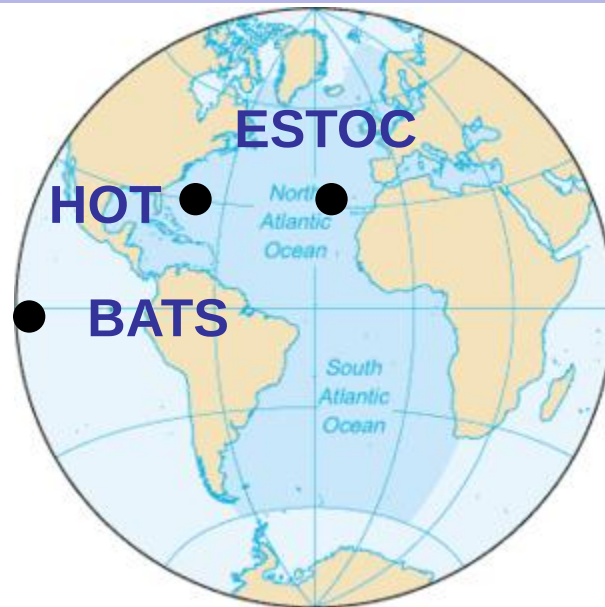
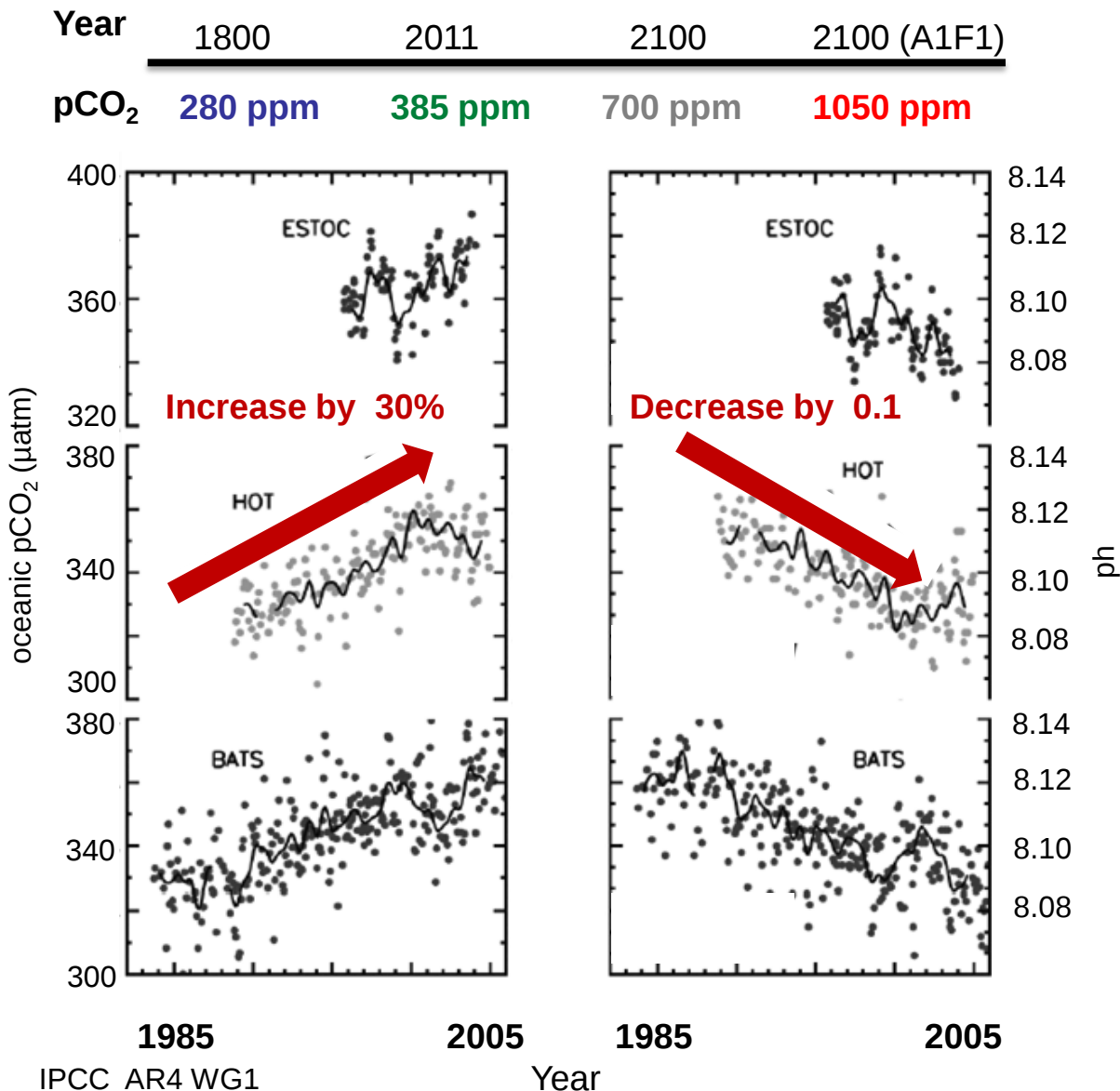


Ocean Acidification and Biogeochemical Cycling

Uta Passow



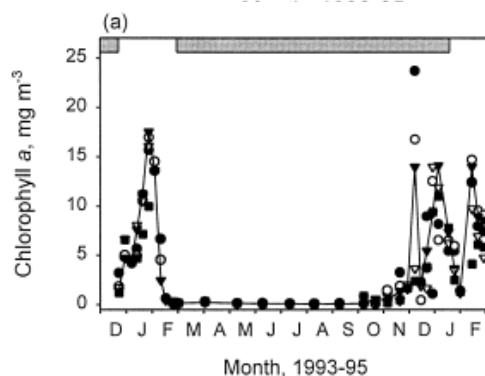
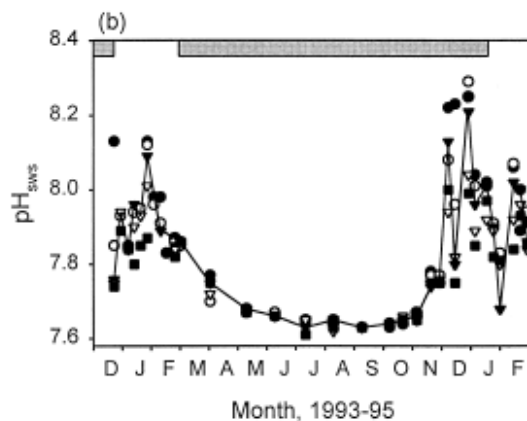
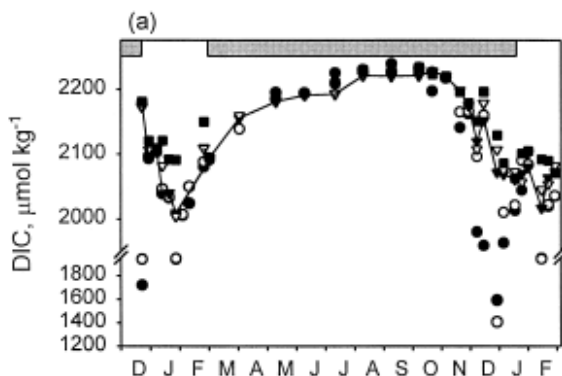
Facts About Ocean Acidification (OA)



- Burning of fossil-fuel lead to increase in $p\text{CO}_2$
- CO₂ dissolves in ocean water
- Decrease in pH, increase in DIC & pCO₂, TA remains constant

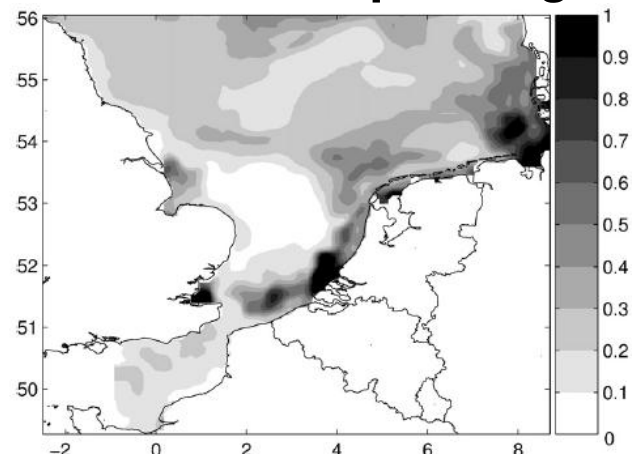
In situ variability of carbonate system parameters

Annual S. Ocean

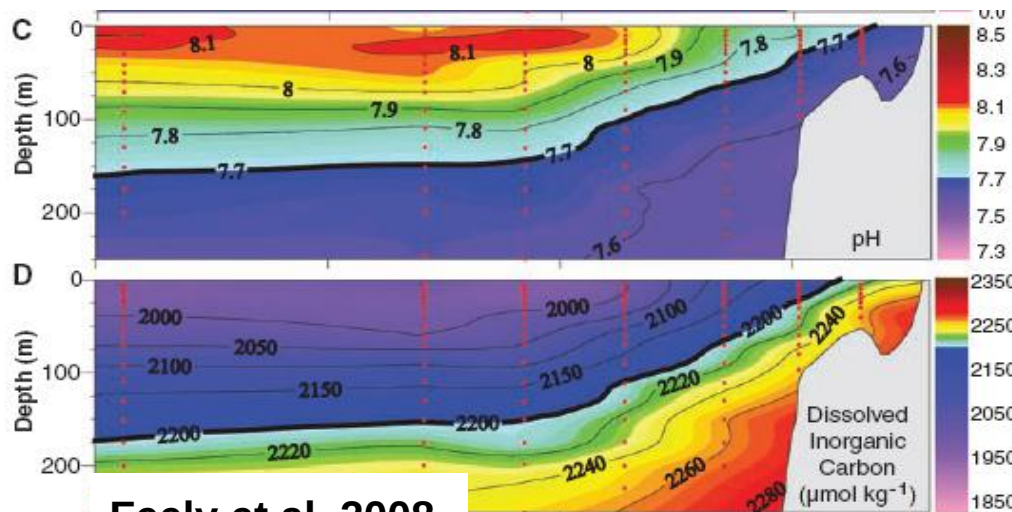


Gibson & Trull 1999

N Sea annual pH range

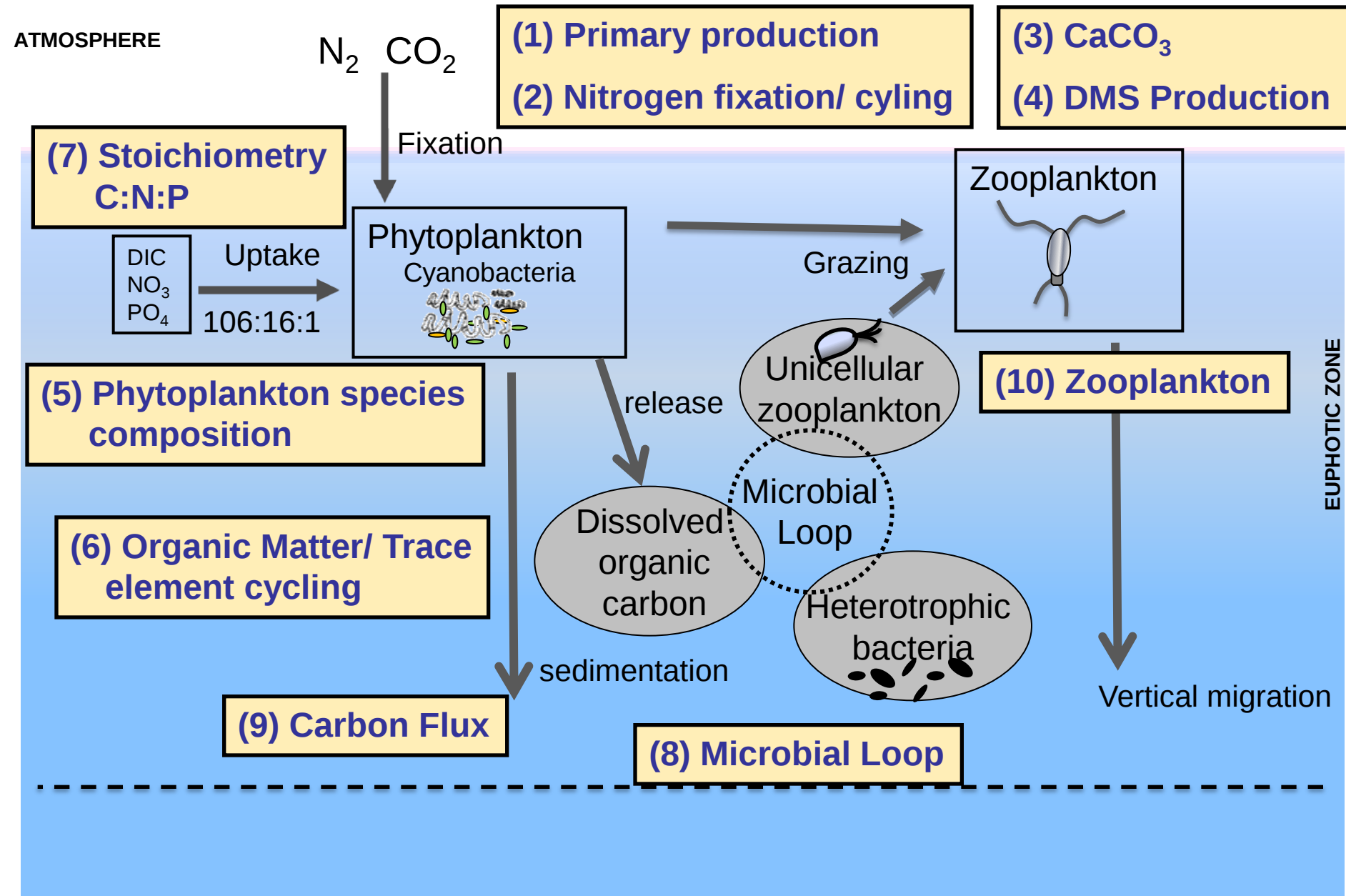


W Coast USA



Feely et al. 2008

Biogeochemical cycles



(1) Primary Production & growth rate

Number of studies

15 + 18 (eukaryotes)

10 (cyanobacteria)

Impact

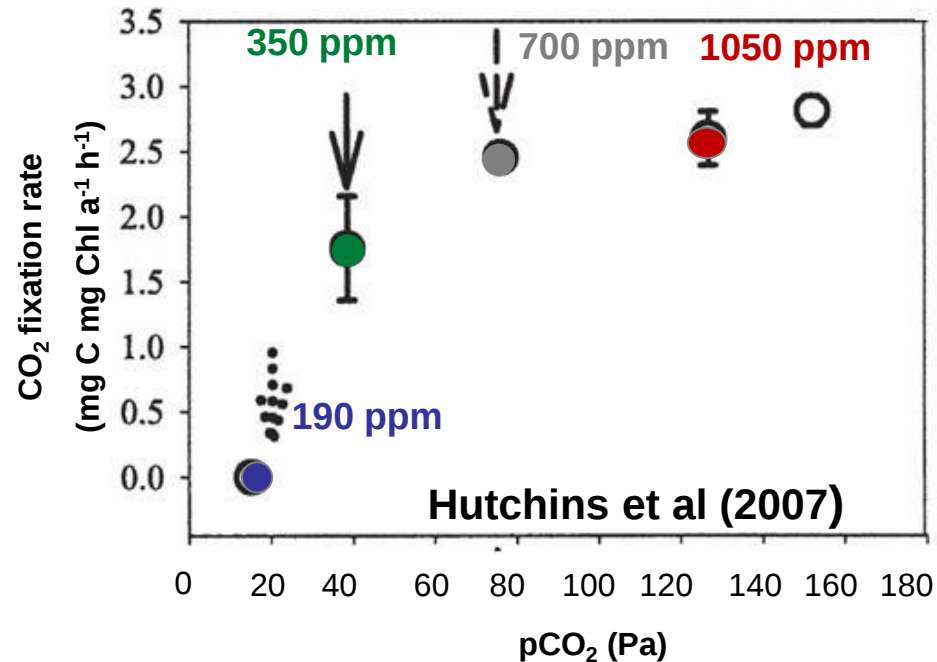
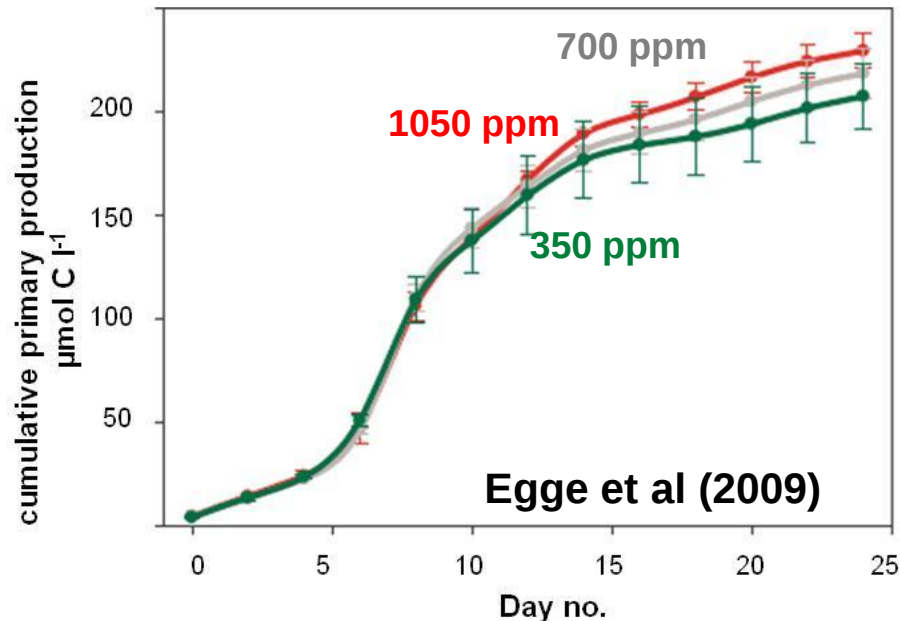
No eff.- Positive

Positive

Range

Increase 10-50%

Increase 15-128%



Pelagic Ecosystem CO_2 Enrichment study
(PeECE III 2005), but no difference PeECE I & II
(2001 & 2003)

(1) Primary Production & growth rate

Number of studies

15 + 18 (eukaryotes)

10 (cyanobacteria)

Impact

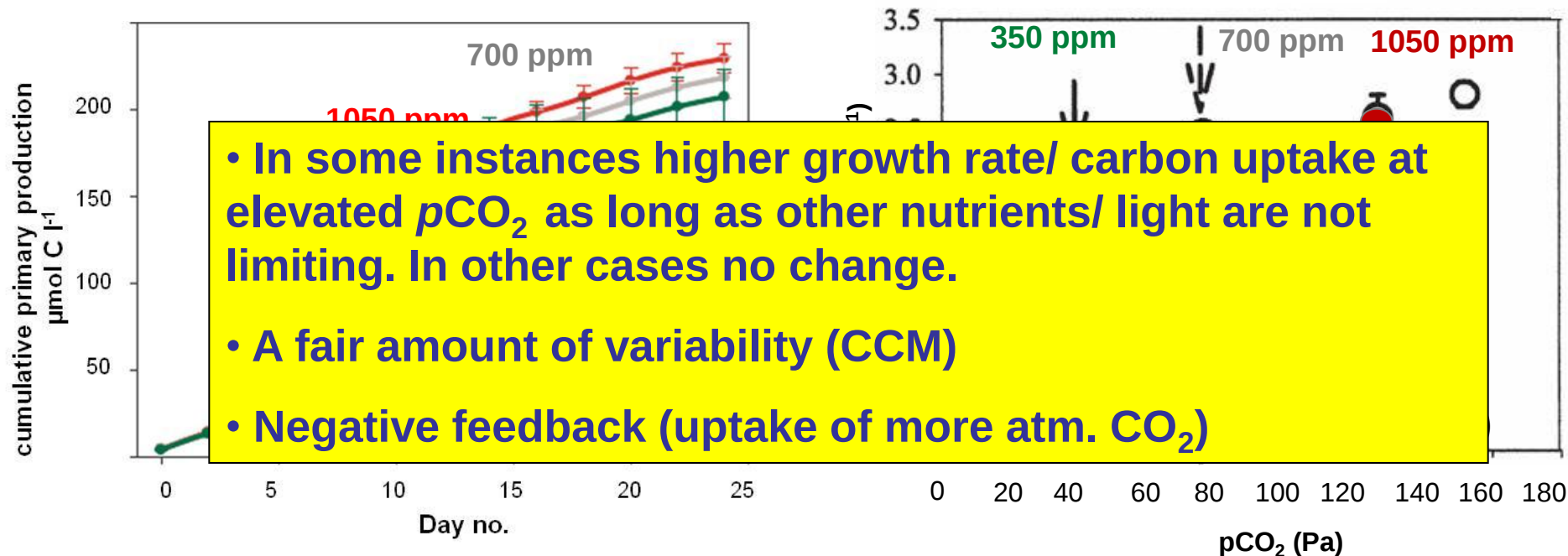
No eff.- Positive

Positive

Range

Increase 10-50%

Increase 15-128%



Pelagic Ecosystem CO_2 Enrichment study
(PeECE III 2005), but no difference PeECE I & II
(2001 & 2003)

(2a) Nitrogen Fixation by Cyanobacteria

Number of studies

10

Impact

Positive /

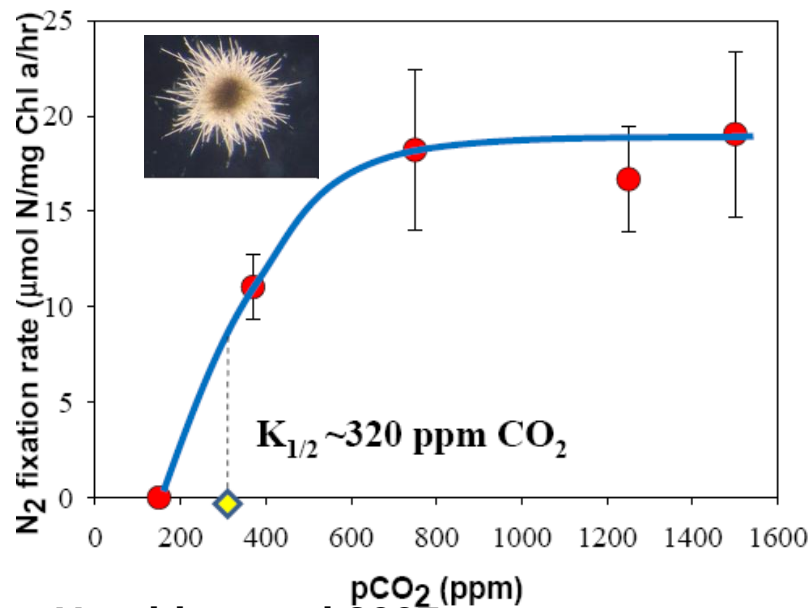
Negat

Range

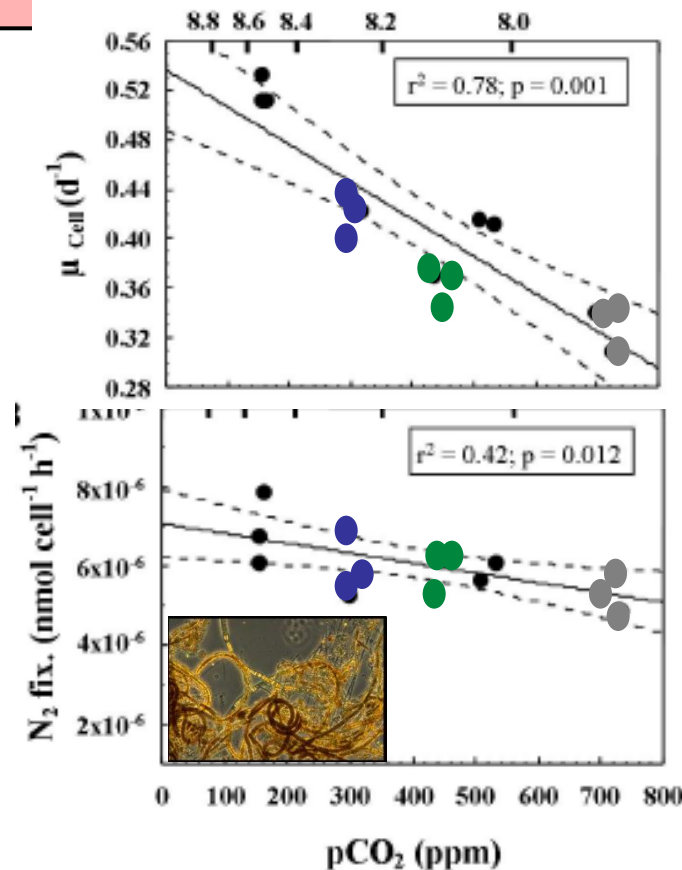
Increase up to 100%

Czerny et al 2009

N₂ fixation saturation kinetics



Hutchins et al 2007



(2a) Nitrogen Fixation by Cyanobacteria

Number of studies

10

Impact

Positive /

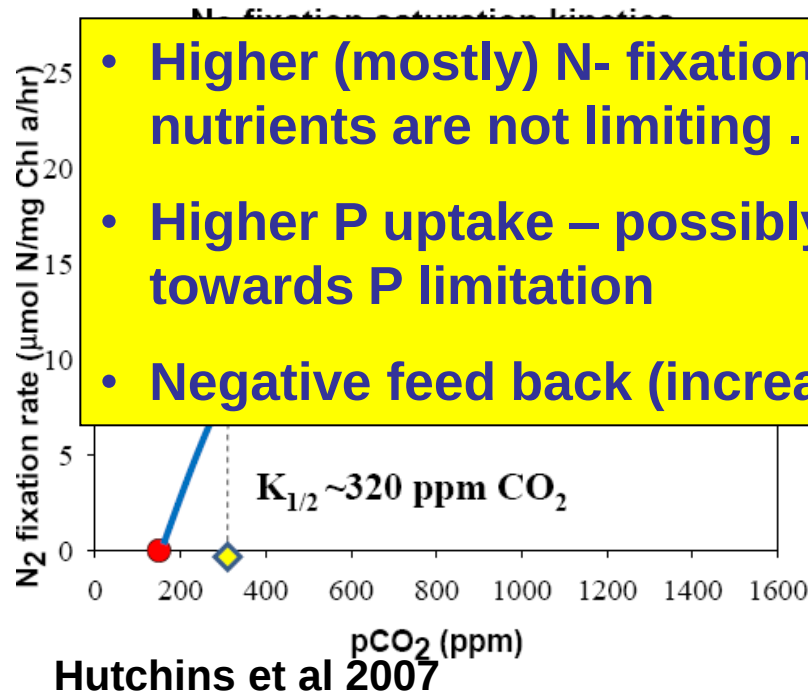
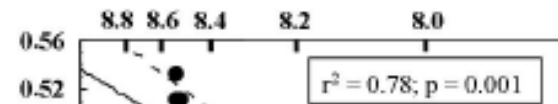
Negat

Range

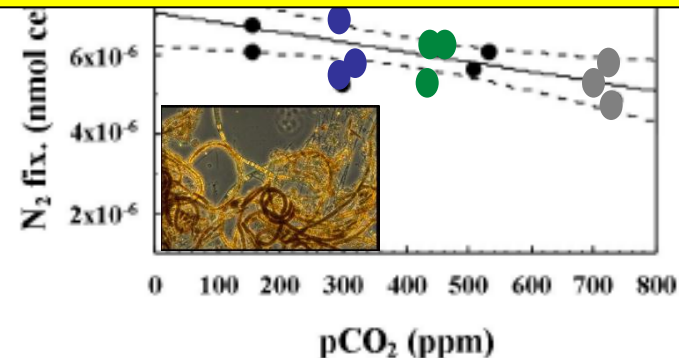
Increase up to 100%

Czerny et al 2009

pH



- Higher (mostly) N- fixation at elevated pCO₂ as long as other nutrients are not limiting . But species specific diversity
- Higher P uptake – possibly driving oligotrophic habitats towards P limitation
- Negative feed back (increase primary production)



(2b) Nitrification

Number of studies

3

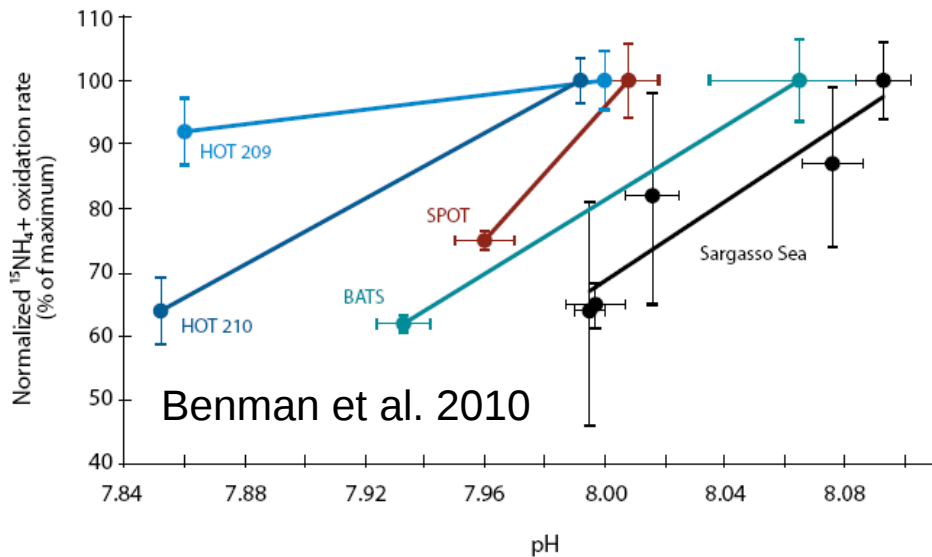
Impact

Negative

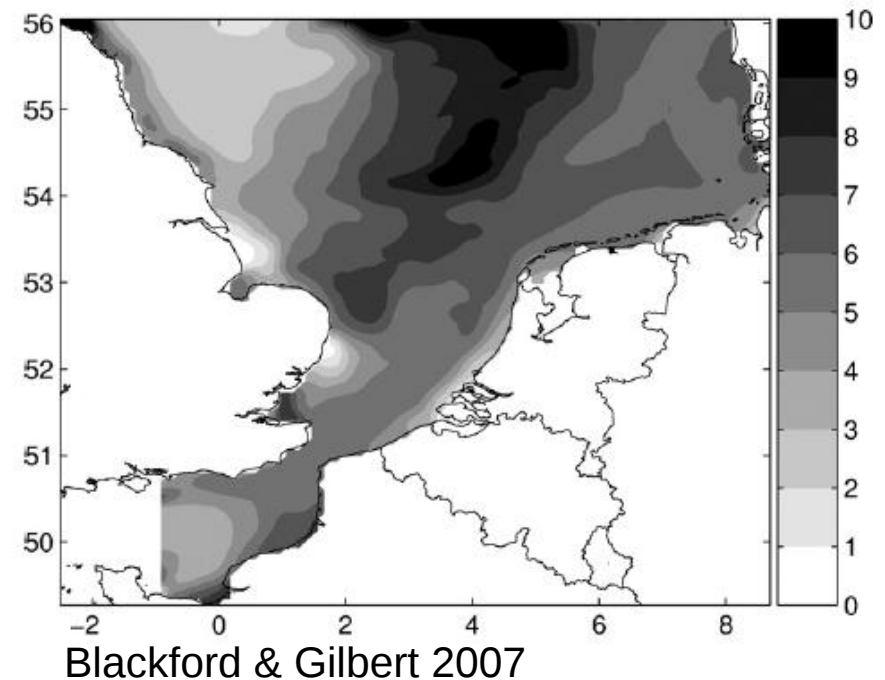
Range

Decrease 10-40%

Nitrification



% Change in NO_3^- : DIN ratio (Δ 385 & 1000 ppm CO_2) based on Husemann et al. 2002.



(2b) Nitrification

Number of studies

3

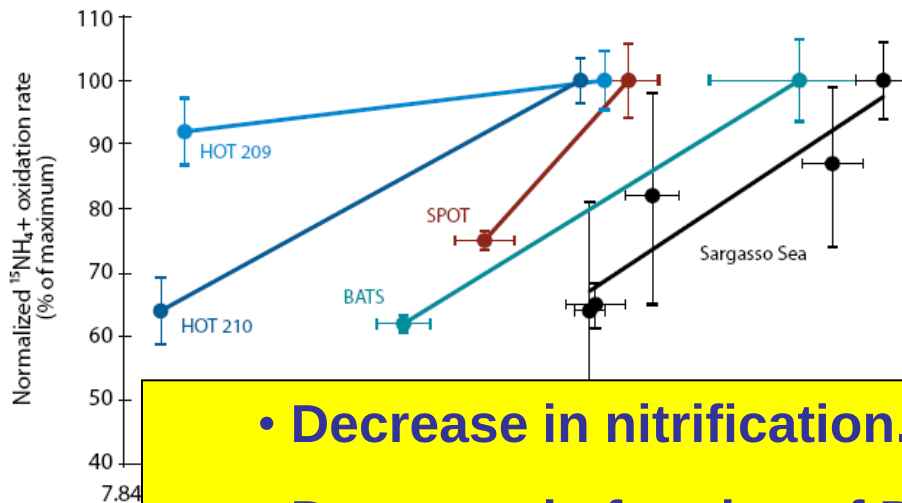
Impact

Negative

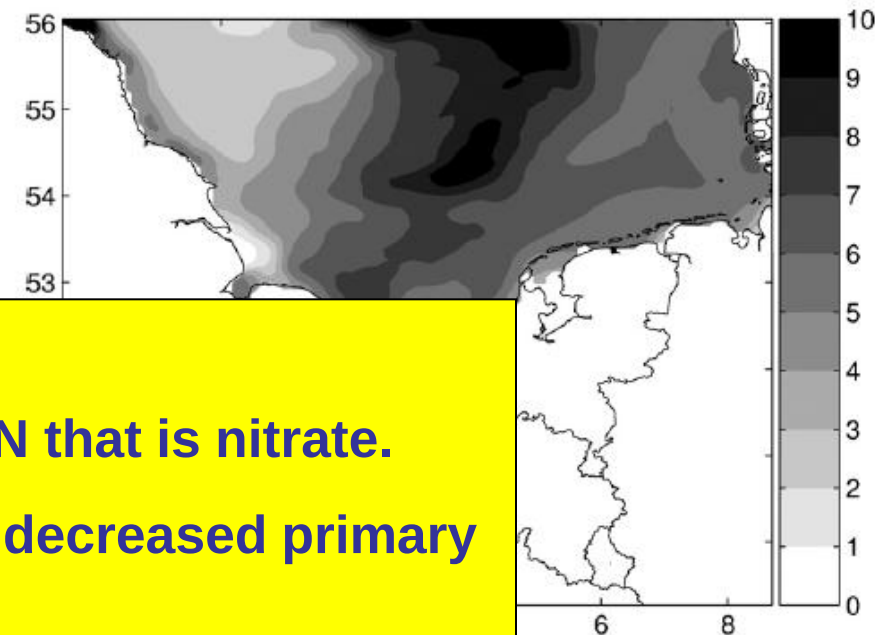
Range

Decrease 10-40%

Nitrification



% Change in NO_3^- : DIN ratio (Δ 385 & 1000 ppm CO_2) based on Husemann et al. 2002.



- Decrease in nitrification.
- Decrease in fraction of DIN that is nitrate.
- Positive feed back due to decreased primary production

Blackford & Gilbert 2007

(2c) Denitrification

Number of studies

3

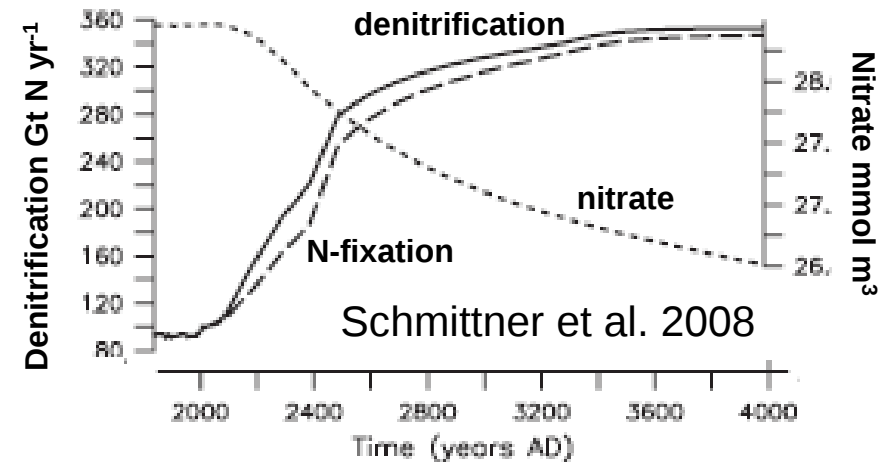
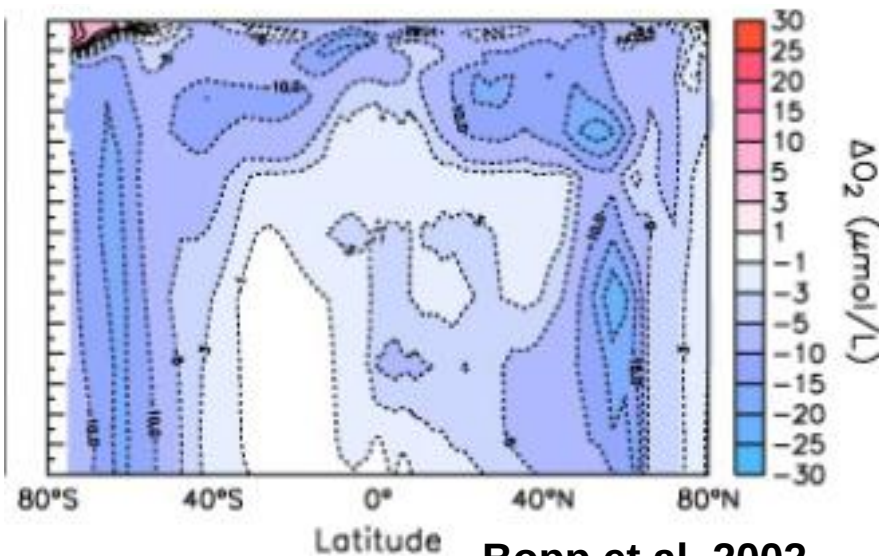
Impact

Increase

Range

quadruple

Δ dissolved of dissolved O_2 between
2080-2100 and 1980-2000



(2c) Denitrification

Number of studies

3

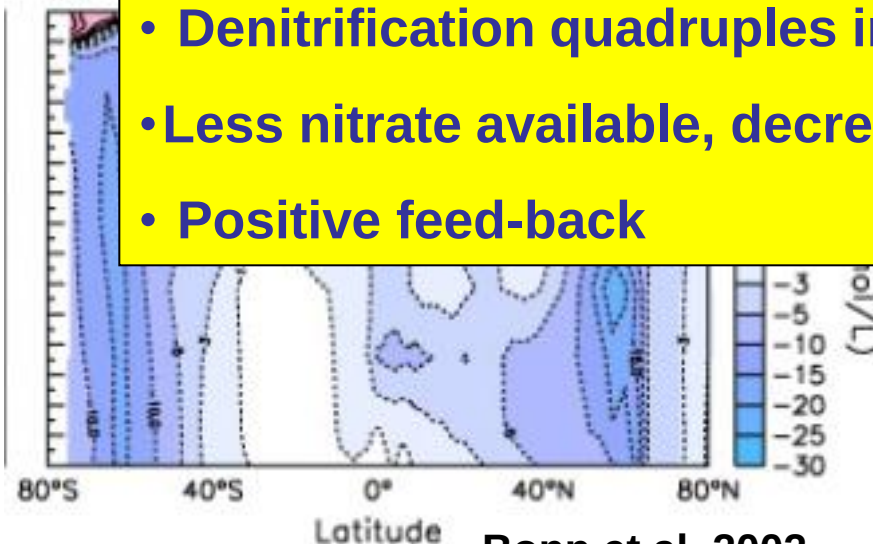
Impact

Increase

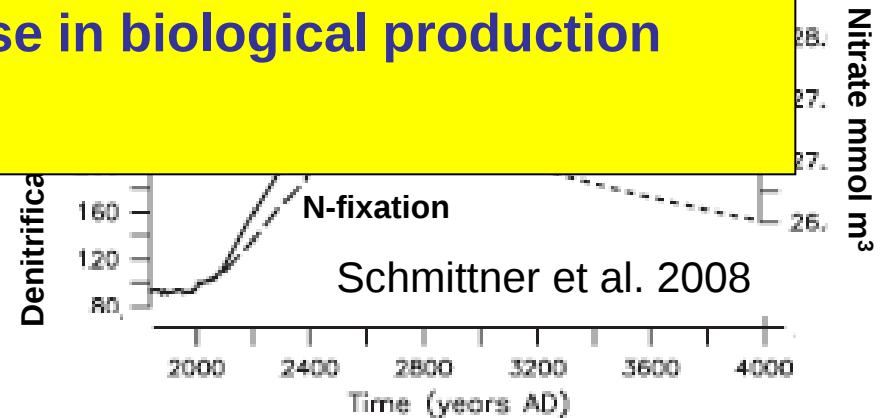
Range

quadruple

- Any OA effect?
- Stratification increases & shallower remineralization
- Suboxic zones in the ocean increase
- Denitrification quadruples in next 2000 years
- Less nitrate available, decrease in biological production
- Positive feed-back

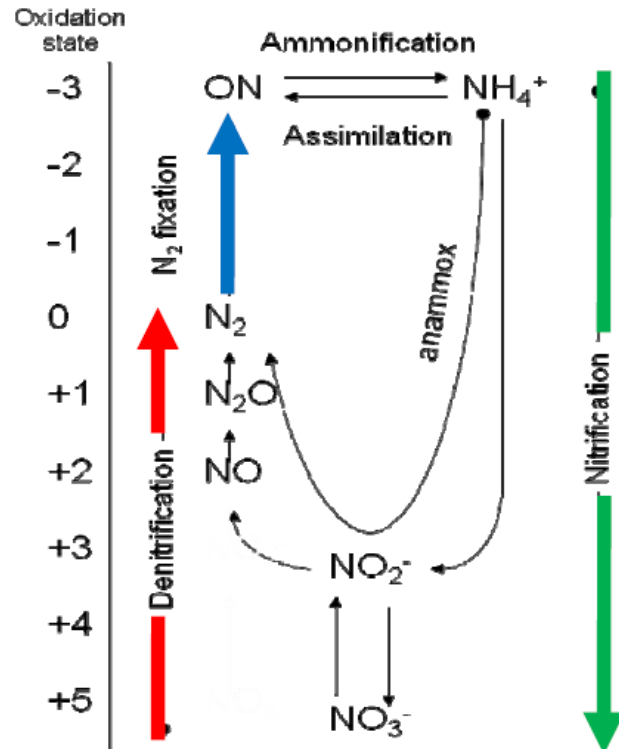


Bopp et al. 2002

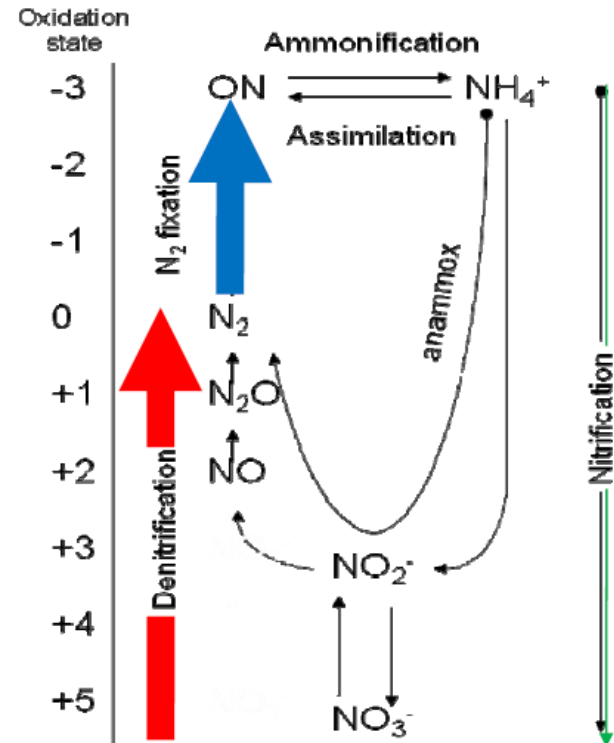


(2) Nitrogen Cycle

Today



Year 2100



Hutchins

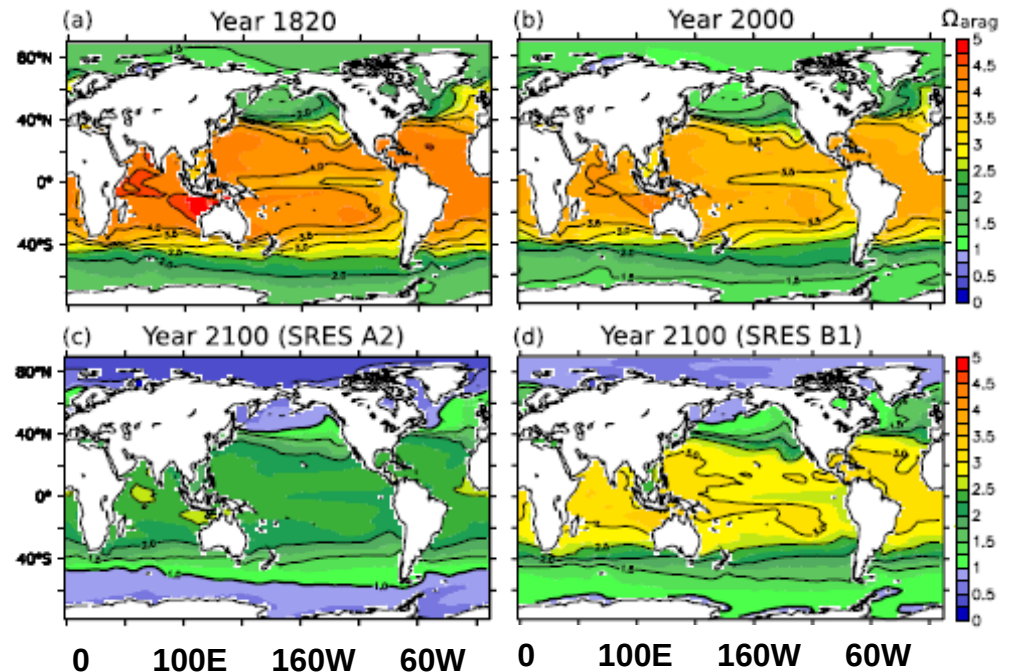
Decrease in fraction of inorganic N that is nitrate

(3a) CaCO₃: Saturation Horizon

Number of studies	Impact	Range
> 6	Decrease of Saturation	Decrease



- Aragonite and Calcite saturation is decreasing rapidly.
- Saturation is spatially variable with low values in the high latitudes



Steinmacher et al. 2009

(3b) (Bio-)Calcification: Coccolithophores & Foraminifera

Number of studies

15 cocco & 5 Forams

Impact

Inconsistent

Range

Increase 100%

Globally 27%

Decrease 25-66%

Doney et al. 2008

Physiological response

Major group

Species studied

Response to increasing CO₂

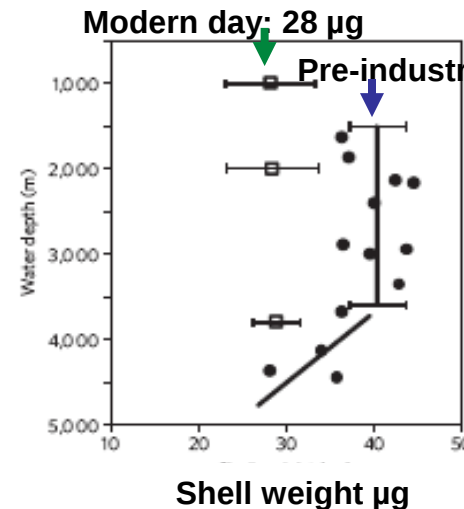


Calcification		Species studied				
	Coccolithophores ¹	4	2	1	1	1
	Planktonic Foraminifera	2	2	–	–	–

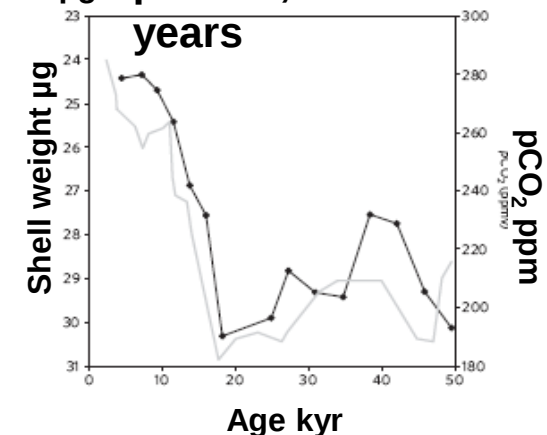
Globigerina bulloides (no algae symbionts)

Irie et al 2010: Optimality-model predicts that natural selection will favor heavy calcification if calcification is a defensive strategy and photosynthesis is enhanced.

Weights of shells 355-425 µm



Shell weights track pCO₂ over past 50,000 years



Moy et al 2009

(3b) (Bio-)Calcification: Coccolithophores & Foraminifera

Number of studies

Impact

Range

Doney et al. 2008

Physiological
res

Species

Response to increasing CO₂

a

b

c

d

Increase 100%
Globally 27%

- Calcification response of Coccolithophores varies (even within one strain)
- Calcification of Foraminifera often decreases with OA, but proxy validation controversially discussed
- Growth conditions (function of a suite of parameters) strongly determine calcification
- CaCO₃ production decrease from 1 Pg C yr⁻¹ to 0.36 – 0.82 Pg C yr⁻¹ by 2100 (Gangsto et al 2011).
- Such a global decrease means a small negative feed back on atm. pCO₂ of -1 to -11 ppm.

Shell weight µg

Age kyr

Moy et al 2009

(3c) CaCO_3 Dissolution

Number of studies

1 (pteropod)

5 carbonate compensation

Impact

Positive

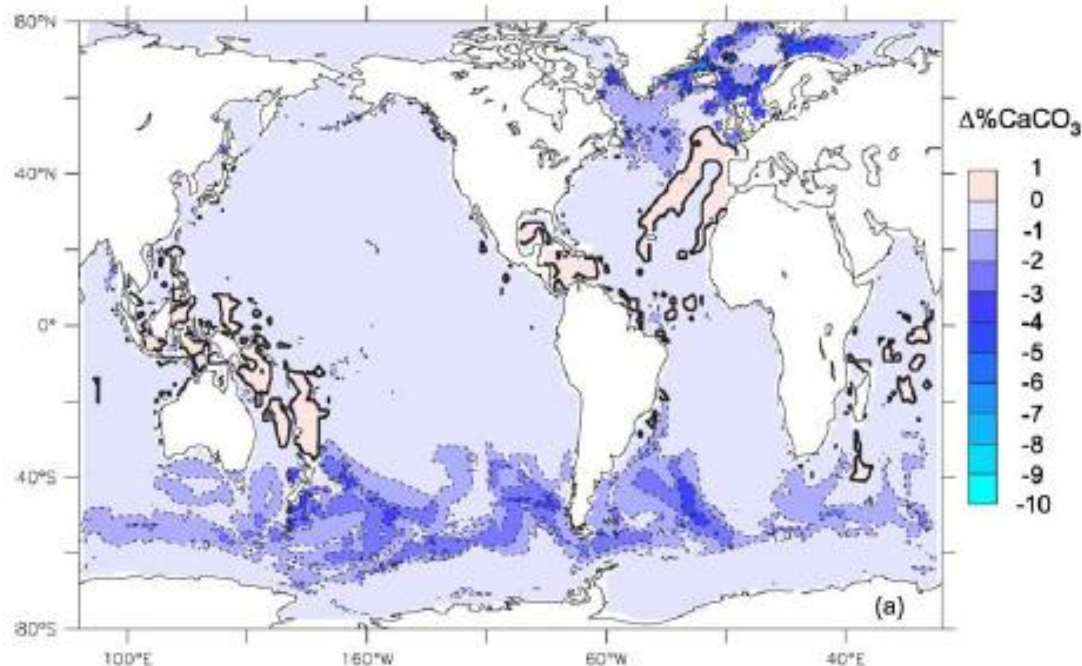
Positive

Range

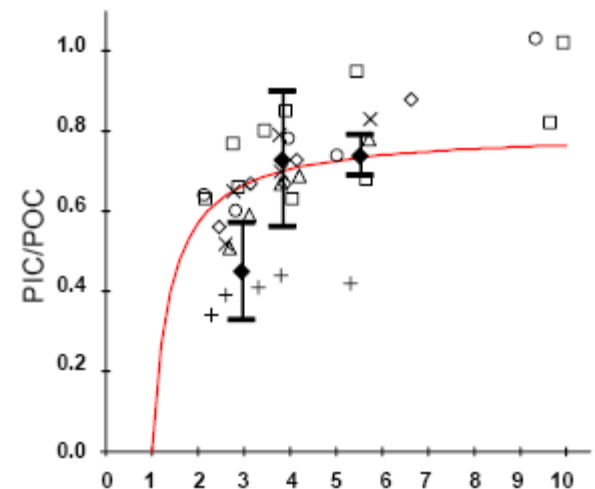
Increase

Increase (geological time scales) globally 11 %

Global CaCO_3 Dissolution:
% ΔCaCO_3 286 ppm to 1144 ppm in 140 years



Change in the rain ratio of sinking carbon



Gehlen et al. 2007 Ω_c

Gehlen & Bopp 2008

(3c) CaCO_3 Dissolution

Number of studies	Impact	Range
1 (pteropod)	Positive	Increase
5 carbonate compensation	Positive	Increase (geological time scales) globally 11 %

- Decrease in calcification & increase in production of POM potentially results in an increase in rain ratio (POC: PIC) in exported material
- Increased rain ratio → promotes dissolution, timescales of 1000-10,000 years).
- However, less ballasting might reduce sedimentation of POC not leading to an increased rain ratio
- Carbonate compensation: Dissolution of CaCO_3 in sediments have a buffer capacity for the deep ocean on geological time scales. Negative feed back!

100°E

160°W

80°W

40°E

(4) DMS, DMSP Production

Number of studies

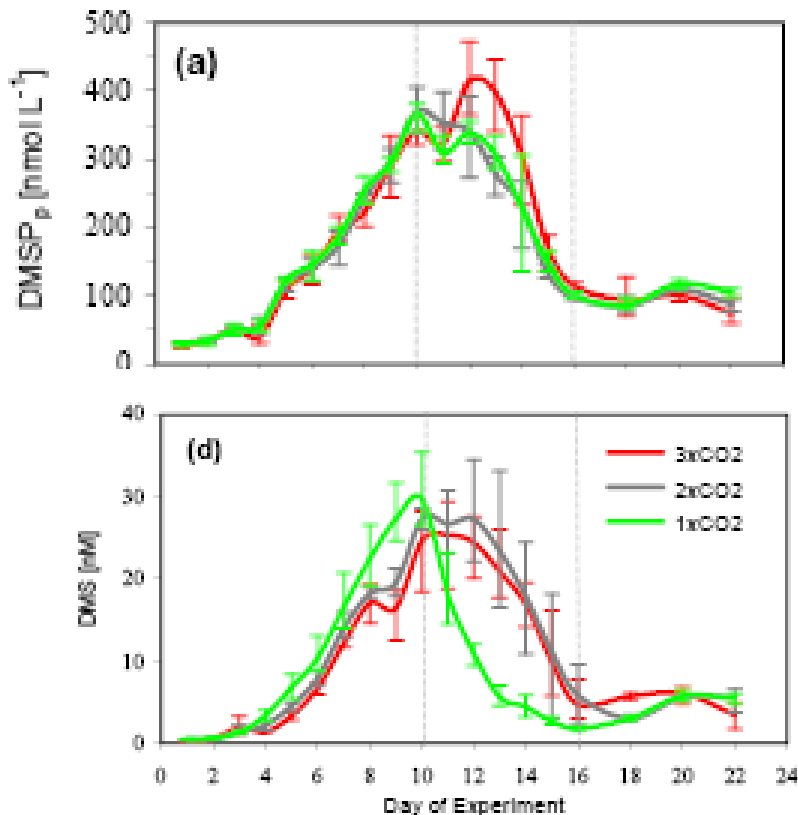
3

Impact

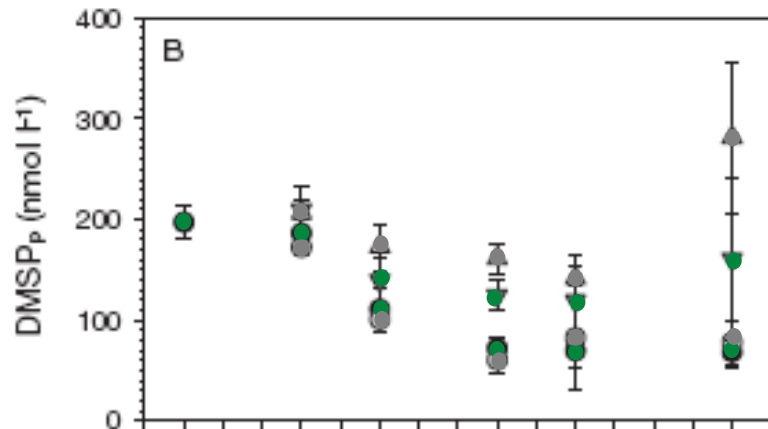
Inconsistent

Range

No change



Vogt et al 2008



Lee et al. 2009

(4) DMS, DMSP Production

Number of studies

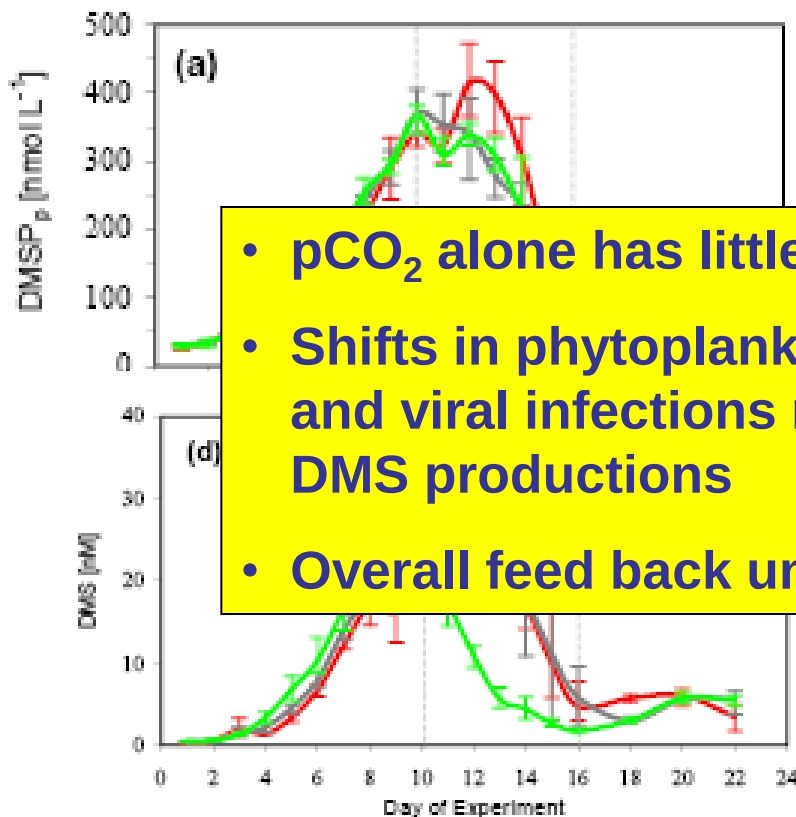
3

Impact

Inconsistent

Range

No change



- pCO₂ alone has little effect on DMSP
- Shifts in phytoplankton species composition, grazing and viral infections may indirectly change DMSP & DMS productions
- Overall feed back unclear

Vogt et al 2008

(5a) Phytoplankton Species Composition

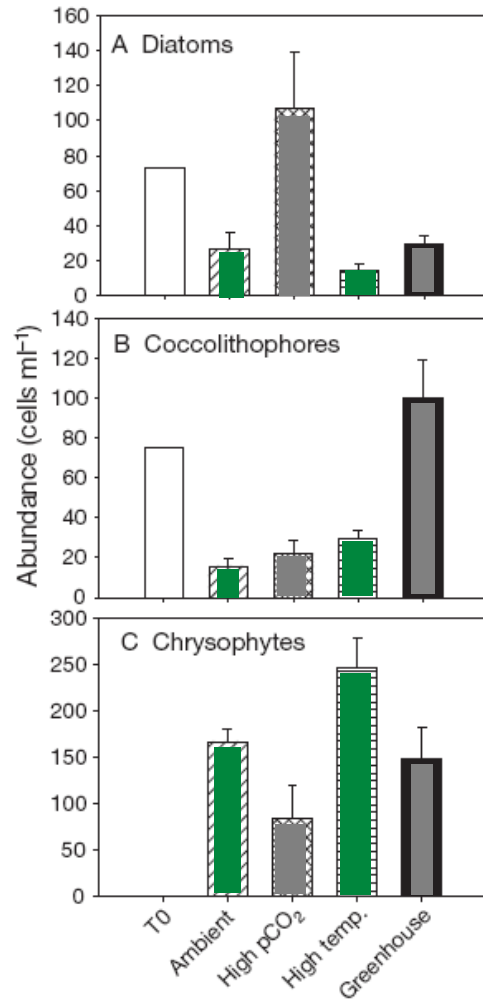
Number of studies

Shift

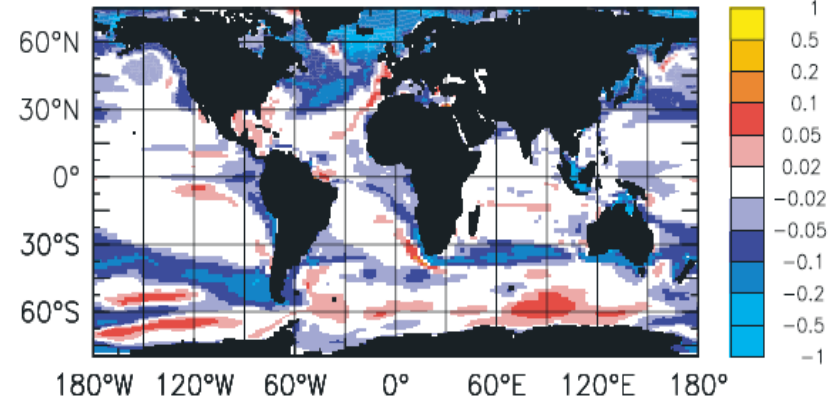
Feng et al. 2009

10

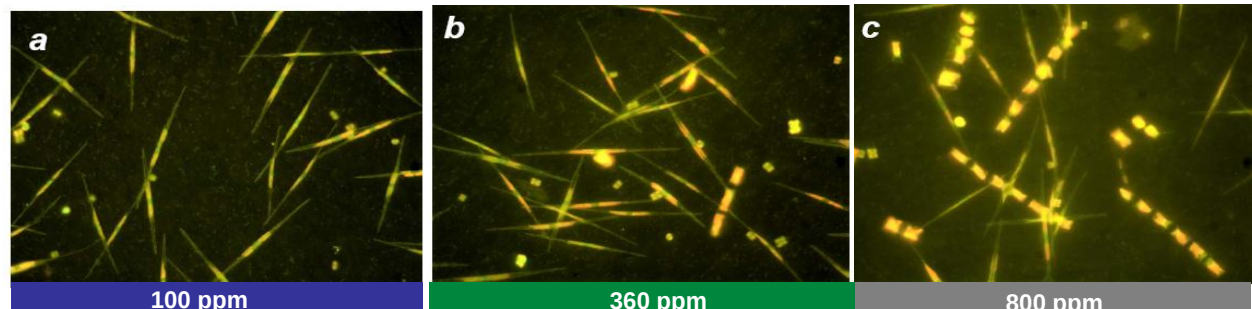
Within groups or between groups



Change in diatom abundance 4xCO₂-1CO₂



Bopp et al. 2005



Tortell et al. 2008

(5a) Phytoplankton Species Composition

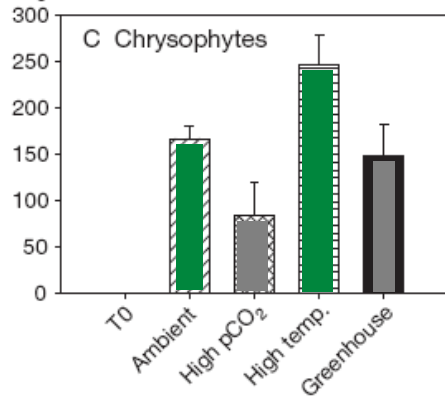
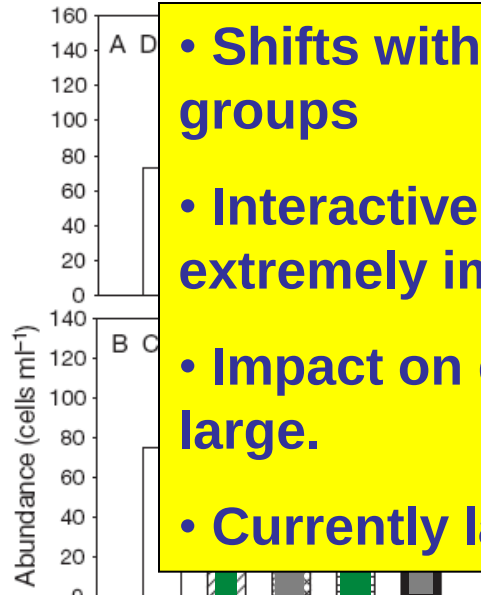
Number of studies

Shift

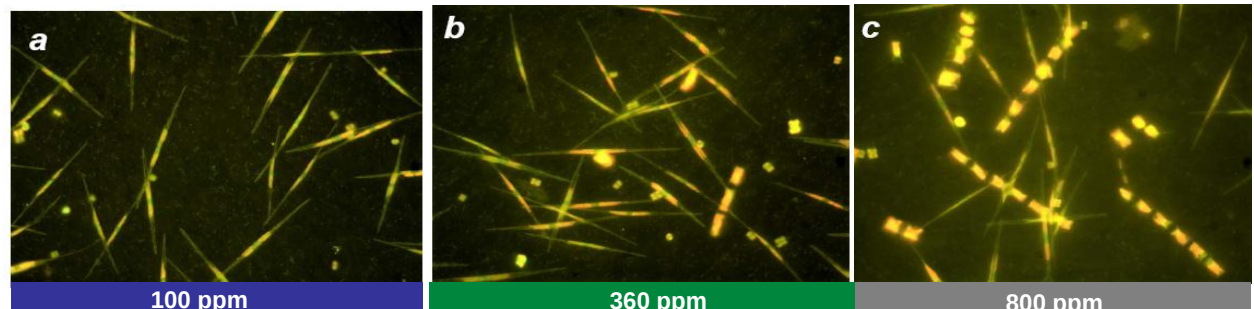
Feng et al. 2009

Within groups or between groups

- Shifts within functional or taxonomic groups and between groups
- Interactive effects with other environmental parameters extremely important. High variability in results
- Impact on export, biogeochemical cycling, stoichiometry large.
- Currently large uncertainty



Bopp et al. 2005



Tortell et al. 2008

(5b) Genetic Acclimation & Adaptation

Number of studies

2 >150 generations

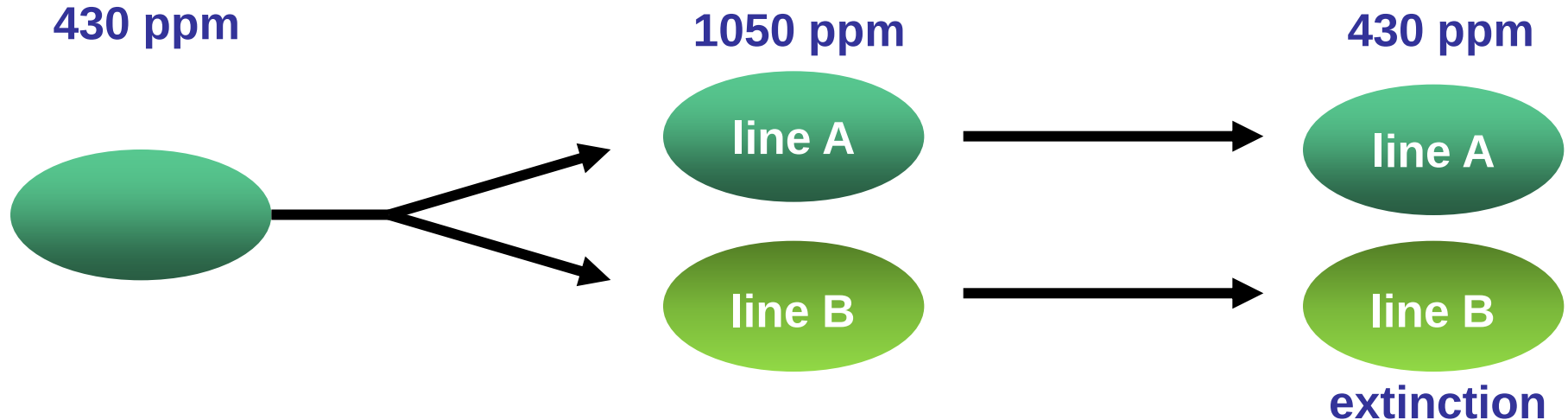
Acclimatisation vs. Adaptation

No difference, loss of flexibility

Stress response: immediate

Acclimatization: (gene expression) 8 - 10 generations

Adaptation: (genetic change) 200 - 1000 generations



(5b) Genetic Acclimation & Adaptation

Number of studies

Acclimatisation vs. Adaptation

2 >150 generations

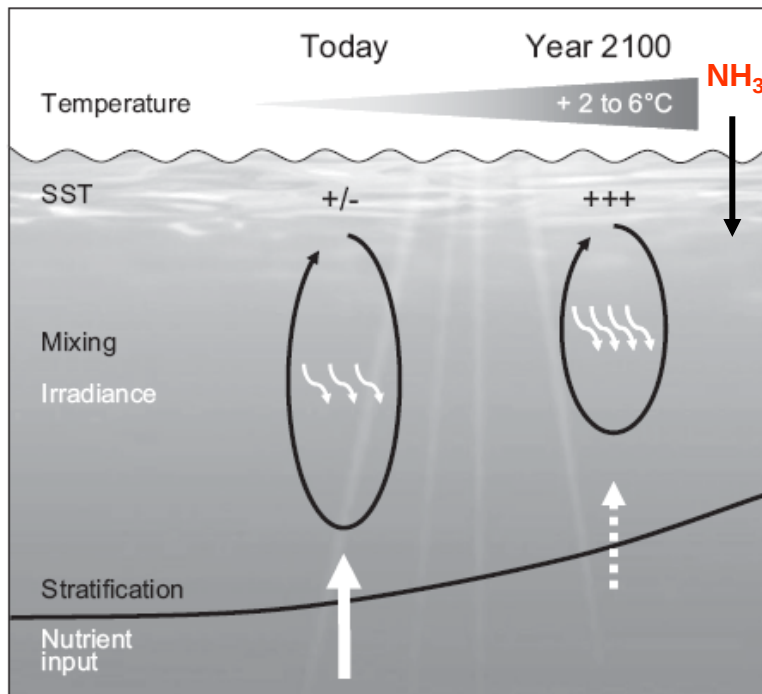
No difference, loss of flexibility

Stress response: immediate

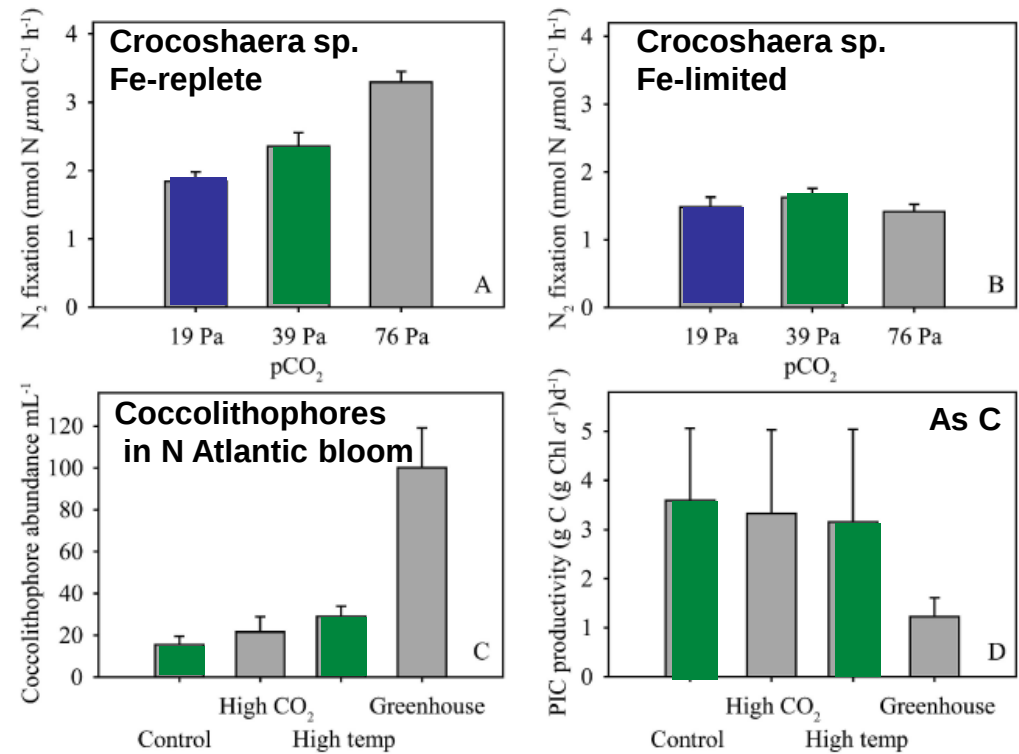
- Green algae *Chlamydomonas* 1000 generations. Some lines did not grow in lower pCO₂ conditions - neutral mutation of CCM making it less efficient - Collins & Bell (2004):
- Similar experiments underway
- Indications from paleo-record of coccolithophores suggest some adaptation
- Evolutionary models
- Impact unknown

Bottom - up Controls of Primary Producers

Synergistic & Antagonistic Interactions between CO₂, temperature, light, nutrients, trace metals



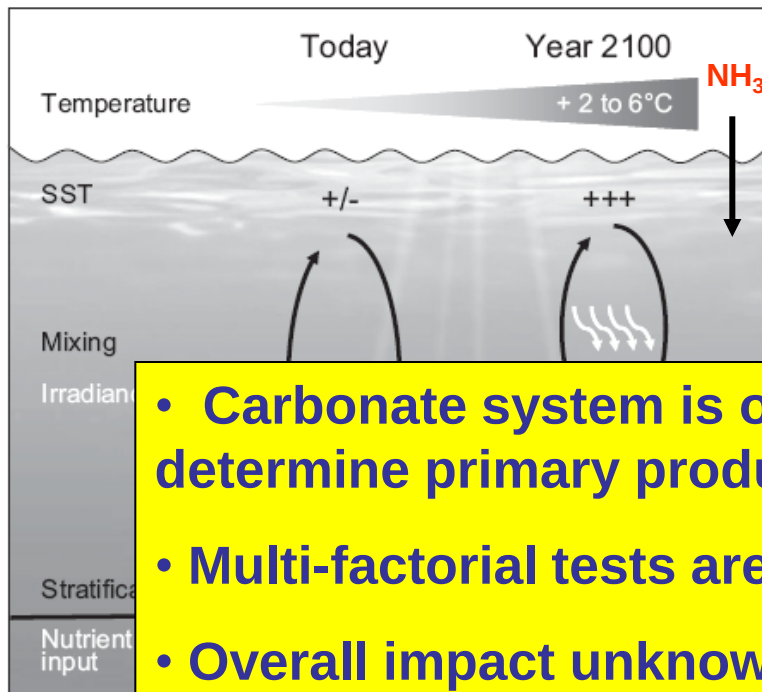
Rost et al. 2008



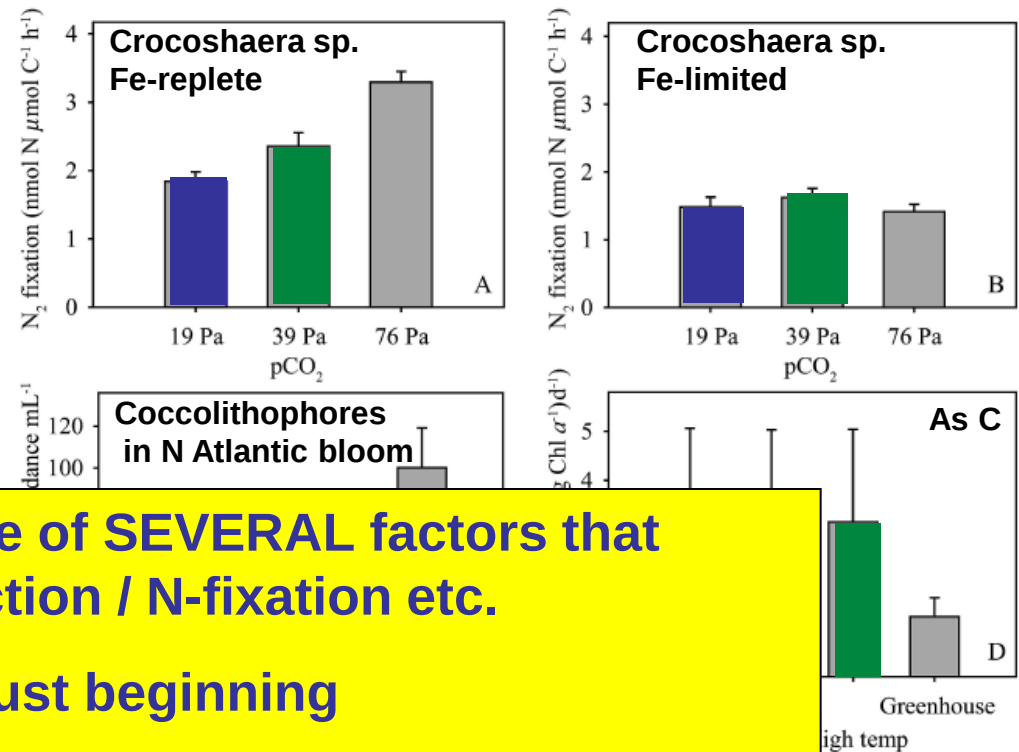
Boyd et al. 2010

Wyatt et al 2010: surface layer NH₄⁺ ↔ NH₃ OA

Bottom - up Controls of Primary Producers

Synergistic & Antagonistic Interactions between CO₂, temperature, light, nutrients, trace metals

Rost et al. 2008



d et al. 2010

Wyatt et al 2010: surface layer NH₄⁺ ↔ NH₃ + H⁺

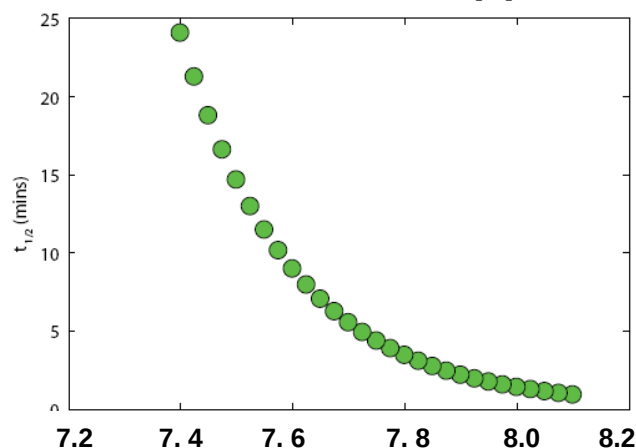
(6) Organic Matter & Trace element cycling

Number of studies

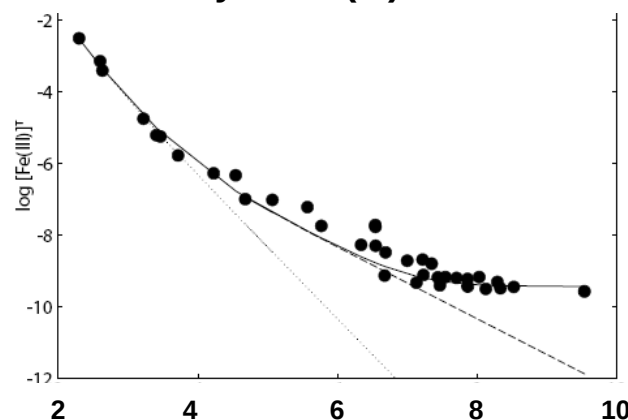
Impact

Range

Half live of Fe (II)

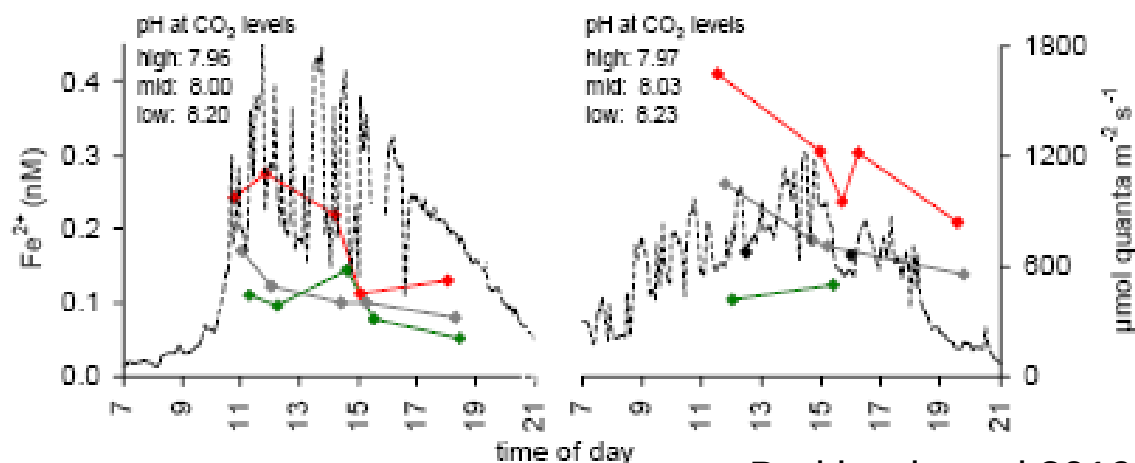


Solubility of Fe (III) in seawater



Millero et al. 2010

Fe²⁺ & PAR days 20 & 22 of PeECE III



Breitbarth et al 2010

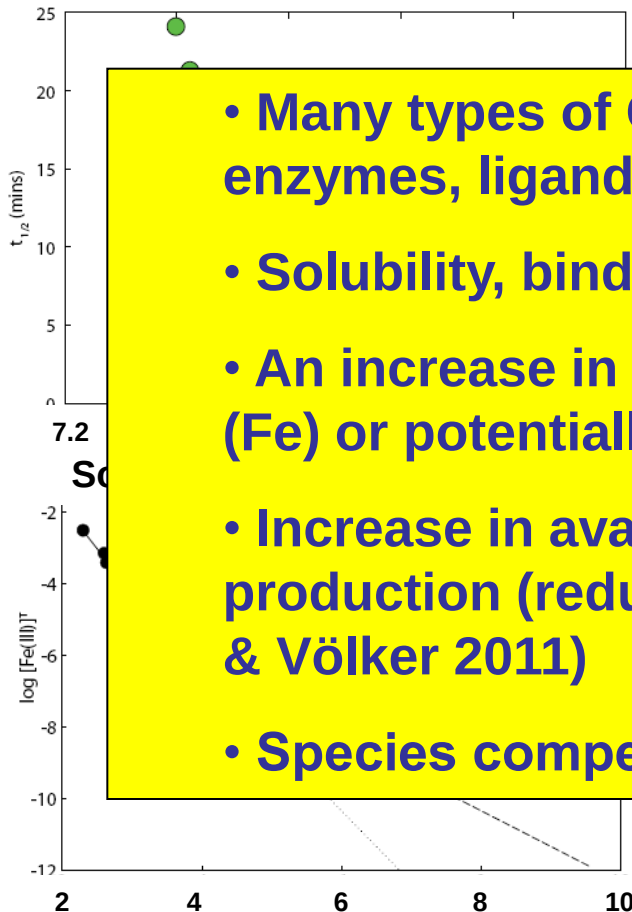
(6) Organic Matter & Trace element cycling

Number of studies

Impact

Range

Half live of Fe (II)



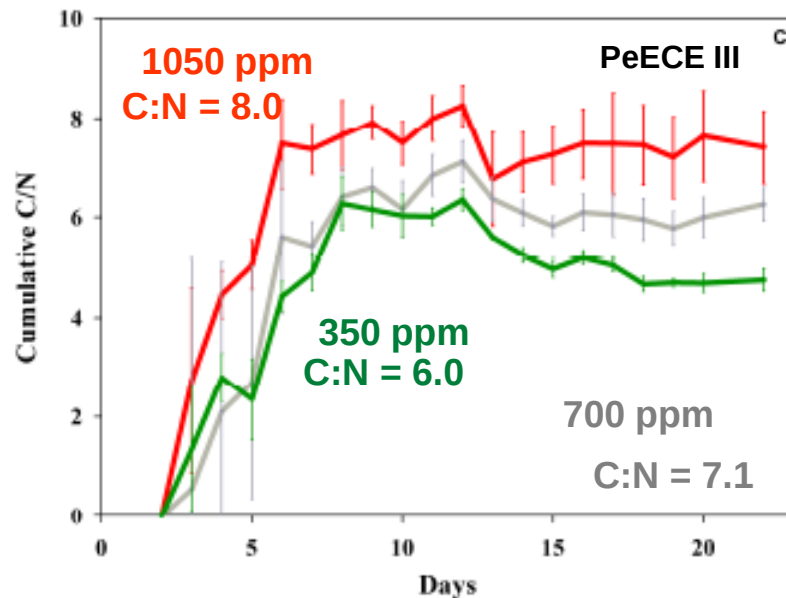
- Many types of OM are sensitive to pH (trace metals, enzymes, ligands, siderophores,)
- Solubility, binding & complexation depends on pH
- An increase in availability of trace metals may be profitable (Fe) or potentially toxic (Cu)
- Increase in availability of iron may increase primary production (reduction of Fe-limited area by 20%; Tagliabue & Völker 2011)
- Species competition may change → shift in composition

$\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$

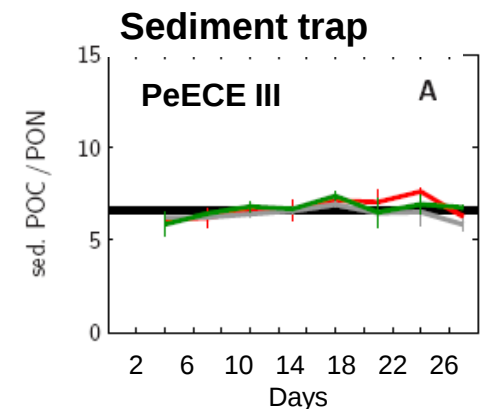
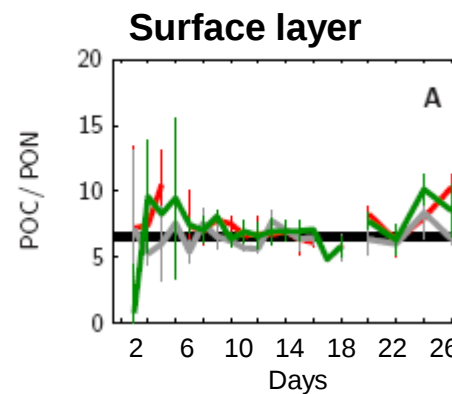
10

(7) Stoichiometry of organic matter

Number of studies	Impact	Direction
13	Positive C:Nutrient	Increase
5	Negative C:Nutrient	Decrease
4	Positive N:P	Increase
Uptake Ratio 5	Negative N:P	Decrease



Bellerby et al (2008)

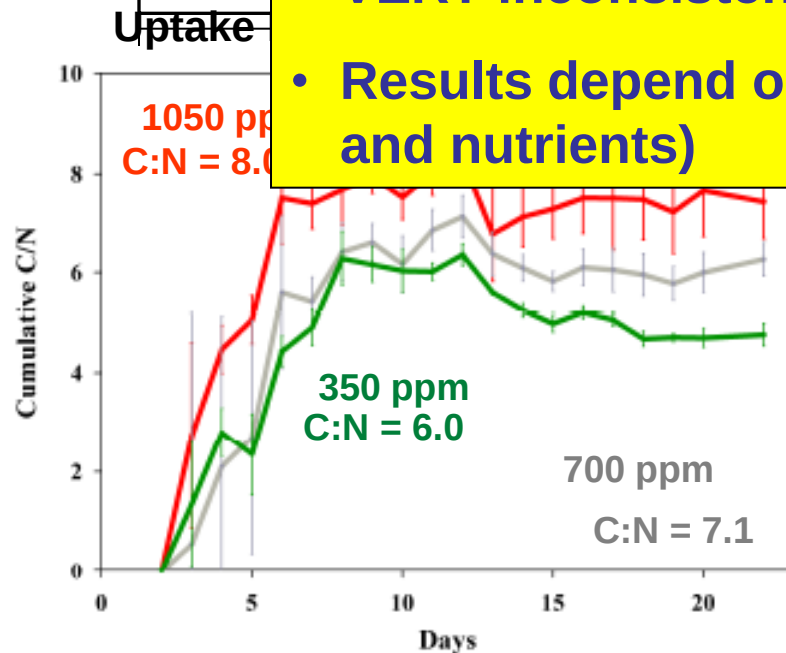


Schulz et al (2008)

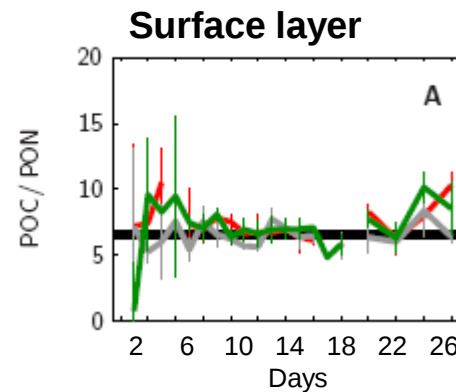
(7) Stoichiometry of organic matter

Number of studies	Impact	Direction
13	Positive C:Nutrient	Increase
5	Negative C:Nutrient	Decrease

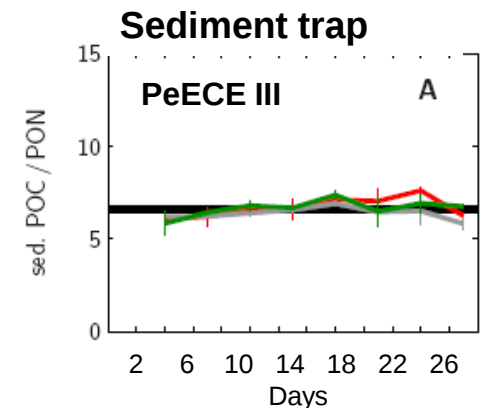
- Enhanced drawdown of CO₂ vs. N, but results VERY inconsistent
- Results depend on experimental conditions (light and nutrients)



Bellerby et al (2008)



Schulz et al (2008)



(8a) Microbial Loop: DOM Production

Number of studies

1 Viruses

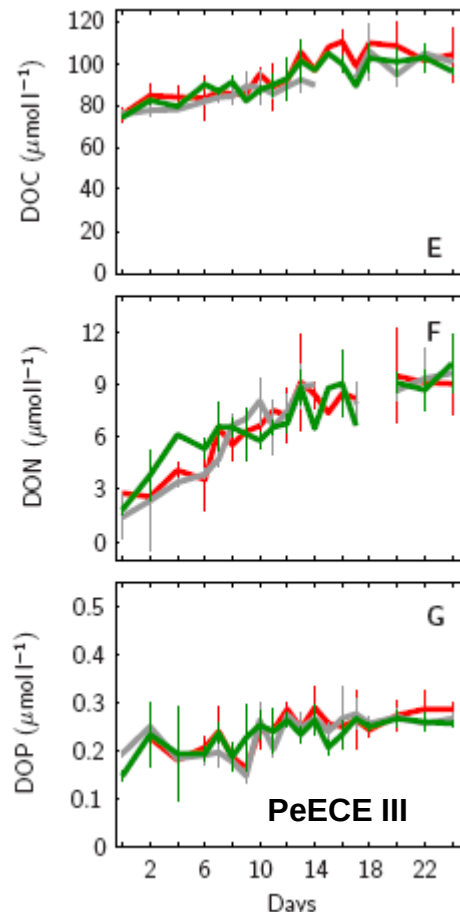
Impact

abundance & diversity

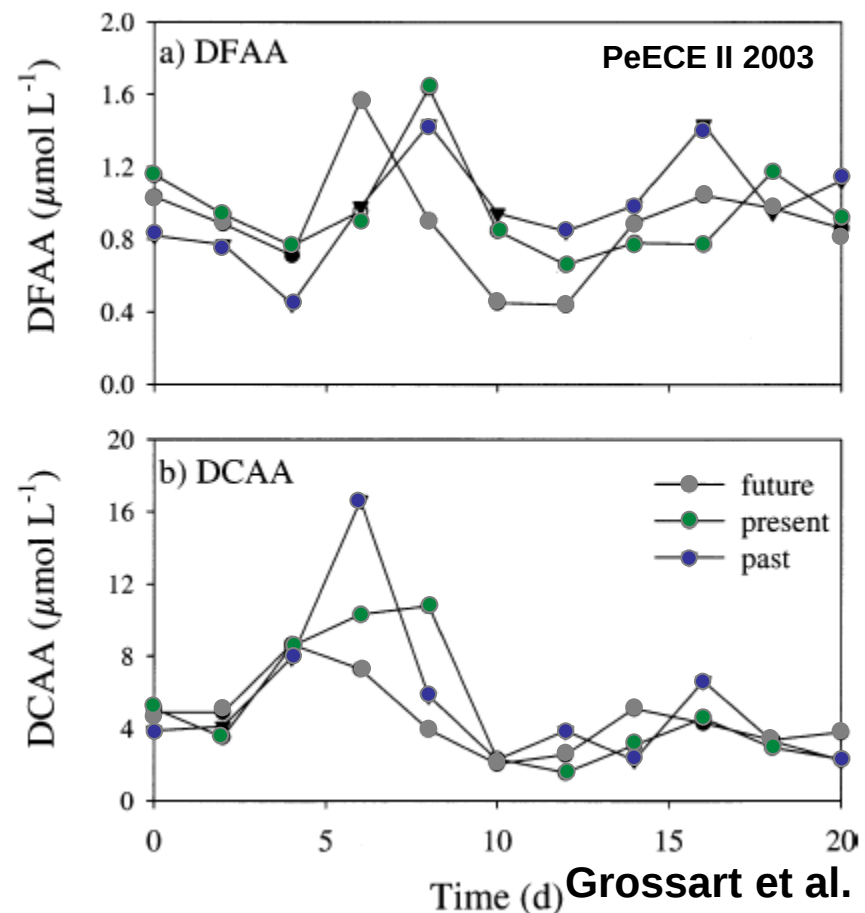
Range

Inconsistent

No change



Schulz et al 2008



Grossart et al. 2006

(8a) Microbial Loop: DOM Production

Number of studies

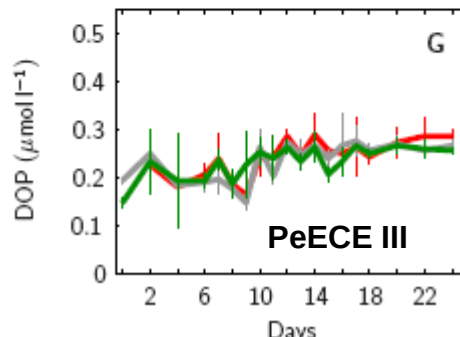
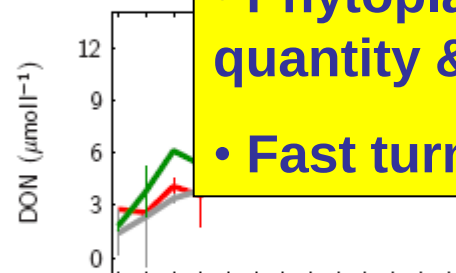
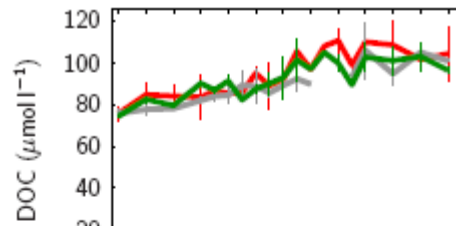
Impact

Range

1 Viruses

abundance & diversity

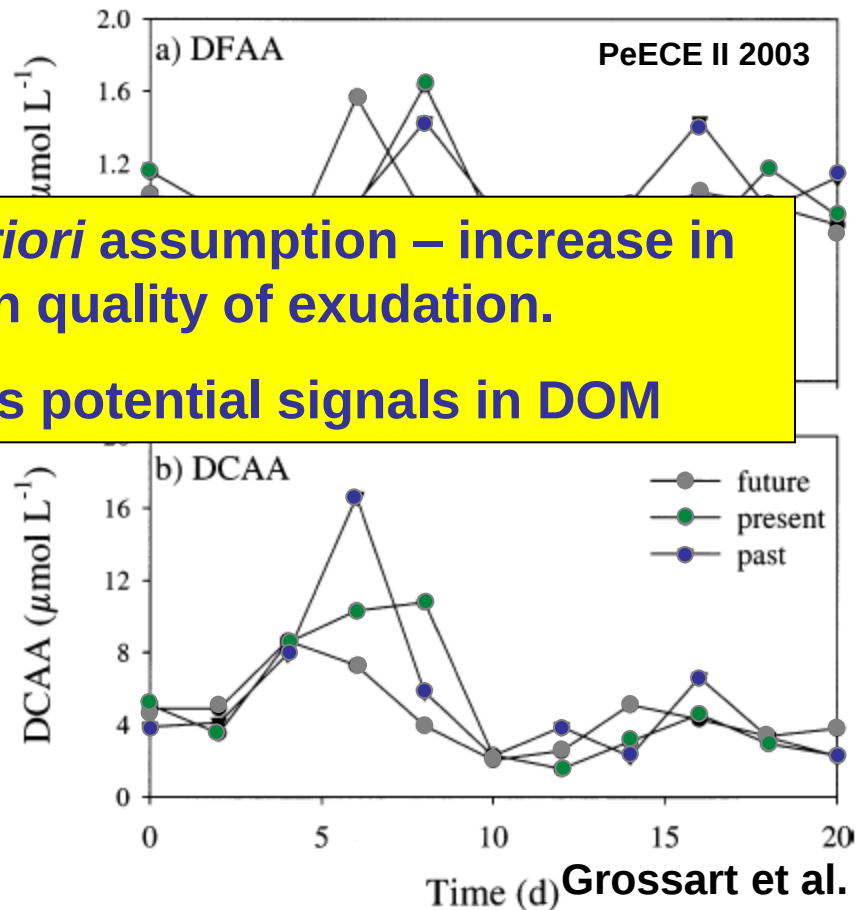
Inco



Schulz et al 2008

- Phytoplankton: *a priori* assumption – increase in quantity & decrease in quality of exudation.

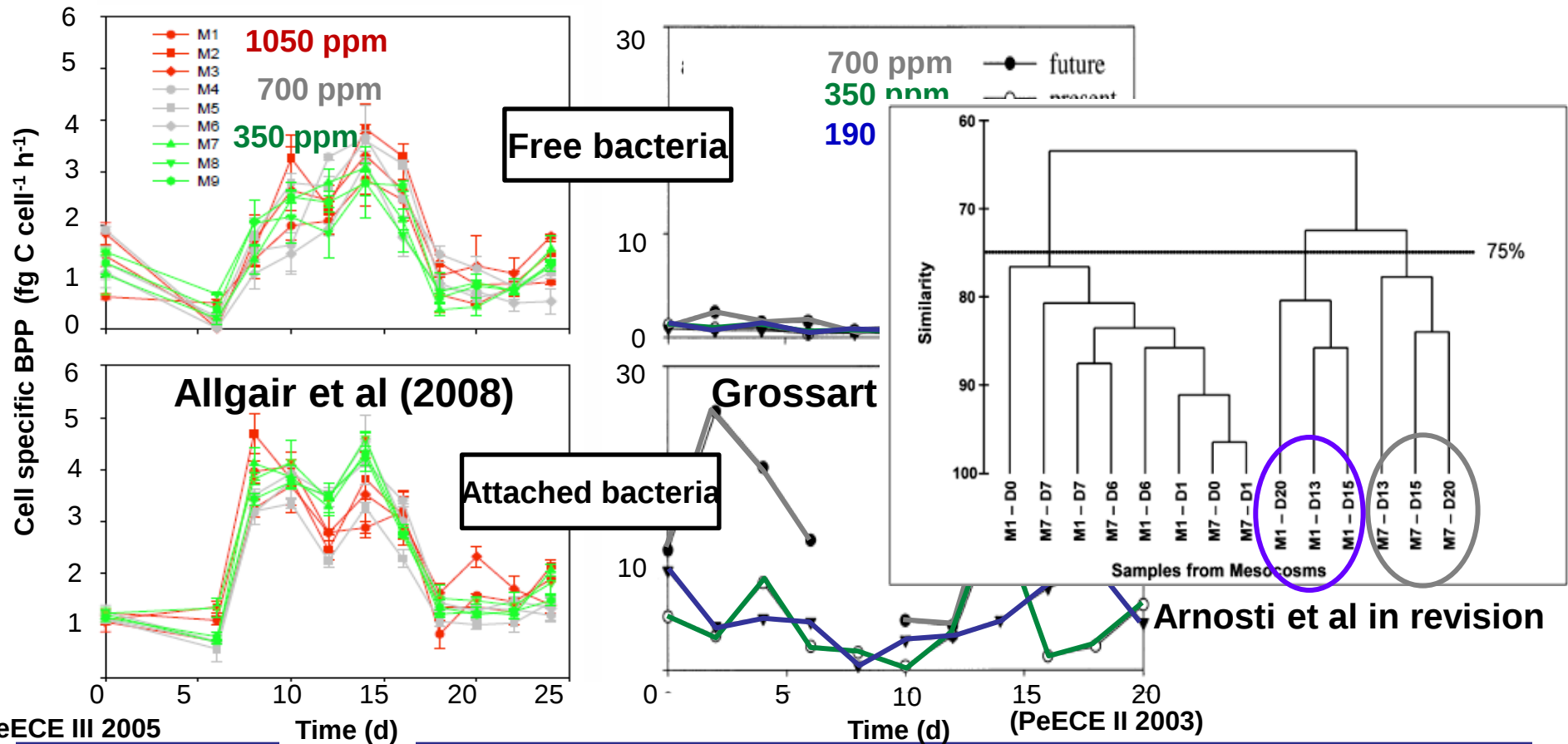
- Fast turn-over masks potential signals in DOM



Grossart et al. 2006

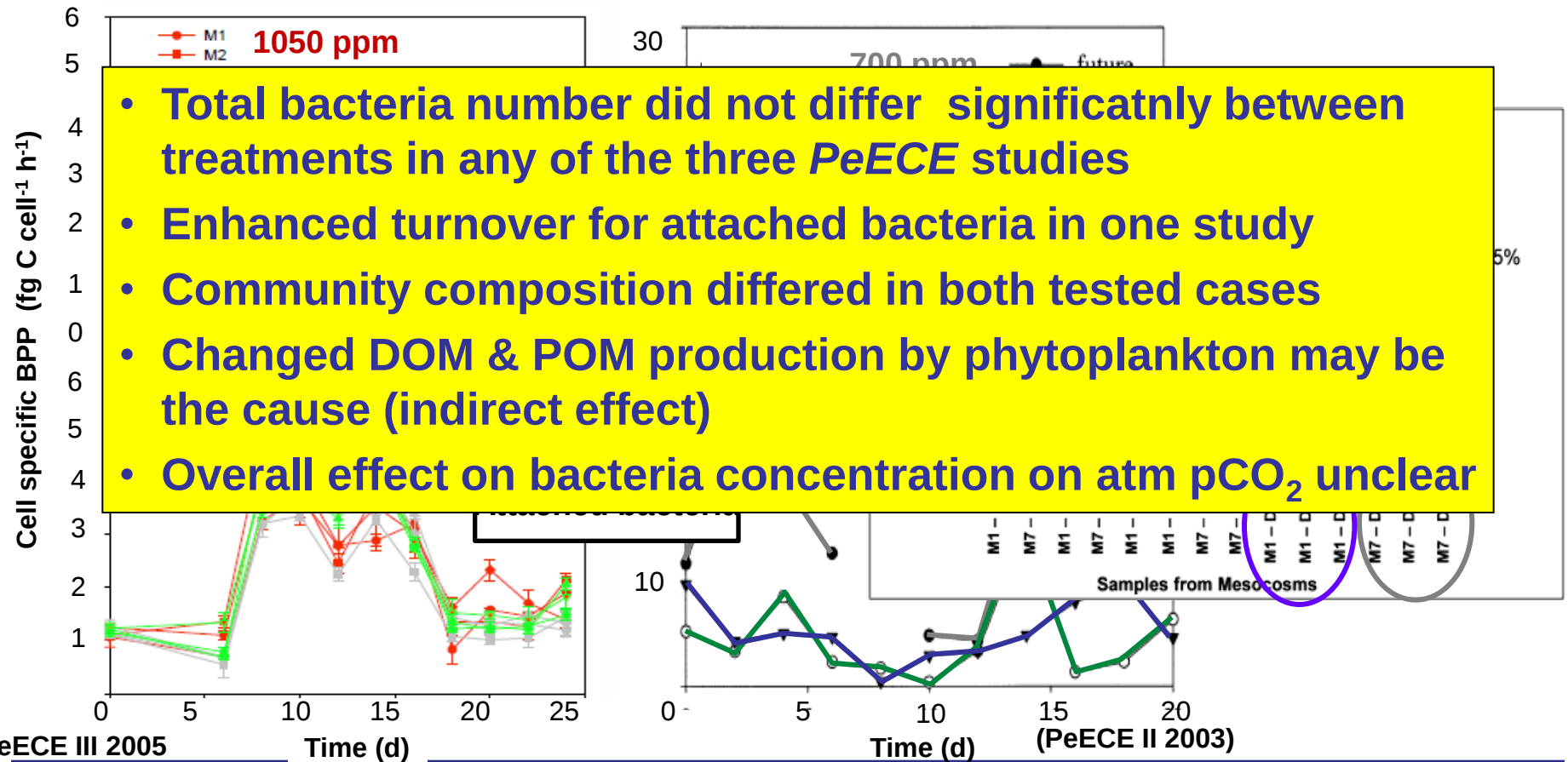
(8b) Microbial Loop: Bacterial Concentration, Turnover and Diversity

Number of studies	Impact	Range
4	Inconsistent	Increase 46% attached bac.



(8b) Microbial Loop: Bacterial Concentration, Turnover and Diversity

Number of studies	Impact	Range
4	Inconsistent	Increase 46% attached bac.



(8c) Microbial Loop: Bacterial Degradation of DOM

Number of studies

3

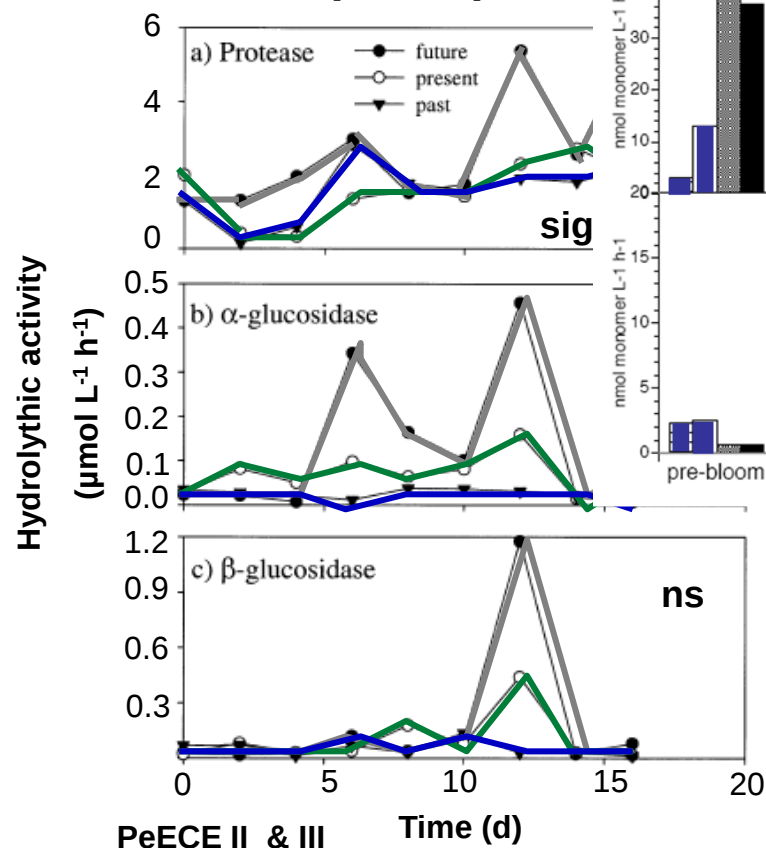
Impact

Positive/ None

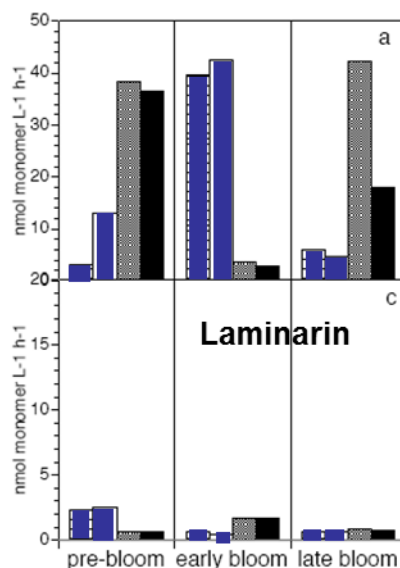
Range

Increase 50-83%

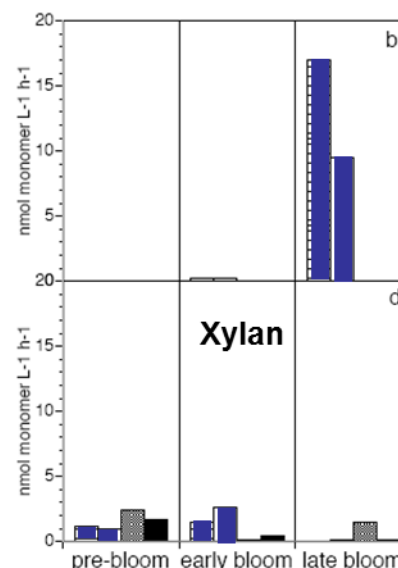
Grossart et al (2006a)



Chondroitin sulfate



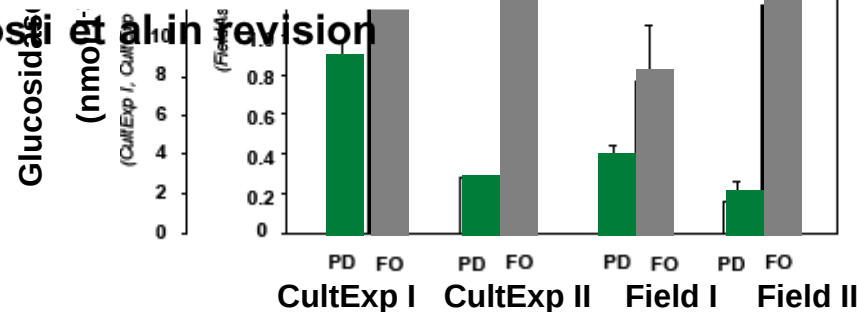
Fucoidan



Montek et al (2009)

Arnold et al in revision

700 ppm
350 ppm
190 ppm

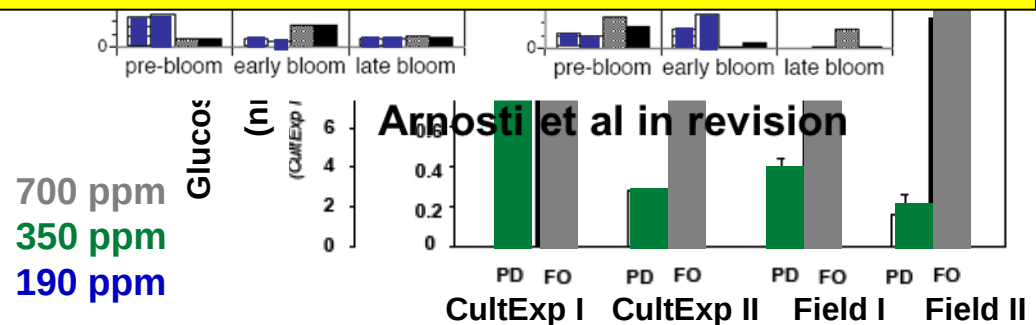
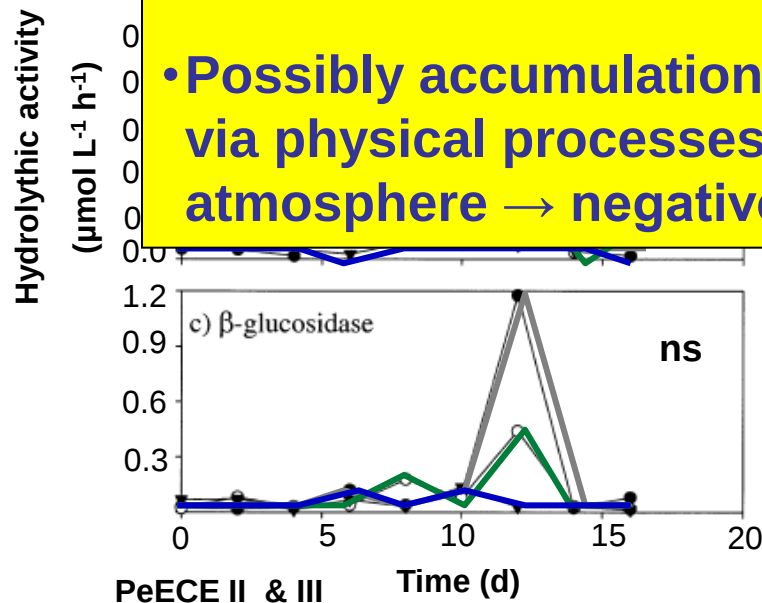


(8c) Microbial Loop: Bacterial Degradation of DOM

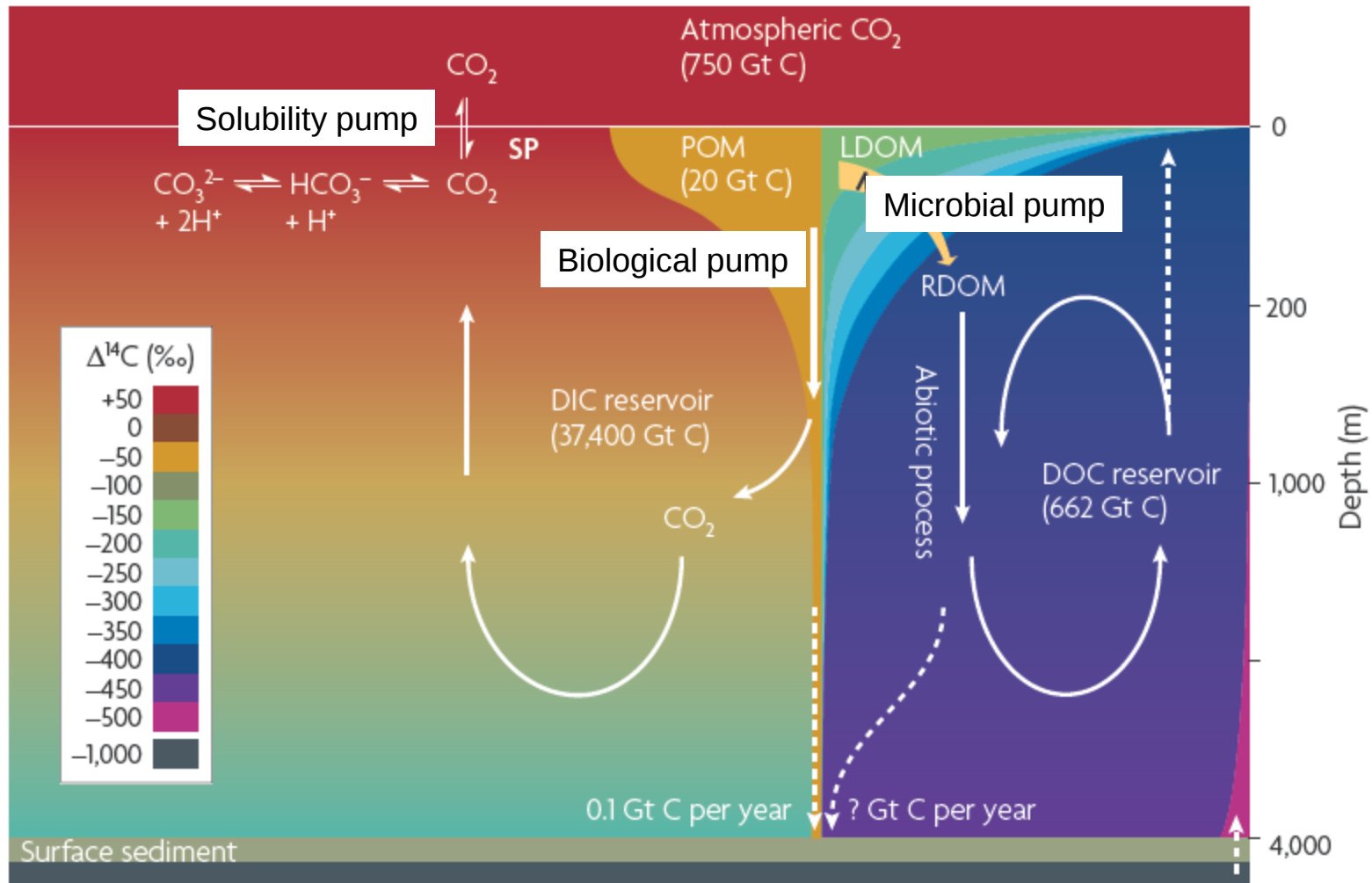
Number of studies	Impact	Range
3	Positive/ None	Increase 50-83%

Gross

- Dependant on DOM and mineral nutrients
- Some studies show enhanced degradation in upper water column others do not. Enhanced degradation of additionally fixed carbon would have no net effect on atm. pCO_2 .
- Possibly accumulation of DOM in surface ocean & subduction via physical processes removes additional CO_2 from the atmosphere → negative feed back

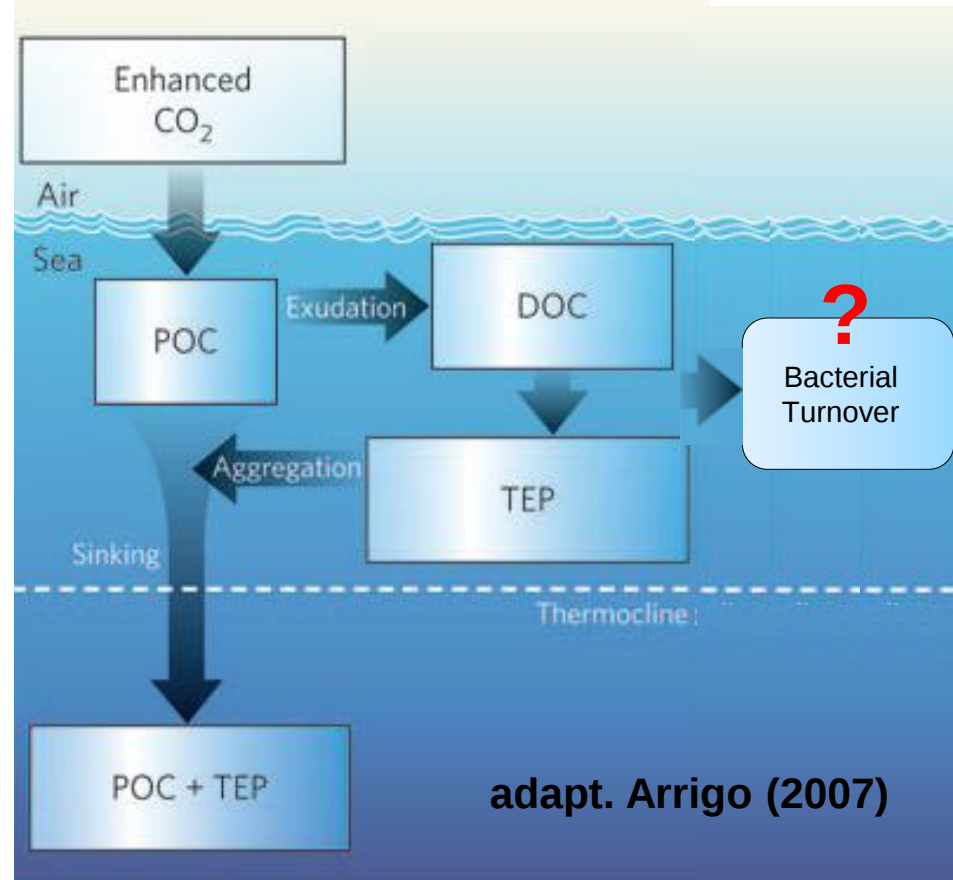
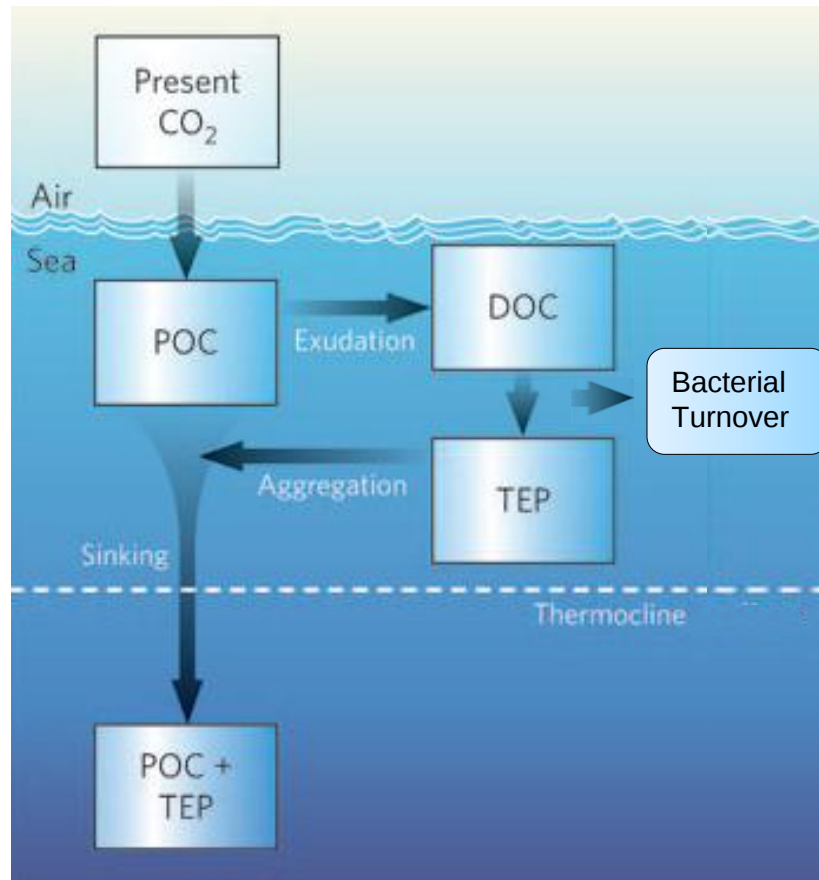


(8) Concept: Microbial Carbon Pump



Jiao et al. Nature Reviews Microbiology 2010

(9) Carbon Flux: Partitioning



(9) Aggregation and Transparent Exopolymer Particles, TEP

Number of studies

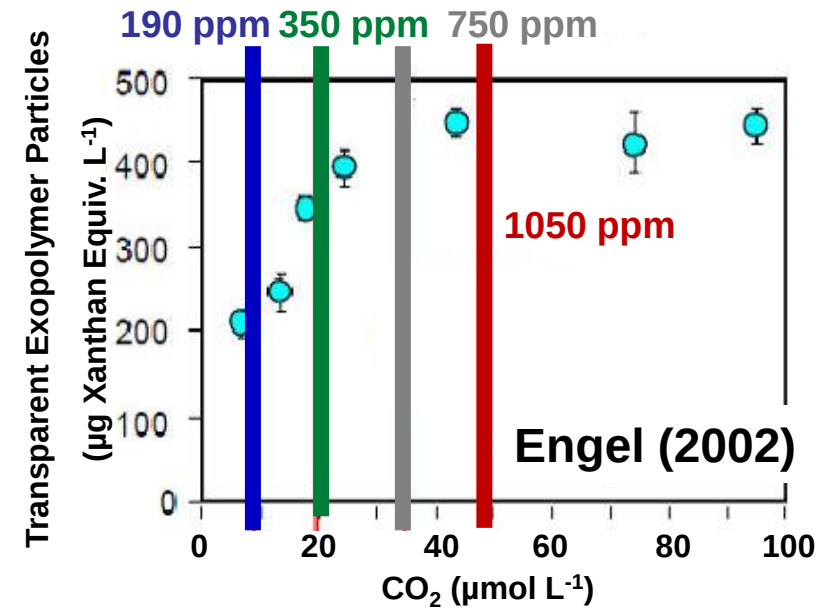
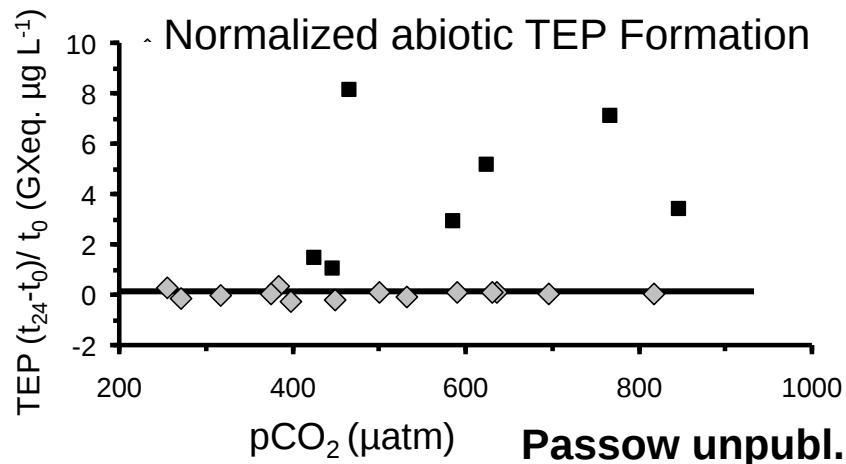
6 (3↑, 3→)

Impact

Inconsistent

Range

Increase 20%



(9) Aggregation and Transparent Exopolymer Particles, TEP

Number of studies

6 (3↑, 3→)

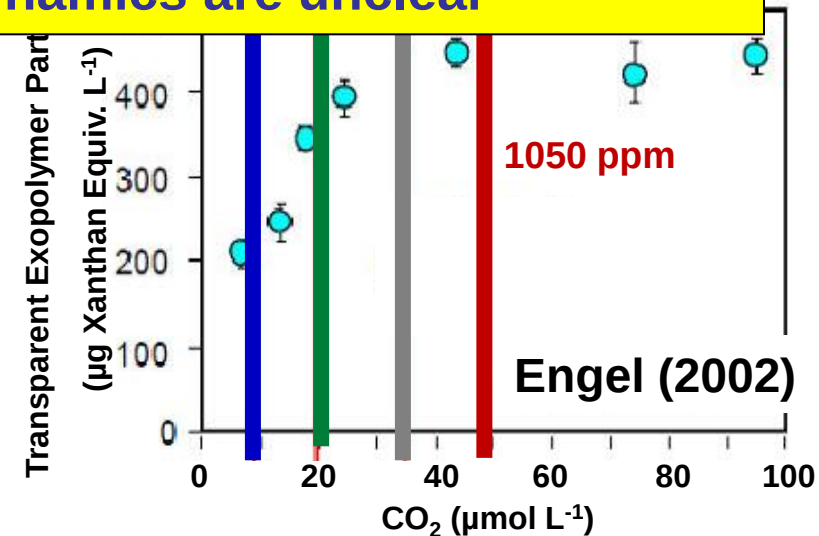
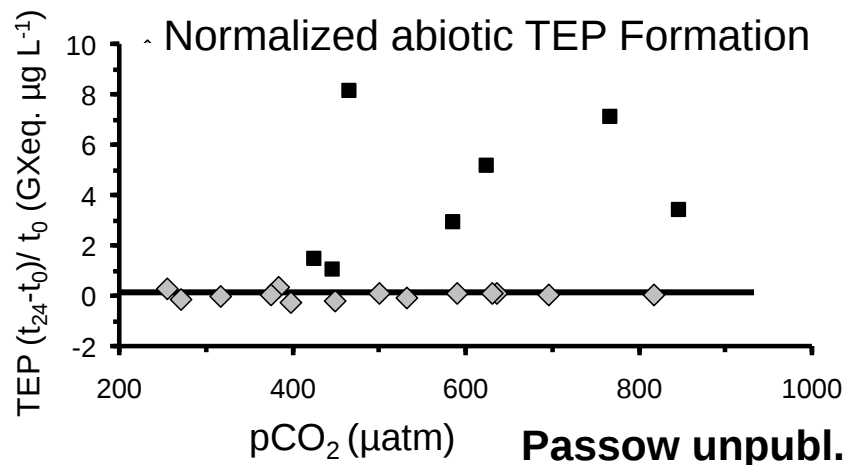
Impact

Inconsistent

Range

Increase 20%

- No change in abiotic TEP formation expected
- Possibly enhanced TEP formation due to increase in DOC exudation but not observed in PeECE II & III.
- Impact for aggregation or microbial dynamics are unclear



(9) Sinking velocity of aggregates

Number of studies

2

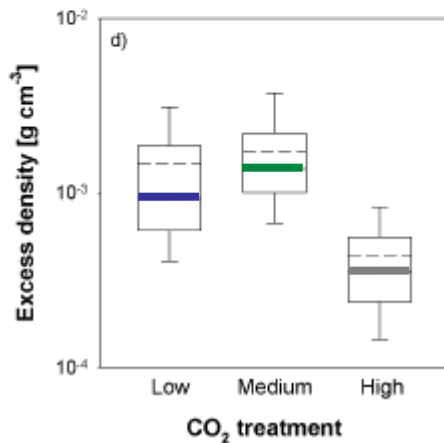
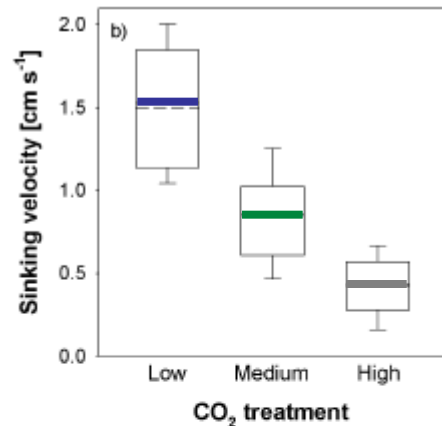
Impact

Decrease

Range

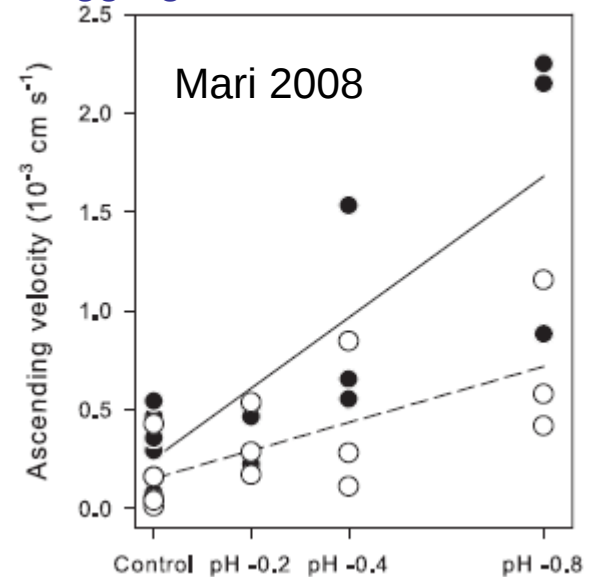
Decrease

Ballasting. Aggregates of *E. hux.*



TEP Fraction:

Aggregates of TEP & beads



Biermann & Engel 2010

(9) Sinking velocity of aggregates

Number of studies

2

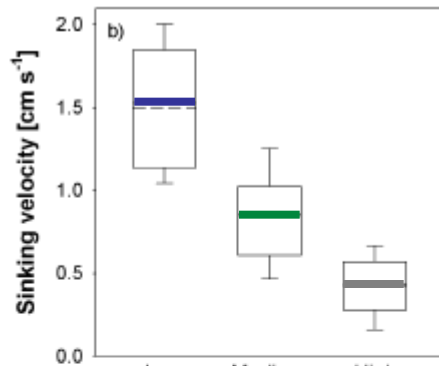
Ballasting. Aggregates of *E. hux.*

Impact

Decrease

Range

Decrease



TEP Fraction:

Aggregates of TEP & beads



- Lack of ballasting due reduction in calcification reduces sinking velocity
- Increase in the volume fraction of TEP in aggregates decreases sinking velocity
- Decrease of flux to deep sea in the future ocean → positive feed back

CO₂ treatment

Biermann & Engel 2010

(9) Efficiency of Biological pump

Number of studies	Impact	Range
3	Increase	PeECE III ^{Mes} , ↓CaCO ₃ Prod ^{Mod.} , Salps vs krill ^{Theo,Field}

- Overall effect on biological pump unknown (regionally different?) :
- Increase in efficiency (negative feed back):
 - C-overconsumption, TEP formation & sedimentation
 - Decrease in calcification
 - Increase in fraction of salps vs krill
- Decrease in efficiency (positive feed back):
 - Decrease in sinking velocity due to increase of TEP in aggregates
 - Decrease in sinking velocity due to lack of ballasting
 - Decrease in diatom abundance

(10) Zooplankton

Number of studies

3

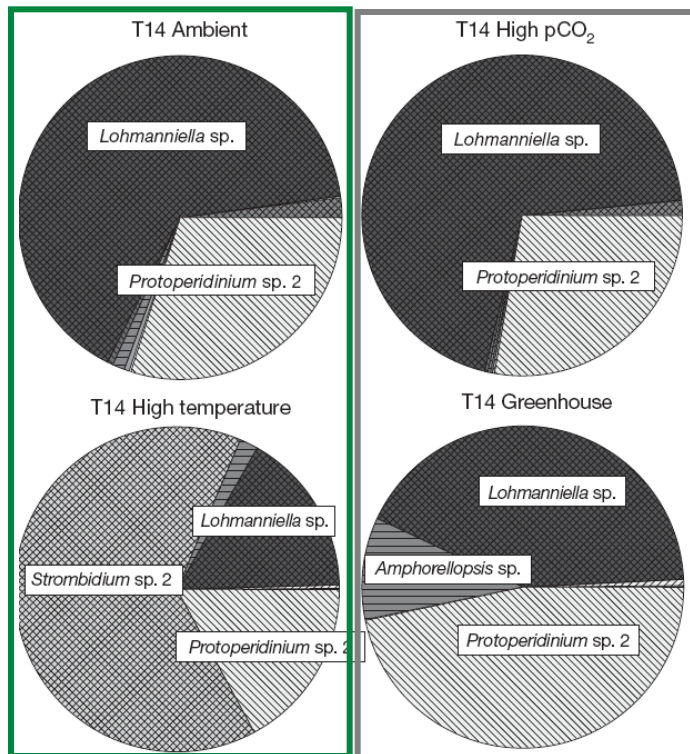
Impact

Subtle

Range

No change

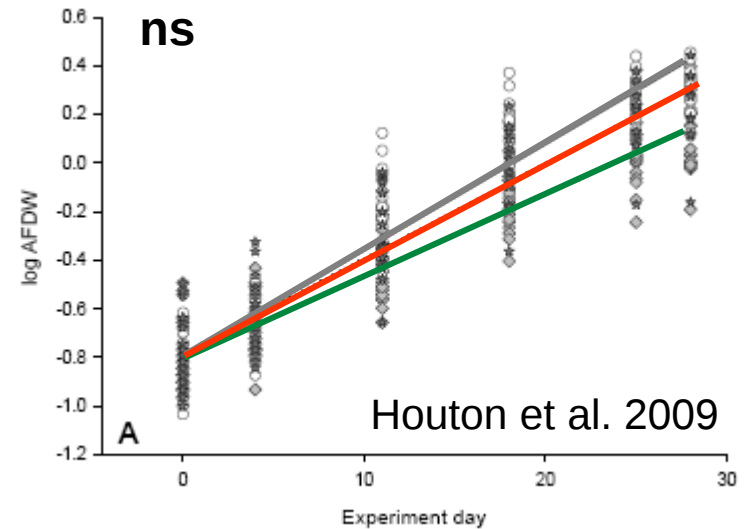
Protozooplankton day 14



Rose et al. 2009

Growth rate of amphipod

ns



Effects on grazing rate & vertical migration

(10) Zooplankton

Number of studies

3

Impact

Subtle

Range

No change

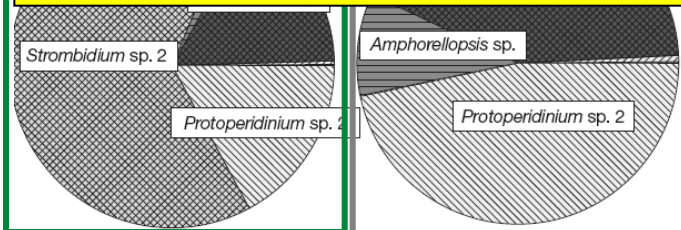
Protozooplankton day 14

Growth rate of amphipod

0.6
ns

- Effects on microzooplankton appear mostly indirect (shift in food source)
- Effects on mesozooplankton subtle, in physiology (gene expression) but not in mortality or growth
- Consequences for biogeochemical cycling impossible to predict at this time

Experiment day



Effects on grazing rate & vertical migration

Rose et al. 2009

Effects on Biogeochemistry on Biological Timescales

**C- fixation
increase →
C-rich POM**

N_2 CO_2
↓
Fixation

**Change in species
composition
Stoichiometry
Feeding
Microbial utilization
Settling flux**

**N_2 fixation
increase →
P-limitation**

DIC
 NO_3
 PO_4
↓
Uptake
106:16:1

Phytoplankton
Cyanobacteria

Grazing

**Nutrition for
higher trophic
level**

**Particle aggregation
→ increase
in sedimentation „??“**

**Calcification reduced →
Less ballasting material →
decrease in sedimentation**

release

Unicellular
zooplankton

Dissolved
organic
carbon

Microbial
Loop

Heterotrophic

EUPHOTIC ZONE

**Microbial loop turnover
enhanced → increased respiration or
decreased → increase of DOM down ward
transport**

Summary

- **Number of available studies very limited considering the complexity of the problem**
- **Ocean acidification seems to significantly alter the environment of microbes**
- **Changes in phytoplankton and bacterial community structure and physiology are likely**
- **Changes in microbial processes and community structure impact biogeochemical cycles**
- **Magnitude and direction of impact presently unpredictable, because of its complexity**
- **Associated changes of climate add to the complexity → need for multifactorial experiments**

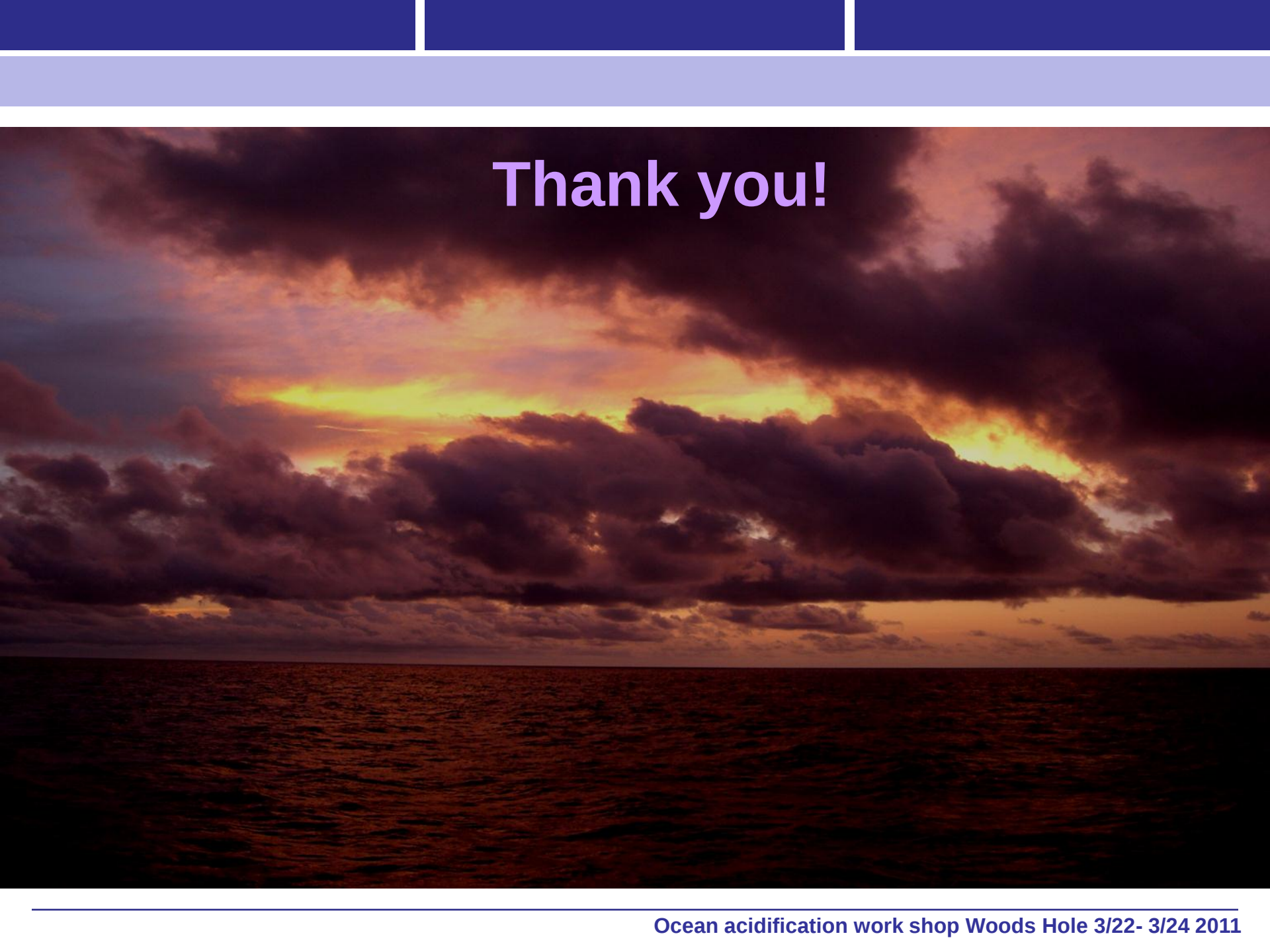
Challenges

1. The carbonate system structures the environment.
 - a) Spatial and temporal fluctuations are large and *will become larger as OA progresses*
 - b) Feed-backs make changes in carbonate system partially unpredictable
 - c) These effect organisms, populations, ecosystems and biogeochemical cycling
 - d) Till recently ignored: Re-evaluate many “pre-OA” results
2. OA does not happen isolated – synergistic and antagonistic interactions with other parameters of major importance.
3. Ability of organisms to acclimatize and adapt unknown.
4. Empirical relationships (*Redfield* ratio, *Martin* curve) may not hold.

Conclusions

Approaches

1. Autonomous CO₂ buoys – understand rate of change and variability
2. Process studies (laboratory or shipboard experiments) isolating individual processes and field surveys evaluating temporal or spatial gradients will give us information on the breadth of possible reactions
3. Explore combined influence of global change relevant parameters (light, nutrients, trace elements, temperature) in experiments. Test for parameter range in expected changes of specific regions.
4. Models could help predict regional specific expected changes of these parameter combinations (tighter collaboration between modelers and experimentalists).
5. Proxy evaluation to utilize past data for analysis of long-term trends.
6. “Evolutionary” Experiments
7. Mesocosm studies look at community level net effects (black box for individual processes)
8. Model processes and feed-backs, e.g. sedimentation – ballasting,

The background of the slide is a photograph of a sunset or sunrise over the ocean. The sky is filled with large, dark, purple and orange clouds. The sun is low on the horizon, creating a bright orange glow that filters through the clouds. The ocean is dark and calm, reflecting the colors of the sky.

Thank you!