Ocean Acidification Impacts on the Surface Ocean: Overview

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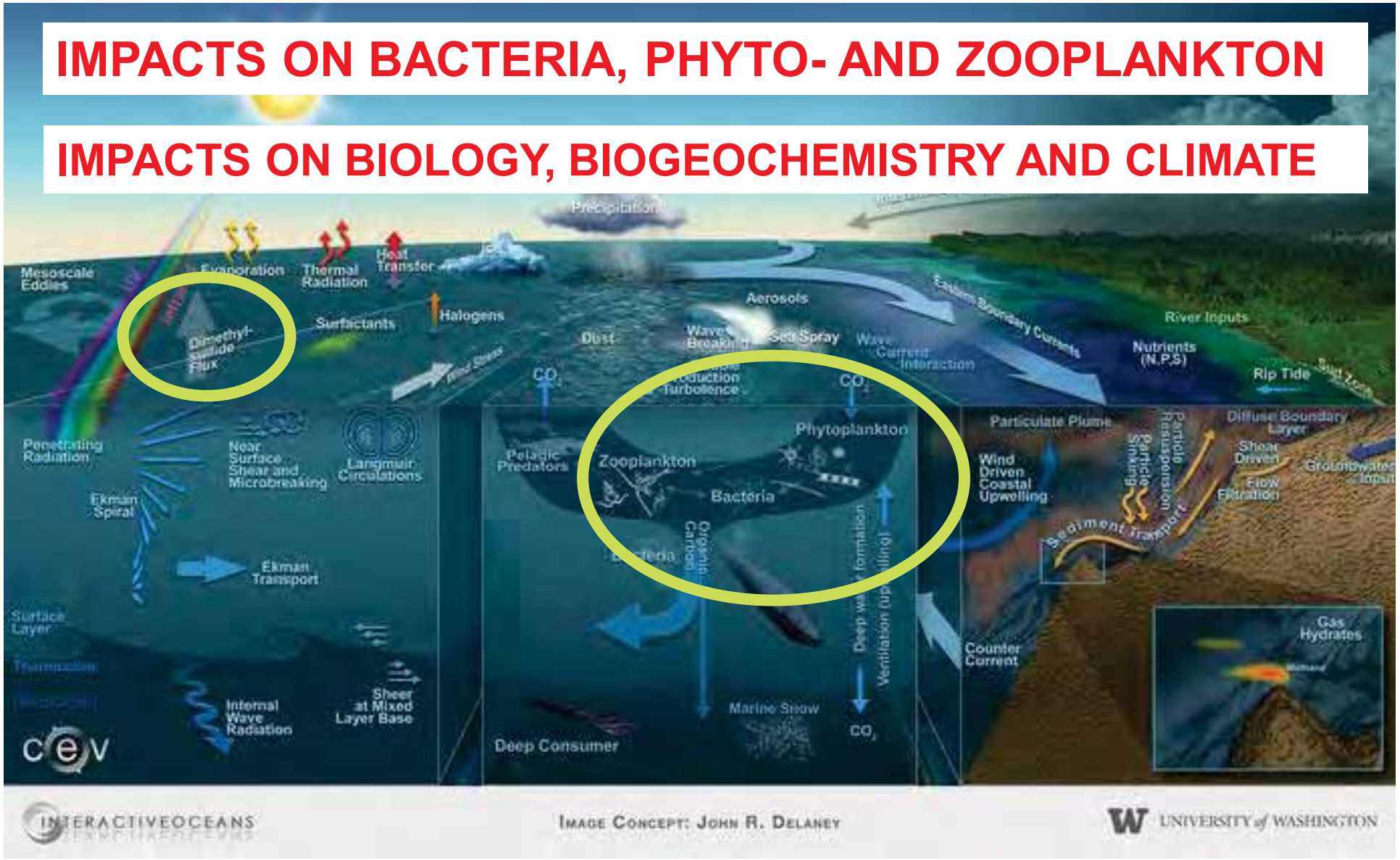
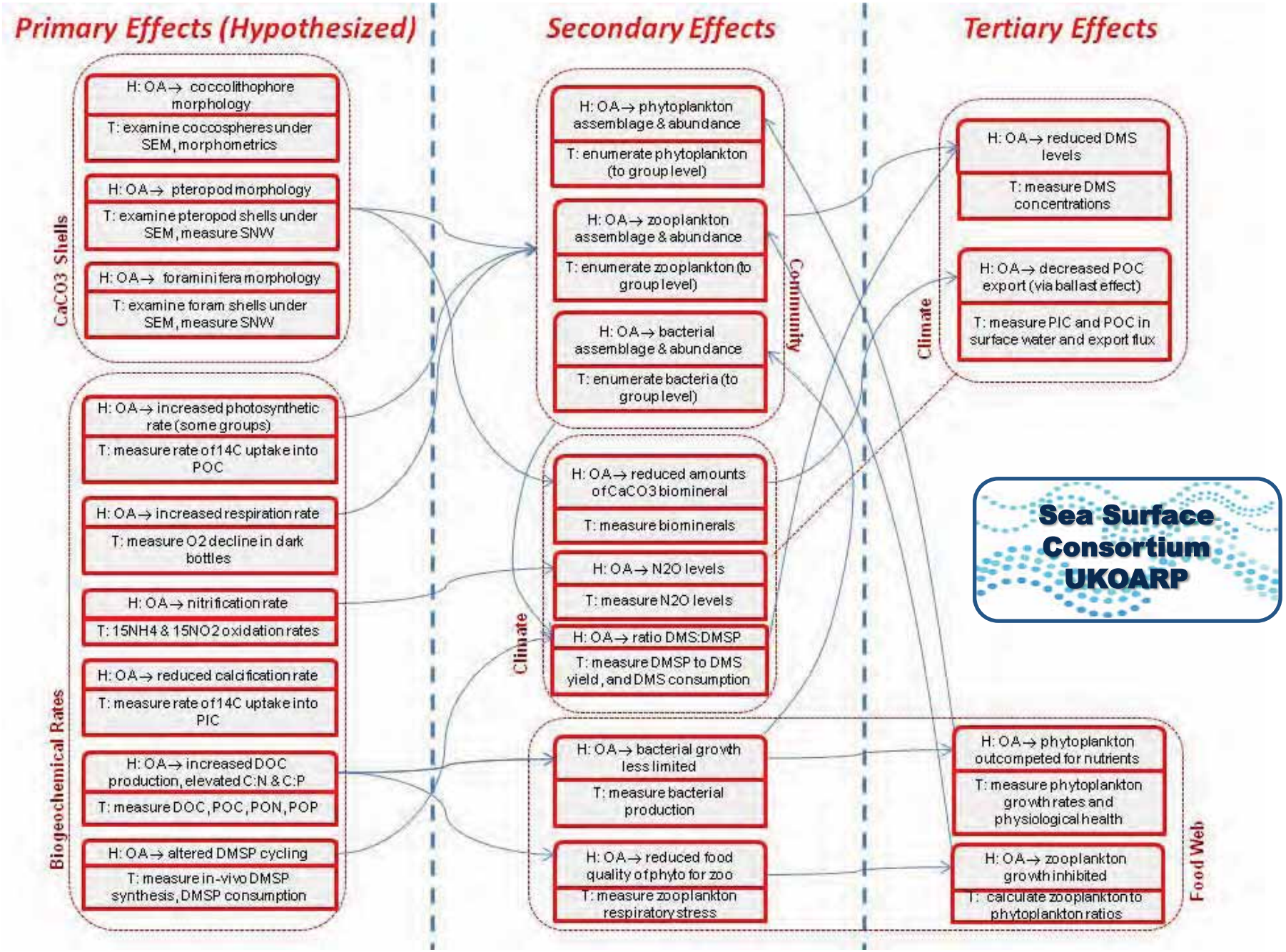
School of Ocean & Earth Sciences
University of Southampton

UK Ocean Acidification Research Programme

Sea Surface Consortium UKOARP

How will OA affect the Surface Ocean?




Primary Effects (Hypothesized)
Secondary Effects
Tertiary Effects
CaCO3 Shells
H: OA→ coccolithophore morphology
T: examine coccospheres under SEM, morphometrics
H: OA→ pteropod morphology
T: examine pteropod shells under SEM, measure SNW
H: OA→ foraminifera morphology
T: examine foram shells under SEM, measure SNW
Biogeochemical Rates
H: OA→ increased photosynthetic rate (some groups)
T: measure rate of 14C uptake into POC
H: OA→ increased respiration rate
T: measure O2 decline in dark bottles
H: OA→ nitrification rate
T: 15NH4 & 15NO2 oxidation rates
H: OA→ reduced calcification rate
T: measure rate of 14C uptake into PIC
H: OA→ increased DOC production, elevated C:N & C:P
T: measure DOC, POC, PON, POP
H: OA→ altered DMSP cycling
T: measure in-vivo DMSP synthesis, DMSP consumption
H: OA→ phytoplankton assemblage & abundance
T: enumerate phytoplankton (to group level)
H: OA→ zooplankton assemblage & abundance
T: enumerate zooplankton (to group level)
H: OA→ bacterial assemblage & abundance
T: enumerate bacteria (to group level)
Community
H: OA→ reduced amounts of CaCO3 biomineral
T: measure biominerals
H: OA→ N2O levels
T: measure N2O levels
H: OA→ ratio DMS:DMSP
T: measure DMSP to DMS yield, and DMS consumption
Climate
H: OA→ bacterial growth less limited
T: measure bacterial production
H: OA→ reduced food quality of phyto for zoo
T: measure zooplankton respiratory stress
H: OA→ reduced DMS levels
T: measure DMS concentrations
H: OA→ decreased POC export (via ballast effect)
T: measure PIC and POC in surface water and export flux
Climate
H: OA→ phytoplankton outcompeted for nutrients
T: measure phytoplankton growth rates and physiological health
H: OA→ zooplankton growth inhibited
T: calculate zooplankton to phytoplankton ratios
Food Web
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Alternative Approaches

Lab experiments have major advantages, e.g. :

(1) control over conditions
(2) everything the same between expts except variable of interest…

But also major disadvantages, e.g. :

(1) insufficient time for adaptation to occur
(2) conditions often not very realistic (high nutrients)
(3) monocultures not very realistic (no competitors, symbionts, prey or predators)
(4) only one species at a time, out of thousands

Other approaches are also needed

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Alternative Approaches

We will adopt a complementary approach, primarily cruise-based:

(1) observations across natural carbonate chemistry gradients

(2) bioassay experiments on complete in situ community

(3) study of mechanistic basis of impacts

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Benefits of Our Approach

- Results directly applicable to real world

- When making observations across carbonate chemistry gradients, organisms will be adapted to the prevailing environment, so evolutionary adaptation is taken into account

- Knowledge of underlying mechanisms will allow improved predictions of impacts

- However, can also be problematic to gain understanding from observations (correlation ≠ causation)

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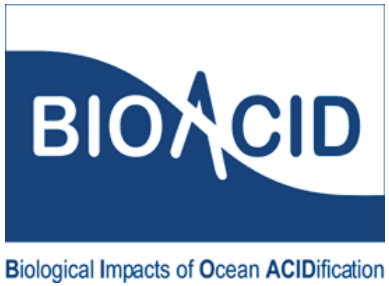
International Context

Focus on laboratory and mesocosm experiments and modelling. Small observational/monitoring component (no dedicated cruises)



Focus on lab expts again. Small amount of work at sea (Baltic only)

Ocean Acidification

Program Solicitation

Announced Sept 2010 – mixture of observational, lab and modelling work

Work Package List

WP 1: Cruises
WP 2: Bioassay Experiments
WP 3: Core Measurements including carbonate chemistry

impacts of OA on:
WP 4: Plankton Community Structure
WP 5: Biogeochemical Rates
WP 6: Biocalcification
WP 7: Food Web Effects
WP 8: Climate

WP 9: Synthesis

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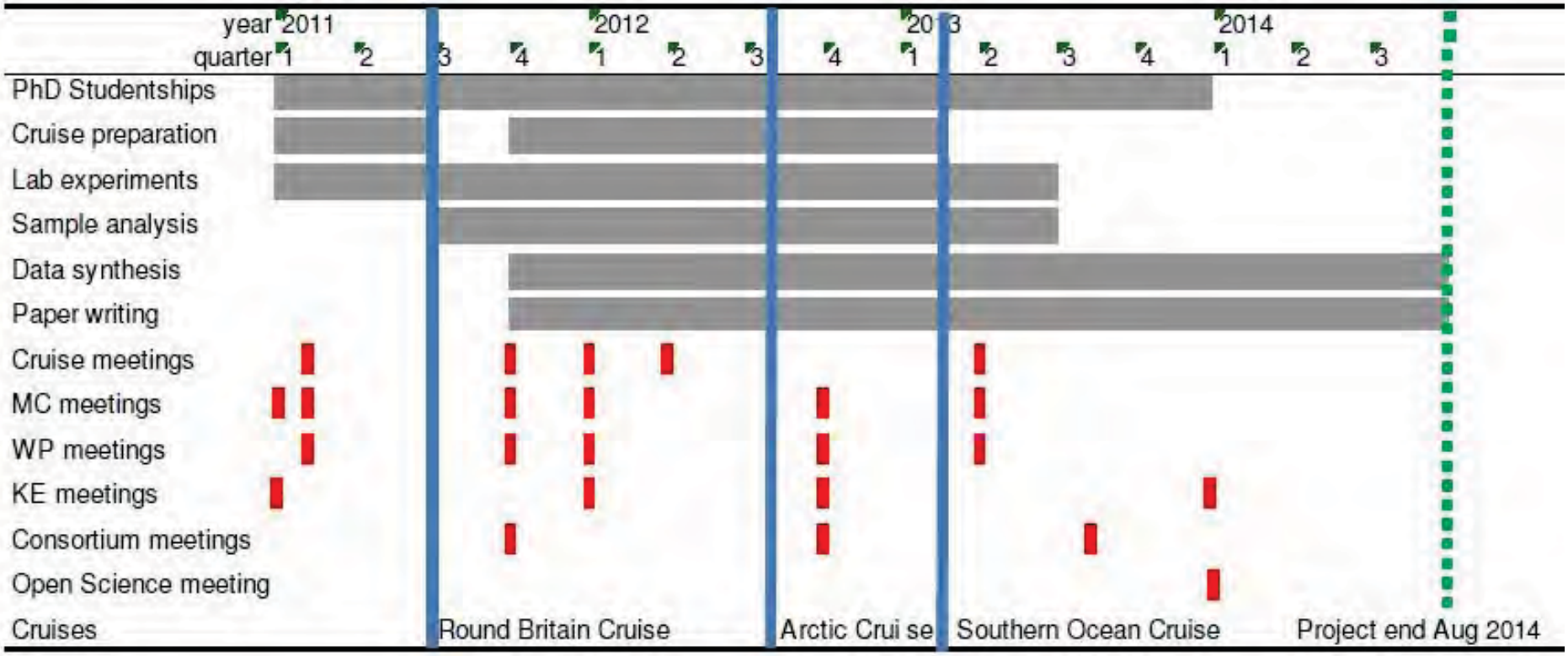

project start (now)

most posts end

synthesis ends

Timeline

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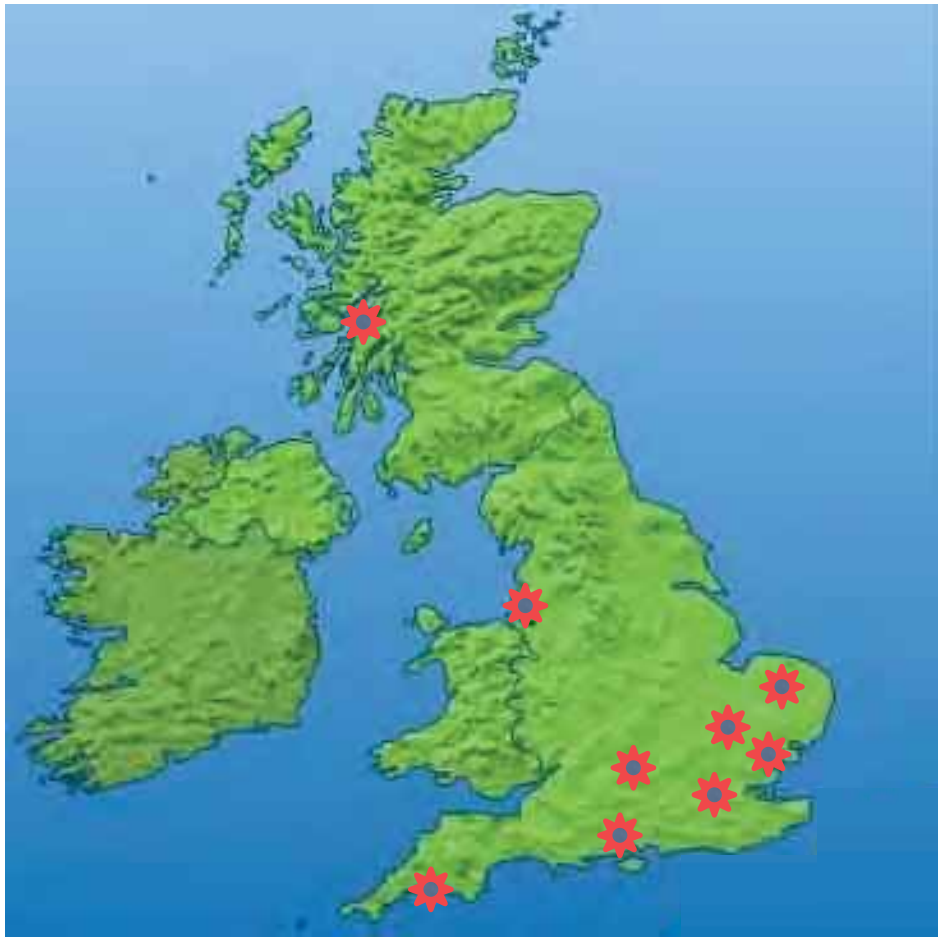
Participating Institutes



NOCS-Univ. Soton
NOC Southampton
PML
Univ. East Anglia
NHM
BAS
NOC Liverpool
SAHFOS
SAMS
Univ. Essex
MBA
Univ. Oxford

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PIs and Co-Is

Toby Tyrrell
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Mark Moore
Alex Poulton
Richard Sanders
Mike Zubkov
Phil Nightingale
Andy Rees
Steve Archer
Darren Clark
Dorothee Bakker
Jeremy Young

Geraint Tarling
Victoria Peck
Peter Ward
Colin Brownlee
Declan Schroeder
Roz Rickaby
Peter Burkill
David Johns
Dave Suggett
Tracey Lawson
Jonathan Sharples
Ray Leakey

Mark Stinchcombe, Gareth Lee, Renee Lee, Susan Kimmance, Matthew Palmer, Andrea Highfield, Frances Hopkins

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Consortium PhD Students

- Laura Bretherton – Uni. Essex
- Helen Smith – NOC Southampton (at sea)
- Tingting Shi – Uni. Southampton
- MBA/Oxford – *to be appointed*

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End Products

- Observational datasets
- Bioassay datasets
- Advanced understanding of mechanisms
- Analyses of OA impacts
- Manuscripts (***both absence of impacts and negative impacts should be published***)
- Improved understanding of OA impacts on the surface ocean
- Any other exciting science we can fit in

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Consortium Cruises

Eric Achterberg

School of Ocean & Earth Sciences, Univ of Southampton

Purpose of the UK sea surface OA consortium cruises:

Undertake joint experimental/observational work at sea through cruises in the NW European shelf region, Arctic and Southern Oceans

Focus of cruises:
-in-situ biological and chemical observations across natural carbonate chemistry gradients
-on-deck CO_2 perturbation incubations

Cruises

Approaches

Collection of in-situ data along many different transects with strong gradients in carbonate chemistry

Use common methods on cruises to facilitate thorough statistical data analysis

Undertake underway sampling (every 20 nm)

Undertake CTD profiles (ca. 50 per cruise) →full depth on European Shelf; 300 m and some full depth on Arctic and Antarctic cruises

Identify and enumerate organisms, and undertake physiology/morphometry and rate measurements

Undertake turbulence measurements

Determine downward fluxes of particulate material (POC/PIC) and also collect sinking material (snowcatcher)

Undertake N_20 and DMS/DMSp measurements

Undertake pCO2 incubation experiments with microbial and planktonic organisms

Cruises

Ship's Core Measurements

DIC , Total Alkalinity, pH in discrete samples

DIC , Total Alkalinity, pH, pCO2 on underway supply

Nutrients

Dissolved Oxygen

Chlorophyll a

Temperature, salinity, fluorescence, light, turbulence

PIC-POC-PON-POP

Dissolved Organic Carbon (DOC)

Transparent Exo Polymers (TEP)

Cruises

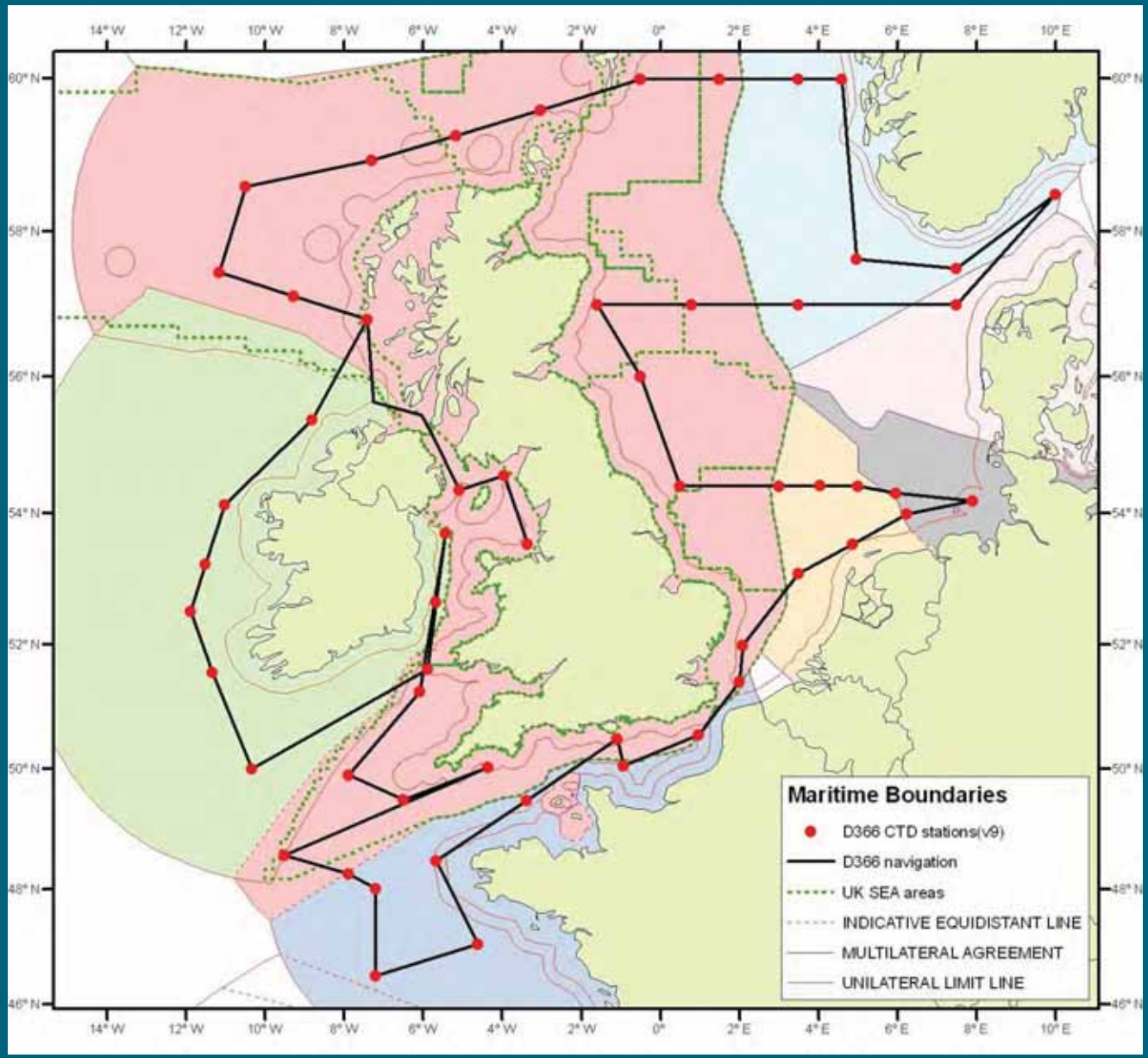
The UK Pelagic OA consortium will have three cruises:

-European Shelf cruise in summer 2011 on *RRS Discovery* (24 science berths).
PSO Eric Achterberg

- Arctic Cruise summer 2012 on *RRS James Clark Ross* (30+ science berths)
PSO Ray Leakey

-Antarctic Cruise Jan-Feb 2013 on *RRS James Clark Ross* (30+ science berths)
-PSO Geraint Tarling

European Shelf Cruise Track; summer 2011



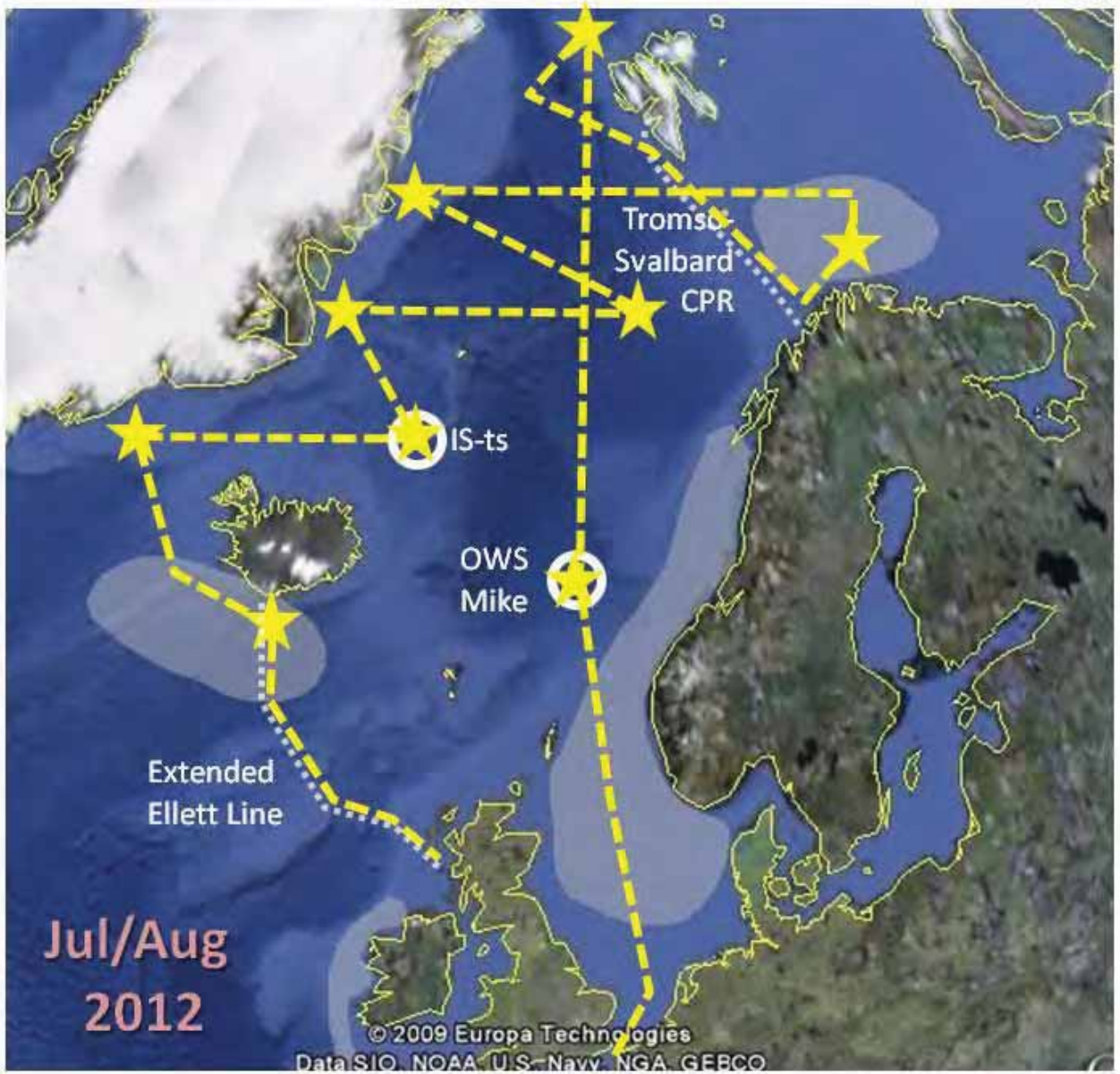
European Shelf Cruise

Rational for cruise & timing

A time of year with enhanced biological productivity and coccolithophore abundance (June/July 2011)

Cruise track will cover UK and European shelf areas of:
-different pH
-seasonally stratified and perennially mixed seas
-areas of coccolithophore abundance and absence
-areas where low alkalinity decouples Ω_{CaCO3} from SST (e.g. eastern North Sea, influence of Baltic inflow)

Arctic Cruise Track summer 2012



Arctic Cruise

Rational for cruise & timing

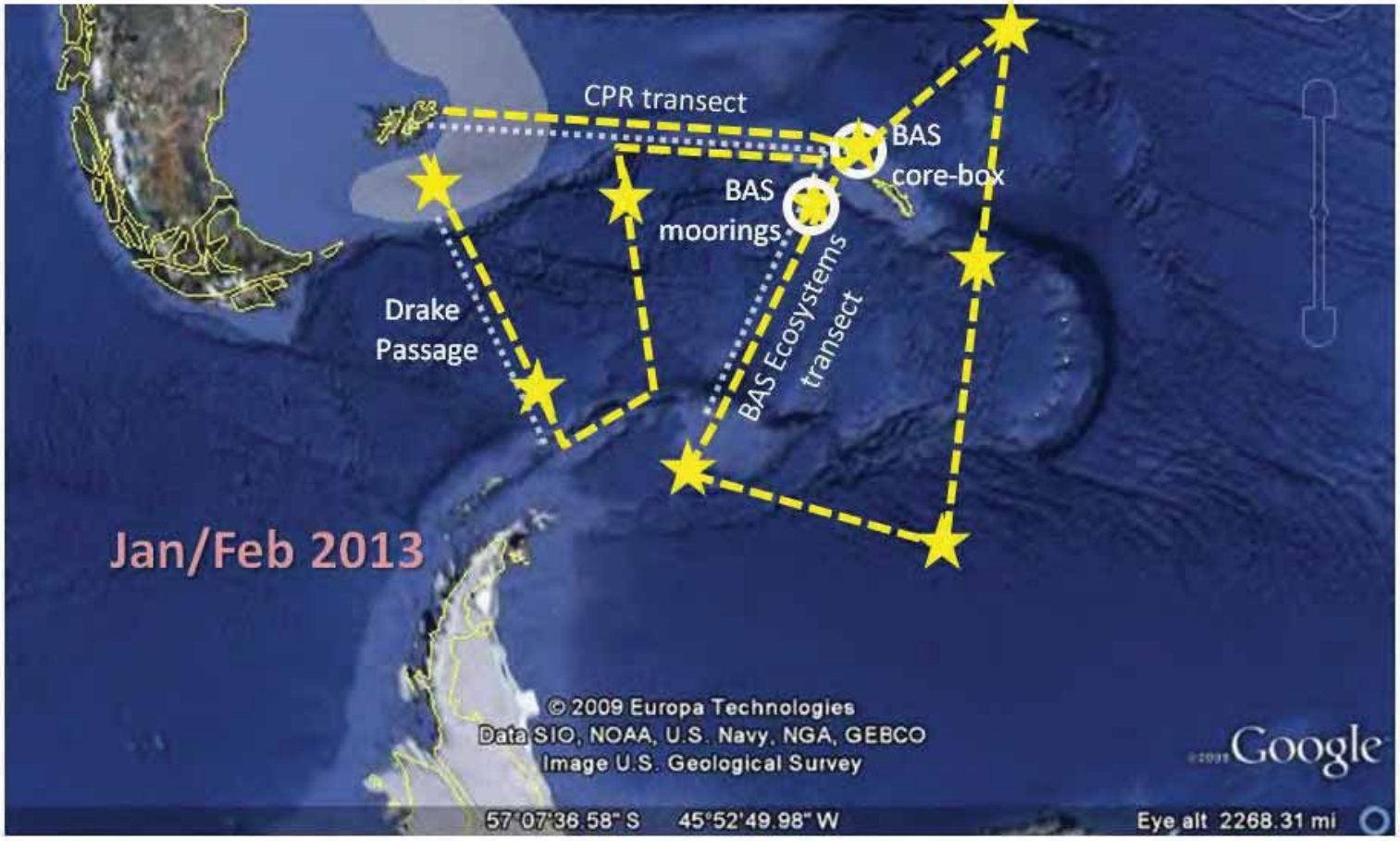
A period of year with enhanced productivity and minimum ice cover (July/Aug 2012)

Cruise track will cover the ice edge region where strong changes in the carbonate system occur

The cruise will sample annually occurring coccolithophore blooms in the Barents Sea and Ω_{CaCO3} gradients along N-S and E-W transects (lower Ω_{CaCO3} in Arctic-sourced waters nearer to Greenland).

The cruise will re-visit locations previously sampled in 2008/2010 as part of the SAMS Arctic cruise programme, and in 2009 by the Norwegian MERCLIM cruise.

Antarctic Cruise Track; Jan-Feb 2013



Antarctic Cruise

Rational for cruise & Timing

Southern Ocean cruise (Jan/Feb 2013) will cover the regularly sampled Drake Passage (recent cruise found surface $\Omega_{aragonite}$ from 1.25 to >2) and (ice permitting) the exceptionally cold Weddell Sea where undersaturation is predicted to occur first in the Southern Ocean.

Strong gradients in Ω_{CaCO3} will be covered along multiple N-S transects at different longitudes, in ice edge regions and in high productivity waters NW of S Georgia.

Previous BAS transects will be traversed, allowing repeat observations (incl. carbonate system).

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Sea Surface Acidification consortium:
Ocean Acidification Impacts on Sea-Surface Biology, Biogeochemistry and Climate

Plans for inorganic carbon manipulation experiments within consortium cruises, „Bioassayexperiments"

Mark Moore

University of Southampton

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National Oceanography Centre, Southampton

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Assessing the impact of pH (pCO_2/carbonate chemistry) on organism physiology/ biogeochemistry in ‗survey mode' is clearly confounded by co-occurring environmental gradients (e.g. nutrients, light availability, temp, salinity).

Deliberate manipulation circumvents this problem, although it comes with a number of additional problems.

Complimentary to other techniques.

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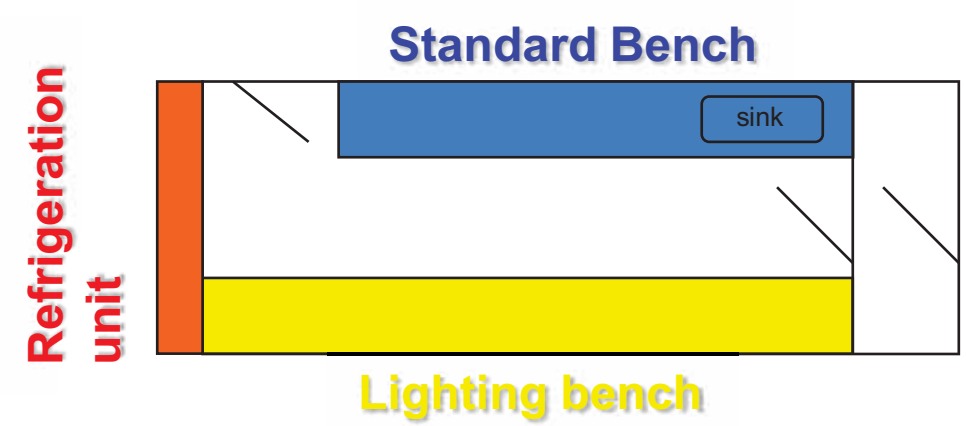
Containerised lab facility



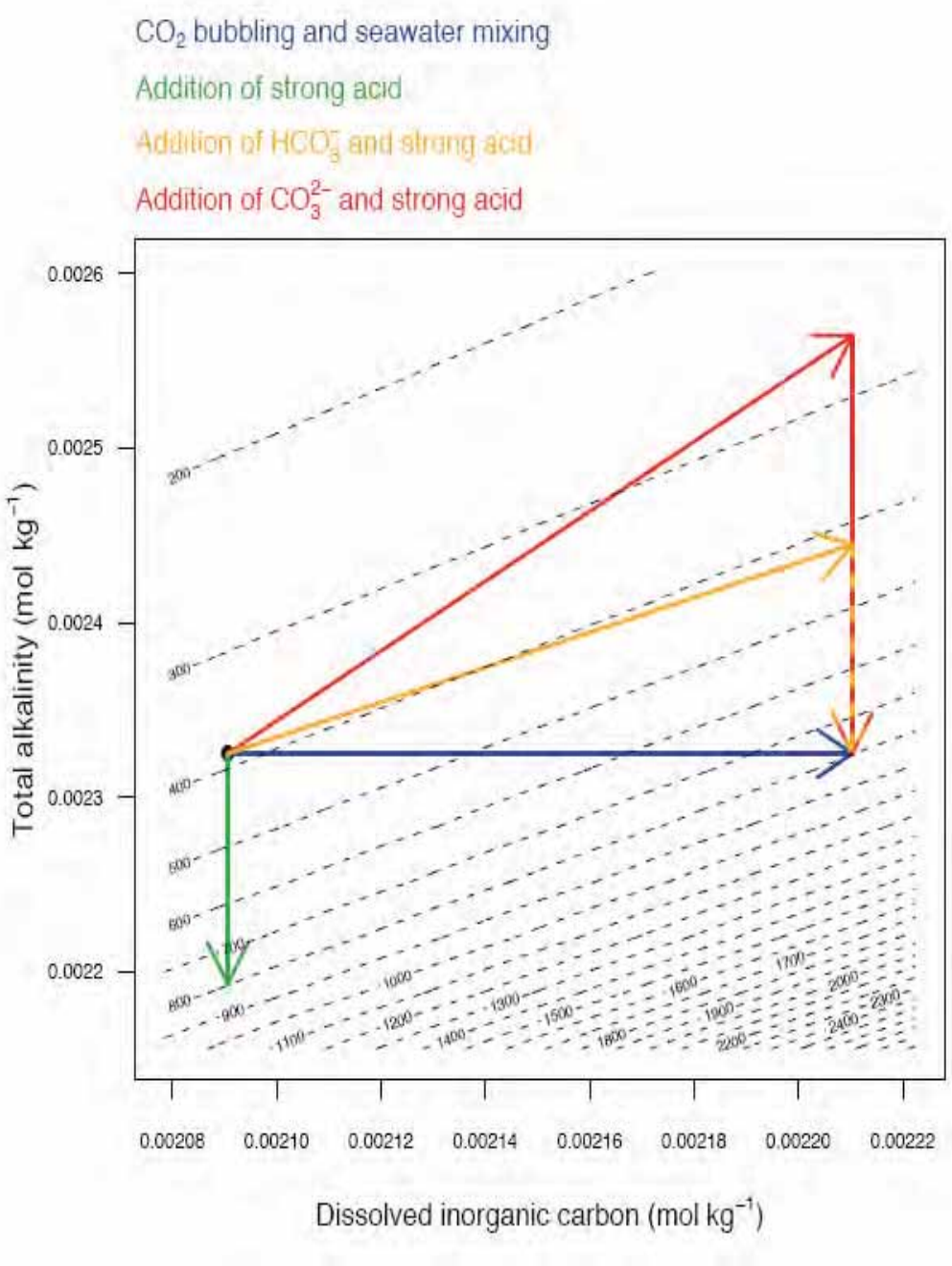
Rather than using on-deck incubators we will use artificial controlled light sources within a dedicated experimental container facility

Experimental work on Arctic and Antarctic cruises will require low temperature and adequate control, => conversion of refrigerated container

Manipulation method

	$pCO_{2\,sw}$ (µatm)	pH_T (–)	$[H^+]$ (a)	TA (b)	DIC (b)	$[CO_2]$ (b)	$[HCO_3^-]$ (b)	$[CO_3^{2-}]$ (b)	Ω_c (–)	Ω_a (–)
Year 2007	384	8.065	8.6	2325	2065	12.8	1865	187	4.5	2.9
Year 2100	793	7.793	16.1	2325	2191	26.4	2055	110	2.6	1.7
Gas bubbling	793	7.793	16.1	2325	2191	26.4	2055	110	2.6	1.7
Addition of high-CO_2 seawater	792	7.793	16.1	2325	2191	26.4	2055	110	2.6	1.7
Addition of CO_3^{2-} and HCO_3^-; closed sys.	793	7.942	11.4	3406	3146	26.4	2901	218	5.2	3.4
Addition of CO_3^{2-} and HCO_3^-; open sys.	384	8.207	6.2	3406	2950	12.8	2580	357	8.5	5.5
Acid addition; closed sys.	793	7.768	17.1	2184	2065	26.4	1940	98	2.3	1.5
Acid addition; open sys.	384	8.042	9.1	2184	194	12.8	1767	167	4	2.6
Addition of:										
CO_3^{2-} and HCO_3^-; closed sys.	400	8.073	8.4	2467	2191	13.3	1977	201	4.8	3.1
followed by acid addition; closed sys.	793	7.793	16.1	2325	2191	26.4	2055	110	2.6	1.7
Manipulation of $[Ca^{2+}]$	384	8.065	8.6	2325	2065	12.8	1866	187	2.6	1.7

Gattuso and Lavinge *Biogeosciences* 6 2121-2133



$$CO_{2(gas)} + H_2 0 \Leftrightarrow H_2CO_3 *$$

$$H_2CO_3 * \Leftrightarrow H^+ + HCO_3^-$$

$$HCO_3^- \Leftrightarrow H^+ + CO_3^{2-}$$

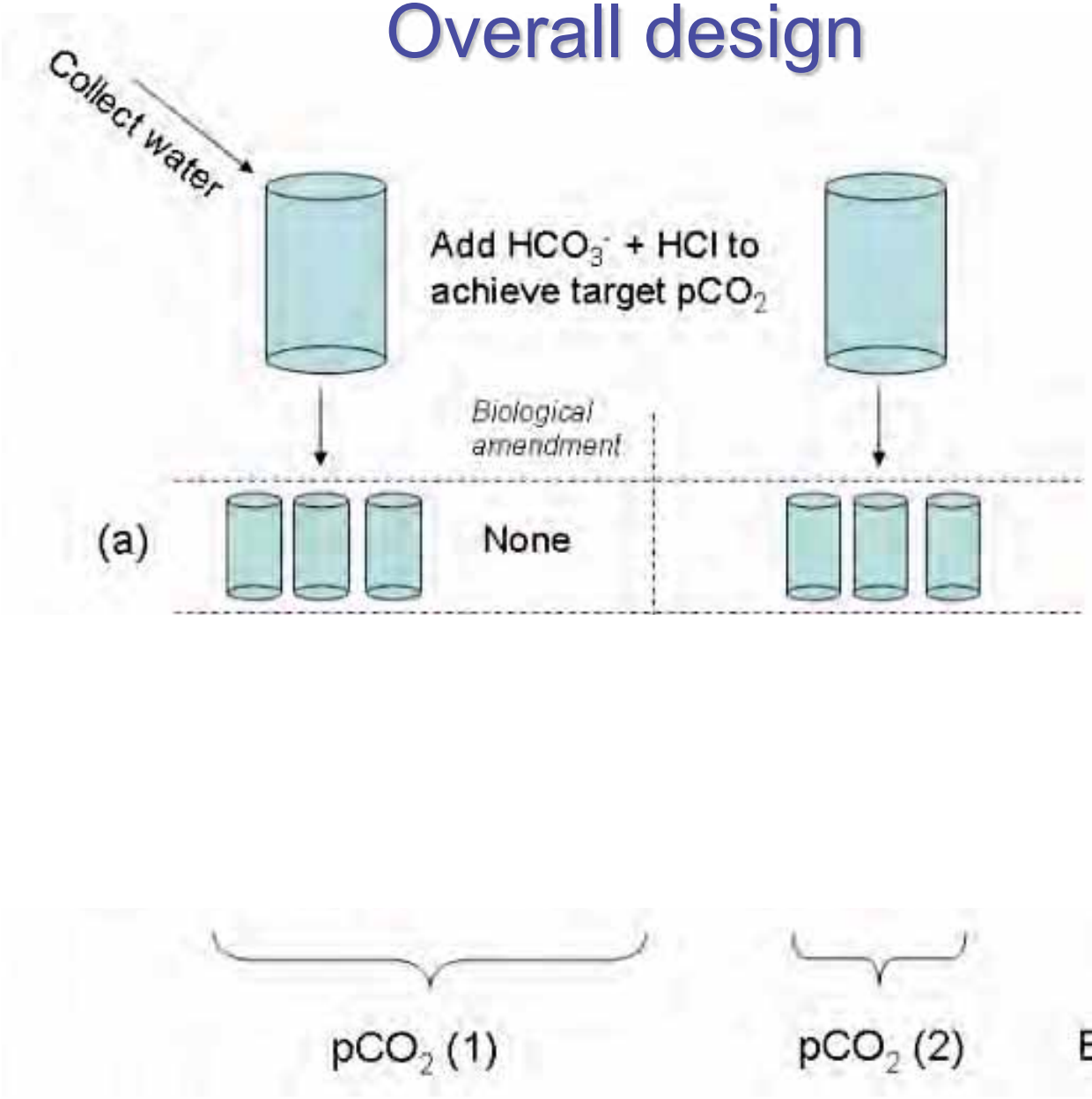
Problems with bubbling (lack of control and mechanical disturbance) avoided.

Closed system.

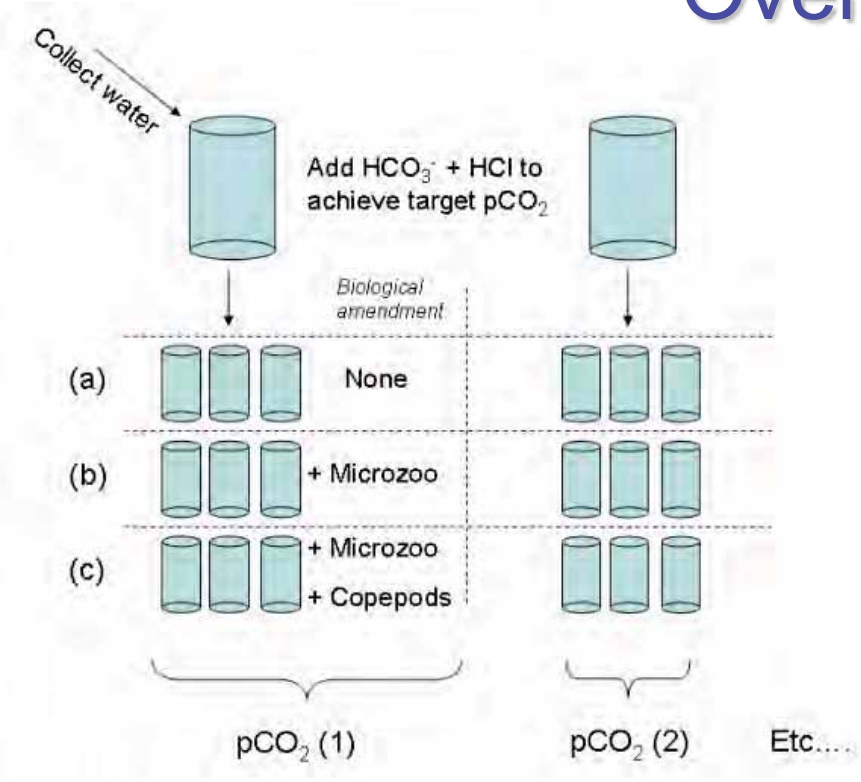
‗Batch type' experiment (i.e. carbonate chemistry will drift ‗naturally' as any ‗bloom' proceeds).

Gattuso et al. *Approaches and tools to manipulate the carbonate chemistry*. Guide to best practices for OA research and data reporting

Overall design



Overall design



4 pCO_2 levels:

ambient, 550, 750, 1000 μatm.

No zooplankton work on first cruise.

Arctic and Antarctic will use trace metal clean techniques.

Initial plan is for ~6 experiments per cruise *(compared ~1 per cruise)*

Experiments within consortium will represent an order of magnitude increase on available data sets.

Measurements

Carbonate system (pre- and post- incubation): *UoSoton*

Calcification, Primary productivity, Community respiration, Phytoplankton physiology, Chlorophyll, POC, PON, POP: *UoSoton, UoEssex, NOCS*

Oxidation rates of NH_4^+ and NO_2^-, DMSP production, DMSP-DMS conversion rates, DMS, DMSP, N_2O: *PML*

Bacterioplankton productivity: *NOCS*

Mesozooplankton processes, Gut fluorescence, Oil sac size: *BAS*

Microbial community structure, incl. Prokaryotes and (both plastidic and aplastidic) protists, particular emphasis on coccolithophores: *NOCS, UoSoton, SAMS*.

Macro-nutrients: *NOCS*

Iron: *UoSoton*

DOC, TEP: *NOCS, UoSoton*

Gene diversity, expression: *UoOxford, MBA*

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Summary

Inorganic carbon manipulation experiments within the Sea Surface Ocean Acidification consortium will be highly complimentary to prior work and survey sampling.

Represents an order of magnitude increase on prior efforts to run at sea manipulation experiments of this type.

Incorporate a novel highly holistic approach addressing multiple potential physiological/ecological responses to OA at a range of trophic levels.

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Assessing Impacts of OA on Calcification

Jeremy Young & Alex Poulton: coccolithophores

Geraint Tarling & Vicky Peck: zooplankton

Declan Schroeder, Colin Brownlee & Ros Rickaby: mechanistic studies

Hypotheses

(H1) *A decline in pH and Ω $CaCO_3$ as a result of rising atmospheric CO_2 concentrations will affect the rate and quality of formation of $CaCO_3$ shells by planktonic calcifiers.*

may occur via

- reduced calcification or even dissolution of shells
- selection of less heavily calcified strains or species
- reduced fitness of calcifying groups vs. other groups

-> cruise + bioassay approach

Pteropods

advantages

- aragonite shells so especially vulnerable
- abundant in high latitudes
- few field studies of effect of OA

methods

- cruises 2 & 3
- plankton tow sampling + bioassays
- size/weight + SEM study of shell surface and margin

Planktonic foraminifera

advantages

- Much evidence of sensitivity to OA
- Size-normalised shell-weight is well-established methodology
- shells accessible for electron microprobe and other refined techniques

challenges

- sampling/low abundances

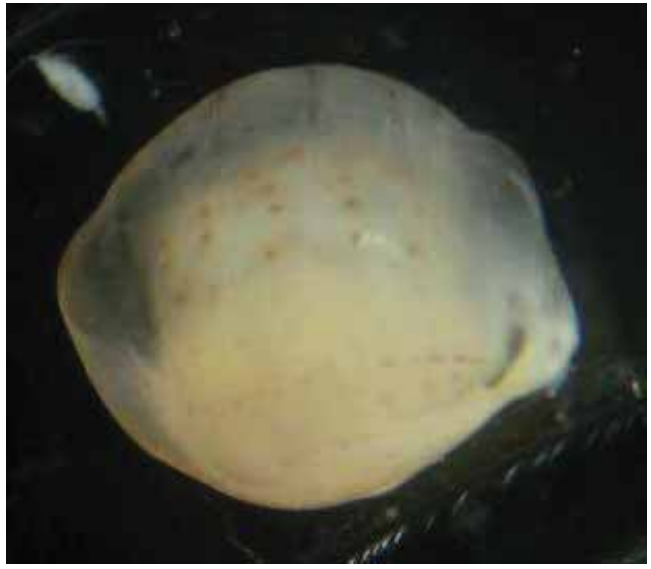
Pelagic ostracods

Opportunities

- abundant and widespread
- vary greatly in degree of calcification
- little previous research on effect of OA

Challenges

- no established methodologies
- few ubiquitous species?
- low perceived importance
- weakly calcified



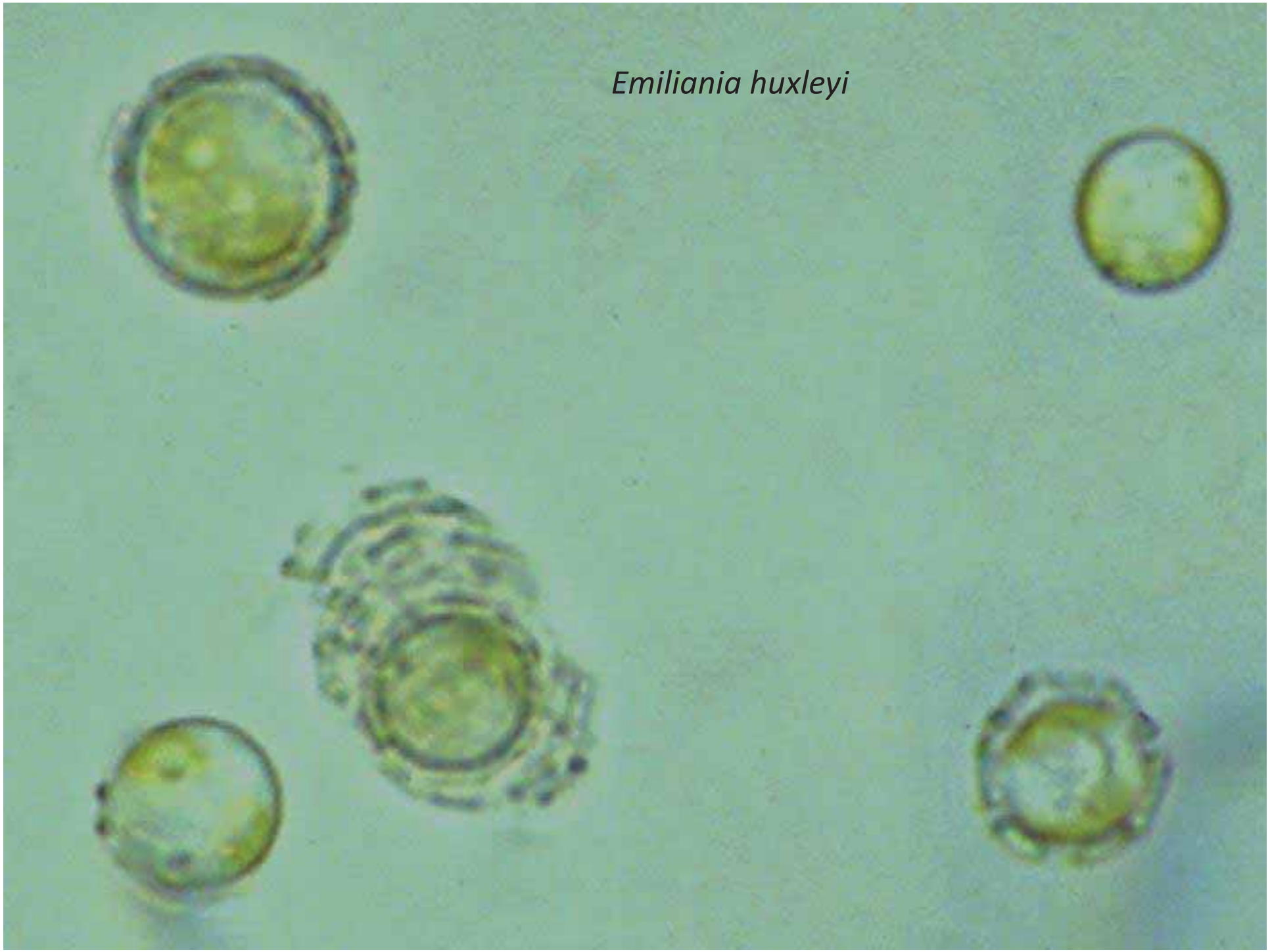
Coccolithophores

advantages

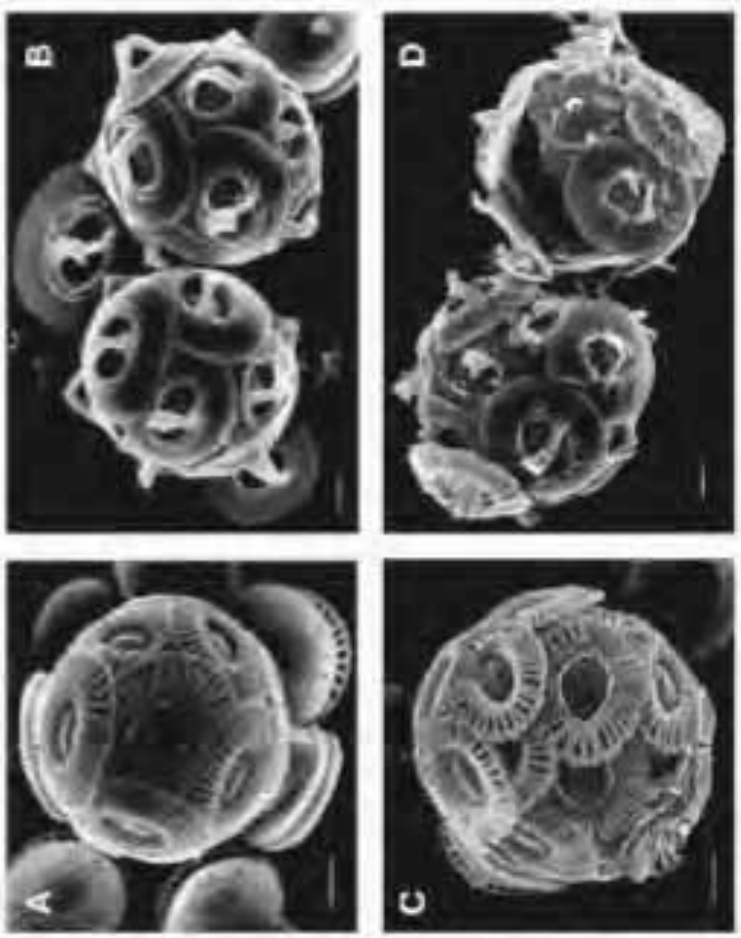
- high abundance/predictable occurrence
- easy to grow in culture
- SYRACO system for rapid size/weight estimation
- molecular tools for strain monitoring

challenges

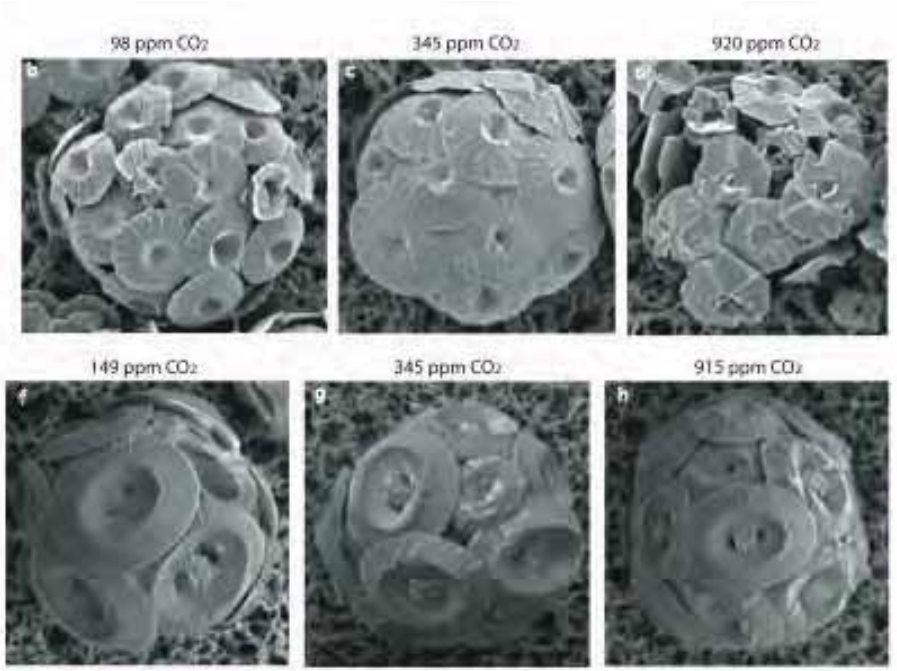
- limited evidence of strong response
- composite skeleton -> what is key parameter?
- ecotype selection or physiological response?


Emiliania huxleyi

Ocean acidification and coccoliths

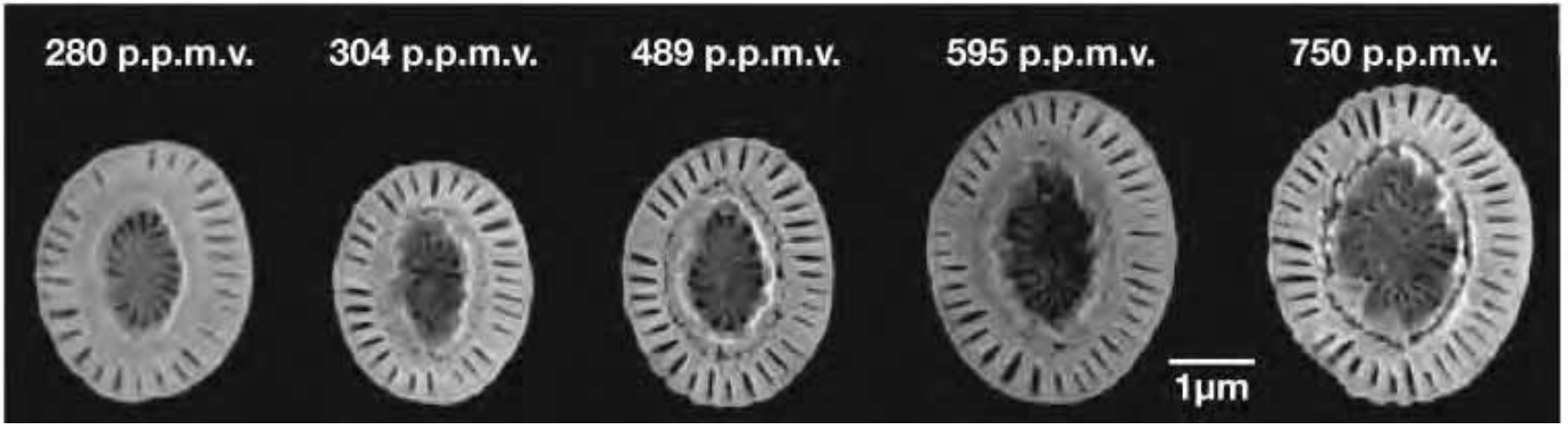


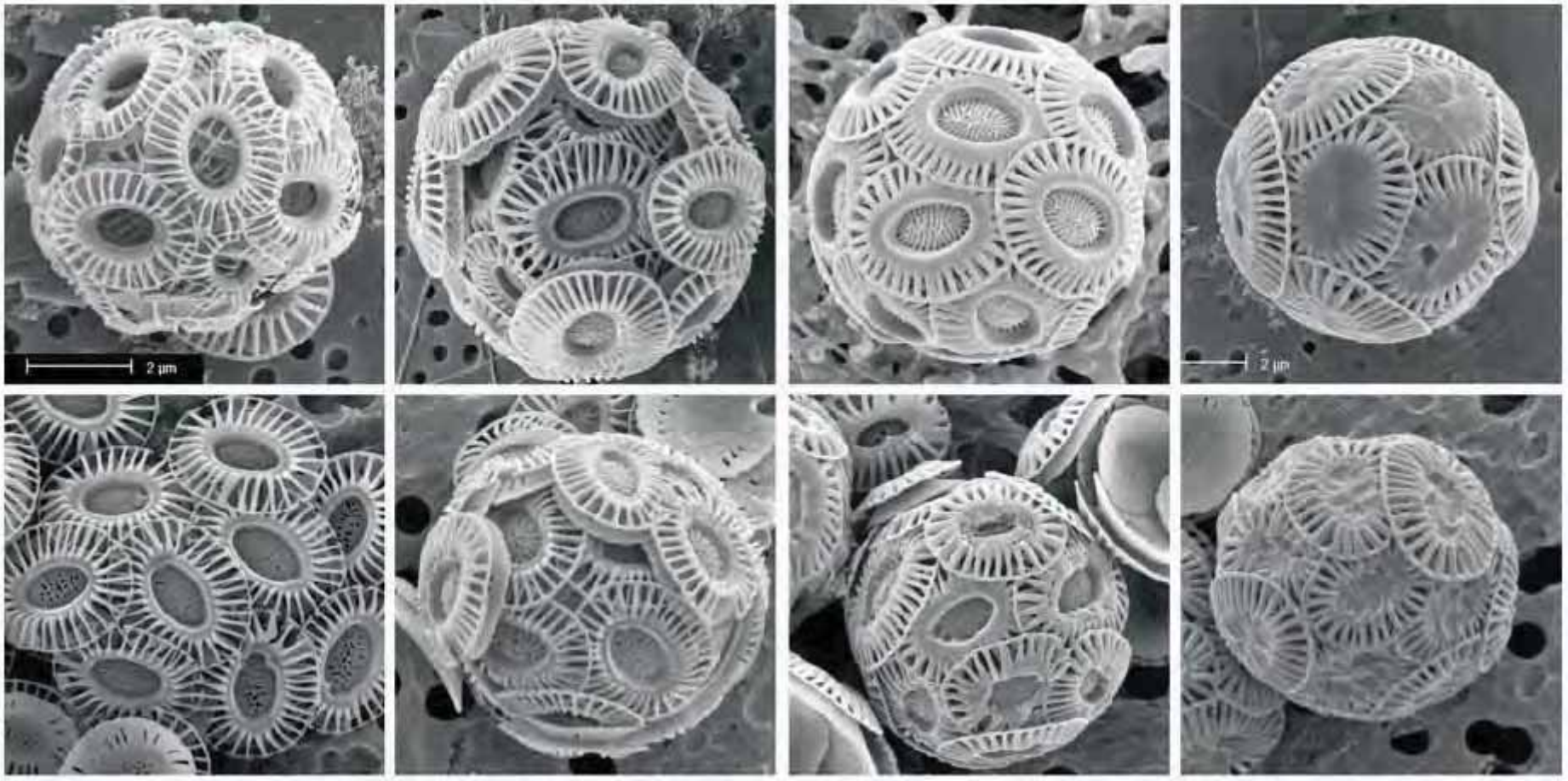
Riebesel et al. 2001



Langer et al. 2005

Iglesias et al. 2008





Ridgwell, et al 2009

inter-strain (i.e. genetic) variability in degree of calcification - are they adapted to different carbonate saturation conditions?

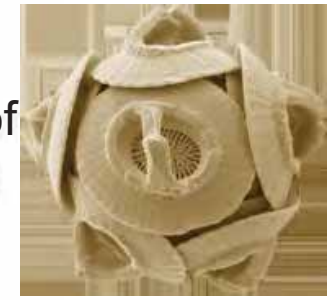
Coccolithophores - approaches

1. *In situ* populations across Ω gradients
2. Bioassay experiments at different CO_2 levels - morphology obs + qPCR monitoring of strain composition
3. Culture isolates from bioassay inocula -> integration of: morphological, physiological and molecular studies

Coccolithophores methodology

- Coccolith size and weight by analysis of cross-polarised light images (SYRACO)
- Automated SEM image capture -> enumeration of morphotypes, calcification state and malformation
- qPCR analysis of population structure (Declan Schroeder)

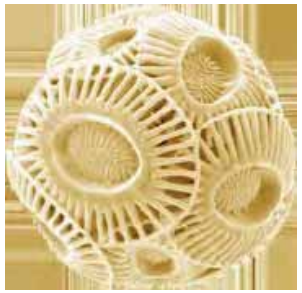
SUMMARY



basic approach is good and integration with other aspects of the project makes it unique study as well as exhaustive test of the core hypothesis

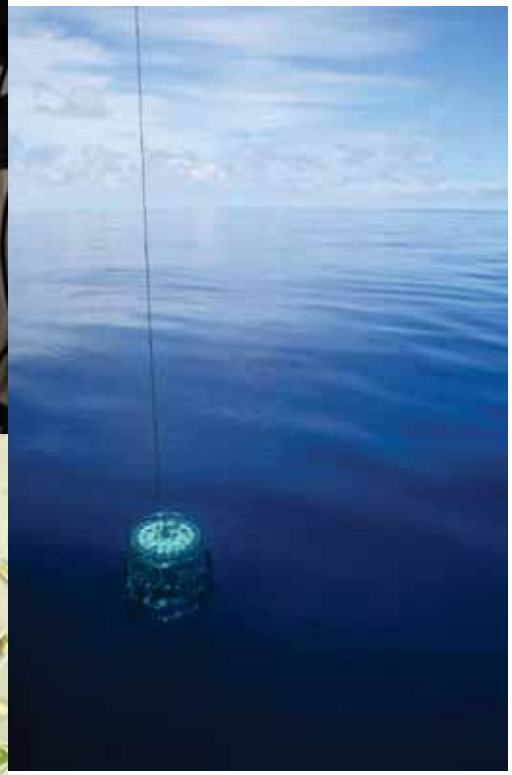
… but a significant amount of effort needed to make it all work smoothly

	gradients	incubations	cultures
Coccolithophores	Y	Y	Y
P. forams	Y		
Pteropods	Y	Y	



Sea-surface impacts of OA: biogeochemical rates

David Suggett, University of Essex



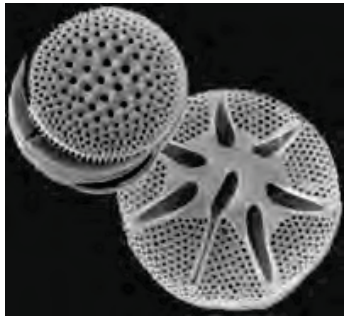
Biogeochemistry objectives (hypotheses)

Characterisation of carbon and nitrogen biogeochemistry using *absolute and biomass normalised rates* measured both in-situ and within bioassays will enable testing of the following hypotheses:

H2a: Elevated surface water pCO_2 levels will enhance photosynthetic rates of CO_2 limited phytoplankton groups;
H2b: Elevated surface water pCO_2 levels will increase ecosystem respiration rates (as a result of increased production of carbon rich compounds such as DOC);
H2c: Lower ΩCaCO3 will reduce calcification rates, at the level of both the community and the individual calcifier;
H2d: Lower pH will result in a decrease in nitrification with consequent biological pump and climate feedback.

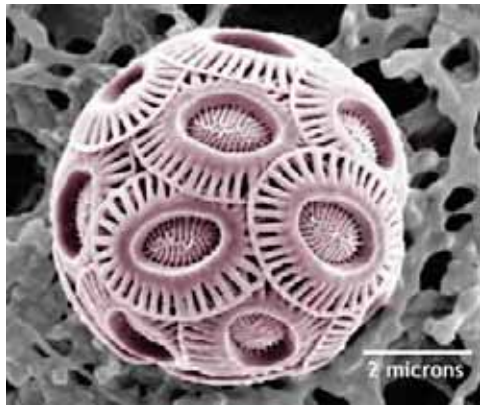
Output (for systems of key biogeochemical/ecosystem service importance):
Net ecosystem metabolism capacity (sink of atmospheric CO_2)
Net productivity (organic carbon) for trophic transfer
Biodiversity impacts on ecology (e.g. species dependencies) and climate (e.g. trace g

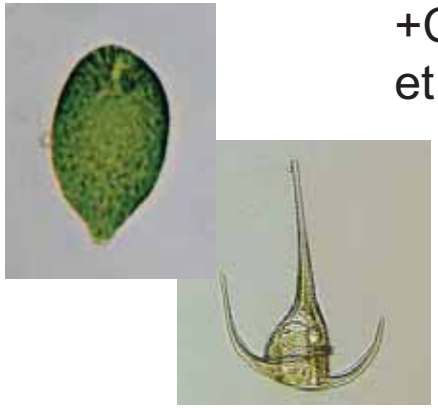
Phytoplankton productivity



Diatoms: little response to +CO_2; highly evolved efficient CCMs (Rost et al. 2009 *MEPS*)

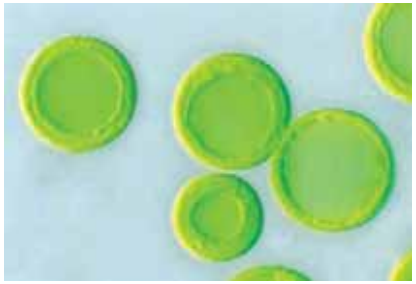
Coccolithophores: various response to +CO_2; greatest response seen when +CO_2 combined with other factors (Rost et al. 2009 *MEPS*)





Raphidophytes only +CO_2 response when +Temp; dinoflagellates strong +CO_2 response (Fu et al. 2008 *Harmful Algae*)

Prochlorophytes unaffected by CO_2 alone (but are temp affected)
(Fu et al. 2007 *J. Phycology*); cyanobacteria widely respond to +CO_2



Phytoplankton productivity

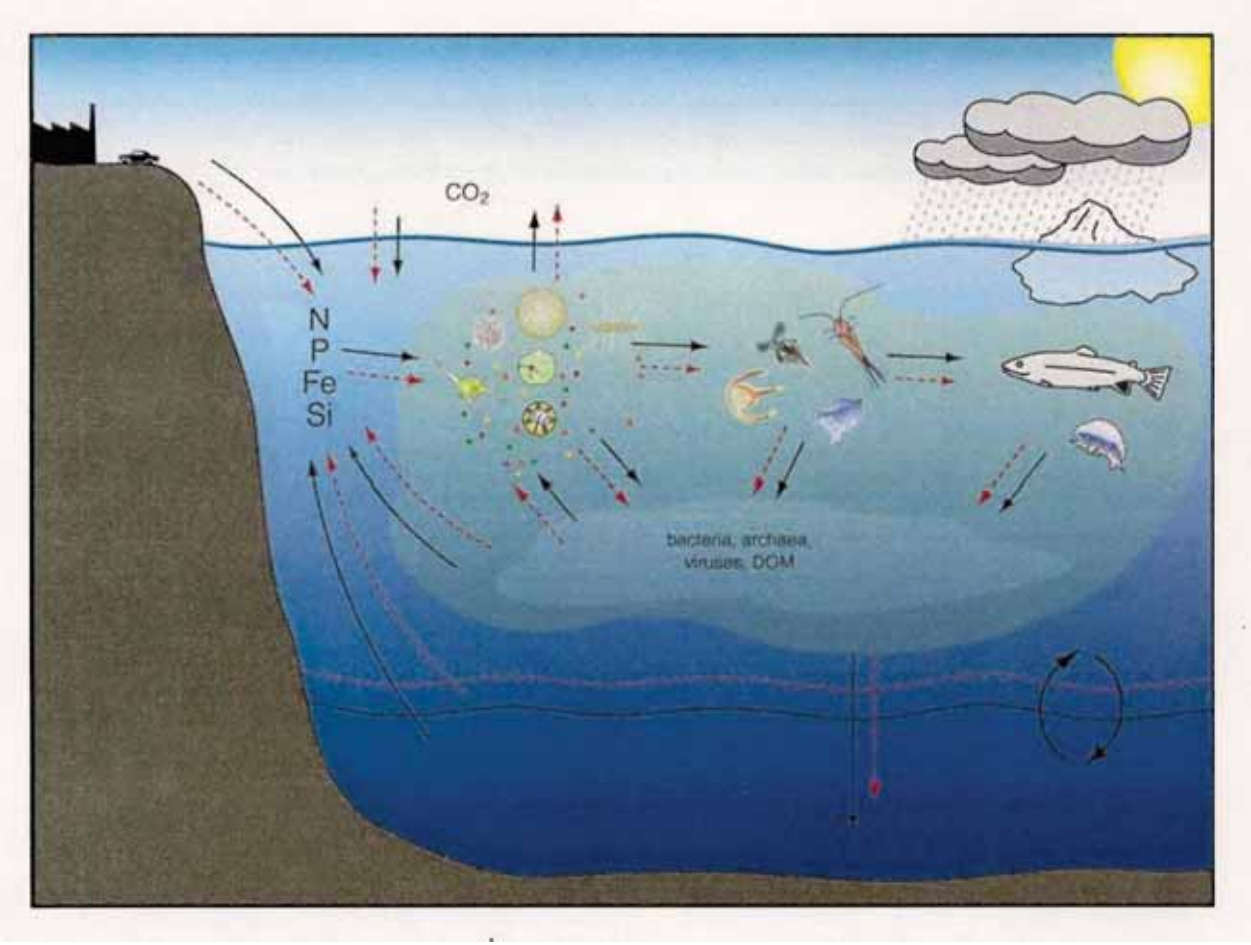
Does OA select within or between taxa?

Strain ID	Location	CO_2	μ	PP	CALC	Citation
88E SMBA-279	G. Maine (1988) n/a	acid/base	n/a n/a	↓ ↑	↓ ↓	Nimer & Merrett (1992)
PML92-11A	N. Sea (1992)	gas; acid/base		(↑) ↑↑	(↓) ↓↓	Riebesell et al., (2000); Zondervan et al. (2002); Rost et al. (2003)
TW1	W. Med (2001)	gas		↓	↓	Sciandra et al. (2003)
n/a (meso.)	N. Sea	gas		↓	↓	Delille et al. (2005); Engel et al. (2005)
PML-92A	n/a	gas	(↓) ↑	(↓) ↓↓	n/a	Leonardos & Geider (2005)
CCMP371	Sargasso (1987)	gas	(-) ↑	(↑) ↑↑	(↓) ↓↓	Feng et al. (2008)
NZEH	S. Pacific (1992)	gas	↓	↑	↑	Iglesias-Rodriguez et al. (2008)
NZEH	S. Pacific (1992)	acid/base	↑	↑	↑	Shi et al. (2009)
PeECE isol.	Norway (2005)	gas	↓	n/a	↓	Müller et al. (2010)

*Note PP changes also for Paasche (1964), Nielsen (1995), Berry et al. (2002); μ for Langer et al. (2009), Gatusso et al. (2010)

Elemental Stoichiometry

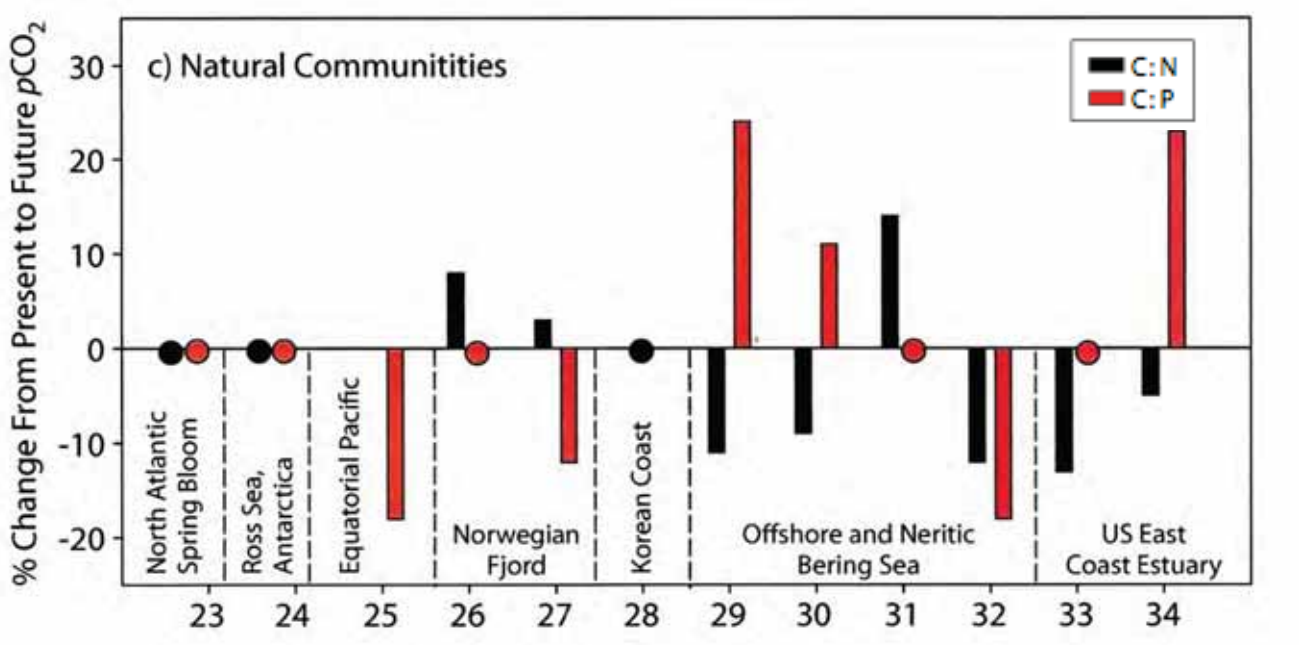
Finkel et al. (2010) *Journal of Plankton Research*



Regulated by different species (sizes) and thus environment for growth

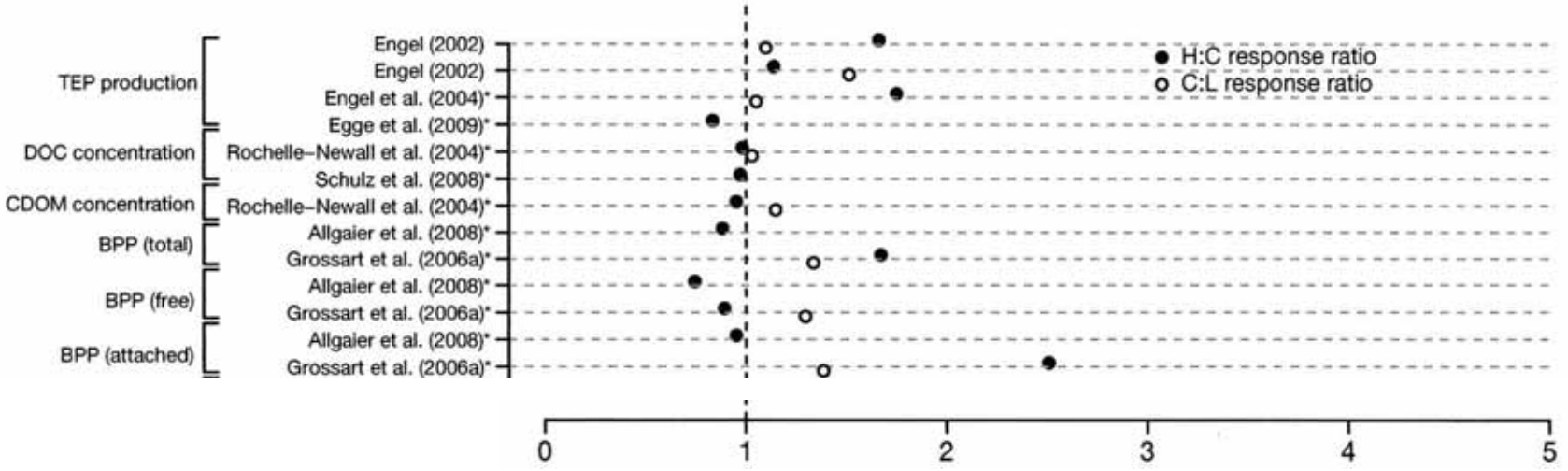
Elemental Stoichiometry

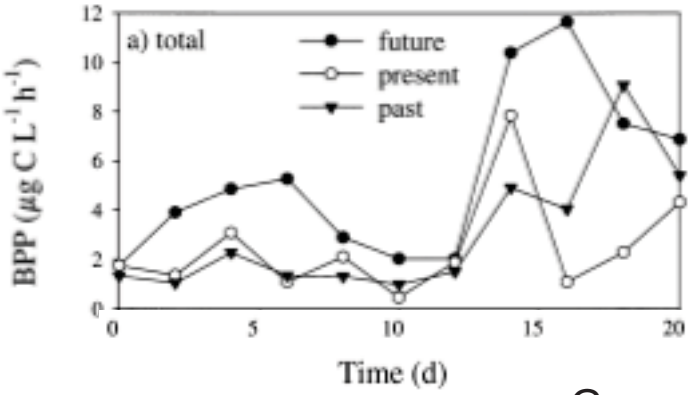
Hutchins et al. (2009) *Oceanography*



Bacterial productivity

Liu et al. (2010) *Aquatic Microbial Ecology*





Grossart et al. (2006) *Limnology & Oceanography*

Temperate (UK) processes

Borges & Gypens (2010) *Limnology & Oceanography*

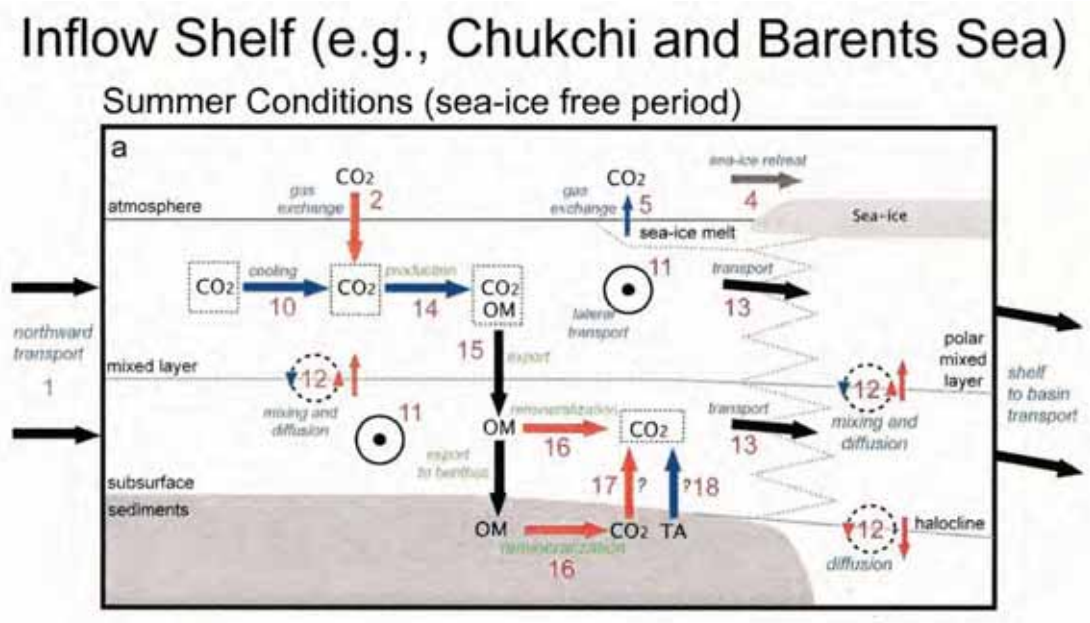
—using a numerical model…the effect of eutrophication on carbon cycling can counter the effect of ocean acidification on the carbonate chemistry of surface waters. Whether antagonistic or synergistic, the response of carbonate chemistry to changes of nutrient delivery to the coastal zone (increase or decrease, respectively) is stronger than ocean acidification."

Lab-based studies (and also Bergen mesocosms) demonstrate a nutrient moderation of the CO_2 response

Therefore broad-scale systems-based approach to test notion of nutrient control of OA in coastal systems (especially where can find HABs) will be a major step forward

Polar processes

Bates & Mathis (2009) *Biogeosciences*



How the environment regulates C-flow still largely unknown for (sub)-Polar systems; in particular, multivariate control of adaptation versus acclimation

UKOARP First Annual Science Meeting

Cambridge (Downing College), 6-7th January 2011

Sea surface impacts of OA (Consortium): WP 4

Plankton Community Composition

Alex Poulton, Mike Zubkov, Polly Hill, Ross Holland (NOC)

Geraint Tarling, Peter Ward, Victoria Peck (BAS)

Ray Leakey (SAMS)

Peter Burkill, David Johns (SAFHOS)

Jeremy Young (NHM)

Colin Brownlee, Declan Schroeder (MBA)

WP 4. Plankton Community Composition

UK Ocean Acidification Research Programme

Motivation

FAQs about Ocean Acidification (Source – EPOCA website)

An increase of CO_2 in seawater increases growth of photosynthetic algae – isn't that a good thing?

The growth and photosynthesis of certain marine phytoplankton and plant species may increase with higher CO_2 levels, but this is by no means a general rule. For other species, higher CO_2 and rising acidity will have either negative or neutral effects on their physiology. Therefore some marine phytoplankton and plants will be —winners," while others will be –losers." This means that instead of benefiting all impartially, future acidification will instead probably cause major shifts in the species composition of ocean phytoplankton communities. Some of the experiments that have been done so far suggest that the likely new dominant phytoplankton species in the future acidified ocean may be less able to support the productive food chains that we presently rely on to support healthy ocean ecosystems and fisheries resources. — *David Hutchins, Professor of Marine Environmental Biology, University of Southern California, USA*

WP 4. Plankton Community Composition

UK Ocean Acidification Research Programme

WP 4. Plankton Community Composition

UK Ocean Acidification Research Programme

WP4 Hypotheses (2009 proposal)

"H3. Community structure will change and calcifying organisms will make up less of the total community [biomass]under lower pH / saturation state conditions.

H3A. Lower saturation state will reduce the representation of calcifying plankton in the total community [biomass].

H3B. Higher saturation state will increase numbers of non-CCM (carbon-concentrating-mechanism) dependent phytoplankton."

Testing the hypotheses:

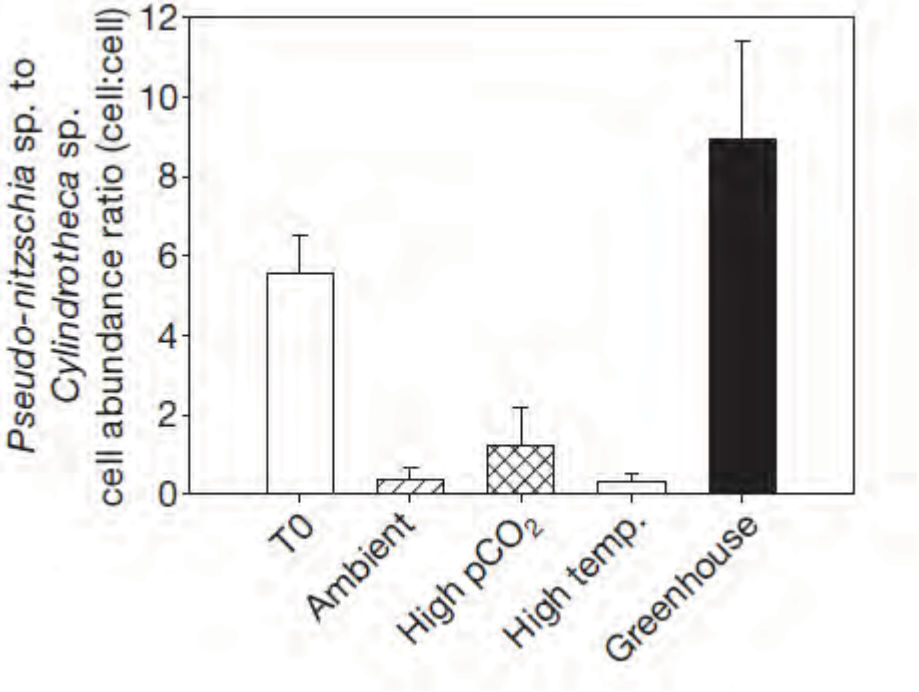
- *Biomass – chosen units of change (physiological basis)*
- *In situ / natural gradients – spatial changes, multivariate approach examining all environmental factors (temp, salinity, nutrients, irradiance, pH, saturation state, etc)*
- *Bioassays – temporal changes relative to control/ambient treatments*
- *Calcifiers – coccolithophores from water-column and bioassays; pteropods and foraminifera from water-column only (no bioassay experiments)*

WP 4. Plankton Community Composition

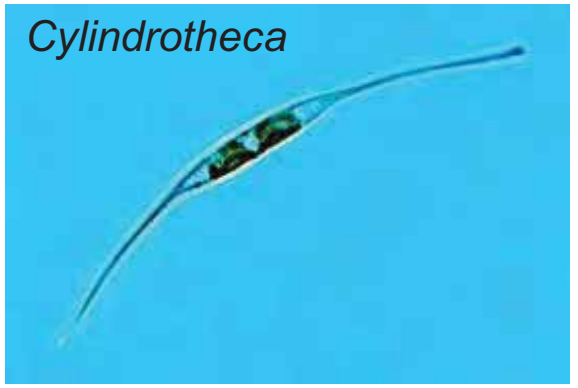
UK Ocean Acidification Research Programme

OA (& climate change) impacts may be species-specific (i.e. dependent on individual physiological / ecological traits)

Feng et al. (2009) NAB



• Greenhouse conditions favoured growth of chain-forming pennate diatom rather than solitary pennate diatom



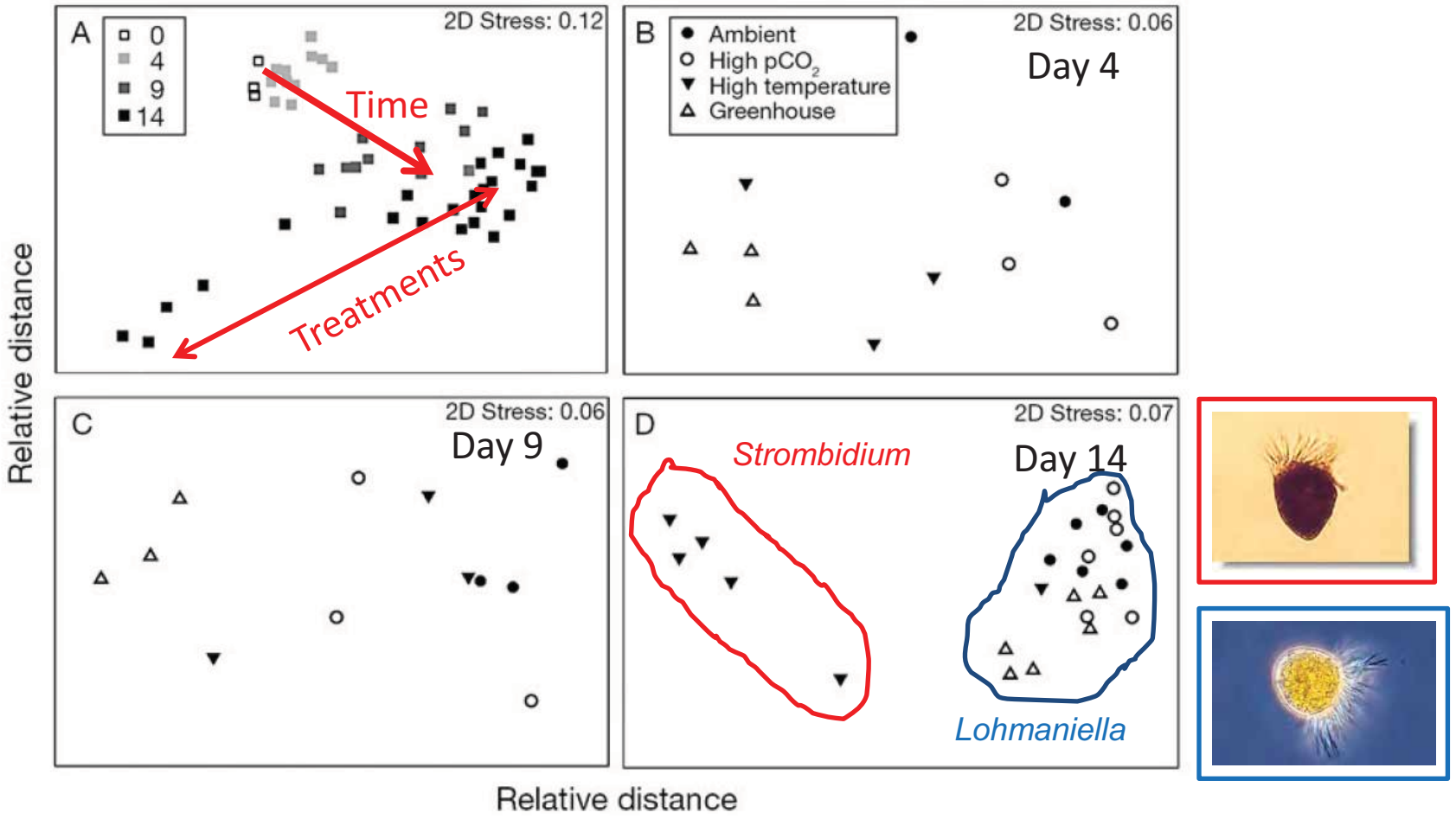
Both appear to be widespread opportunists (Marchetti et al. 2009, Hinz et al. submitted, Poulton pers. obs)

WP 4. Plankton Community Composition

UK Ocean Acidification Research Programme

Requires a multivariate approach to analyse community composition

Rose et al. (2009) NAB

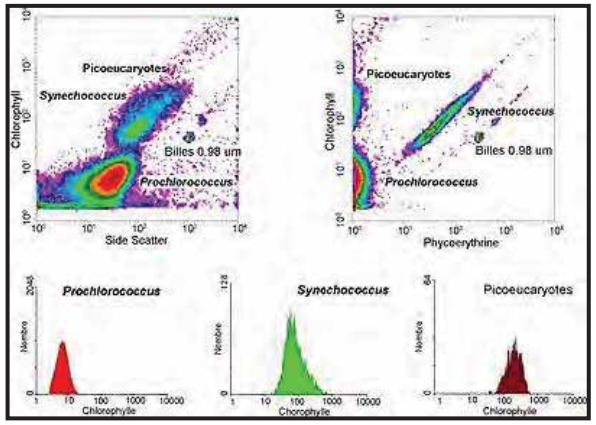


Challenge is to link changes in natural communities to environmental drivers (and partition their relative roles in causing change)

WP 4. Plankton Community Composition

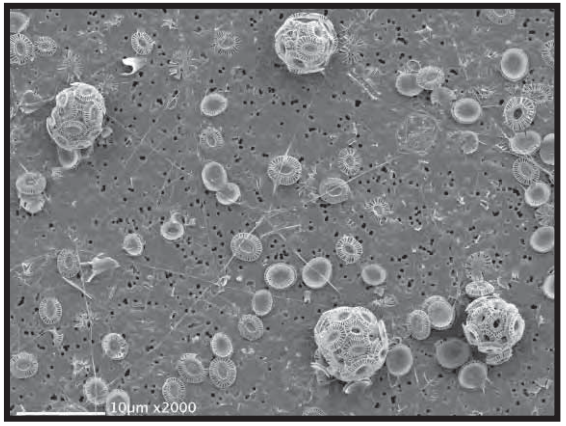
UK Ocean Acidification Research Programme

Our plans – Combination of techniques

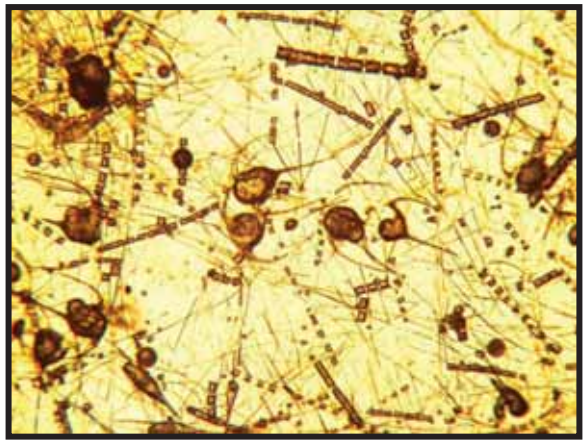


Flow cytometry

FlowCAM

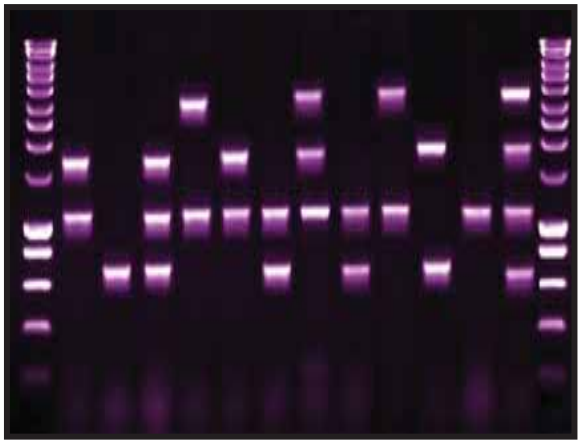


Scanning Electron Microscopy



Light Microscopy

Light Microscopy



Genotyping

WP 4. Plankton Community Composition

UK Ocean Acidification Research Programme

People & tasks

Mike Zubkov, Polly Hill, Ross Holland (NOC) – Flow Cytometry & FlowCAM

Alex Poulton (NOC) & Ray Leakey (SAMS) – Microplankton, Light Microscopy

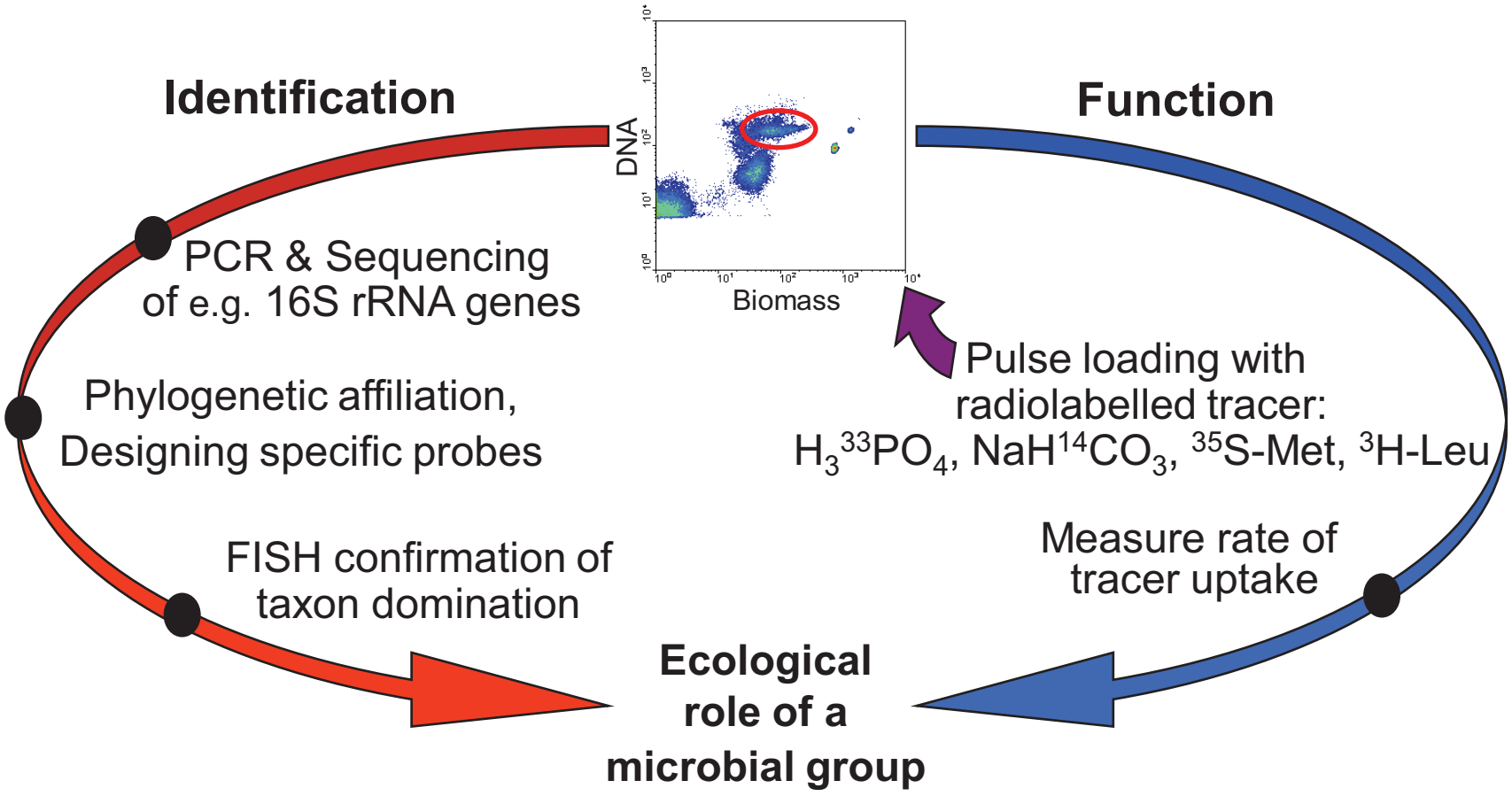
Geraint Tarling, Peter Ward, Victoria Peck (BAS) – Vertical net hauls; plankton; foraminifera & pteropods

Peter Burkill, David Johns (SAFHOS) – CPR; plankton; foraminifera & pteropods

Jeremy Young (NHM) – Coccolithophores; small diatoms & other mineralisers

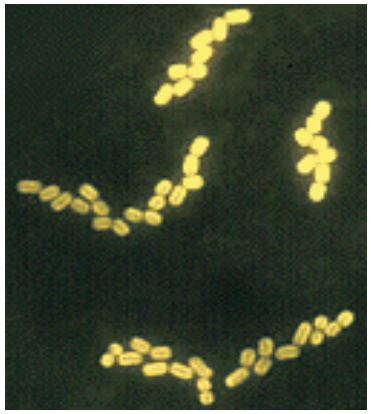
Colin Brownlee, Declan Schroeder (MBA) – Genotyping; *E huxleyi* morphotypes

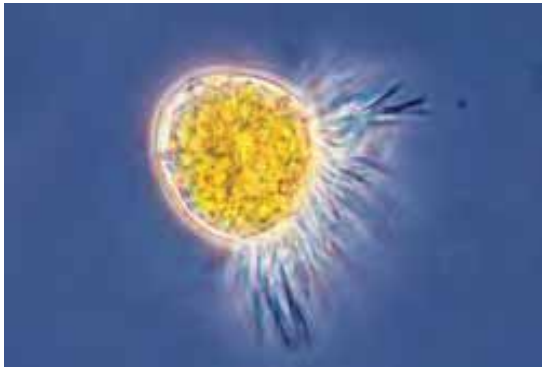
Approach to study microbial interactions
using
flow cytometric sorting



Zubkov et al., 2001, Appl. & Environ. Microbiol., 67:5210-5218

Food web interactions





Experimental addition of individual microzooplankton and mesozooplankton to bottles containing pCO2 manipulated phytoplankton

Gut fluorescence / grazing rate

UKOARP – Sea Surface Consortium

6th January 2011

Assessing impacts of OA on Climate

Andy Rees, PML

H4a: *OA will impact on the efficiency of the biological carbon pump by reducing CaCO3 concentrations and hence ballast efficiency (NOCS-NERC).*

H4b: *OA will decrease nitrification rates and hence decrease the sea to air flux of N_2O (PML).*

H4c: *OA will lead to reduced DMS flux from the oceans to the atmosphere (PML).*

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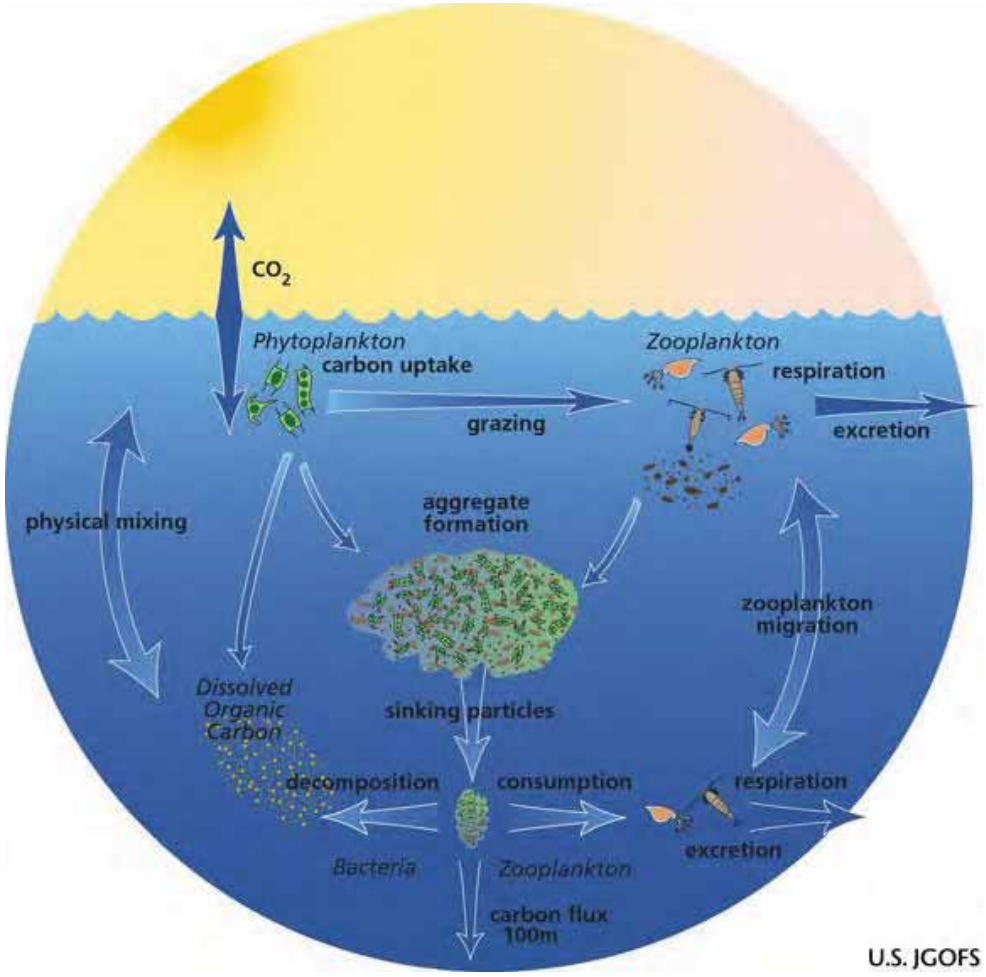
PML | Plymouth Marine Laboratory

Ocean Acidification (OA) and efficiency of the Biological Carbon Pump (BCP)



- Tied studentship (2010-2014)
- Helen Smith
- Supervisors: Alex Poulton, Richard Lampitt, Richard Sanders
- Complex issue – Possible direct OA impact on several aspects of BCP, including:

  1) Ballast material (calcite, opal)

  - Production / dissolution

  2) Aggregation processes

  - TEP (‚the glue‘) production / degradation

- Pelagic consortium – strong regional and experimental components
- Need to adopt an approach which addresses both regional and mechanistic differences in fluxes

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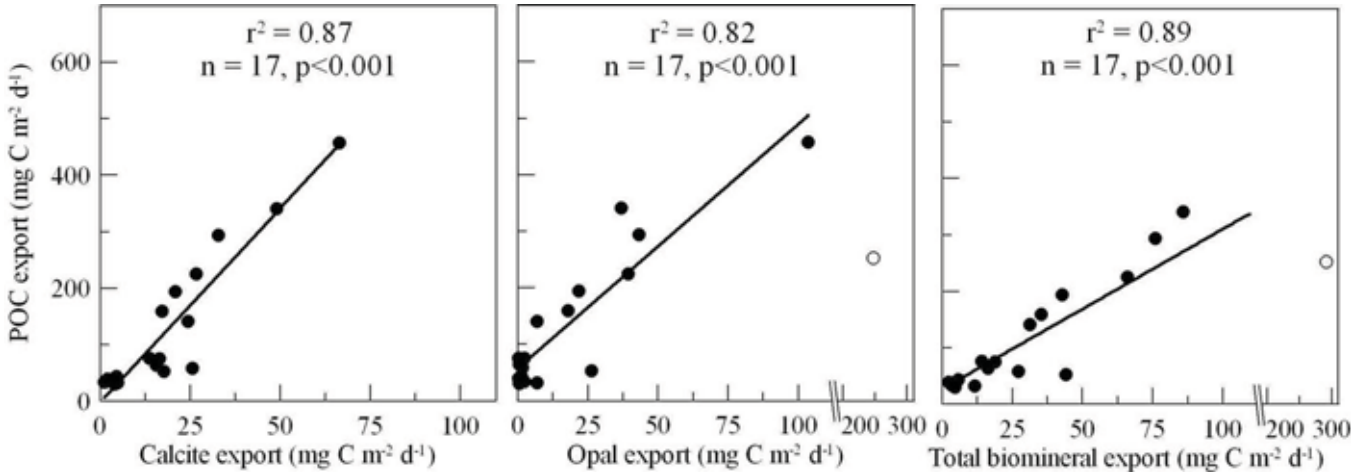
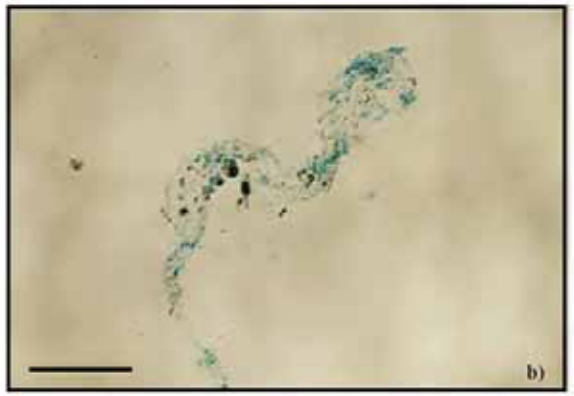
Ocean Acidification (OA) and efficiency of the Biological Carbon Pump (BCP)

Klaas & Archer 2002 GBC: **Deep (>1 km) correlations between opal, calcite and POC fluxes in material caught in sediment traps – "***Most of the organic carbon rain in the deep sea is carried by calcium carbonate, because it is denser than opal and more abundant than terrigenous material."*

Sanders et al. 2010 GRL: **Shallow (<0.1 km) correlations between opal, calcite and POC fluxes derived from ^{234}-Thorium disequilibrium –** *"Correlations found in deep-sea originate in the surface ocean"*



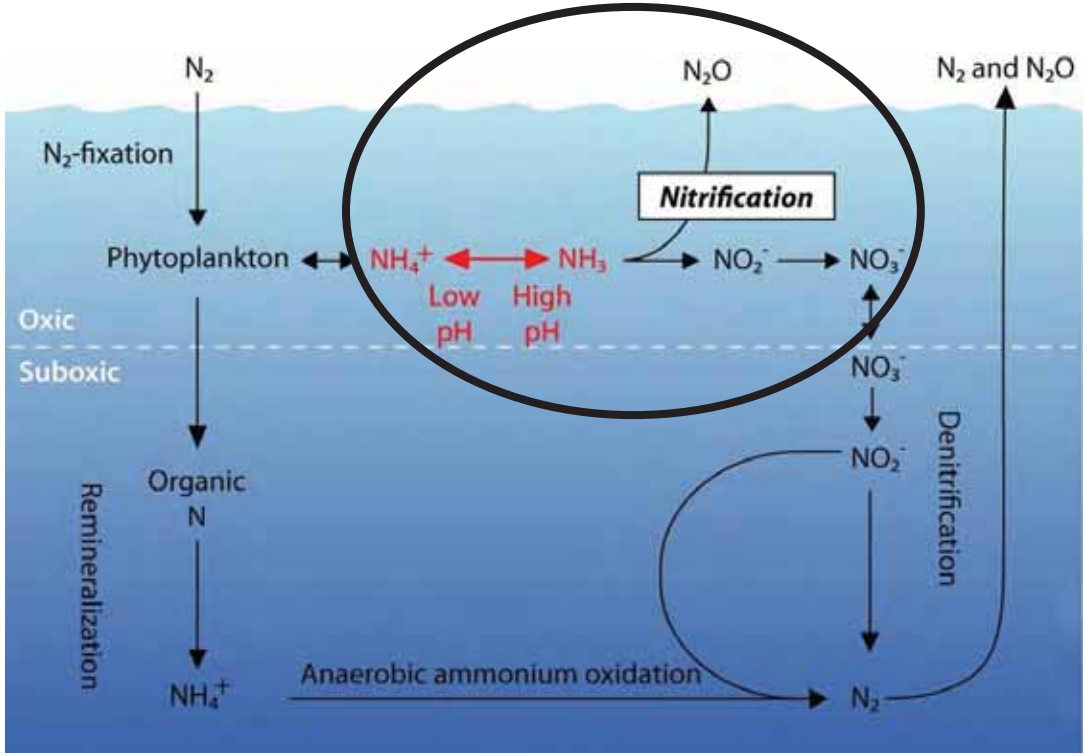


Microscopic view of TEP retained on a filter stained with Alcian Blue (Passow 2002)

- TEP are very sticky particles that exhibit the characteristics of gels, predominantly acidic polysaccharides (Passow 2002 Prog Ocean 55)
- TEP enhance or even facilitate the aggregation of particles (precursers), matrices of all marine aggregates (Passow 2002 Prog Ocean 55)
- TEP abundance and size distribution linked to plankton composition, higher in coastal and shelf waters (Passow & Alldredge 1994 MEPS 113)
- TEP production linked to CO_2 concentration (Engel 2002 JPR 24)
- Rich source of carbon to microbial system – linked to bacterial production (Ortega-Retueta et al. 2010 Micro Ecol 59)

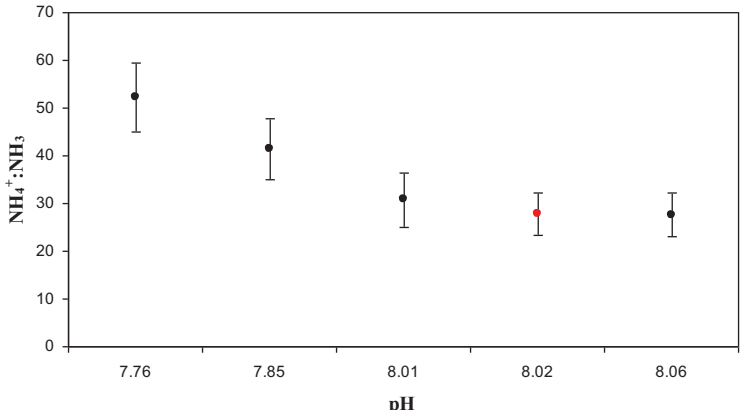
Ocean acidification and N_2O flux

Andy Rees, Darren Clark, Ian Brown

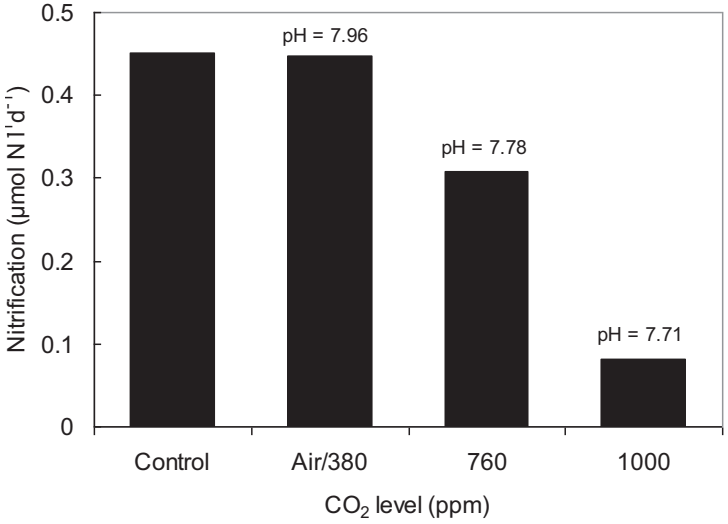


- N_2O highly potent greenhouse gas and key factor in stratospheric ozone destruction.
- release during nitrification
- All published data (for all environments) indicate that ammonia oxidation slows as pH decreases.
- 0.1 decrease in ocean pH (20-30 y) predicted decrease of 3-44% in NH_3.Ox rates will result in ***reduced N_2O emissions comparable to current production from fossil fuel combustion and industry*** (Beman et al 2010).

Ocean acidification and N_2O flux



Increased ratios of NH_4^+ to NH_3 at L4 with decreasing pH during late March and April. Values are shown as mean ratio with standard deviation representing natural variation. Ambient ratio is shown in red



Nitrification rates determined by 14C uptake and ATU inhibition at Station L4 in the western English Channel during July 2008

- pH may affect ammonia monooxygenase directly but observations indicate that declining NH_3 with OA is the driving factor in NH_3Ox reduction. (*Beman et al 2010).*

- NH_4^+:NH_3 equilibrium is sensitive to pH

  $NH_3 + H^+ \Leftrightarrow NH_4^+$

- Our data from L4 confirm sensitivity of NH_4^+:NH_3 (*Wyatt et al 2010*) and nitrification (*Rees et al 2009*) to OA.

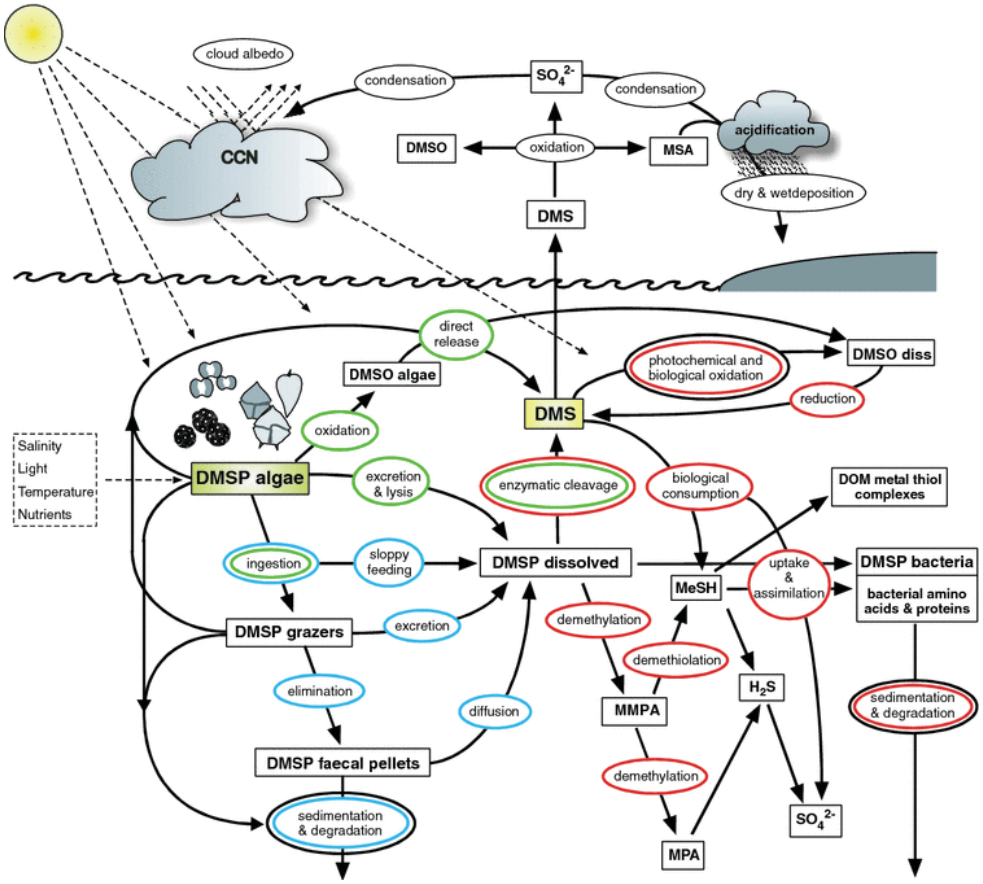
- BUT: —Marine N_2O production may rise substantially as a result of eutrophication, warming and OA" – *Codispoti 2010*

-N_20 yield increases with decreasing O_2

- OA decrease of ballast (H4a) reduces sinking favouring respiration => hypoxia
- Warming => deoxygenation

Ocean acidification and DMS emissions

Archer, Hopkins, Stephens, Kimmance, Nightingale



Mesocosm studies have shown (3 out of 4) that DMSP and DMS concentrations alter in the face of altered CO_2.: But there is limited mechanistic understanding of why.

Altered pCO_2 could impact on DMS production by:

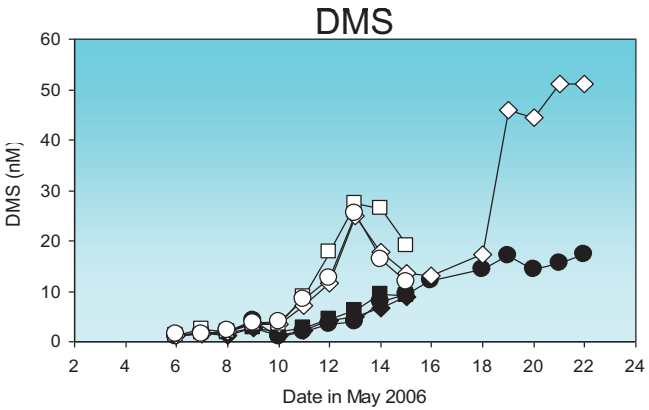
+ or – calcifyers (high DMS producers?)

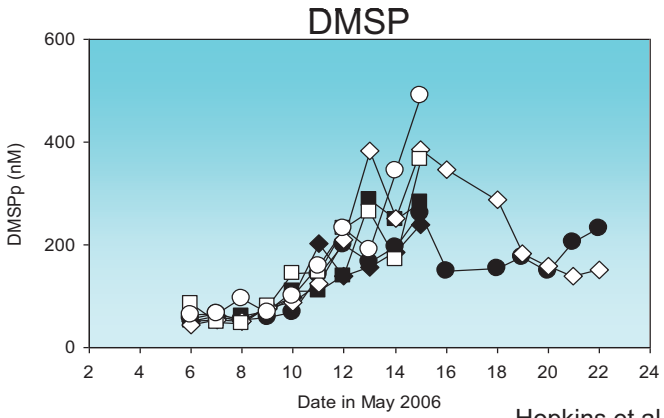
1. altered phytoplankton compatible solute / antioxidant requirements: (+ or – DMSP)
2. physiological forcing of taxonomic change (+ or – DMSP)
3. affect on total primary production (+ or – DMSP)
4. heterotrophic utilisation of DMSP and DMS (+ or – DMS)

OA and DMS: previous results

Bergen, Norway, mesocosms: *E. huxleyi* bloom conditions

300 µatm vs. 750 µatm

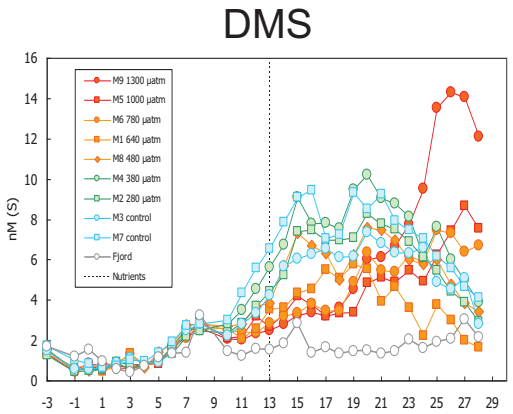


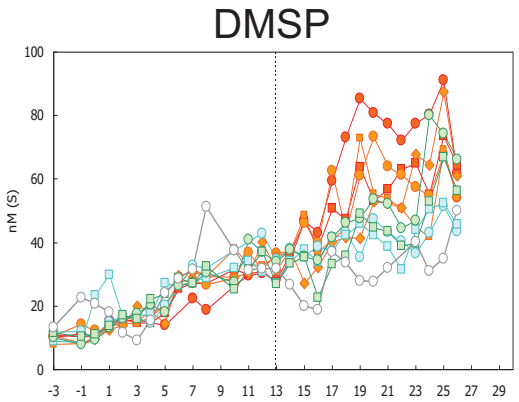


Hopkins et al. **2010 PNAS**

Svalbard, Arctic, pelagic mesocosms: complex taxonomic succession

190 µatm to ~1300 µatm





Experimental day

Stephens et al. EPOCA 2010

- high CO_2 appears to result in reduced DMS production,
- possibly driven by reduced DMSP production,
- but more likely a result of the complex processes that govern DMSP conversion to DMS

Plans for OA project: what we'll do

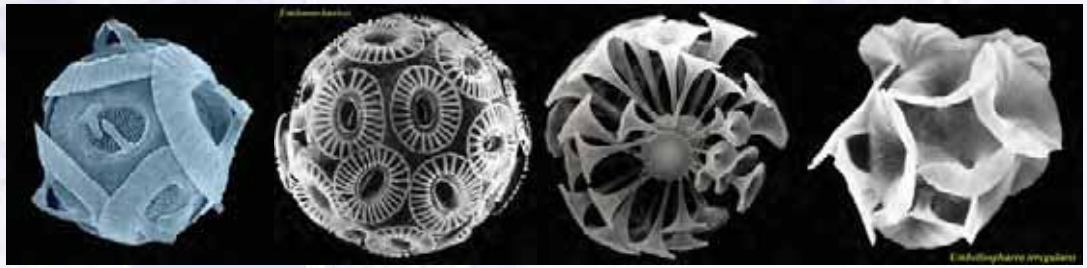
During cruises to European shelf, Arctic, Antarctic under natural conditions and manipulated experiments:

- Measurements of TEP abundance and production
- Export fluxes (POC, PIC & Opal) via 234Thorium disequilibrium
- Snow Catcher to characterise sinking particles

- Nitrification rates
- N_2O concentration and air-sea flux

- Determine DMS, DMSP and DMSO concentrations
- Eco-physiological changes in DMSP production
    - DMSP specific synthesis rates
    - determination of taxon-specific DMSP content

- Heterotrophic DMSP conversion to DMS and DMS loss



Mechanistic understanding of OA impacts on coccolithophores

Colin Brownlee, Declan Schroeder, Andrea Baker (MBA)
Ros Rickaby (Oxford)

- Calcification and other responses -variability
- Calcification mechanism – Identify pH-dependent processes: potential mechanisms of adaptation
- Population-level responses - Genetic and physiological variability and adaptation

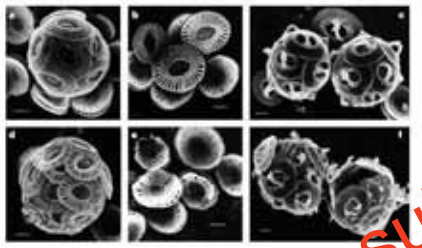
THE MARINE BIOLOGICAL ASSOCIATION

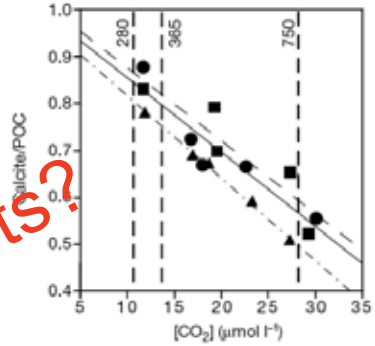
UNIVERSITY OF OXFORD

Reduced calcification of marine plankton in response to increased atmospheric CO_2

Ulf Riebesell *, Ingrid Zondervan*, Björn Rost*, Philippe D. Tortell*
Richard E. Zeebe*‡ & François M. M. Morel†

NATURE | VOL 407 | 21 SEPTEMBER 2000 | www.nature.com





Species-specific responses of calcifying algae to changing seawater carbonate chemistry

Gerald Langer and Markus Geisen
Biogeosciences, Biological Oceanography, Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, D-27570 Bremerhaven, Germany (glanger@awi-bremerhaven.de; mgeisen@awi-bremerhaven.de)

Karl-Heinz Baumann
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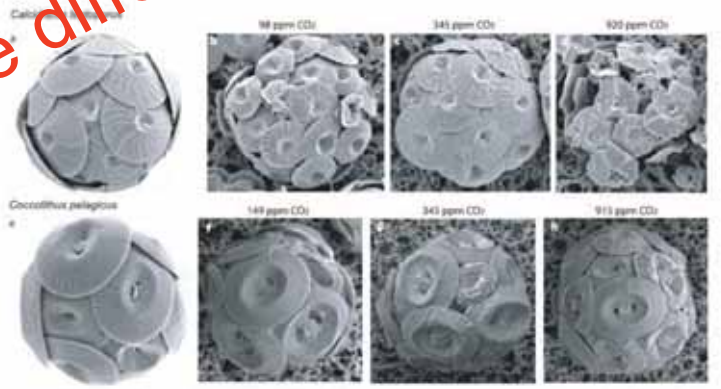

Geochemistry Geophysics Geosystems
AN ELECTRONIC JOURNAL OF THE EARTH SCIENCES
Research Letter
Volume 7, Number 9
20 September 2006
Q09006, doi:10.1029/2006GC001227
ISSN: 1525-2027

Why do different studies give different results?

Phytoplankton Calcification in a High-CO_2 World

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18 APRIL 2008 VOL 320 **SCIENCE** www.sciencemag.org

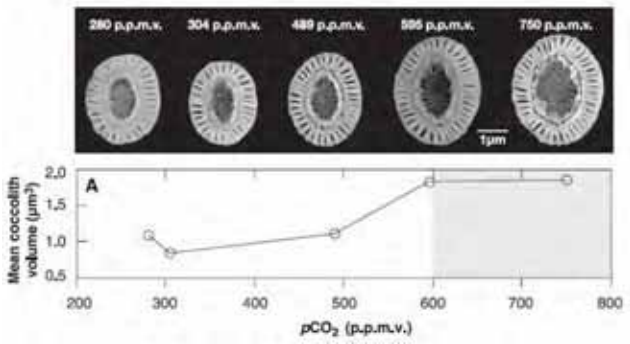


Table 1. Synthesis of available coccolithophorid calcification carbonate chemistry manipulation experiments.

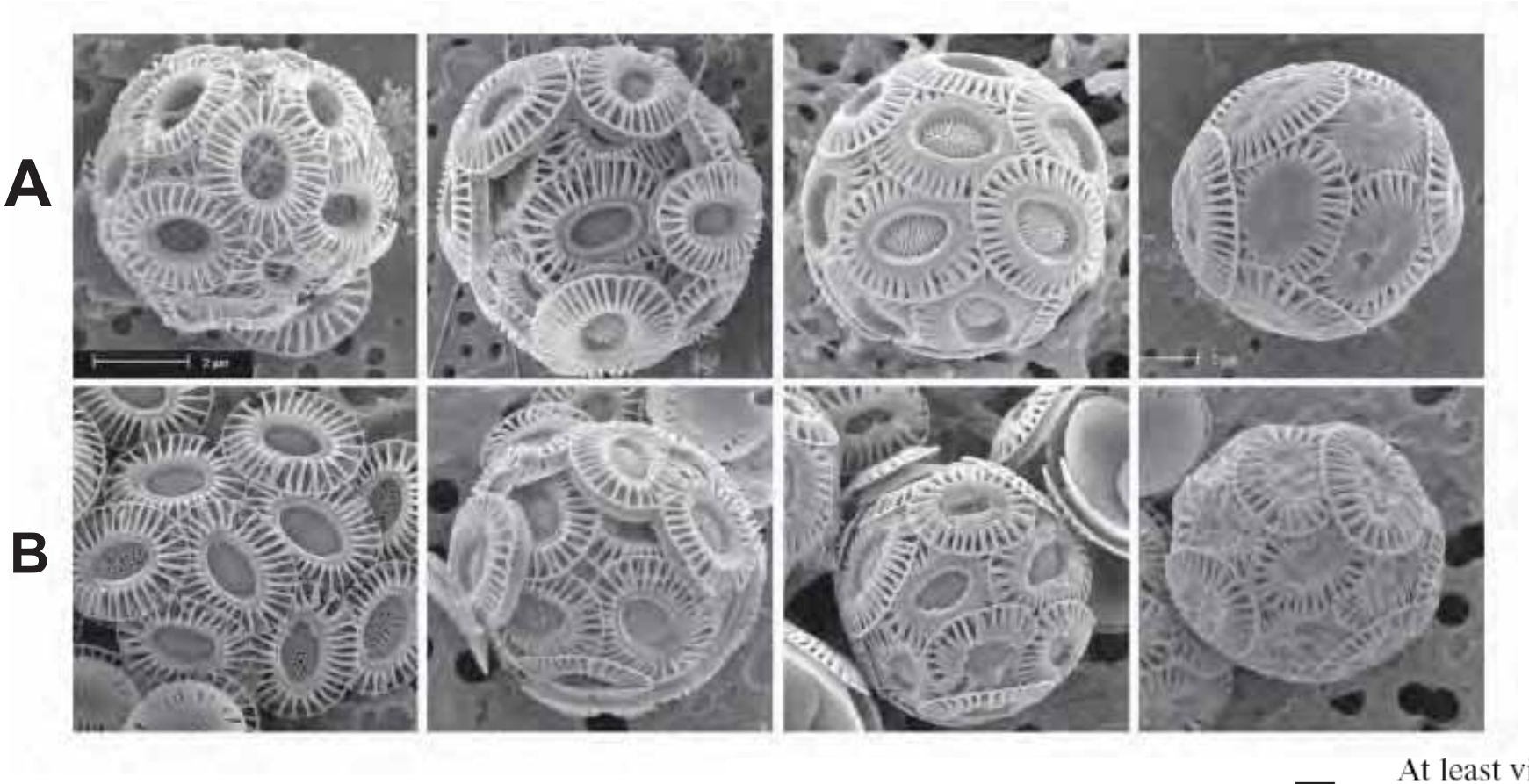
Species	Strain (Clone)	Isolation date and location	Experimental design	Ambient light environment [1]	Carbonate chemistry manipulation	Calcification response [2]	Calcification response [3]	$CaCO_3$/POC response [10]	Reference [11]
Emiliania huxleyi	NZEH (CAWPO6)	1992 South Pacific	laboratory culture	12:12 h L:D 150 µmol m^{-2} s^{-1}	CO_2 bubbling	↑	↑	↔	*1*
Emiliania huxleyi	MBA 61/12/4	1991 North Atlantic	laboratory culture	12:12 h L:D 150 µmol m^{-2} s^{-1}	CO_2 bubbling	↑	↑	n/a	*1*
Emiliania huxleyi	PML B92/11A	1992 North Sea	laboratory culture	18:6 h L:D 150 µmol m^{-2} s^{-1}	acid/base	n/a	↓	↓	*2,5*
Emiliania huxleyi	PML B92/11A	1992 North Sea	laboratory culture	24:0 h L:D 150 µmol m^{-2} s^{-1}	acid/base	n/a	↓	↓	*2,5*
Emiliania huxleyi	CCMP 371	1987 Sargasso Sea	laboratory culture	12:12 h L:D 50 µmol m^{-2} s^{-1}	CO_2 bubbling	↔	n/a	↓	*3*
Emiliania huxleyi	CCMP 371	1987 Sargasso Sea	laboratory culture	12:12 h L:D 400 µmol m^{-2} s^{-1}	CO_2 bubbling	↓	n/a	↓	*3*
Emiliania huxleyi	TW1	2001 W Mediterranean	laboratory culture	24:0 h L:D 570 µmol m^{-2} s^{-1}	CO_2 bubbling	↓	↓	↔	*4*
Emiliania huxleyi	88E	1988 Gulf of Maine	laboratory culture	24:0 h L:D 50 µmol m^{-2} s^{-1}	acid/base	n/a	↔ [4]	↔ [4]	*9*
Emiliania huxleyi	Ch 24-90	1991 North Sea	laboratory culture	16:8 h L:D 300 µmol m^{-2} s^{-1}	CO_2 bubbling	n/a	↔ [5]	↔ [5]	*10*
Emiliania huxleyi	NZEH (PLY M219)	1992 South Pacific	laboratory culture	24:0 h L:D 150 µmol m^{-2} s^{-1}	acid/base	↑	↑	↔	*11*
Gephyrocapsa oceanica	PC7/1	1998 Portuguese shelf	laboratory culture	18:6 h L:D 150 µmol m^{-2} s^{-1}	acid/base	n/a	↓	↓	*2,5*
Calcidiscus leptoporus	AC365	2000 South Atlantic	laboratory culture	16:8 h L:D 350 µmol m^{-2} s^{-1}	acid/base	n/a	↓ [6]	↓ [6]	*6*
Coccolithus pelagicus	AC400	2000 South Atlantic	laboratory culture	16:8 h L:D 350 µmol m^{-2} s^{-1}	acid/base	n/a	↔	↔	*6*
Emiliania huxleyi [7]	n/a	n/a (North Sea)	mesocosm [8]	95% of ambient surface irradiance	CO_2 bubbling	n/a	↓ [9]	↓ [9]	*7,8*
subarctic North Pacific natural assemblages	n/a	n/a (N. Pacific)	ship-board incubation	30% of ambient surface irradiance	CO_2 bubbling	n/a	↓ [9]	↓ [9]	*2*
subarctic North Pacific natural assemblages	n/a	n/a (N. Pacific)	ship-board incubation	30% of ambient surface irradiance	acid/base	n/a	↓ [9]	↓ [9]	

- **CO_2 manipulation conditions**
- **Species/strain optima: "Eppley" response**
- **Previous culture history**
- **Difficult to disentangle!**

A. Ridgwell et al.:

Biogeosciences, 6, 2611–2623, 2009

Natural variability in coccolithophopre populations:



A: Variability in plankton samples

B: Different strains

—At least visually, the natural variability present between different strains appears equal to or exceeds that due to culturing experiments under varying pCO_2 (e.g., Riebesell et al., 2000). Arguably we should regard *E. huxleyi* as a diverse assemblage of genotypes with highly variable calcification characteristics and ecological adaptations. The substantial variability in degree of calcification between genotypes suggests that future changes in genotype assemblage could be important.—

A. Ridgwell et al.: Biogeosciences, 6, 2611–2623, 2009

How might ocean pH affect the calcification mechanism?

NATURAL ENVIRONMENT RESEARCH COUNCIL

Need to understand:

Oceans 2025

- Transport pathways

BBSRC bioscience for the future

- Rate-limiting pH-dependent processes

- Energetics

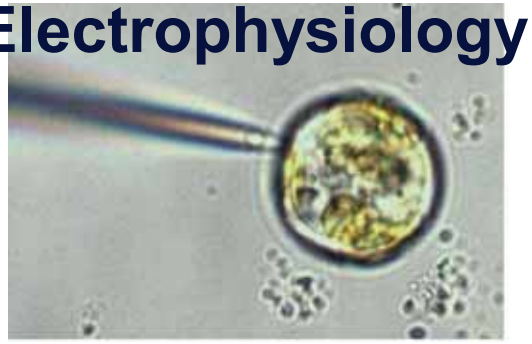
EPOCA European Project on Ocean Acidification

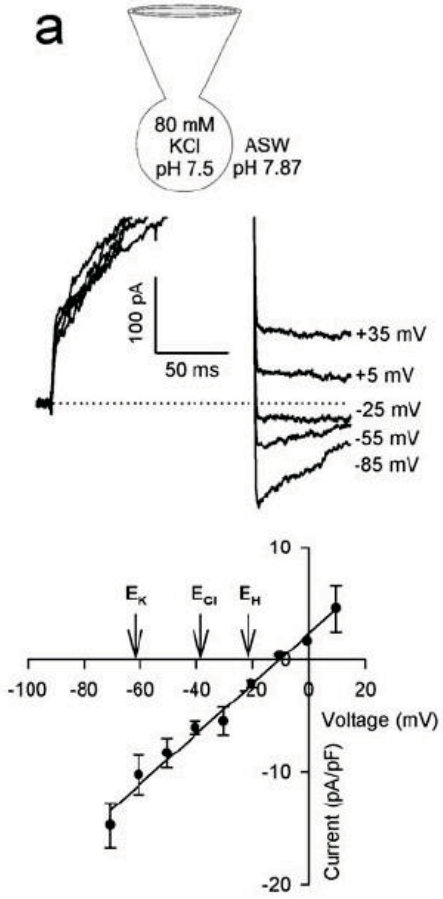
- Celullar homeostasis mechanisms

cal.mar.o

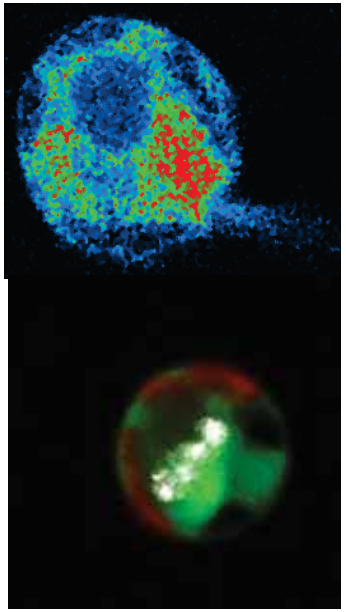
Approaches to identify pH-dependent mechanisms

Electrophysiology



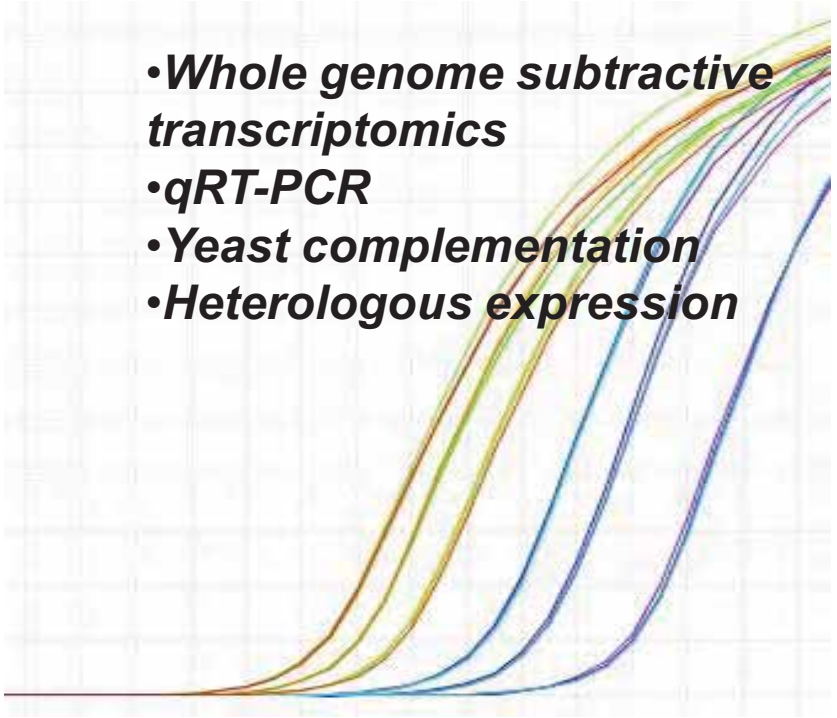


pH imaging



Functional genomics

- ***Whole genome subtractive transcriptomics***
- ***qRT-PCR***
- ***Yeast complementation***
- ***Heterologous expression***



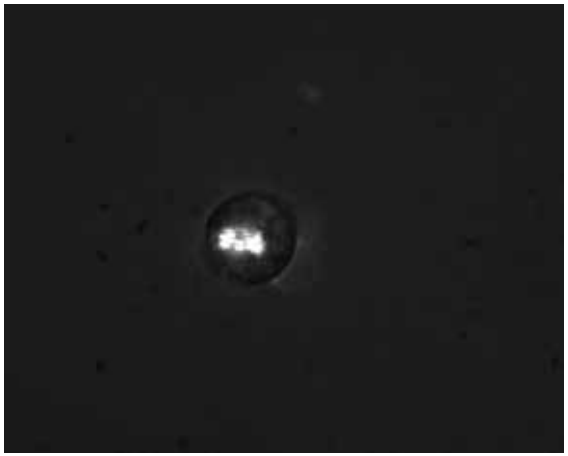
Examples:

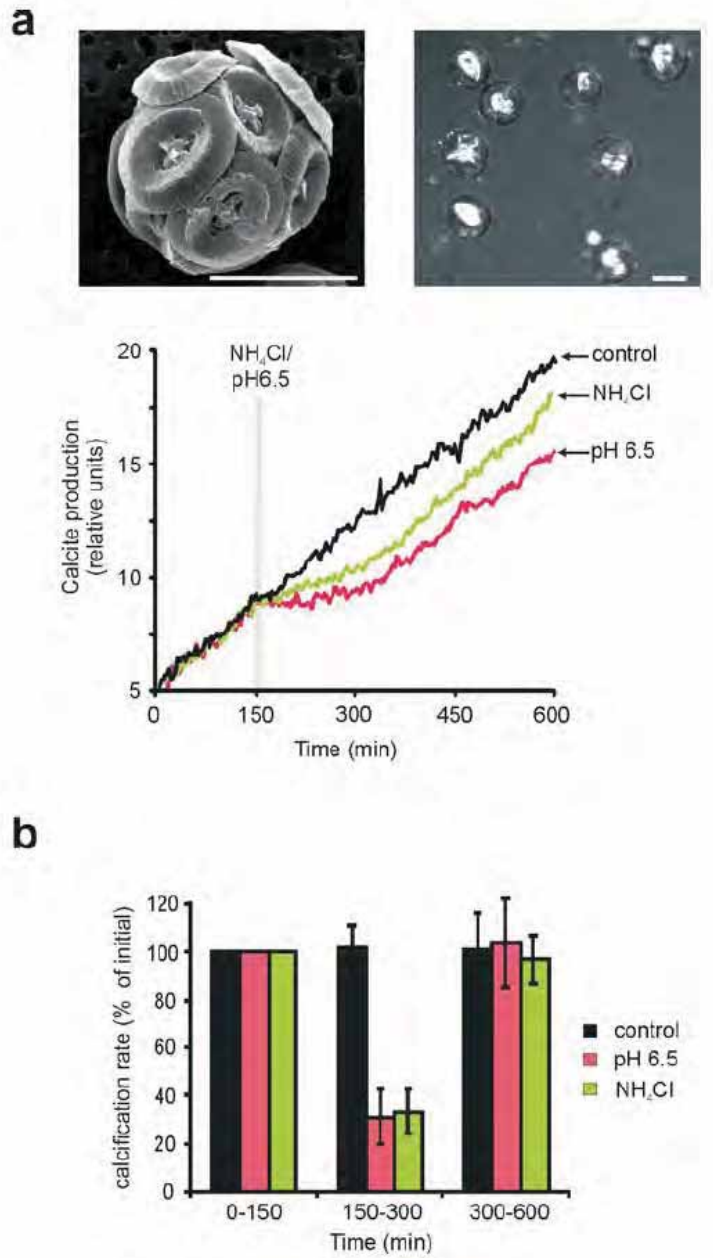
SLC4** ECA2*
(Ca ATPase)
CAX3****
γCA*
V-ATPAse*
Na/Ca exchanger*

GPA*
CAX4*

Single cell or population calcification rate in vivo

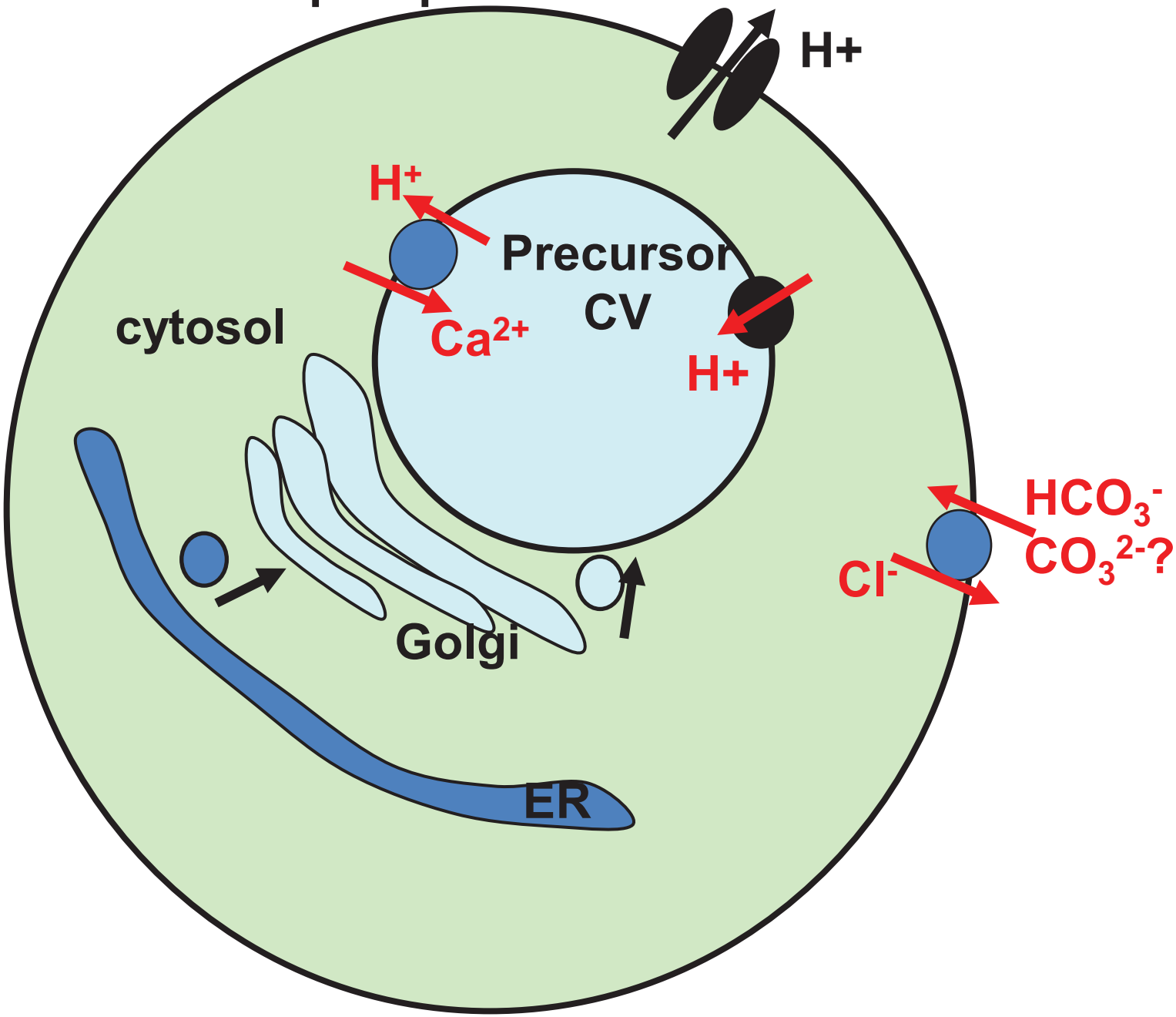
Calcification is dependent on maintenance of cytoplasic pH





Taylor et al PLoS biology (submitted)

pH-dependent transport processes



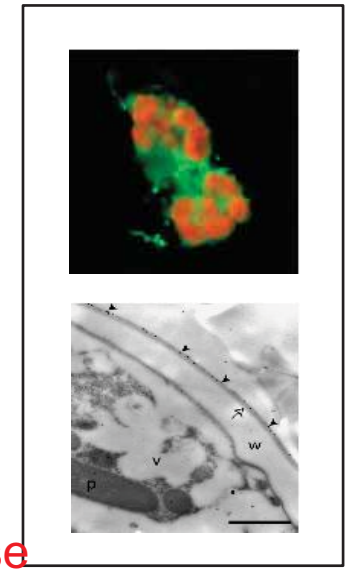
Candidate CCM genes

e.g. δ-CA, HCO_3^- transporter (e.g. NAR 1.2), pyrenoids

$$CO_2 + H_2O \longleftrightarrow HCO_3^- + H^+$$

Carbonic anhydrase

- δ-CA First characterized in *T. weissflogii* (Roberts *et al.* 1997)
- Subsequently characterized in *E. huxleyi (*Soto *et al.* 2006) and *L. polyedrum* (Lapointe *et al.* 2008)
- Localized to the cytosol in *T. weissflogii* and plasma membrane in *L. polyedrum*



Morel *et al.* (2002) Funct Plant Biol
Lapointe *et al.* (2008) Plant Phisiol

We have performed TWCA1 cloning, overexpression, extraction and detection and demonstrated δ-CA is both a functional esterase (nitrophenyl acetate hydrolysis assay) and CA

CA activity assay

Electrometric assay

$$CO_2 \quad H_2O \xrightarrow[CA]{+} H_2CO_3$$

Wilbur & Anderson 1948

- Time required for a saturated CO_2 solution to lower the pH of the Tris-HCl buffer from 8.3 to 6.3 at 0°C

Specific activity

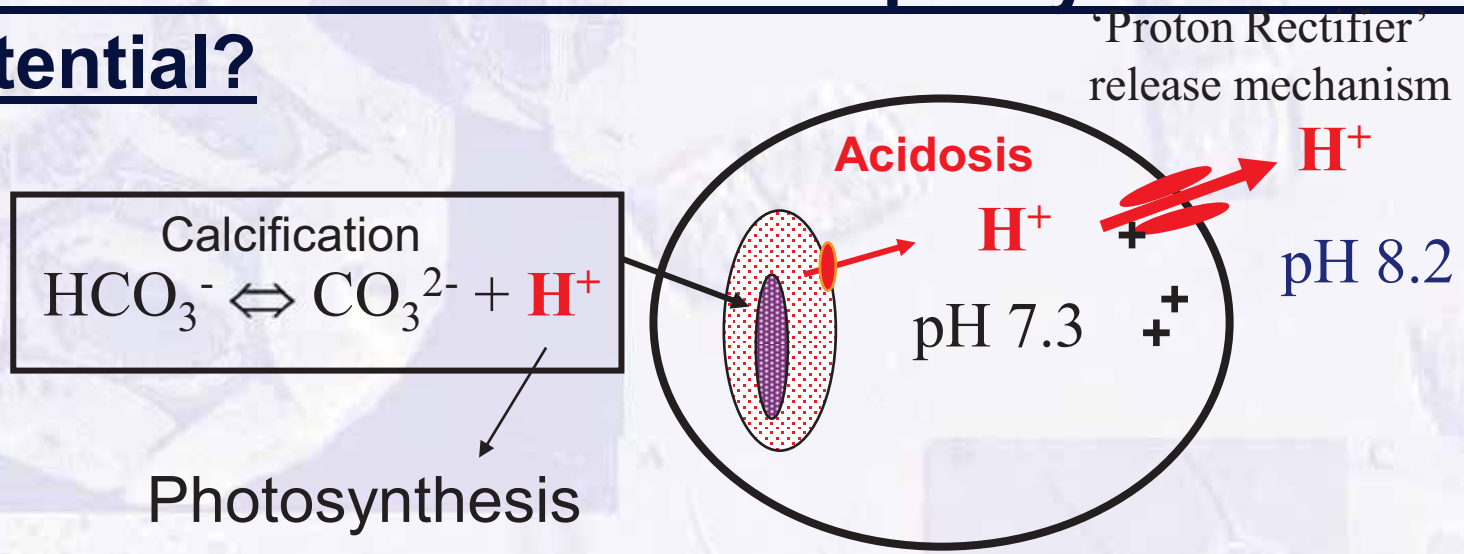
Measured

TWCA1 : 281 WA U/mg	Positive control (α-CA) : 723 WA U/mg

Published

csoS3 (ε-CA) : 234 WA U/mg [1]	*P. tricornutum* (β-CA) : 1144 WA U/mg [2]	*T. elongatus* (γ-CA) : 445 WA U/mg [3]

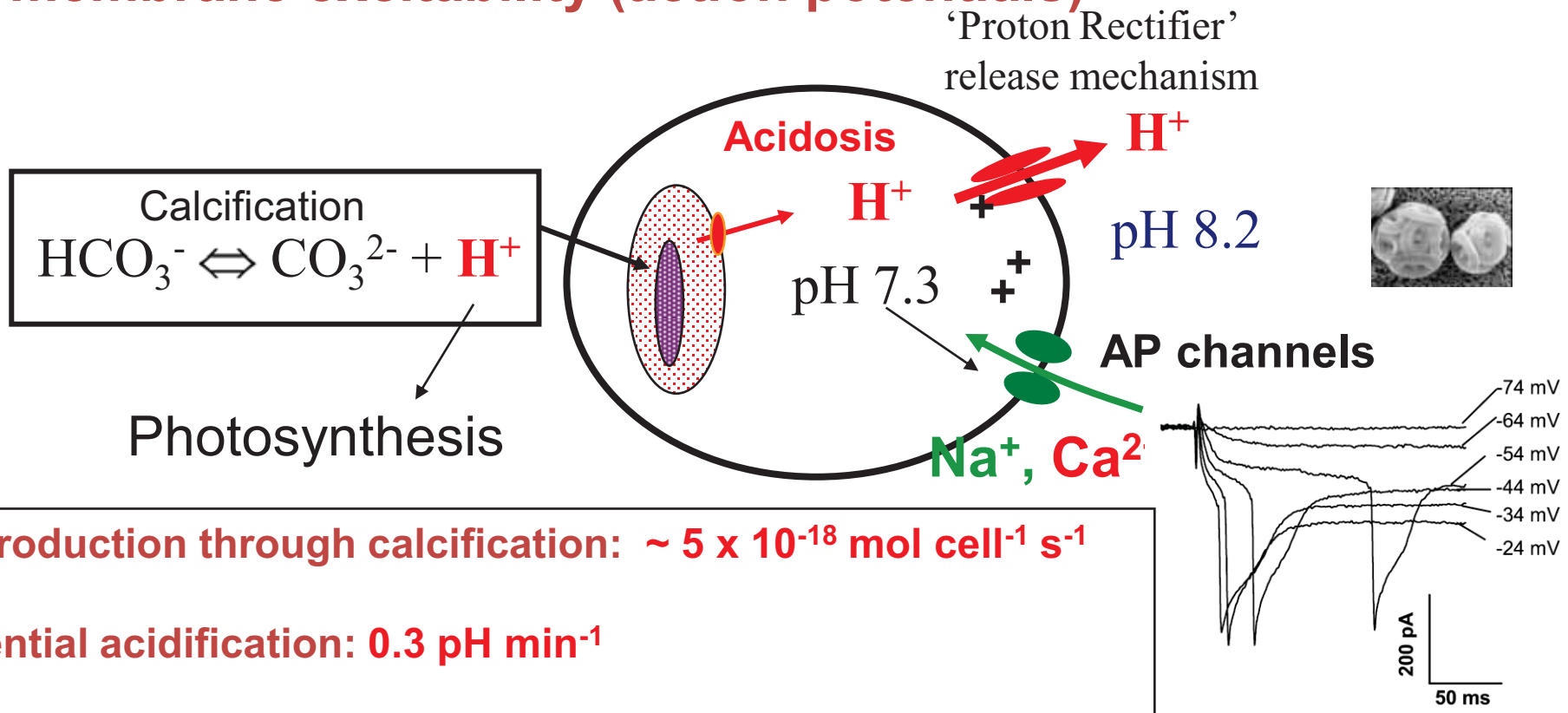
Fine control of intracellular pH by membrane potential?



- *H^+ conductance in the membrane is the major mechanism for pH regulation*
- *pH homeostasis can be maintained by regulation of the membrane potential*
- *Metabolic cost ($kJmol^{-1}$ H^+) can be calculated in terms of ATP for average decreases in external pH*

Strategies for membrane control of pH_i at lowered pH_o

Via membrane excitability (action potentials)



Coccolithophore AP

Taylor & Brownlee 2003
Plant Physiology

H^+ production through calcification: ~ 5 x 10^{-18} mol $cell^{-1}$ s^{-1}

Potential acidification: 0.3 pH min^{-1}

H^+ current required to balance H^+ production: 0.3 pA $cell^{-1}$

AP currents: ~200 pA

Vm only needs to be depolarized via APs for <<1% of time ~ 1 AP s^{-1}

Key questions:

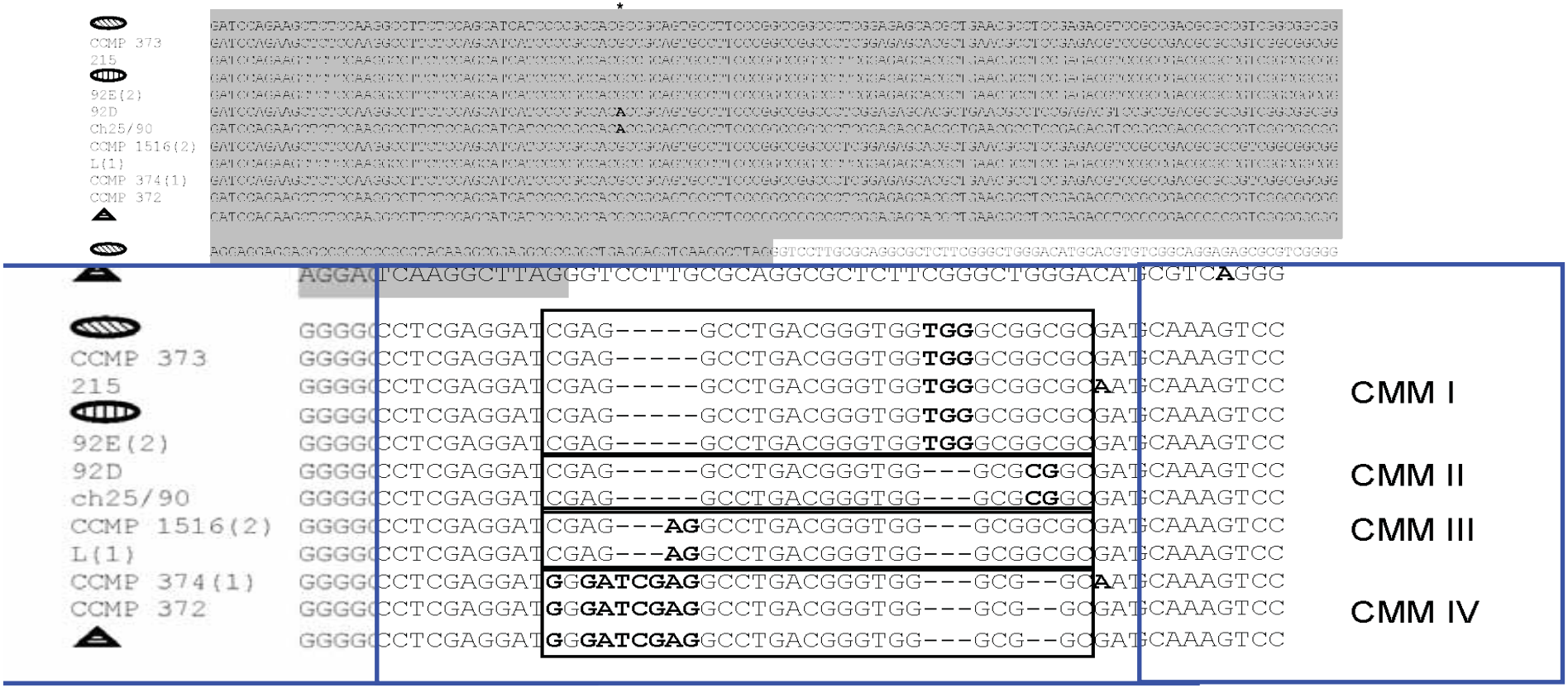
Given what is now known about potential physiological adaptations to lower ocean pH, can any relevant variability/adaptation be detected in natural populations?

How variable are natural populations?

Objectives: Assess physiological and genetic variability relevant to calcification in freshly isolated natural populations.

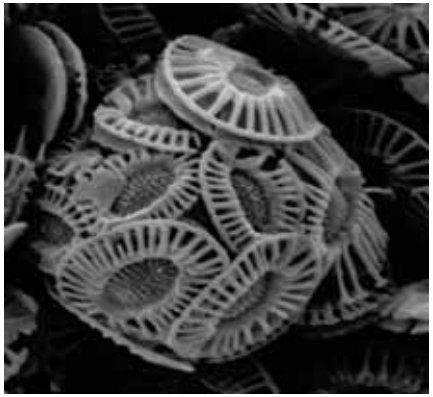
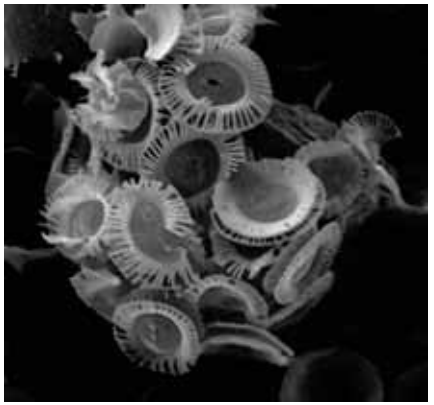
How much *relevant* genetic variability exists in natural populations?

e.g. GPA gene : morphotype-specific sequences



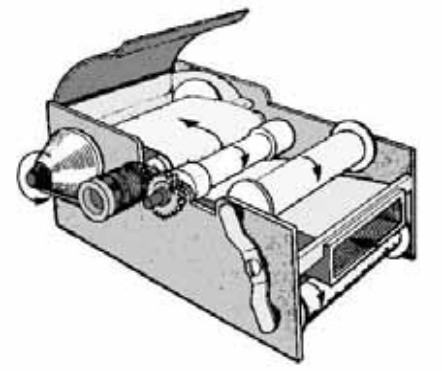
Declan Schroeder
Steve Ripley
Andrea Baker
Matt Hall

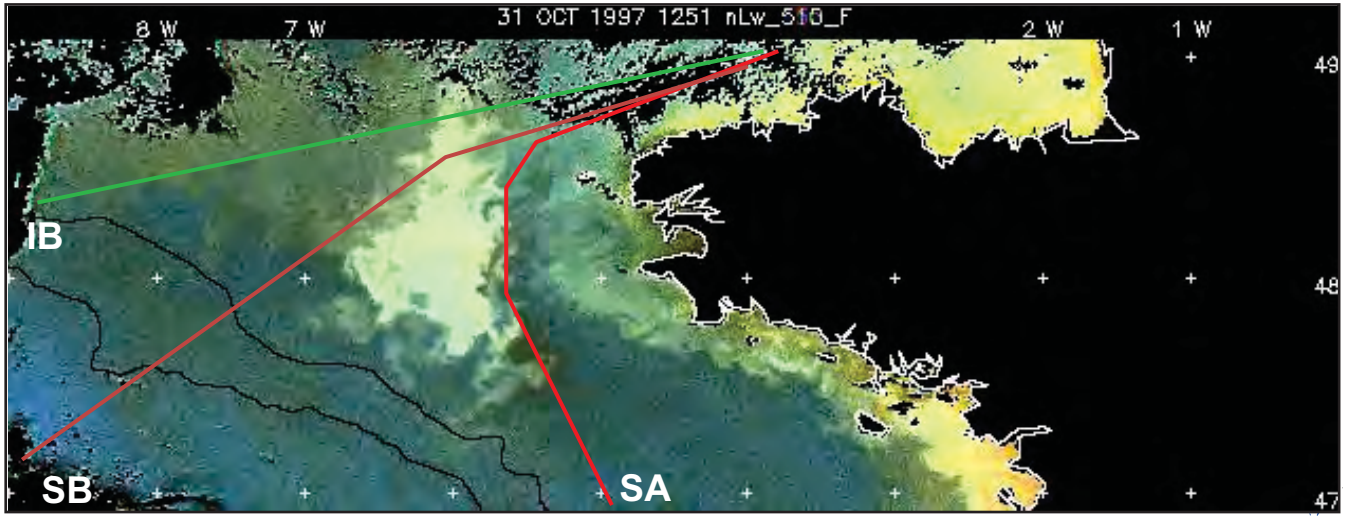
Calcification marker

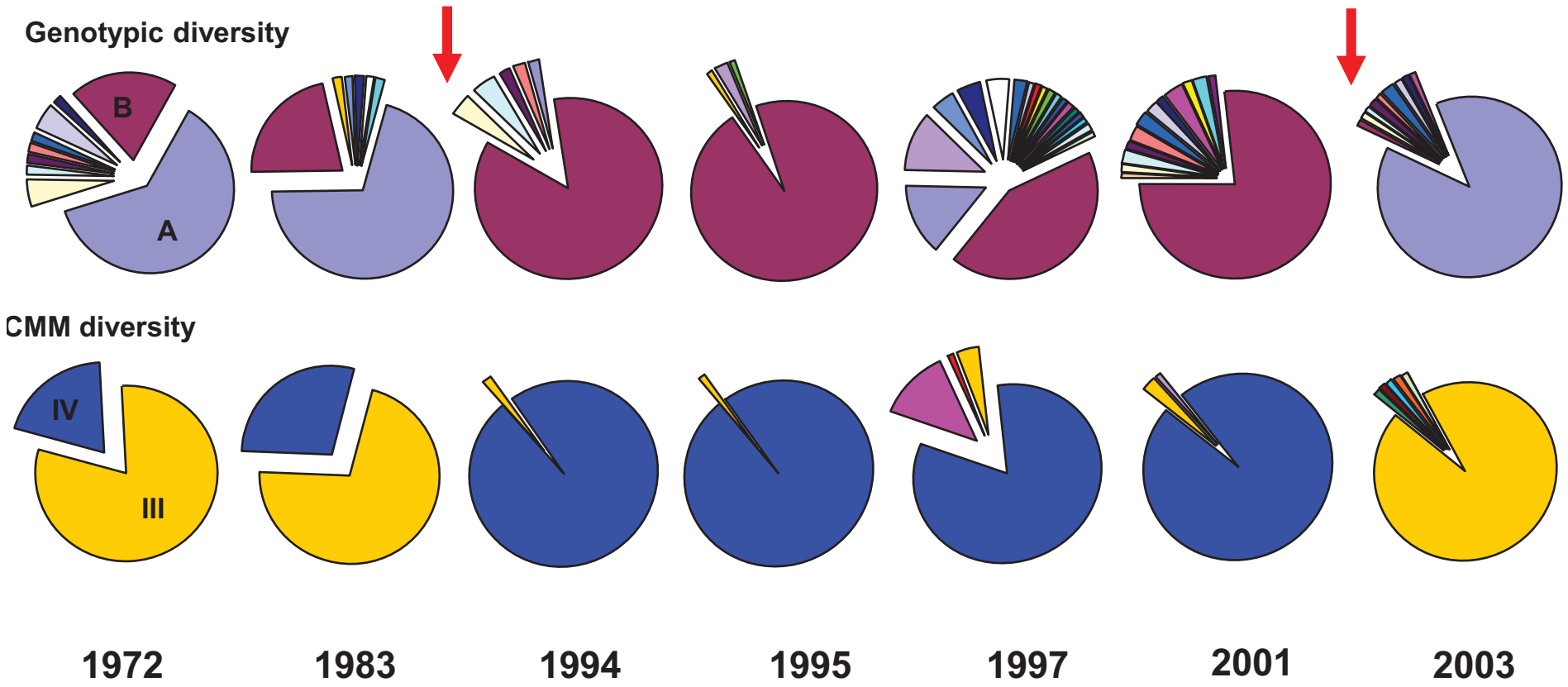
CMM IV	CMM I/III	CMM II	CMM VI
			
CCMP 1516	L	92D	NZEH
A		B	R

Environmental samples

- CPR silks with high coccolithophore count
  - Assessed by visual interrogation by light microscopy
- Regular coccolithophore blooms in Ushant
- >50 years of samples preserved in formalin - DNA extraction






Genotypic diversity
B
A
CMM diversity
IV
III
1972
1983
1994
1995
1997
2001
2003

Cruise sampling

- *UK: June/July 2011 (PDRA)*
- *Arctic: July/Aug 2012 (PDRA + PhD?)*
- *S. Ocean (PhD)*

PhD studentship (MBA/Oxford) available!

50 stations per cruise. (Focus on coccolithophore populations)
On board:
-Calc rate, photosynthesis, morphology (bioassays)
$-\delta^{13}C$ (parallel samples)

Uniclonal isolates (on board) + samples **to lab**. Max 10 isolates per sample.

Samples for genetic variability (e.g. GPA) and other calcification and CCMgenes

Samples for gene expression (e.g. **CCM: CA, RubisCO, anion transporters, GPA, CAX**)

Physiological variability (high throughput) on ***fresh isolates***
Calcification, PS, growth, morphology,
Gene expression (GPA, CAX, SCL4 (AE1), H+ channel, CCM)
pH regulation experiments (selected strains)

3 acidification scenarios (closed batch cultures)

Genetic characterisation of clones