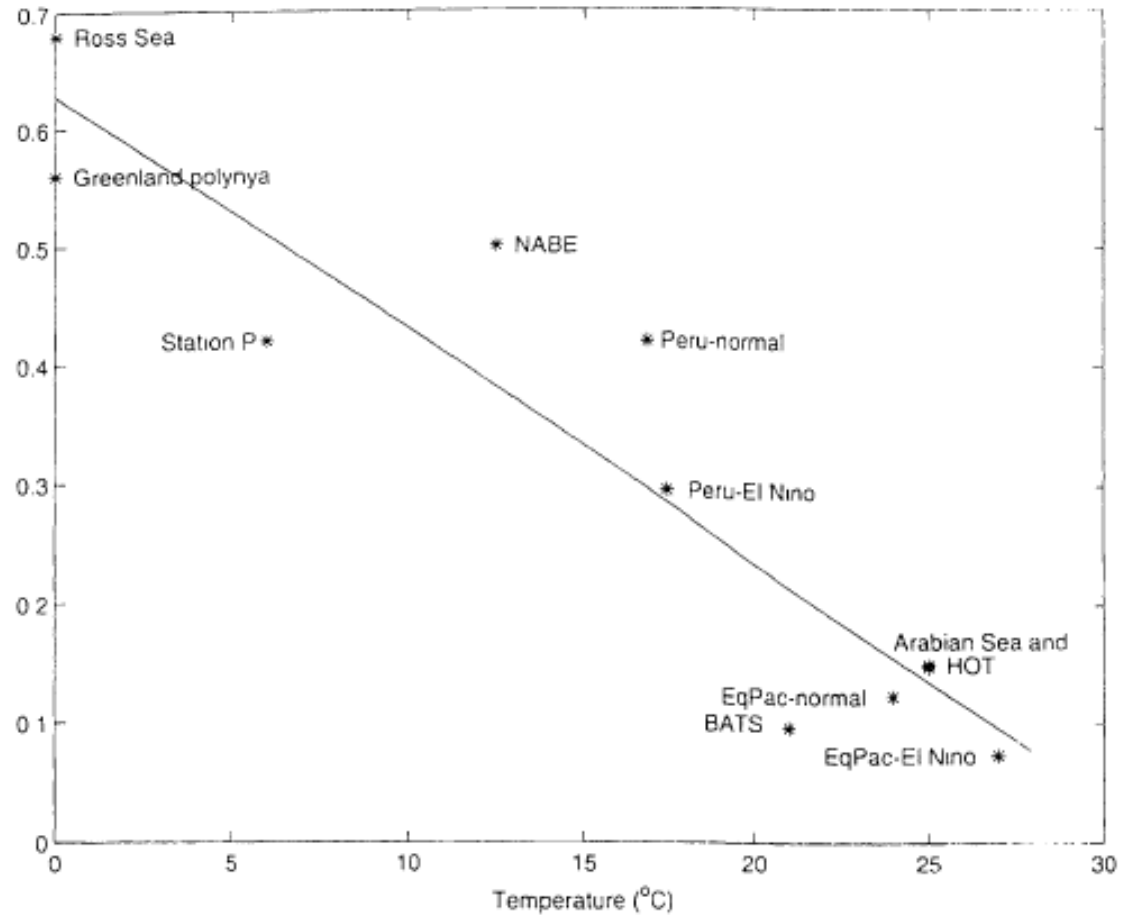
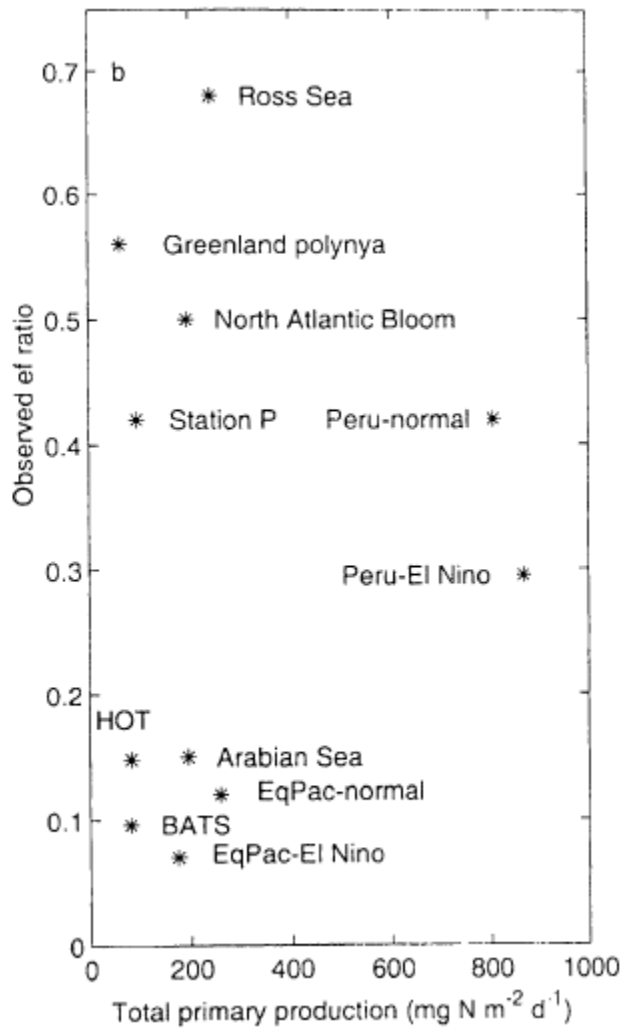
The spatial gradients in  $E_{\text{eff}}$  and  $T_{\text{eff}}$  suggest that in high latitudes, more of the PP is exported below the mixed layer than in low latitudes, but that this material is not effectively sequestered.

Global means vary widely...

$E_{\text{eff}} \sim 10\%$  to  $40\%$  and  $T_{\text{eff}} \sim 1\%$  to  $20\%$

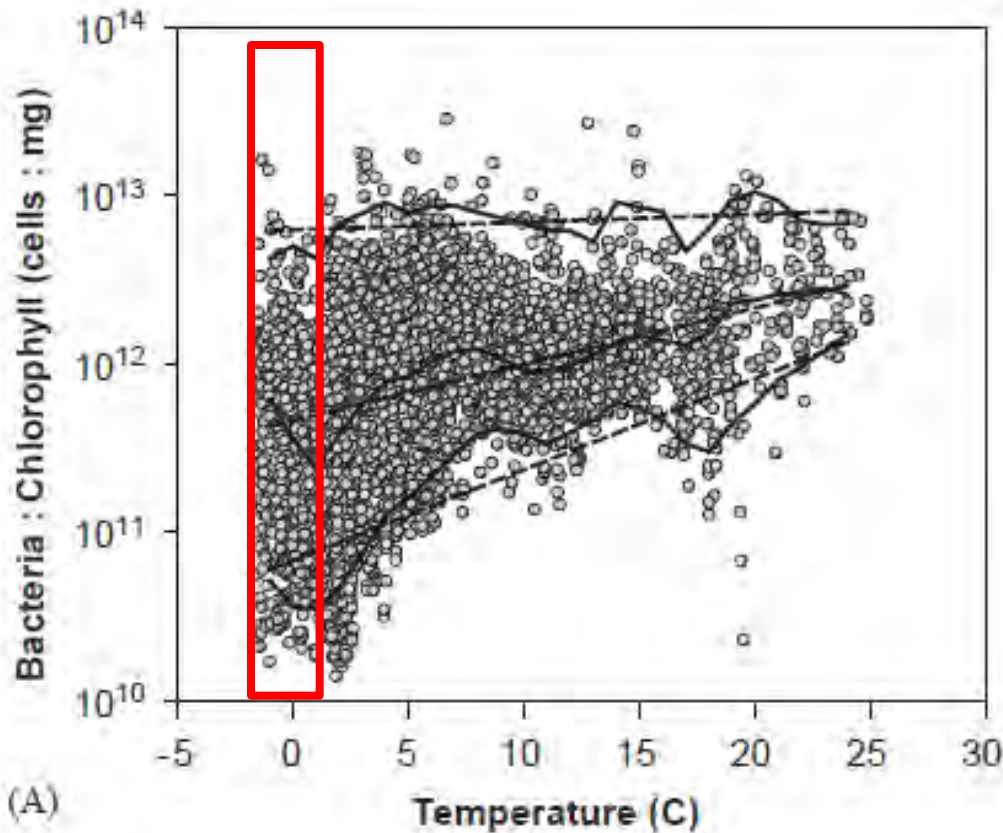
JGOFS-era studies demonstrated particle flux from the surface related to size-spectra and composition of the pelagic food web.

# Laws et al. 2000



$E_{\text{eff}} = \text{ef-ratio} = \text{ratio of export (or new production) to total primary production}$



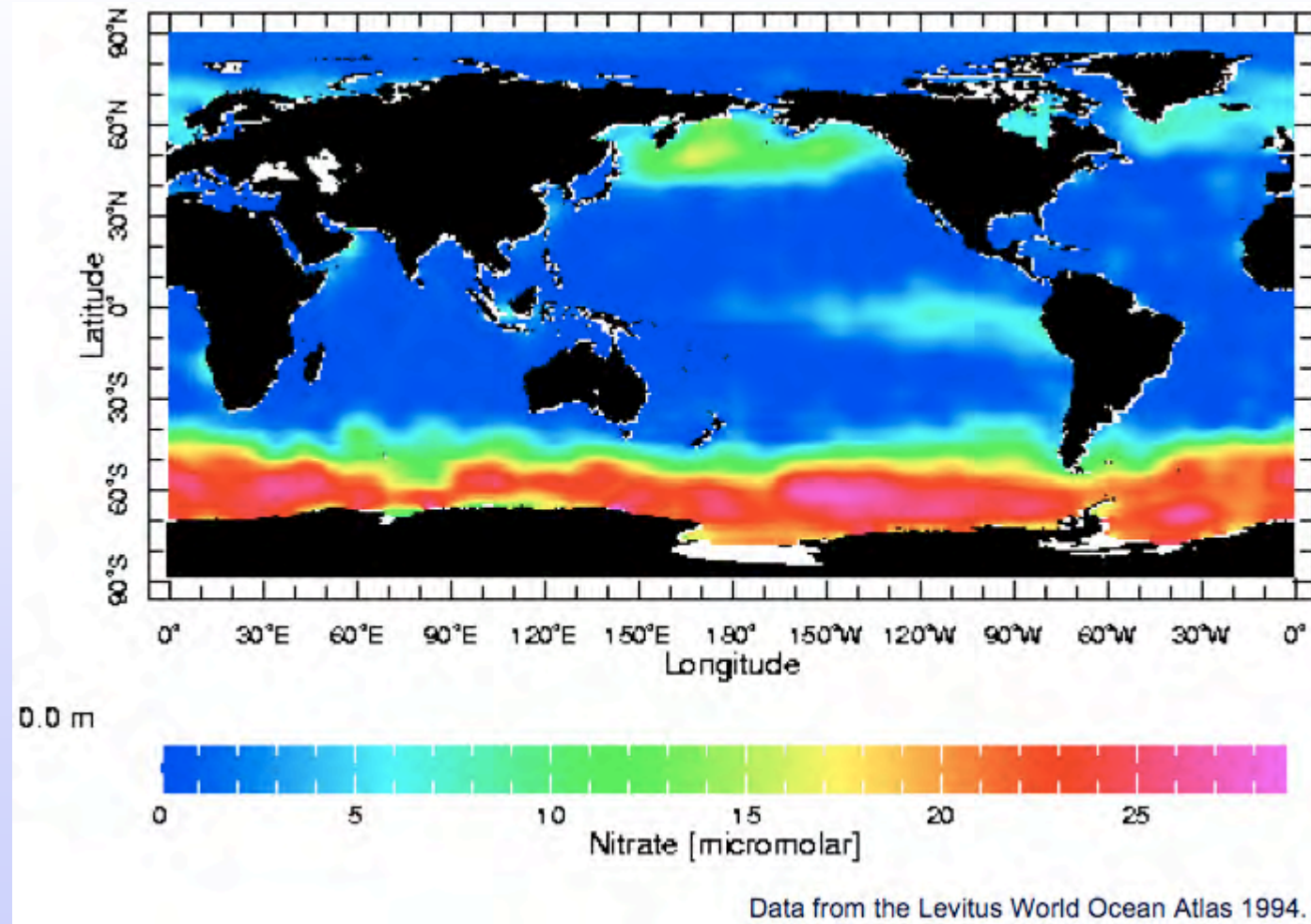


The bacteria : chlorophyll ratio is temperature dependent and the greatest range and variability is at low temperatures, typical of polar regions.

Is the high  $E_{\text{eff}}$  (or ef-ratio) at high latitudes due to the uncoupling of phytoplankton and bacterial processes at low temperatures?

Is this important and how can this be tested?

Phytoplankton biomass in some nutrient rich areas of the contemporary oceans is low and thought to be iron limited.



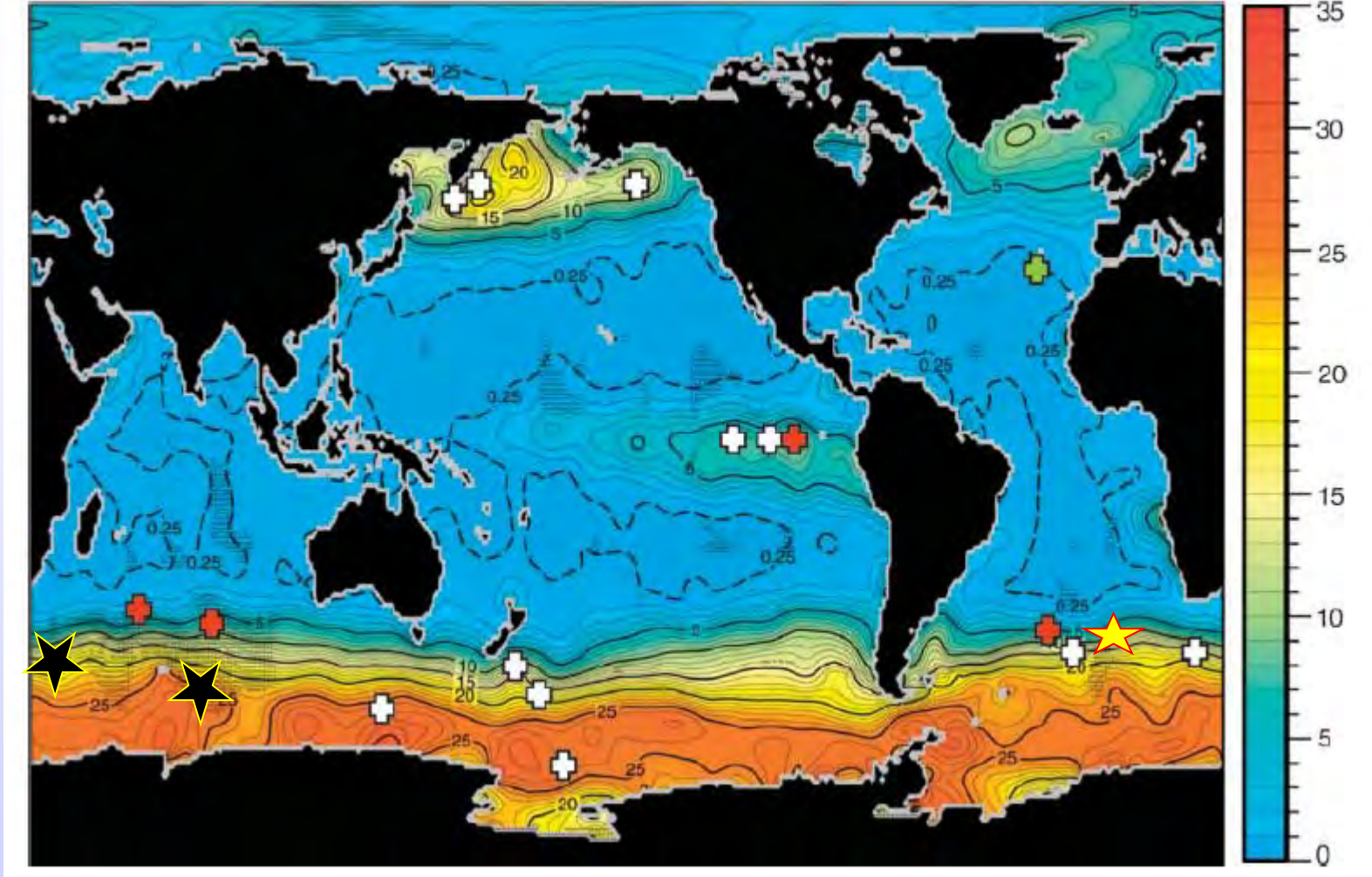
Phytoplankton biomass in some nutrient rich areas of the contemporary oceans is low and thought to be iron limited.

Enhanced supply of iron-bearing dust to these regions during the recent glacial maxima stimulated phytoplankton blooms and *the sinking of phytoplankton to the deep ocean sequestered carbon* preventing its exchange with the atmosphere over millennial time scales.

Ocean iron fertilization experiments tested this hypothesis have provided unambiguous support for the first condition: that iron addition generates phytoplankton blooms in regions with high nutrient but low chlorophyll concentrations.

Experiments have not unequivocally demonstrated the sinking of bloom biomass to depth. Thus second condition of the iron hypothesis has yet to be confirmed.

# Mesoscale Iron Enrichment Experiments 1993–2005 (Boyd et al. 2007):



- ★ Natural iron fertilization; CROZEX and KEOPS 1 & 2
- ★ Mesoscale Iron Enrichment; LOHAFEX



## Synthesis of iron fertilization experiments: From the Iron Age of Enlightenment

Hein J. W. de Baar,<sup>1,2</sup> Philip W. Boyd,<sup>3</sup> Kenneth H. Coale,<sup>4</sup> Michael R. L. Atsushi Tsuda,<sup>6</sup> Philipp Assmy,<sup>7</sup> Dorothee C. E. Bakker,<sup>8</sup> Yann Bozec,<sup>1</sup> Richard T. Barber,<sup>9</sup> Mark A. Brzezinski,<sup>10</sup> Ken O. Buesseler,<sup>11</sup> Marie Boyer,<sup>12</sup> Peter L. Croot,<sup>1,13</sup> Frank Gervais,<sup>7</sup> Maxim Y. Gorbunov,<sup>14</sup> Paul J. Harrison,<sup>15</sup> William T. Hiscock,<sup>16</sup> Patrick Laan,<sup>1</sup> Christiane Lancelot,<sup>17</sup> Cliff S. Law,<sup>18</sup> Maurice Levasseur,<sup>19</sup> Adrian Marchetti,<sup>20</sup> Frank J. Millero,<sup>16</sup> Jun Nishioka,<sup>21</sup> Yukihiro Nojiri,<sup>22</sup> Tim van Oijen,<sup>2</sup> Ulf Riebesell,<sup>13</sup> Micha J. A. Rijkenberg,<sup>23</sup> Hiroaki Saito,<sup>23</sup> Shigenobu Takeda,<sup>24</sup> Klaas R. Timmermans,<sup>1</sup> Marcel J. W. van Meurs,<sup>25</sup> Anya M. Waite,<sup>25</sup> and Chi-Shing Wong<sup>26</sup>

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## ARTICLES

### A massive phytoplankton bloom induced by an ecosystem-scale iron fertilization experiment in the equatorial Pacific Ocean

Kenneth H. Coale\*, Kenneth S. Johnson\*<sup>†</sup>, Steve E. Fitzwater\*, R. Michael Gordon\*, Sara Tanner\*, Francisco P. Chavez<sup>†</sup>, Laurie Ferioli\*<sup>†</sup>, Carole Sakamoto<sup>†</sup>, Paul Rogers<sup>†</sup>, Frank Millero<sup>‡</sup>, Paul Steinberg<sup>‡</sup>, Phil Nightingale<sup>§||</sup>, David Cooper<sup>§||</sup>, William P. Cochlan<sup>†</sup>, Michael R. Landry<sup>#</sup>, John Constantinou<sup>#</sup>, Gretchen Rollwagen<sup>#</sup>, Armando Trasvina<sup>☆||</sup> & Raphael Kudela<sup>¶||</sup>



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nature

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## LETTERS

### Effect of natural iron fertilization on carbon sequestration in the Southern Ocean

Stéphane Blain<sup>1</sup>, Bernard Quéguiner<sup>1</sup>, Leanne Armand<sup>1</sup>, Sauveur Belviso<sup>2</sup>, Bruno Bombled<sup>2</sup>, Laurent Bopp<sup>2</sup>, Andrew Bowie<sup>3,4</sup>, Christian Brunet<sup>5</sup>, Corina Brussaard<sup>6</sup>, François Carlotti<sup>1</sup>, Urania Christaki<sup>7</sup>, Antoine Corbière<sup>5</sup>, Isabelle Durand<sup>8</sup>, Frederike Ebersbach<sup>3</sup>, Jean-Luc Fuda<sup>9</sup>, Nicole Garcia<sup>1</sup>, Loes Gerringa<sup>6</sup>, Brian Griffiths<sup>10</sup>, Catherine Guigue<sup>11</sup>, Christophe Guillemin<sup>12</sup>, Stéphanie Jacquet<sup>13</sup>, Catherine Jeandel<sup>14</sup>, Patrick Laan<sup>6</sup>, Dominique Lefèvre<sup>11</sup>, Claire Lo Monaco<sup>5</sup>, Andrea Malits<sup>15</sup>, Julie Mosseri<sup>1</sup>, Ingrid Obernosterer<sup>16</sup>, Young-Hyang Park<sup>8</sup>, Marc Picheral<sup>15</sup>, Philippe Pondaven<sup>17</sup>, Thomas Remenyi<sup>3</sup>, Valérie Sandroni<sup>1</sup>, Géraldine Sarthou<sup>17</sup>, Nicolas Savoye<sup>13,18</sup>, Lionel Scouarnec<sup>12</sup>, Marc Souhaut<sup>14</sup>, Doris Thuiller<sup>5</sup>, Klaas Timmermans<sup>6</sup>, Thomas Trull<sup>3,10</sup>, Julia Uitz<sup>15</sup>, Pieter van Beek<sup>14</sup>, Marcel Veldhuis<sup>6</sup>, Dorothee Vincent<sup>7</sup>, Eric Viollier<sup>19</sup>, Lilita Vong<sup>1</sup> & Thibaut Wagener<sup>15</sup>

## ARTICLES

### Phytoplankton bloom induced by mesoscale iron fertilization in the equatorial Pacific Ocean

S. Johnson<sup>\*†</sup>, Steve E. Fitzwater<sup>\*</sup>, R. Michael Gordon<sup>\*</sup>, Sara Tanner<sup>\*</sup>, Francisco P. Chavez<sup>†</sup>, Laurie Ferioli<sup>\*†</sup>, Carole Sakamoto<sup>†</sup>, Paul Rogers<sup>†</sup>, Frank Millero<sup>‡</sup>, Paul Steinberg<sup>‡</sup>, Phil Nightingale<sup>§||</sup>, David Cooper<sup>§||</sup>, William P. Cochlan<sup>†</sup>, Michael R. Landry<sup>#</sup>, John Constantinou<sup>#</sup>, Gretchen Rollwagen<sup>#</sup>, Armando Trasvina<sup>☆||</sup> & Raphael Kudela<sup>¶||</sup>

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**Mesoscale Iron Enrichment Experiments 1993–2005: Synthesis and Future Directions**

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ARTICLE

doi:10.1038/nature11229

**Deep carbon export from a Southern Ocean iron-fertilized diatom bloom**

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ARTICLES

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LETTERS

**Southern Ocean deep-water carbon export enhanced by natural iron fertilization**

H. Coale,<sup>7</sup>  
 eur,<sup>11</sup>  
 Smetacek,<sup>16</sup>

Raymond T. Pollard<sup>1</sup>, Ian Salter<sup>1,2</sup>, Richard J. Sanders<sup>1</sup>, Mike I. Lucas<sup>3</sup>, C. Mark Moore<sup>1</sup>, Rachel A. Mills<sup>1</sup>, Peter J. Statham<sup>1</sup>, John T. Allen<sup>1</sup>, Alex R. Baker<sup>4</sup>, Dorothee C. E. Bakker<sup>4</sup>, Matthew A. Charette<sup>5</sup>, Sophie Fielding<sup>6</sup>, Gary R. Fones<sup>7</sup>, Megan French<sup>4</sup>, Anna E. Hickman<sup>8</sup>, Ross J. Holland<sup>1</sup>, J. Alan Hughes<sup>1</sup>, Timothy D. Jickells<sup>4</sup>, Richard S. Lampitt<sup>1</sup>, Paul J. Morris<sup>1</sup>, Florence H. Nédélec<sup>9</sup>, Maria Nielsdóttir<sup>1</sup>, Hélène Planquette<sup>10</sup>, Ekaterina E. Popova<sup>1</sup>, Alex J. Poulton<sup>1</sup>, Jane F. Read<sup>1</sup>, Sophie Seeyave<sup>1</sup>, Tania Smith<sup>1</sup>, Mark Stinchcombe<sup>1</sup>, Sarah Taylor<sup>1</sup>, Sandy Thomalla<sup>11</sup>, Hugh J. Venables<sup>6</sup>, Robert Williamson<sup>11</sup> & Mike V. Zubkov<sup>1</sup>

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**Deep carbon export from a Southern Ocean iron-fertilized diatom bloom**

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ARTICLES

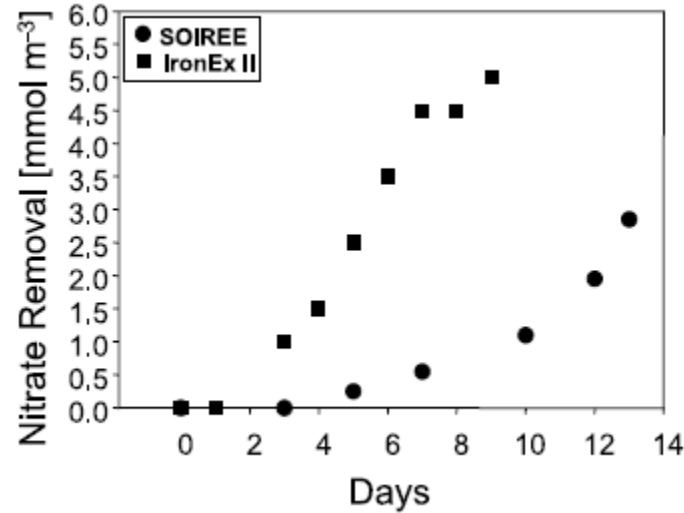
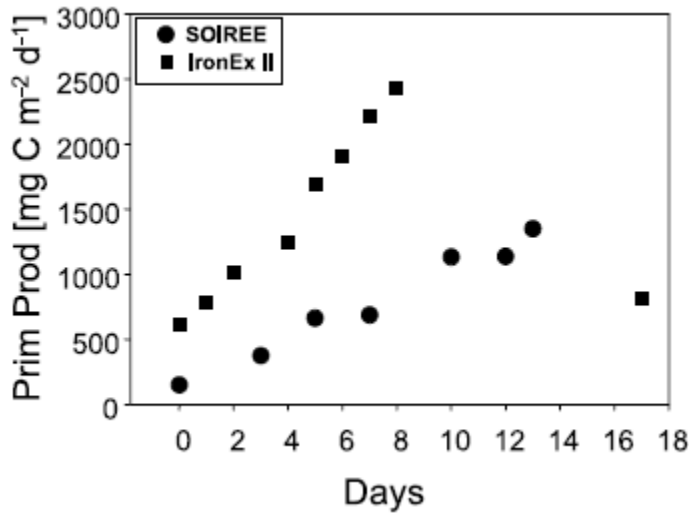
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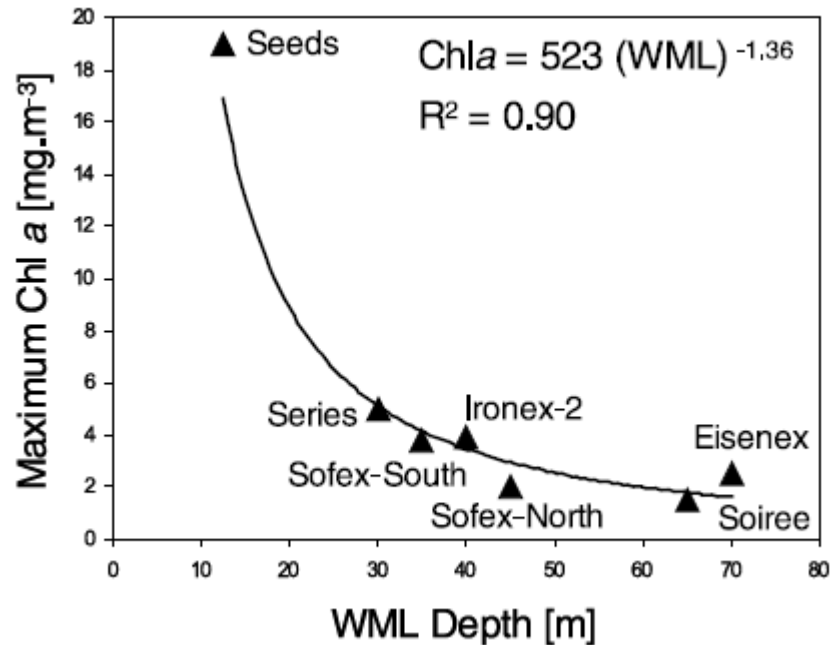
deBaar et al. 2005



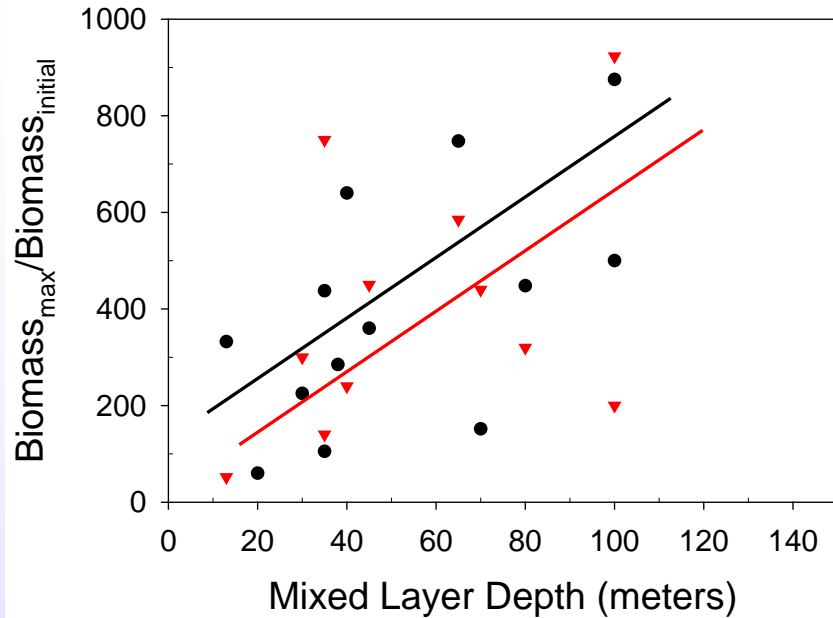
More rapid rates at higher temperatures.

Inverse relationship between Chl a concentration and mixed layer depth.

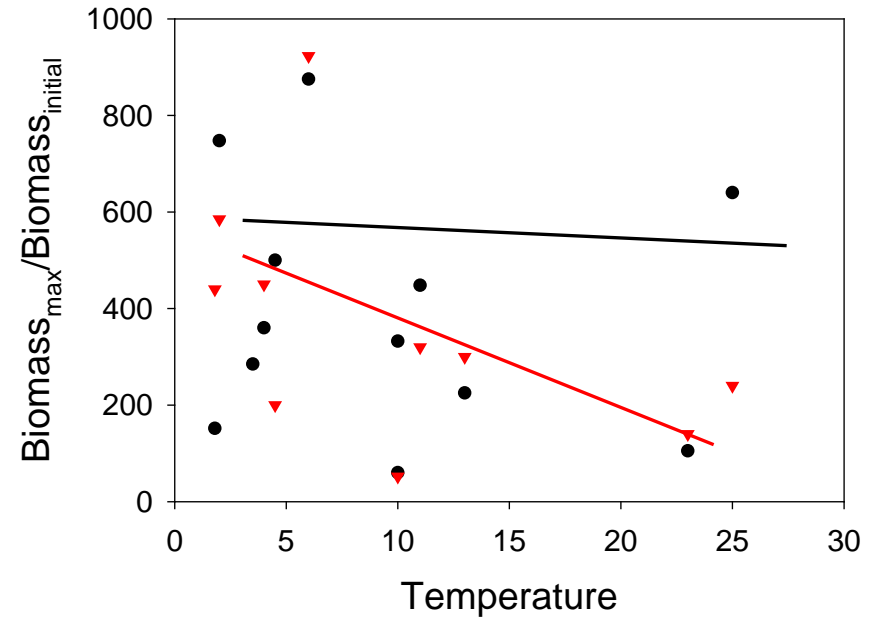
Not all sites characterized heterotrophic microbes.



## Phytoplankton



## Bacteria



Significant and positive relationship between relative biomass increases and MLD.

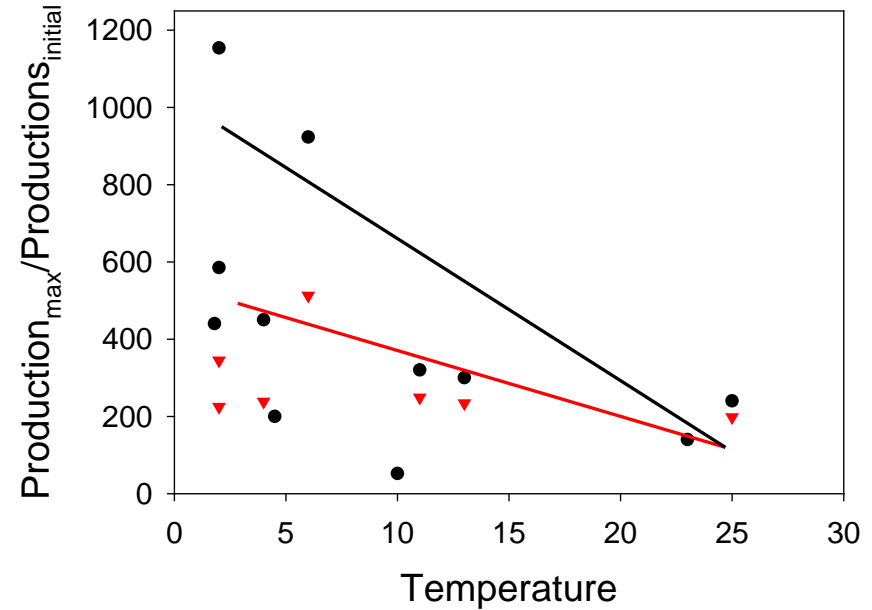
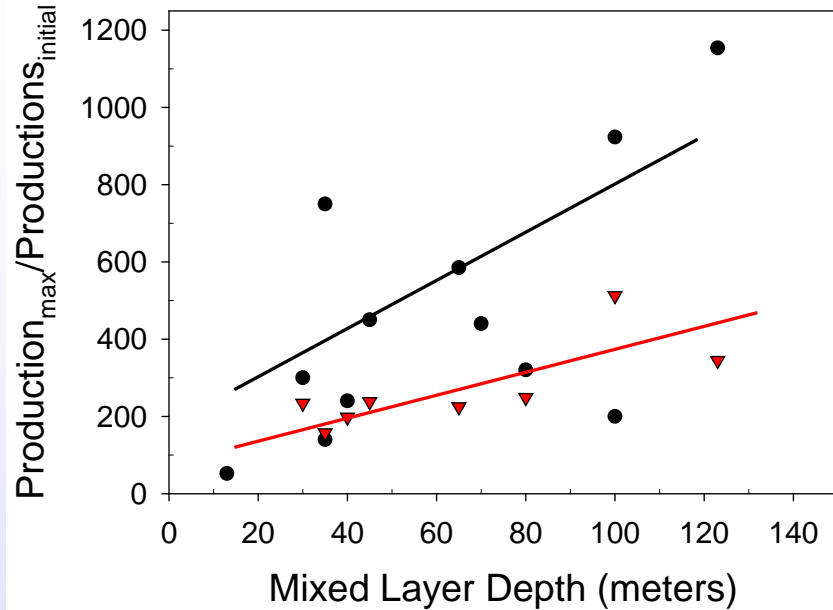
MLD is deeper in polar regions.

Significant inverse relationship between bacterial biomass and temperature.

Bacteria dynamics are more sensitive than phytoplankton to temperature... Higher 'loss' rates at high temperature.

# Phytoplankton

# Bacteria



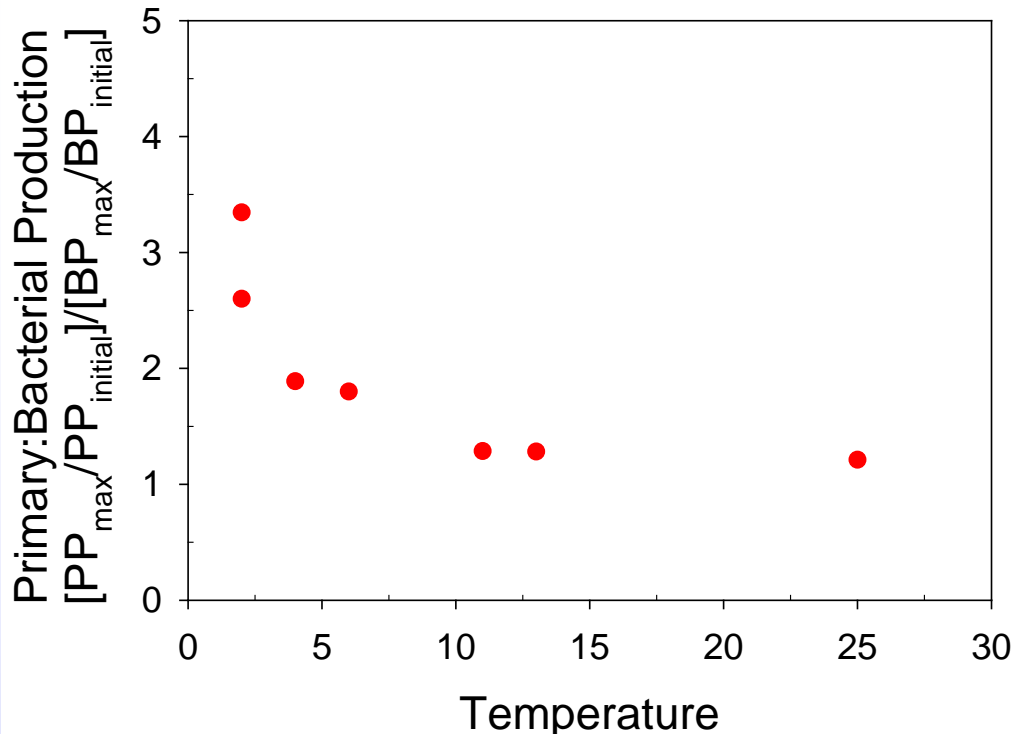
Significant positive relationship between the relative increase in production and MLD.

Significant inverse relationship between increased production and temperature.

Bacteria dynamics are more sensitive than phytoplankton to temperature... Higher loss rates at high temperature.

Different response for phytoplankton biomass *vs.* production suggests mortality is an important process.





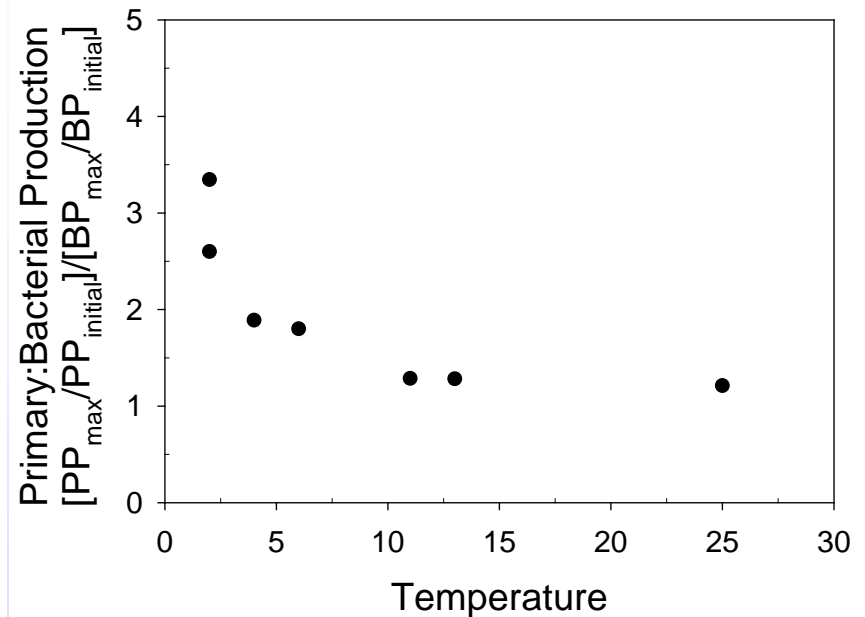
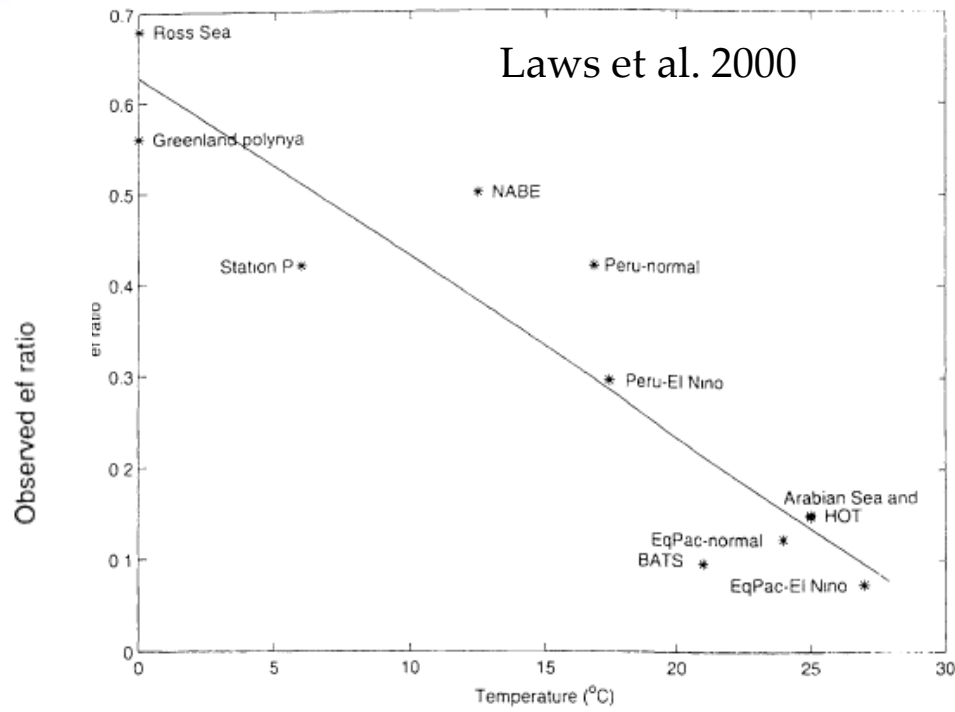
$[PP_{max}/PP_{initial}]/[BP_{max}/BP_{initial}]$

Relative change in the phytoplankton production to bacterial production as a function of temperature during iron fertilization experiments.

The decrease in the ratio implies that there is a smaller bacterial demand for PP carbon at low than high temperatures. More PP available for export.

This is not an absolute value for PP:BP, it is a non dimensional scaling parameter that allows a comparison among iron fertilization experiments.

**ef-ratio** = ratio of export to total primary production



Iron-stimulated carbon export has been ('sorta') observed at the CROZEX and KEOPS natural fertilization sites and to a lesser extent during at the EIFEX and SOFEX-S study sites in the Southern Ocean. Consistent with temperature dependence of bacteria-phytoplankton relationships.

## Summary

Bacteria and phytoplankton have co-evolved and their intimate biological interactions influence ocean biogeochemical processes.

Bacteria directly influence phytoplankton aggregation, dissolution and remineralization processes that leads to differential retention *vs.* export of phytoplankton carbon from the upper ocean, and these processes are temperature dependent.

Mesoscale iron fertilization experiments have not consistently demonstrated carbon export/sequestration, however those carried in the Southern Ocean suggest that a combinations of fertilization durations and microbial dynamics may be important factors.



**Thank you for your attention**