ULB UNIVERSITÉ LIBRE DE BRUXELLES, UNIVERSITÉ D'EUROPE

Coccolithophores at the continental margin: Biogeochemical aspects of bloom formation and development

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Collaborators

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Steve Groom, PML

ROLE OF PELAGIC CALCIFICATION AND EXPORT OF CARBONATE PRODUCTION IN CLIMATE CHANGE

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PEACE

Outline

- Preambule:
  - Problematic of coccolithophorid studies
  - Internal calcification
  - Lessons from the cultures
  - Ecological niche
- Results:
  - Bay of Biscay
  - Multidisciplinary cruises
  - 2004
  - 2006
  - 2008
- Perspectives:
  - Synthesis of field data
  - Mechanism of bloom development in the Bay of Biscay
  - Conceptual model for coccolithophorid calcification

Introduction

Coccolithophores play a major role in the biogeochemical cycle of the world ocean:

- Primary producers:

$$106CO_2 + 16NO_3^- + H_2PO_4^- + 17H^+ + 122H_2O \leftrightarrow (CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 138O_2$$

- Key role in total alkalinity (TA) distribution:

$$2HCO_3^- + Ca^{2+} \leftrightarrow CaCO_3 + CO_2 + H_2O$$

- $CaCO_3$ ballasts particulate organic carbon (POC) and maintains the biological pump that removes CO_2 from the surface ocean to the ocean interior.

Understanding the functioning and characteristics of coccolithophorid blooms is of crucial importance to describe the efficiency of the biological pump (Climate Change perspective).

Problematic

How important are pelagic calcifiers in the biogeochemical C cycle?

- "Carbonate rocks" is the most important reservoir of C on the Earth system

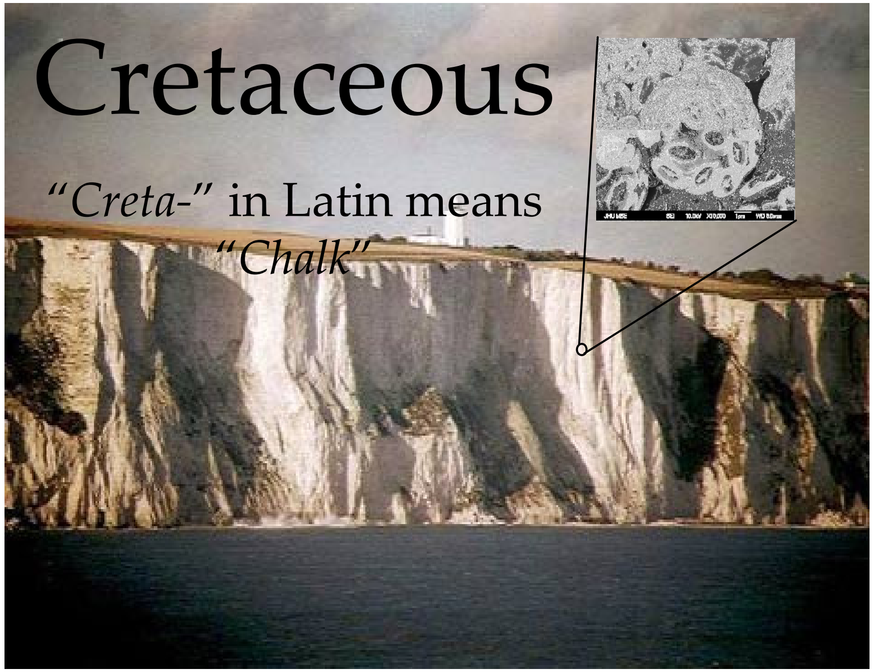
location	mass (10^{18} g of C)
carbonate in rocks	60 000
organic C in rocks	15 000
ocean $HCO_3^- + CO_3^{-2}$	42
soil carbon	4
atmospheric CO_2	0.7
biosphere	0.6

Berner, 1998

- $CaCO_3$ production is a biotic process

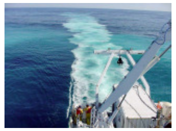
- Ocean acidification and Global Warming will affect the distribution and the abundance of the pelagic calcifiers.

(The Royal Society Report, 2005, IPCC, 2007)



Coccolithophorid science

Regional field surveys



Balch *et* al., 1992; Robertson *et* al., 1993; Holligan *et al.*, 1993, Fernandez *et al.*, 1993; Garcia-Soto *et al.*, 1995; van der Wal *et al.*, 1995; Head *et* al., 1998; Rees *et al.*, 1999; Maranon and Gonzalez, 1997; Graziano *et al.*, 2000; Lampert *et al.*, 2001; Rees *et al.*, 2002; Robertson *et al.*, 2002

PEACE project…

Laboratory experiments

By Paasche in the 60-70s

By Nimer-Merrett-Brownlee in the 80-90s

pCO_2 manipulations in the 2000th

Biogeochemical models

Six and Maier-Reimer, 1996; Heinze, 2004

Phytoplankton functional type-based models

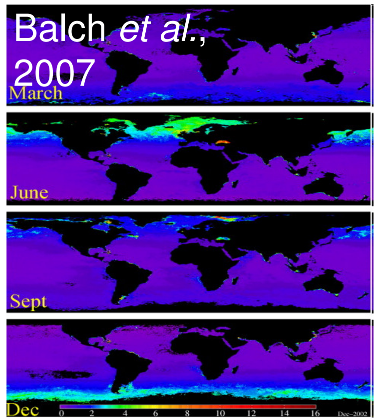
Gregg *et al.*, 2003; Le Quéré *et* al., 2005; Gregg and Casey, 2007

Phytoplankton Individual-based models

Merico *et* al., 2004; Pasquer *et al.*, 2005; Joassin *et al.*, 2008

Remote sensing

Holligan *et al, 1983; GREPMA*, 1988*;* Brown and Yoder, 1994; Balch *et al.*, 2005; 2007



Sediment trap synthesis

Milliman *et* al., 1999; Honjo, 2008

Global Calcification estimates

Table 5
Summary of global calcification estimates made in this study compared to estimates of other workers

Author	Technique	Global $CaCO_3$ production ($Pg\ PIC\ y^{-1}$)
This study	^{14}C measurements and remote sensing algorithm	1.6 ± 0.3
Feely et al. (2004)	Seasonal cycle of euphotic zone alkalinity	0.8–1.4
Wollast (1994)	Chemical state of the carbonate system	1.1
Morse and Mackenzie (1990)	Geochemistry of sedimentary carbonates	1.0
Archer and Maier-Reimer (1994) and Archer (1996b)	Gridded maps of calcite and diagenetic model of $CaCO_3$ preservation	1.0
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Considering that this study reflects coccolithophorid calcification!

Coccolithophores (Balch *et al.*, 2007)

~1.6 Pg PIC yr^{-1}

Foraminifera (Langer *et al.*, 1997)

~0.16 Pg PIC yr^{-1}

Coral Reefs (Vescei, 2004)

~0.09 Pg PIC yr^{-1}

Pteropods ~10% of the global flux

(Honjo, 1981)

Benthic Molluscs, Echinoderms… ?

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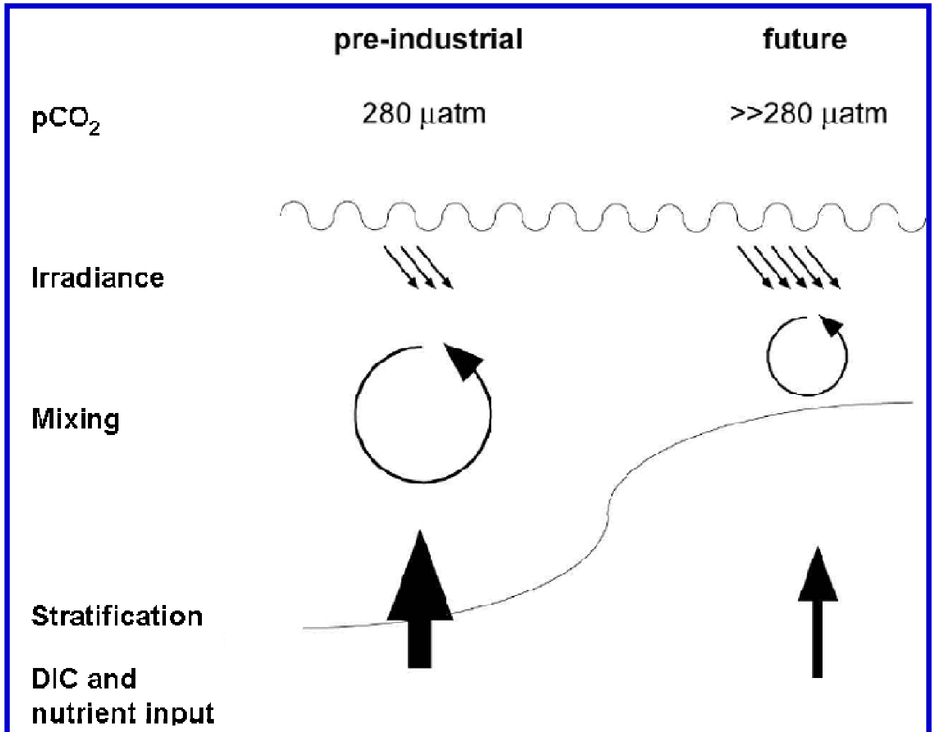
Coccolithophores are the most important calcifier, actually!!

The high-CO_2 World

Ocean acidification would reduce the ability of calcifying organisms to form $CaCO_3$ structures.

Global warming in surface waters:

- decreases **CO_2 solubility**
- decreases **water mixing**
  - enhances **stratification**
  - decreasing the **mixed layer depth**
  - reducing the **DIC inputs**
  - reducing the **nutrient inputs**
  - providing **higher irradiance** for the marine biota



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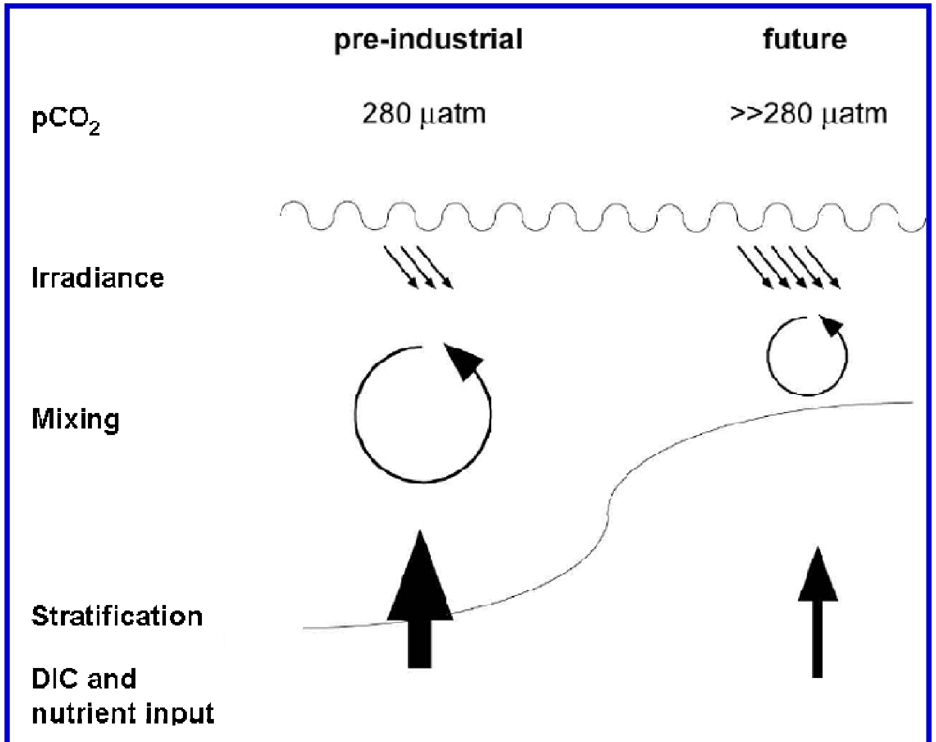

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Setup of new conditions → No good prediction!!

Scientific background

"… **the time taken for a patch to disappear on satellite images can be calculated as >200 days**. **The maximum lifetime of such patches on satellite images is 30-40 days**, **suggesting that processes other than sinking are important in their disappearance**."
(Holligan *et al*., 1993)

FISHERIES OCEANOGRAPHY
Fish. Oceanogr. 2:3/4, 175–183, 1993

What controls the distribution of the coccolithophore, *Emiliania huxleyi,* in the North Sea?

PATRICK M. HOLLIGAN,[1] STEPHEN B. GROOM,[2] AND DEREK S. HARBOUR[1]

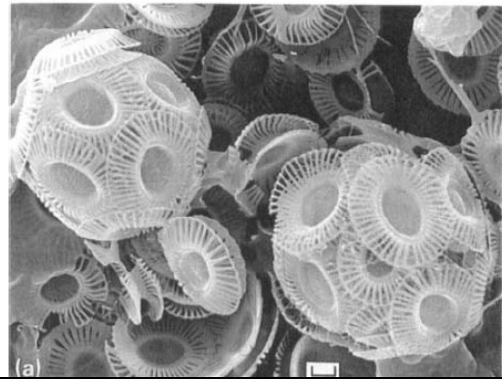
[1]*Plymouth Marine Laboratory, West Hoe, Plymouth PL1 3DH, United Kingdom*
[2]*NERC Image Analysis Unit, University of Plymouth, Plymouth PL4 8AA, United Kingdom*

ABSTRACT

Satellite data show that the distribution of *Emiliania huxleyi* in the North Sea is characterized by considerable spatial patchiness as well as large annual differences in abundance within any particular area. The causes of this variability are largely unknown, and therefore unpredictable, reflecting a paucity of information on the ecophysiology of the species.

Key words: *Emiliania huxleyi*, coccolithophore, North Sea, remote sensing, bloom.

Figure 1. Scanning electron micrographs of type B *Emiliania huxleyi* cells (a) and coccoliths (b) from a water sample collected in shallow water (~15 m) off north-west Scotland on 12 July 1985. Scale bars represent 1 μm.



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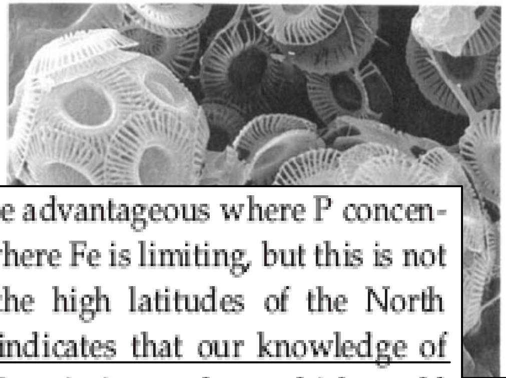

Global Change Biology (2005) 11, 2016–2040, doi: 10.1111/j.1365-2486.2005.01004.x

Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models

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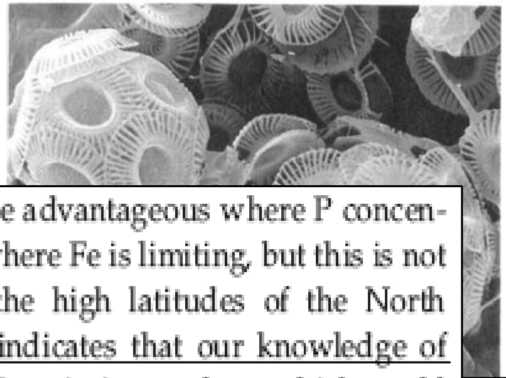

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Our knowledge of coccolithophrid blooms is insufficient!!!

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Coccolithophores are the most important calcifier, actually!!

Setup of new conditions → No good prediction!!

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What do we know ?

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  - Problematic of coccolithophorid studies
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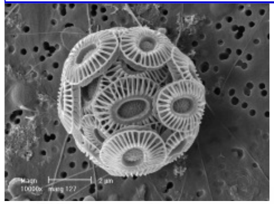
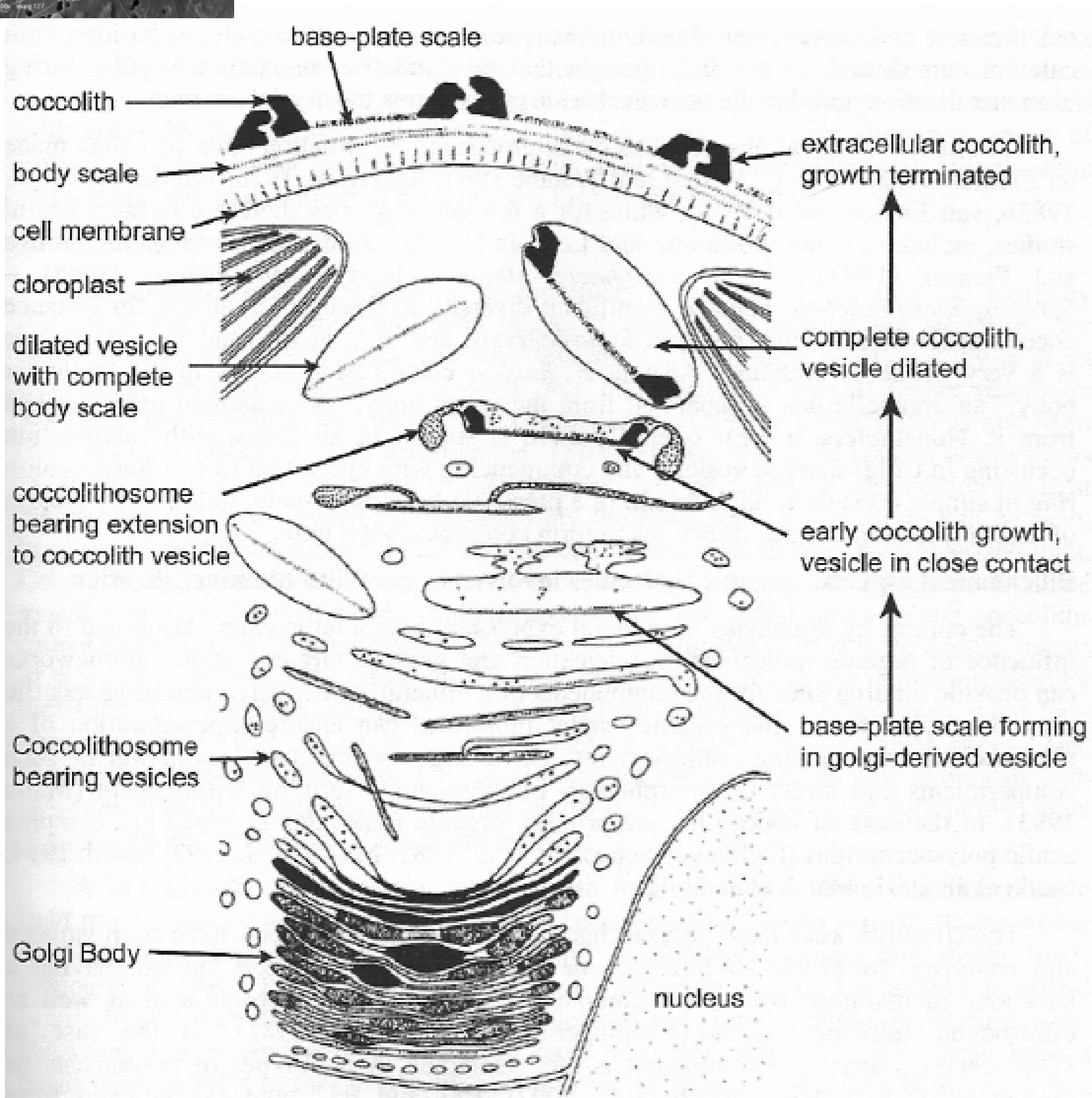
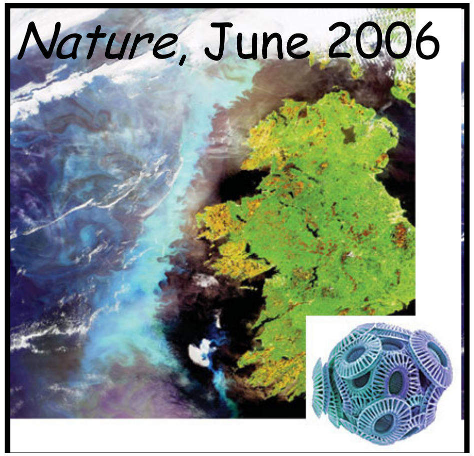


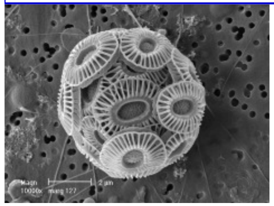
Internal calcification



van der Wal et al., 1983

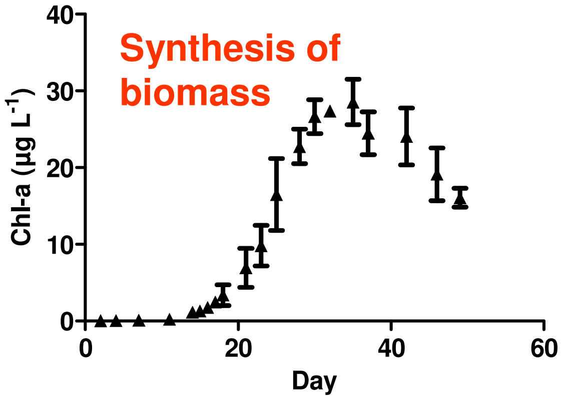
- Takes place in **vesicles** derived from the Golgi apparatus
- Nucleation occurs around a **fibrillar base-plate**
- Involves specific **polysaccharides**
- The new **coccolith** migrates into the cytoplasm and is released by **exocytosis** to the cell periphery
- Coccoliths are produced in excess and detach from the cell





Lessons from cultures

Schematic development of a coccolithophorid bloom



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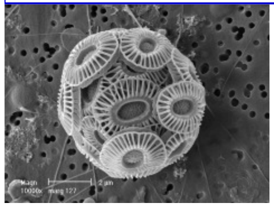

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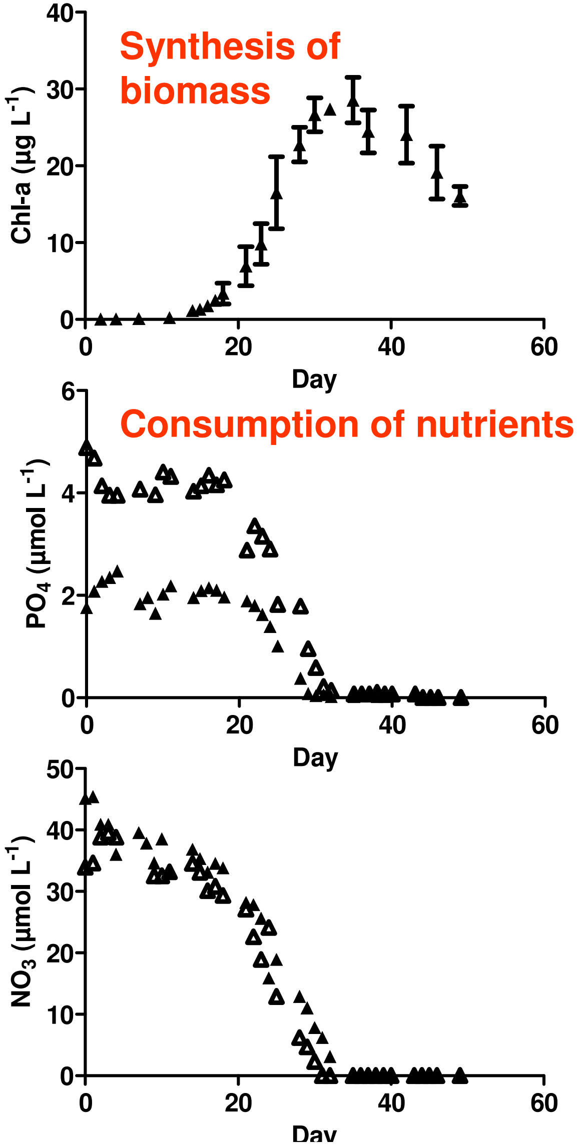

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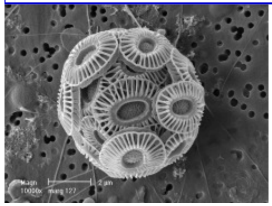

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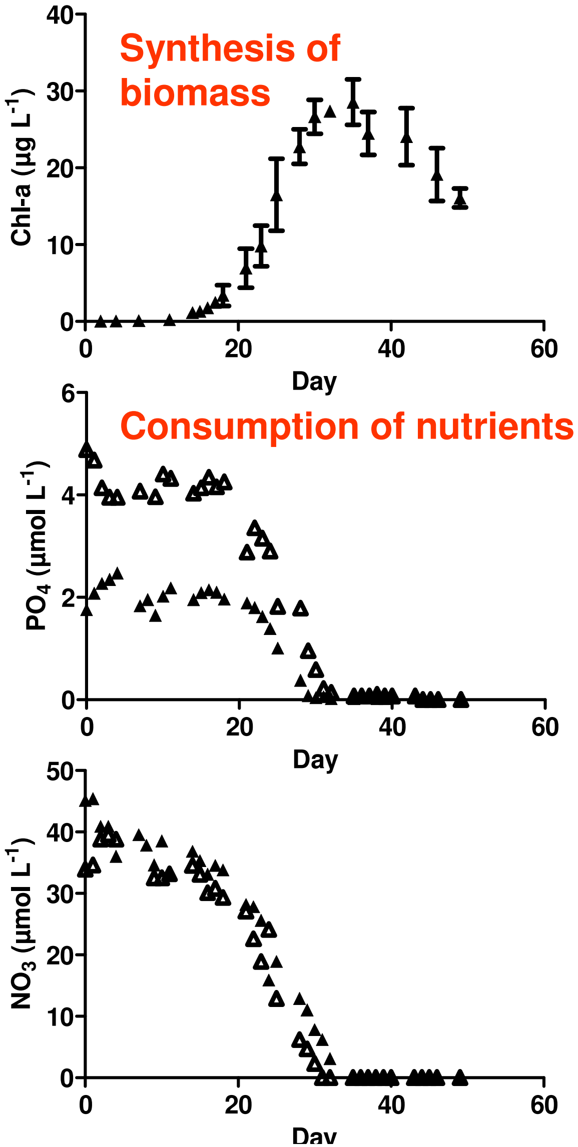

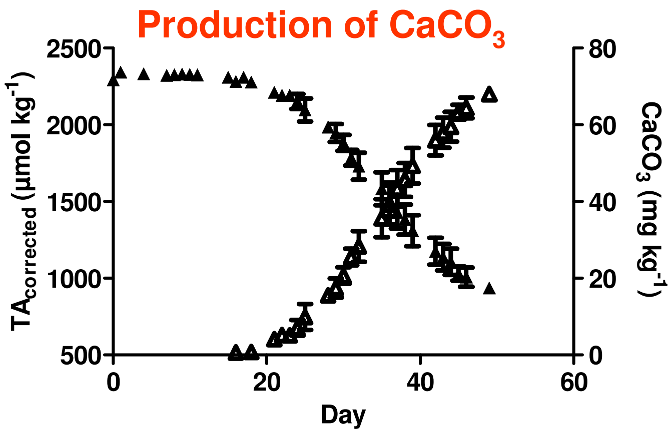

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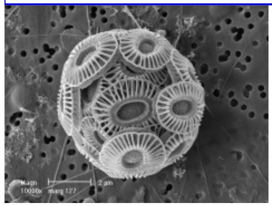

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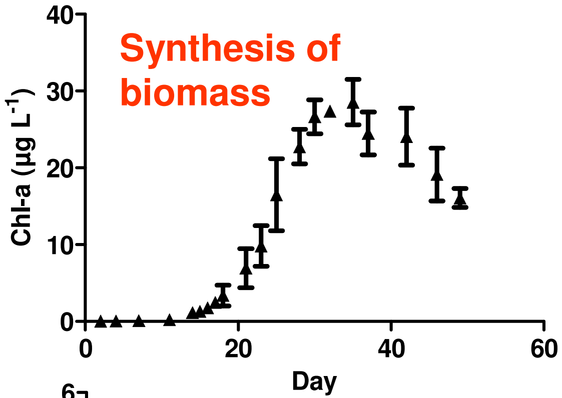

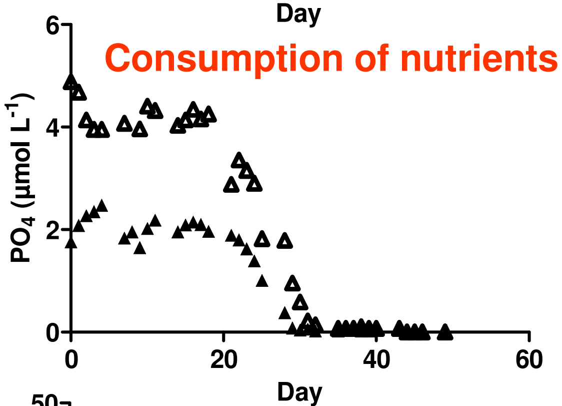

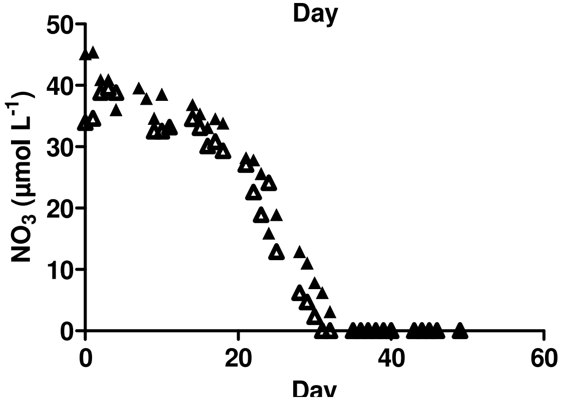

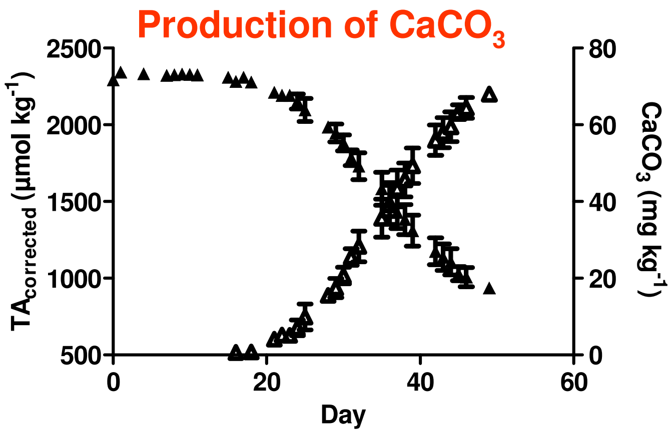

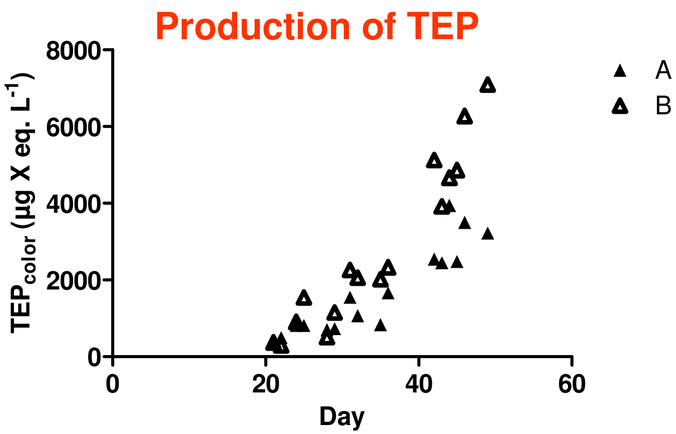

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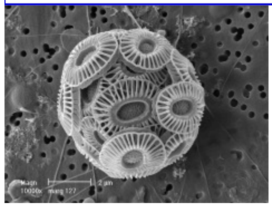

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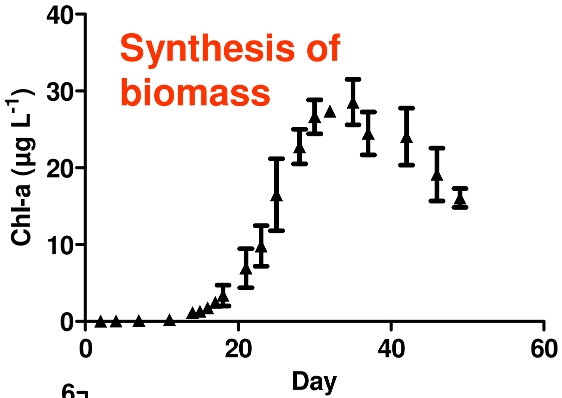

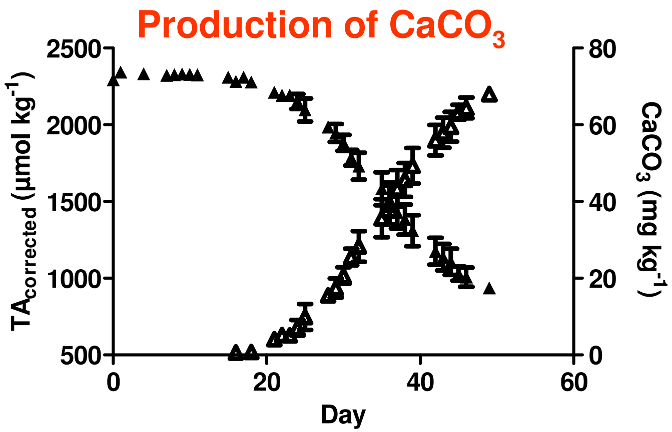

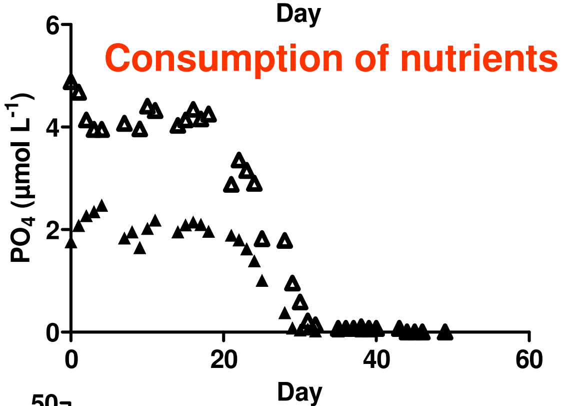

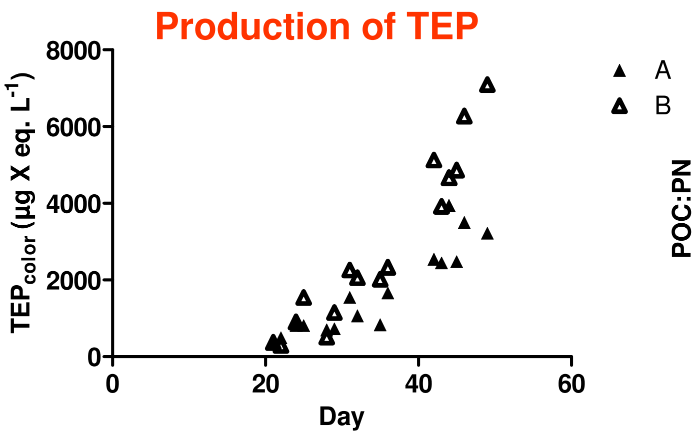

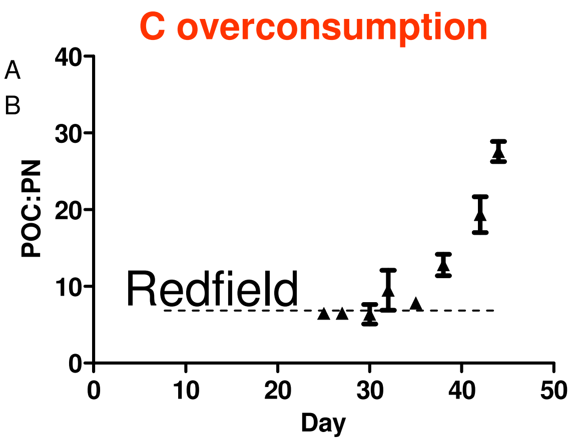

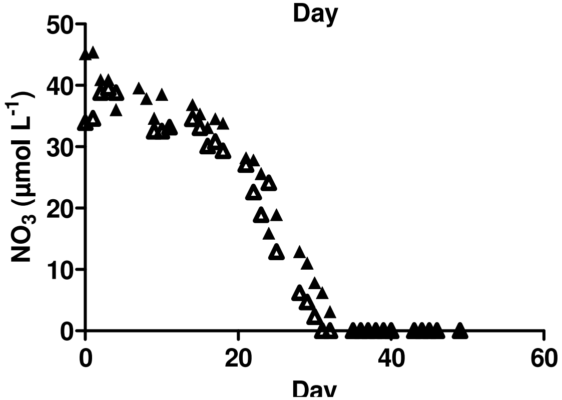

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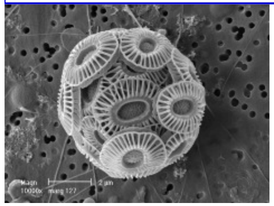

Ecological niche

Ubiquitous species (r-strategy) that develop huge blooms

(Tyrrel and Merico, 2004) *Emiliania huxleyi* is generally found in:

- High light
- Stratified waters
- Low dissolved silicate (DSi) waters: competition with K-selected diatoms
- Phosphate (P) more limiting than nitrate (N) (= high N:P ratio)

Reassessed by (Lessard, Merico and Tyrrell, 2005): *E. huxleyi* grows on organic P (Riegmann *et al.*, 2000) and N (Palenik and Henson,1997). The high N:P is not sufficient to explain the presence of *E. huxleyi* but could prevent any other r-selected phytoplankton (*Phaeocystis* spp.) to bloom.

- Low CO_2

But mesocosm studies show that *E. huxleyi* develops in either high or low CO_2 (e.g. Engel *et al.*, 2005)

- High saturation state with respect to calcite (Ω_{cal})

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  - Problematic of coccolithophorid studies
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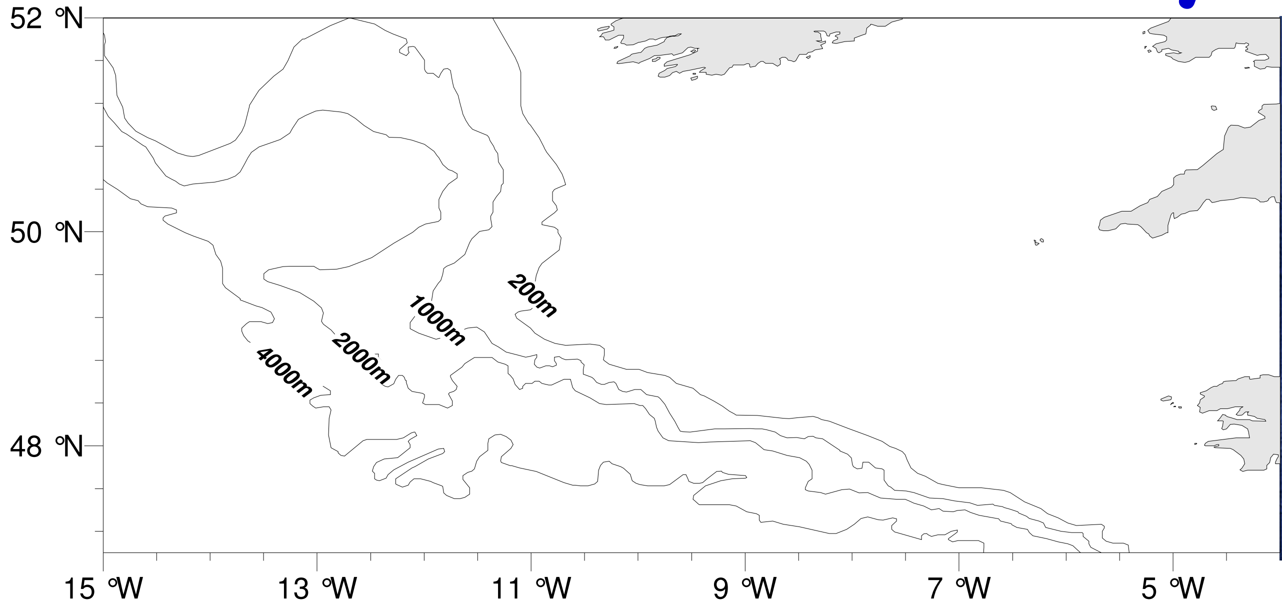
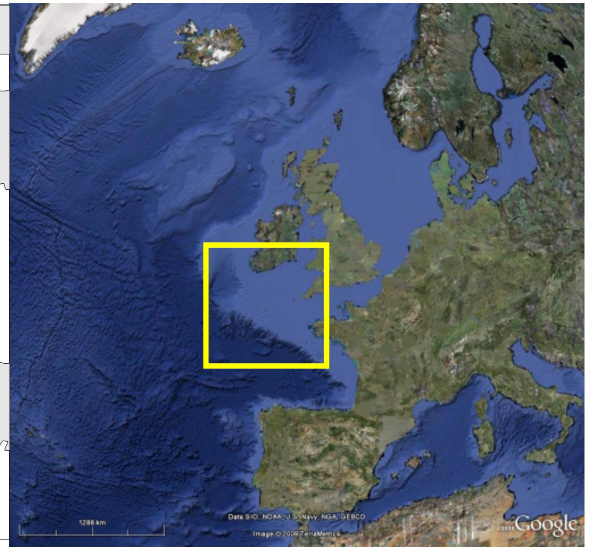
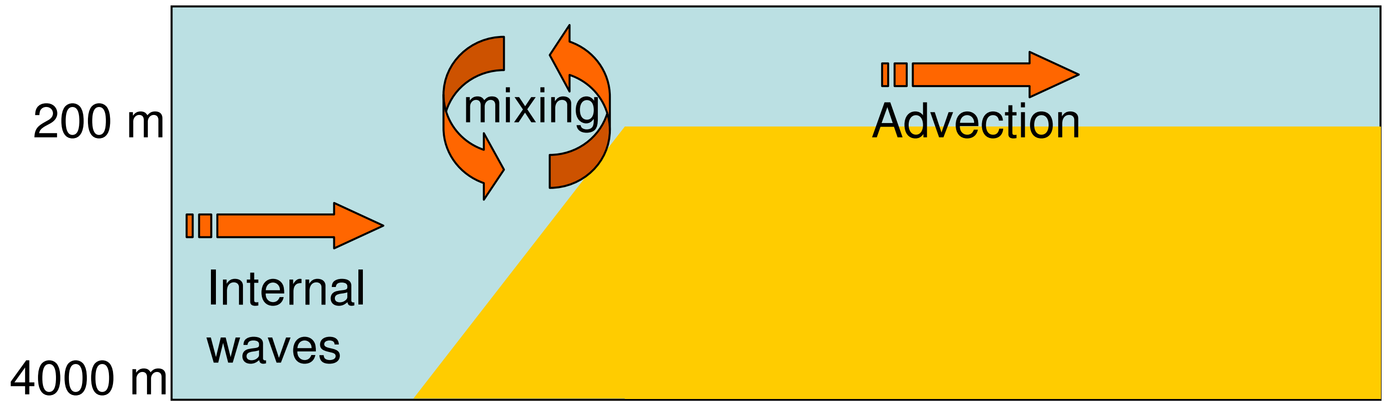
  - Lessons from the cultures
  - Ecological niche
- Results:
  - Bay of Biscay
  - Multidisciplinary cruises
  - 2004
  - 2006
  - 2008
- Perspectives:
  - Synthesis of field data
  - Mechanism of bloom development in the Bay of Biscay
  - Conceptual model for coccolithophorid calcification

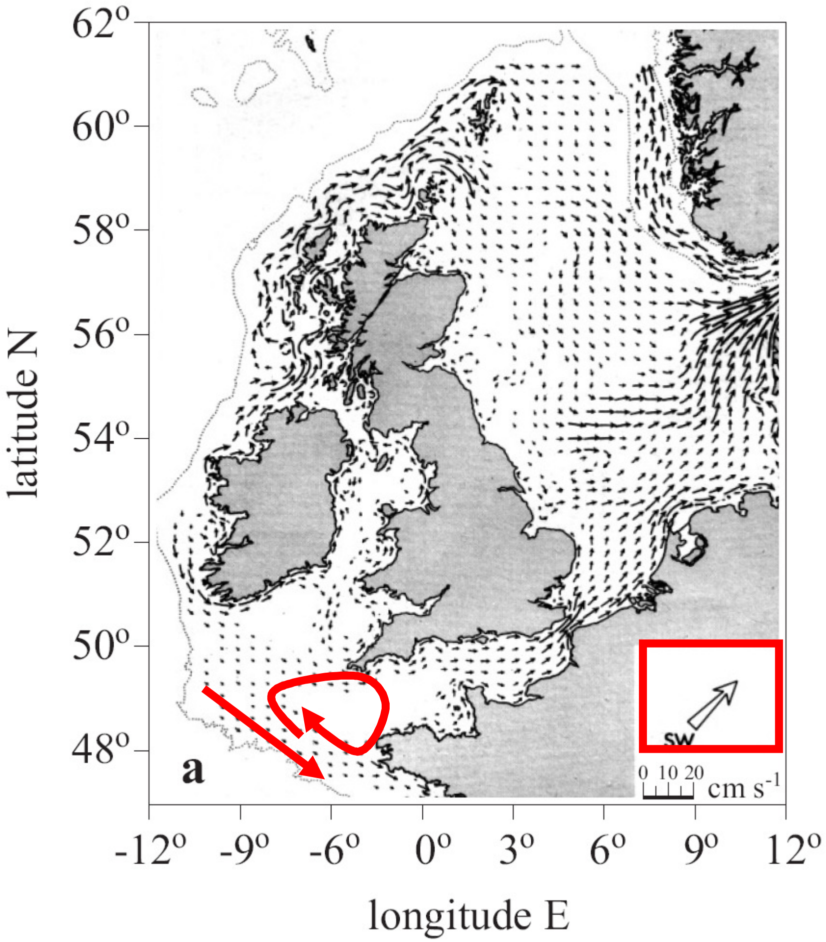
The northern Bay of Biscay

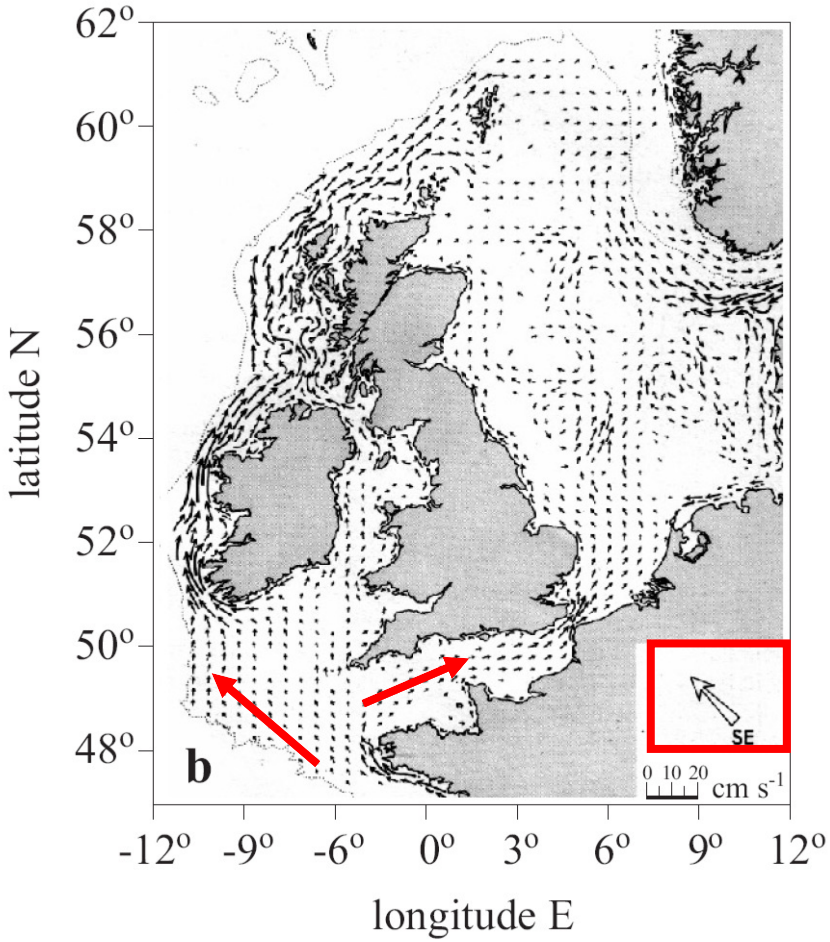




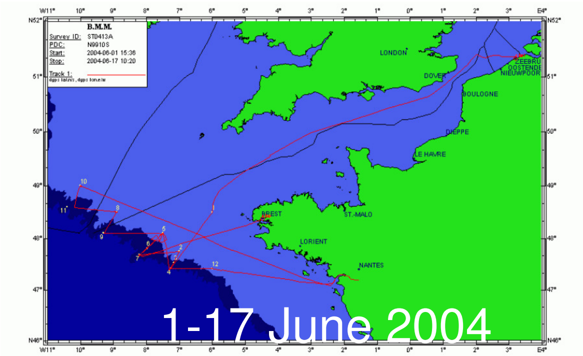


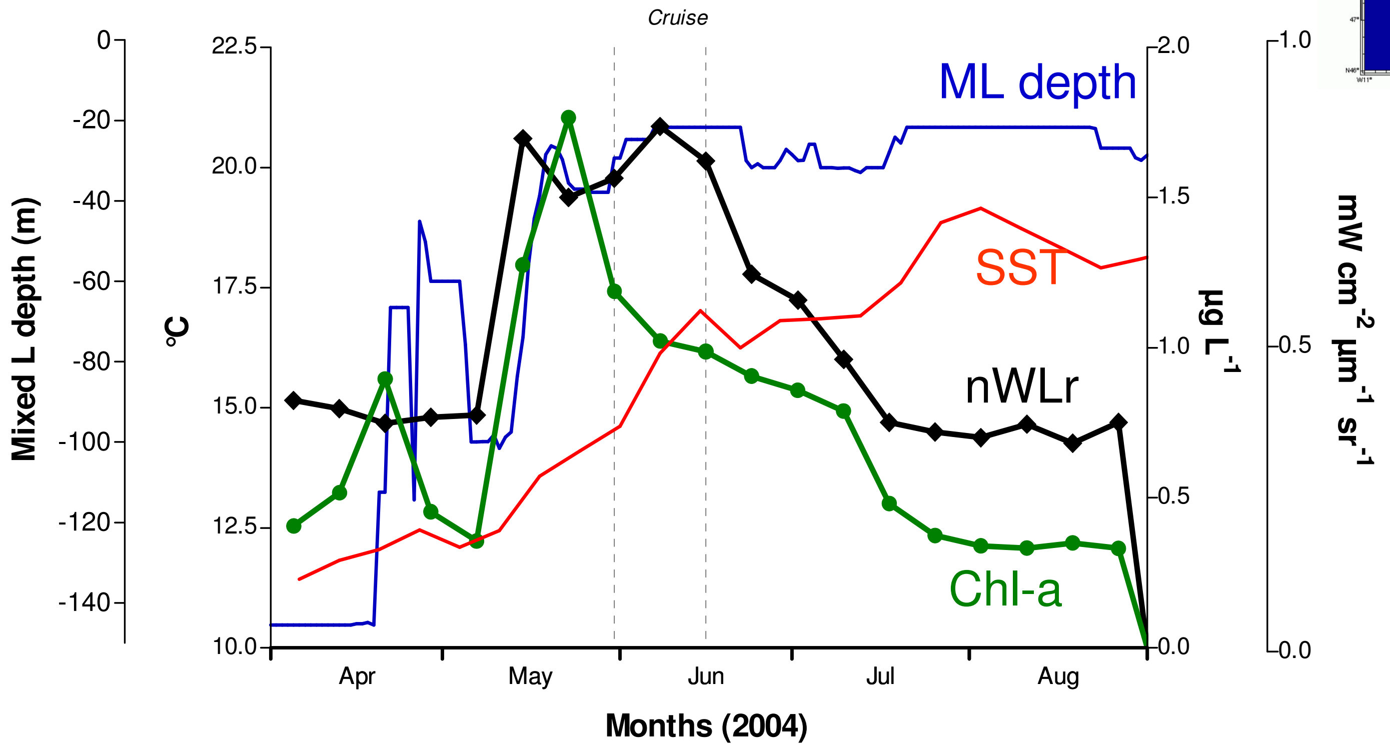
Climatic component: wind-driven residual currents (Leterme *et al.*, 2008)





Time Series





(1) Normalized water-leaving radiance @555nm (mW cm $^{-2}$ µm^{-1} s^{-1})

(1) Chl-a (µg L^{-1})

(2) SST (°C)

(3) Mixed layer depth (m)

1 Ocean Color Time-Series Online Visualization and Analysis web site, Level-3 Sea-viewing Wide Field-of-view Sensor (SeaWiFS), http://reason.gsfc.nasa.gov/Giovanni/
2 Met Office National Centre for Ocean Forecasting for the North-East Atlantic (1/8°) extracted from http://www.nerc-essc.ac.uk/godiva/
3 Reynolds *et al.* (2002) weekly SST climatology (http://iridl.ldeo.columbia.edu/)

Multidisciplinary Cruises

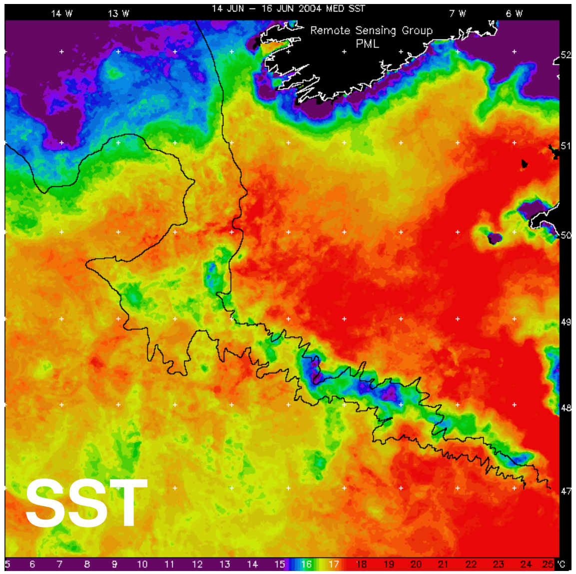
Eulerian studies in the Bay of Biscay in 2002-2004 and 2006-2008:

• T, S	→ Hydrography
• TA, pH, pCO_2	→ Dissolved inorganic C chemistry
• PO_4, DSi	→ Nutrient status
• Chl-a, Phaeo • POC, PIC • TEP	→ Standing stocks
• ^{14}C PP, ^{14}C CAL • BPP, O_2-PCR	→ Processes
• SEM	→ Biodiversity, preservation of $CaCO_3$
• Satellite imagery	→ Snapshots, Time-series

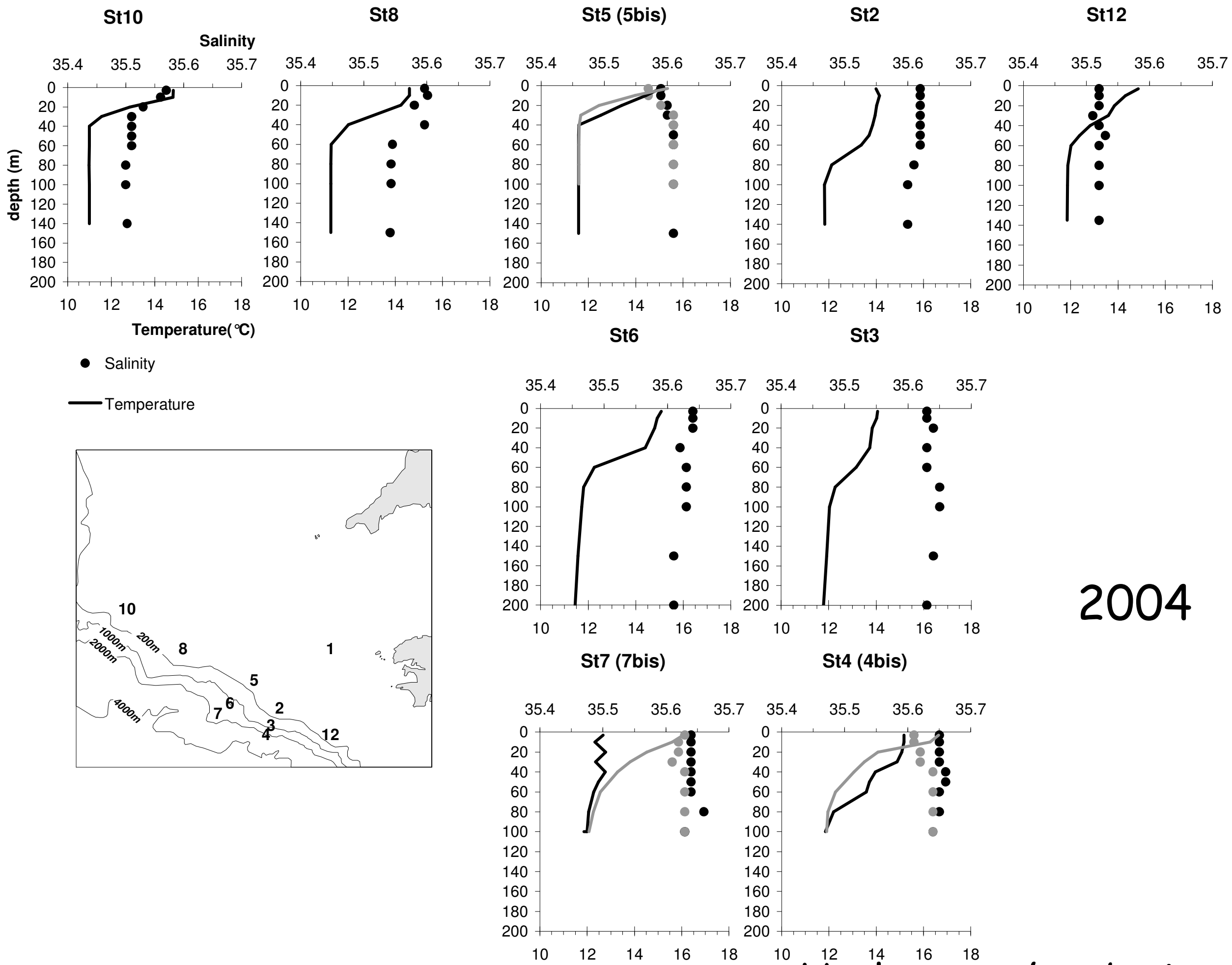
Hydrography

<u>Temperature and salinity profiles:</u>

Thermal stratification in surface waters over the continental shelf



Composite image (14-16 June 2004)



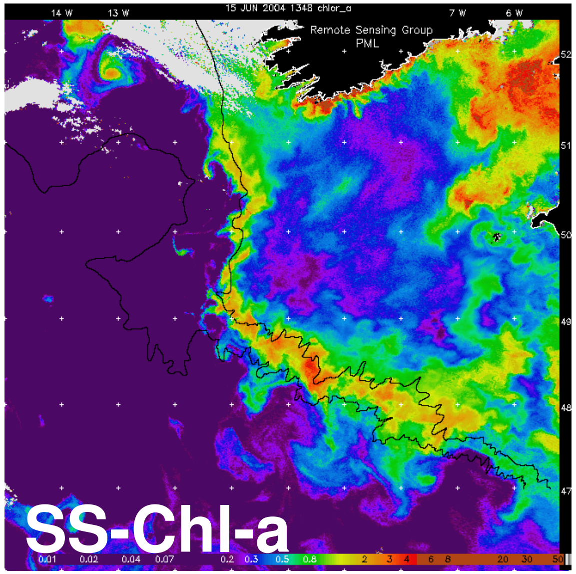
2004

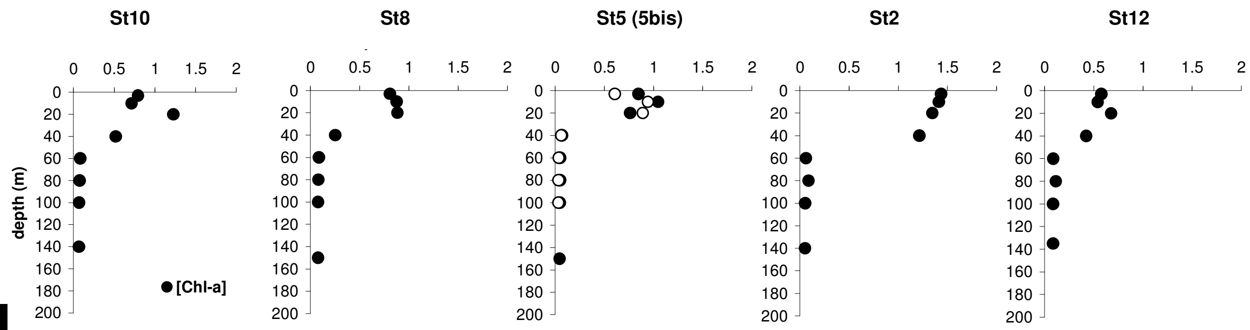
Harlay *et al.*, submitted

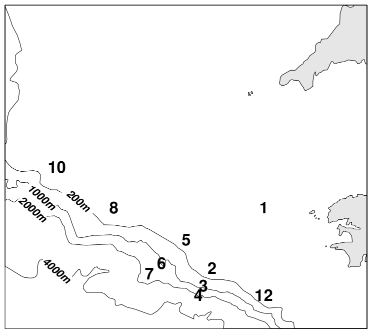
Phytoplankton biomass

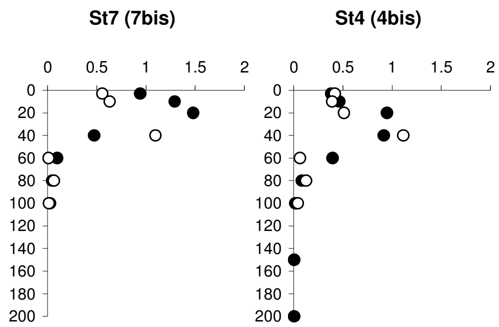
<u>Chl-a profiles:</u>

Chl-a maximum in surface or subsurface









2004

Harlay *et al.*, submitted

Nutrient distributions

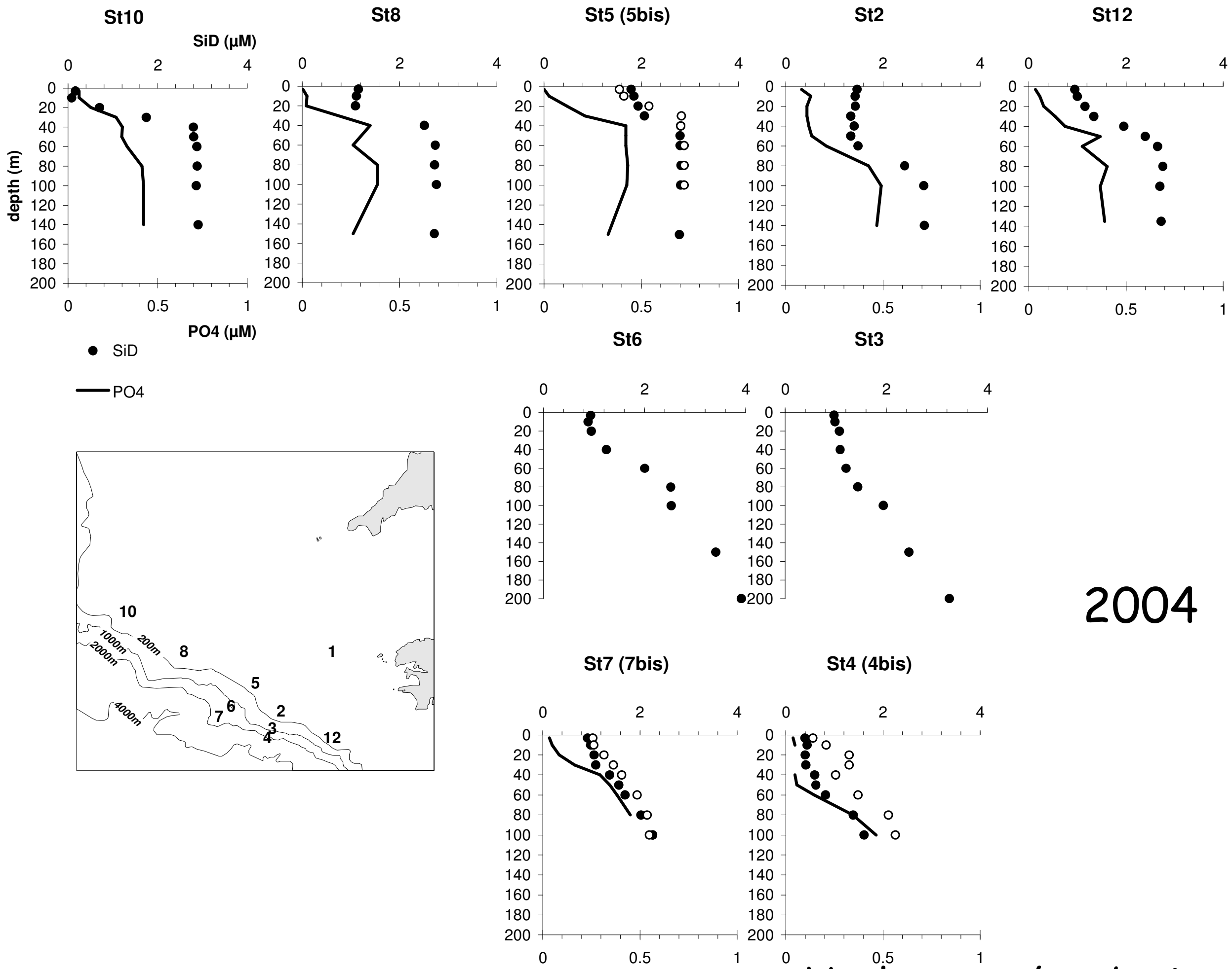
<u>Nutrient profiles:</u>

Nutrient exhaustion in surface waters over the continental shelf

PO_4 ~0 µM

DSi <2.0 µM*

(*probably limiting for diatom's growth)



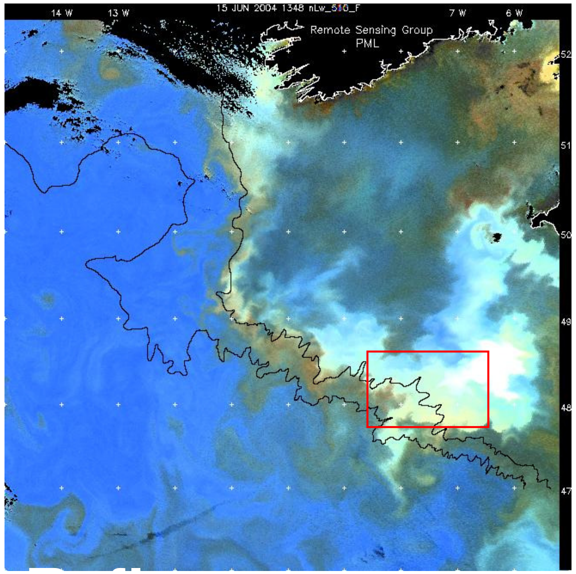
2004

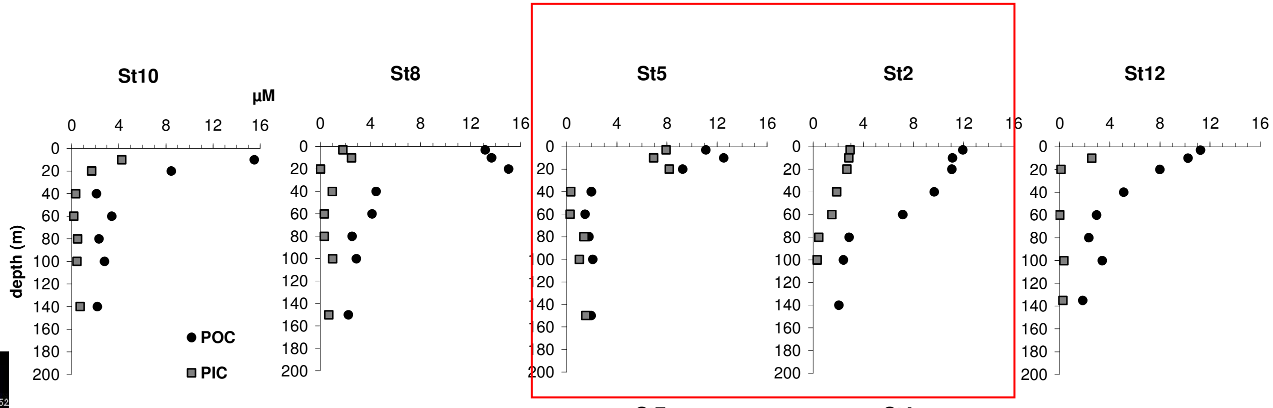
Harlay *et al.*, submitted

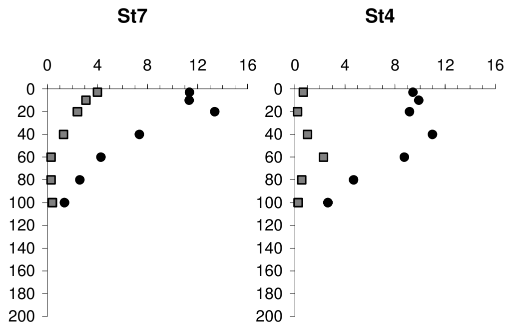
POC and PIC profiles

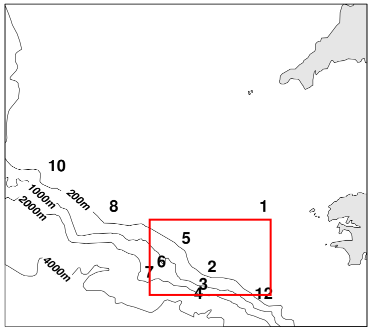
POC and PIC:

Highest PIC in surface or subsurface within the core of the HR patch.









2004

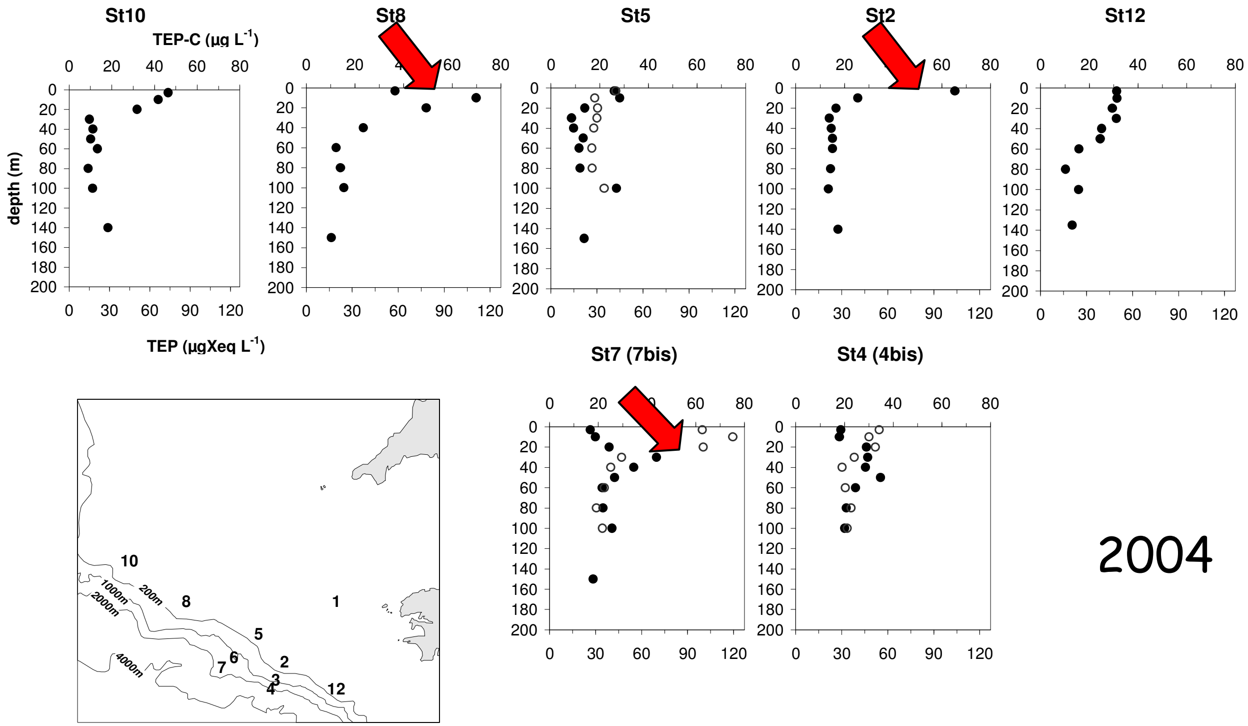
Harlay *et al.*, submitted

Transparent exopolymer particles

<u>TEP$_{color}$ profiles:</u>

TEP-C were derived from TEP$_{color}$ using the 63% (w/w) conversion factor (Engel, 2004).

TEP-C:POC represents 12-24 %



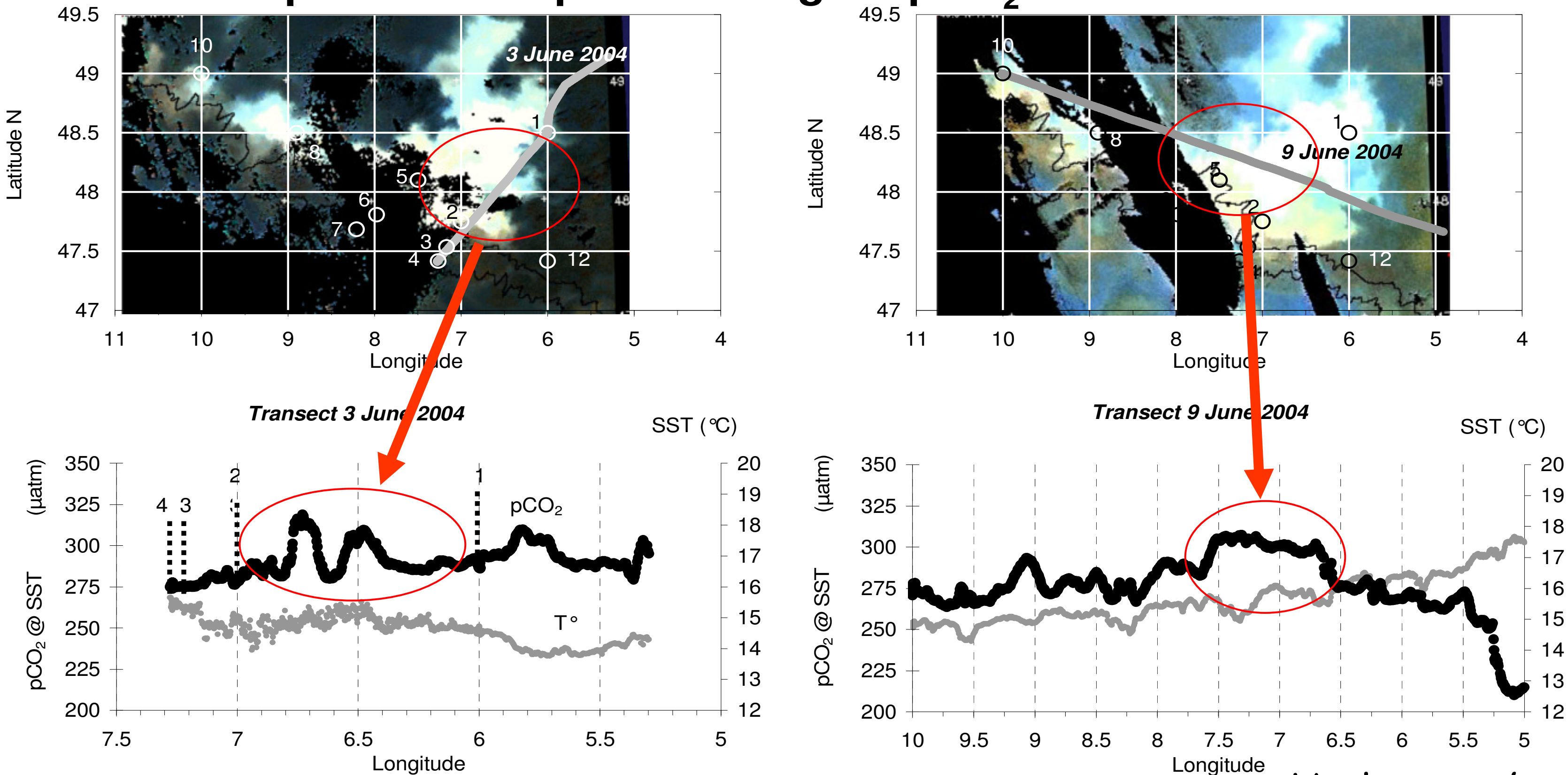
2004

Harlay *et al.*, submitted

pCO_2

Coccolithophorid blooms affect the **Air-Sea fluxes of CO_2**

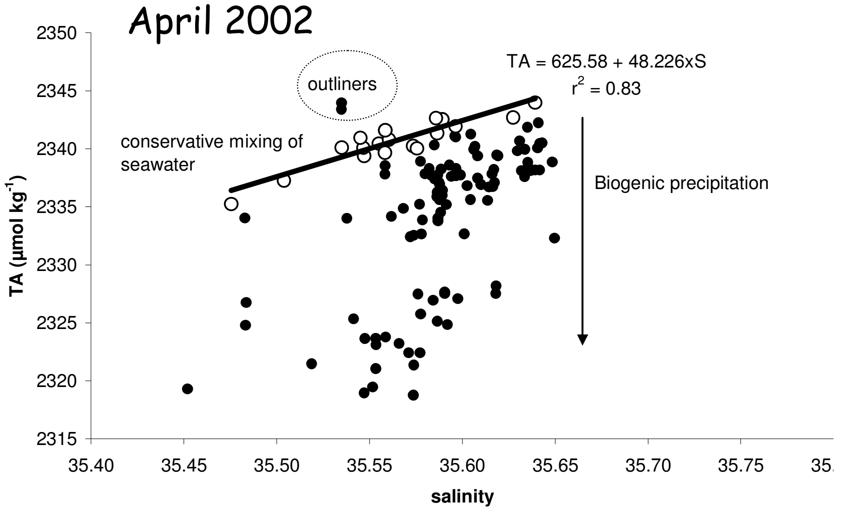
The HR patch corresponds to higher pCO_2



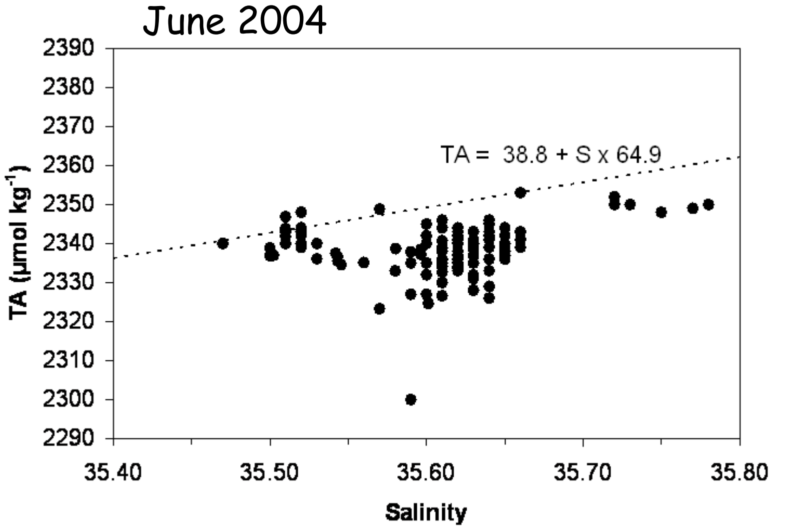
Harlay *et al.*, submitted

Multidisciplinary Cruises

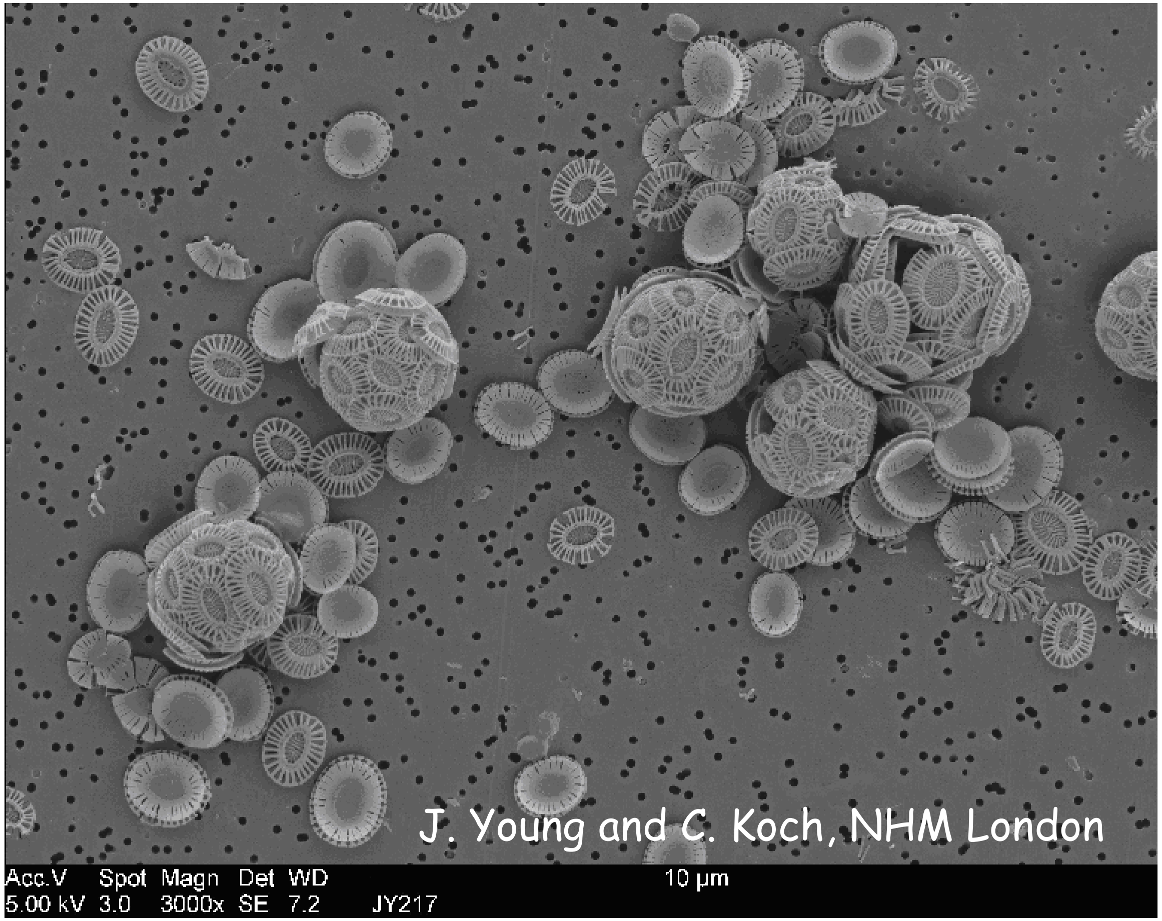
Fingerprint of calcification in the photic zone based on TA



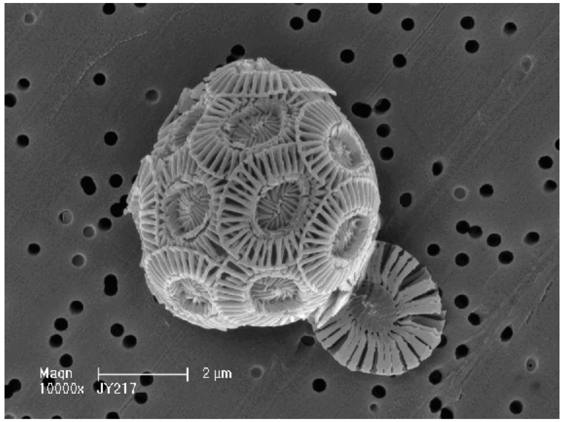
TA measurements by B. Delille (2002)



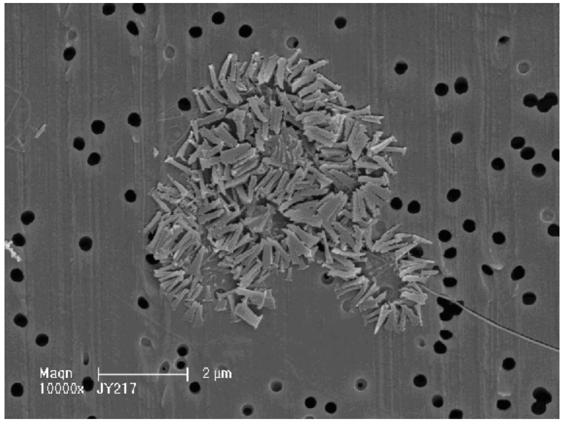
SEM



Intact coccospheres and coccoliths



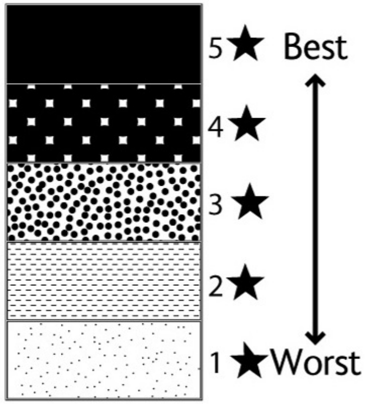
"Corroded" coccoliths

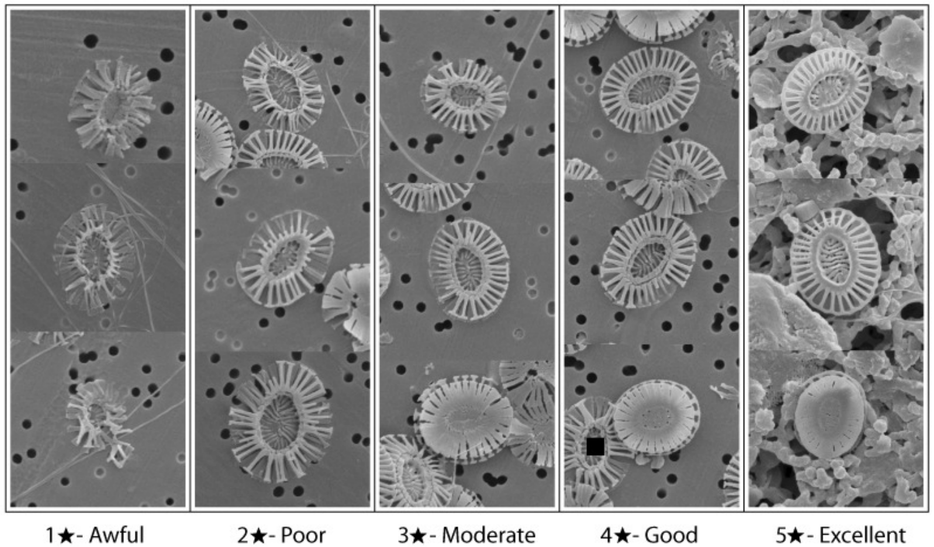


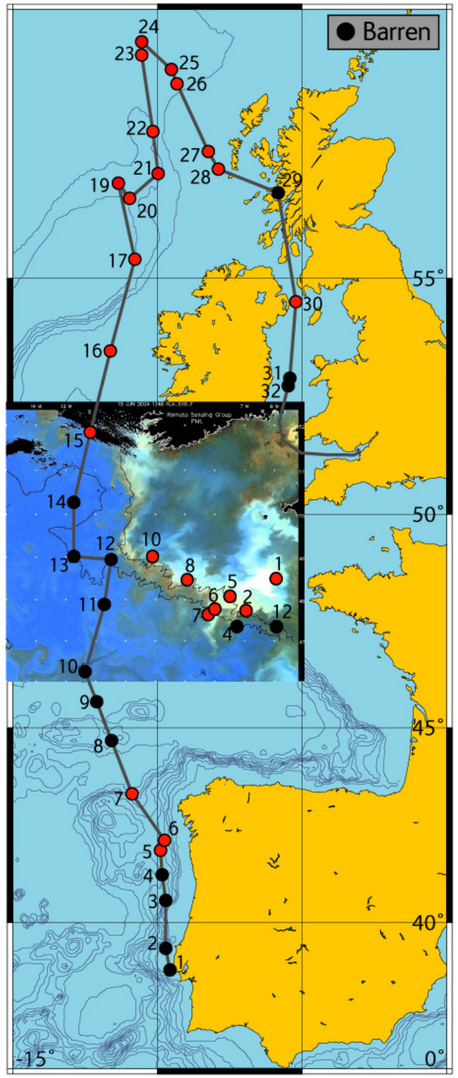
(Harlay *et al.*, in prep)

$CaCO_3$ preservation

Description of **coccolith preservation** in the photic zone (2004).

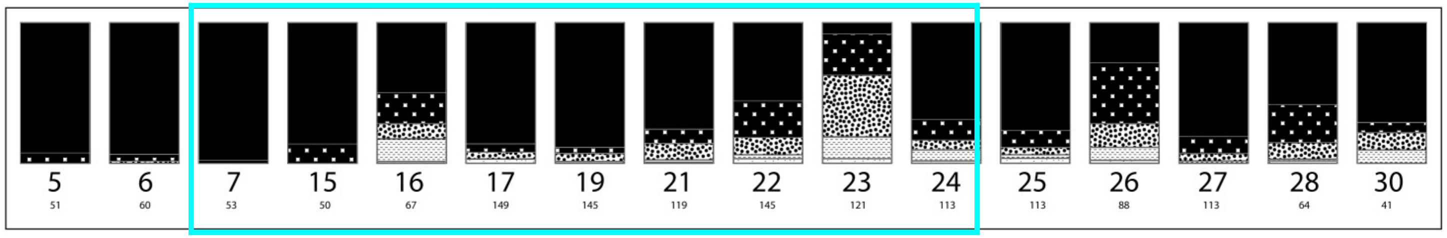


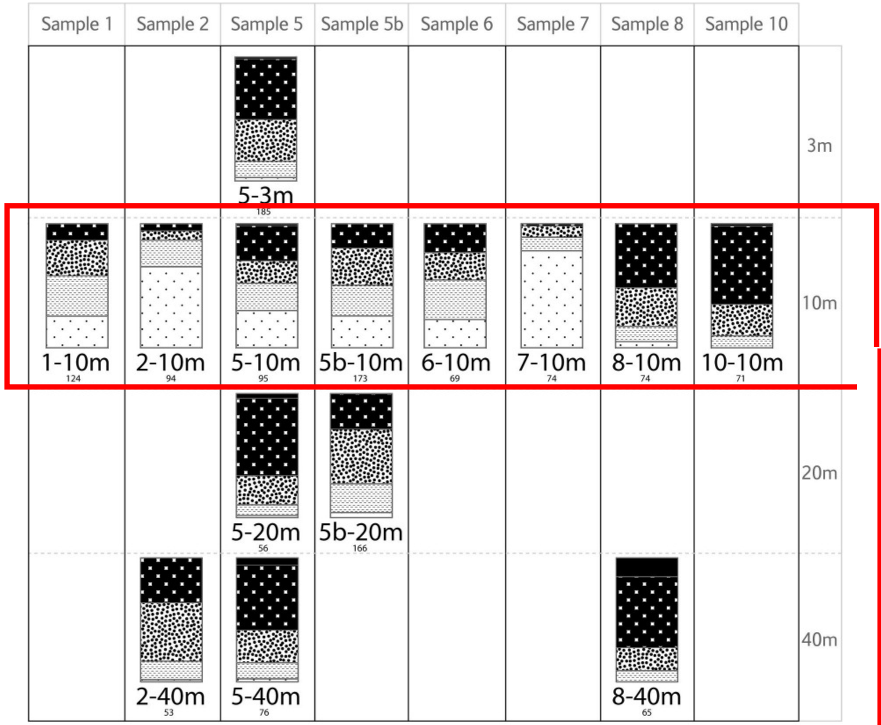




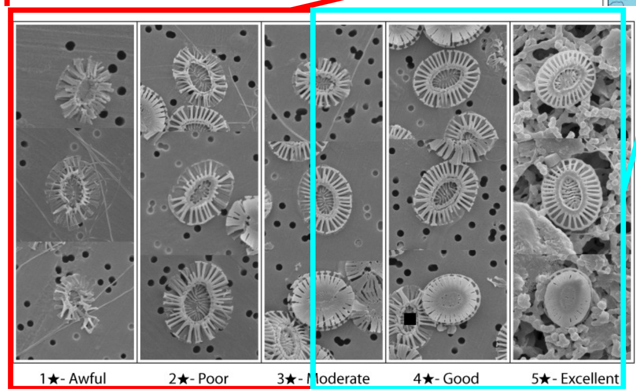
(Harlay *et al.*, in prep)

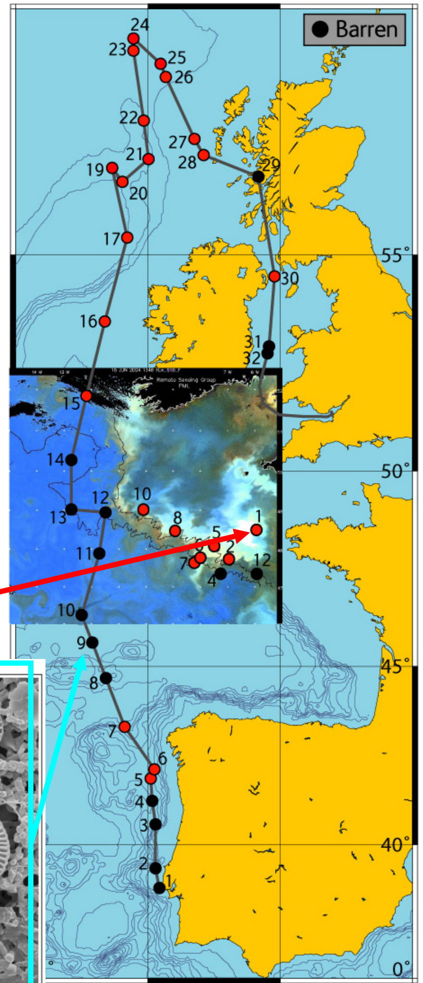
$CaCO_3$ preservation





Supra-lysiclinal dissolution of $CaCO_3$ leading to **coccolith corrosion**





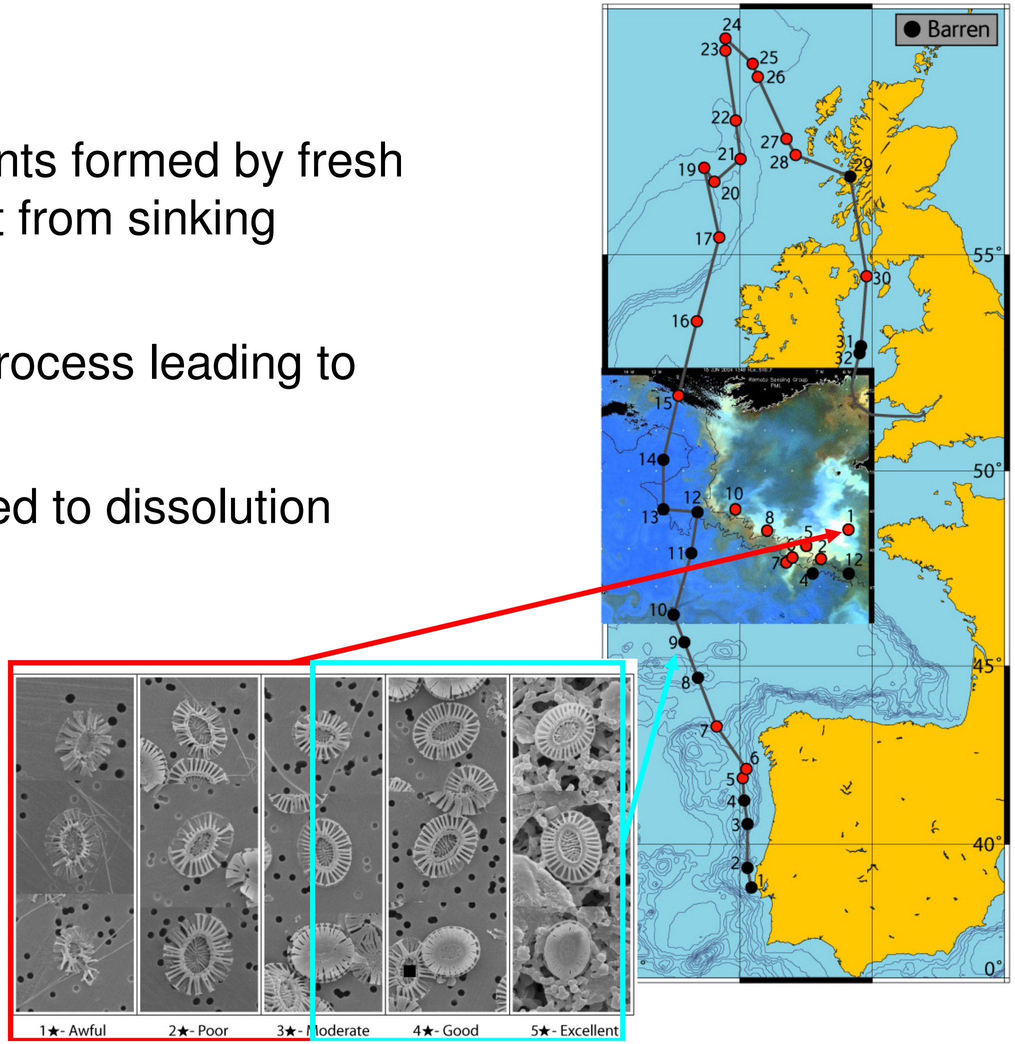
$CaCO_3$ preservation

Hypothesis:

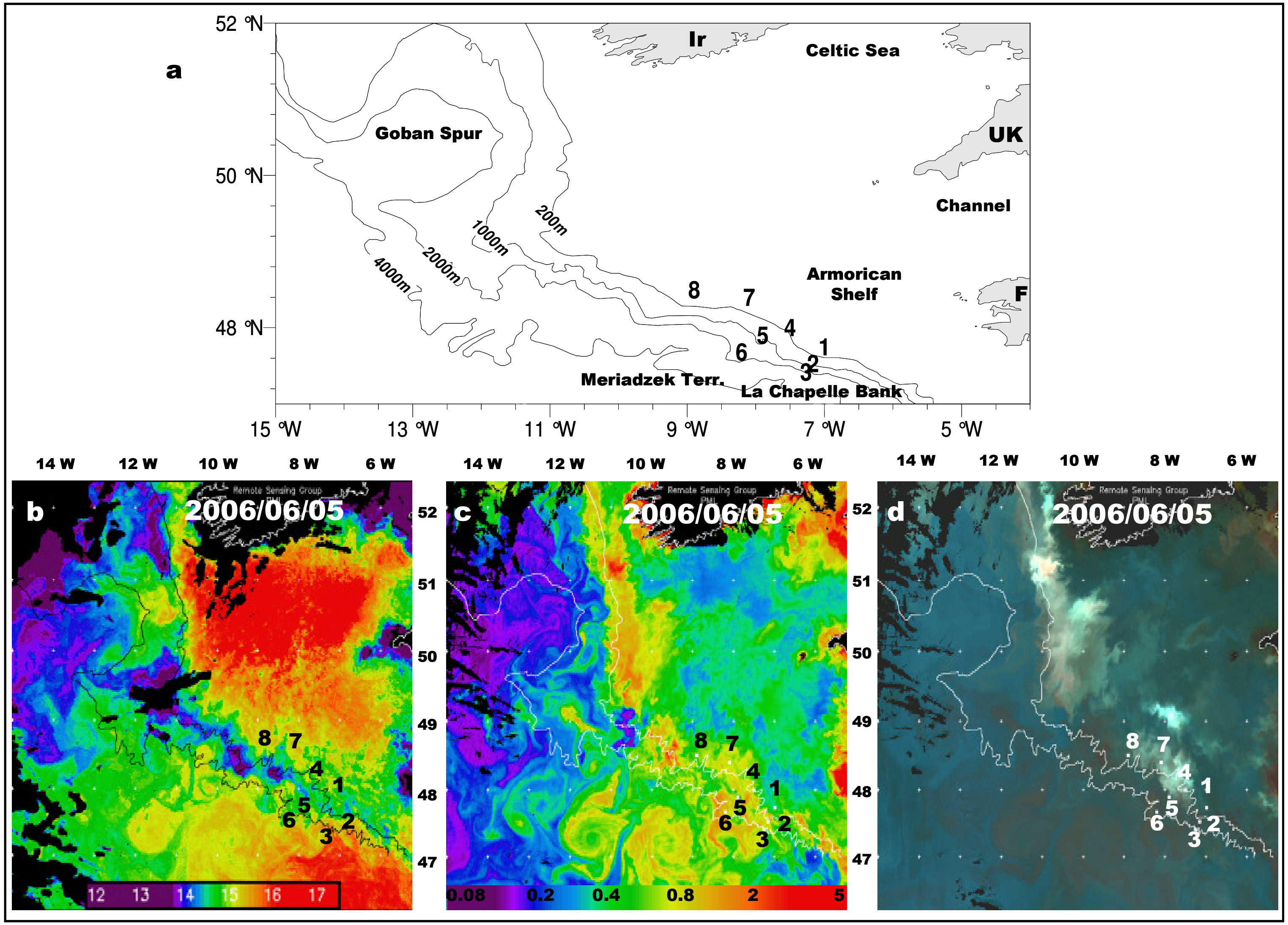
Corrosion happens in microenvironments formed by fresh TEP and suspended material (different from sinking aggregates).

Heterotrophic respiration is the main process leading to acidification within microenvironments.

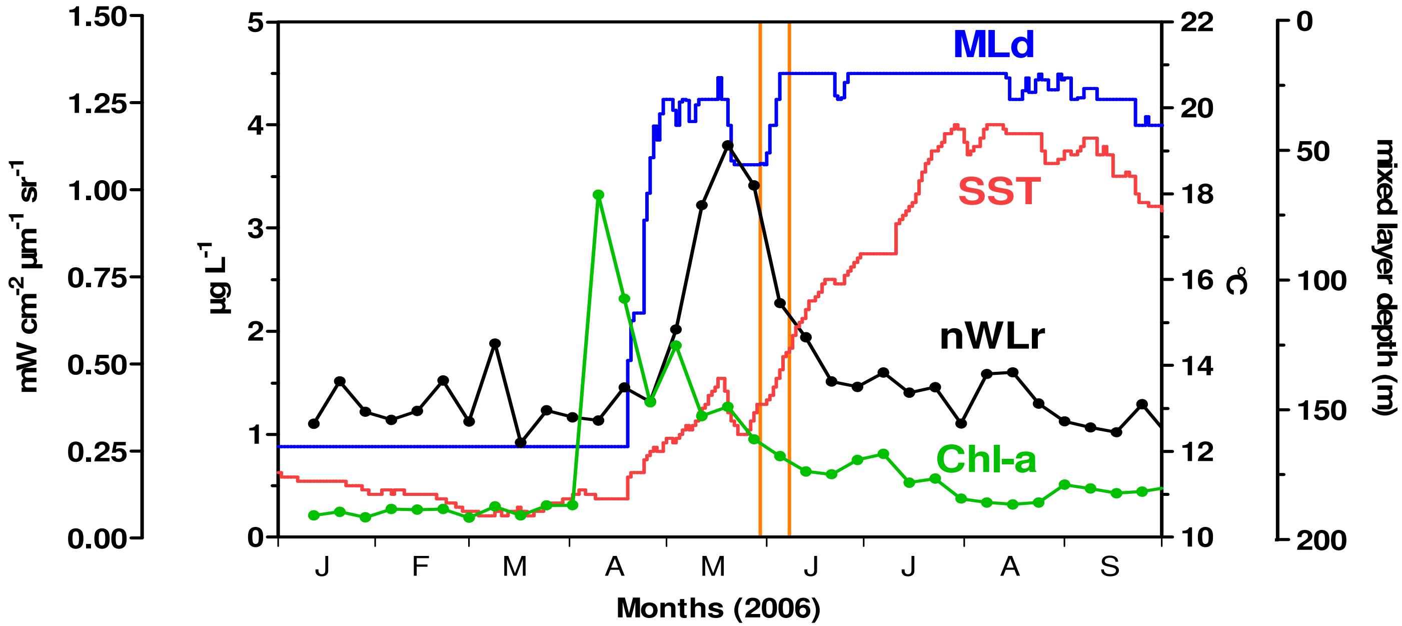
No evidence of faecal pellets associated to dissolution features.



Cruise 2006


a
52 °N
50 °N
48 °N
15 °W
13 °W
11 °W
9 °W
7 °W
5 °W
Ir
Celtic Sea
UK
Channel
Goban Spur
200m
1000m
2000m
4000m
Armorican Shelf
F
Meriadzek Terr.
La Chapelle Bank
8
7
4
5
1
6
2
3
b
c
d
14 W
12 W
10 W
8 W
6 W
2006/06/05
52
51
50
49
48
47
12 13 14 15 16 17
0.08 0.2 0.4 0.8 2 5

Cruise 2006

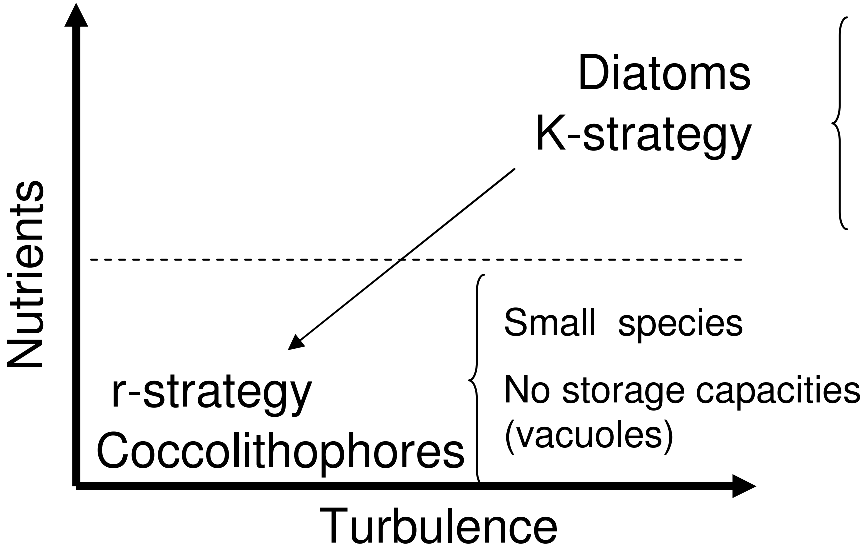


The onset of the coccolithophorid bloom (nWLr) coincides with a **warming** (SST) and a **shoaling of the mixed layer depth** after the first peak of Chl-a in early April.

Cruise 2006

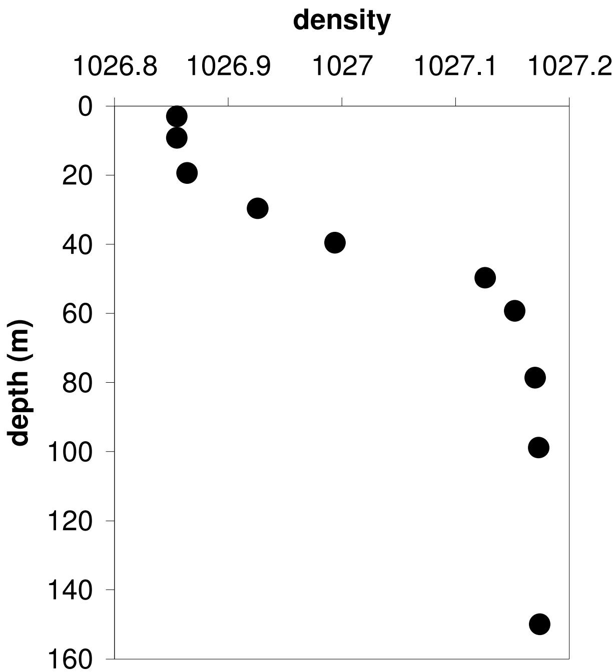
We applied an original approach based on Margalef's Mandala (Margalef, 1997).

→ *A shift towards oligotrophy is accompanied by a change in the relative dominance of phytoplankton species.*

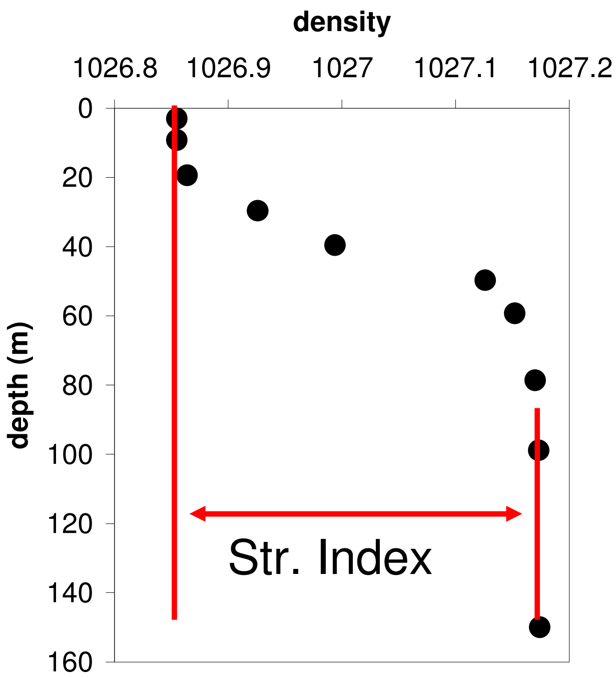


We used the water column **density gradient** to build a **stratification index** as an indicator for the preferential niche of coccolithophores to characterize the status of the different stations regarding of **bloom development**.

Stratification index

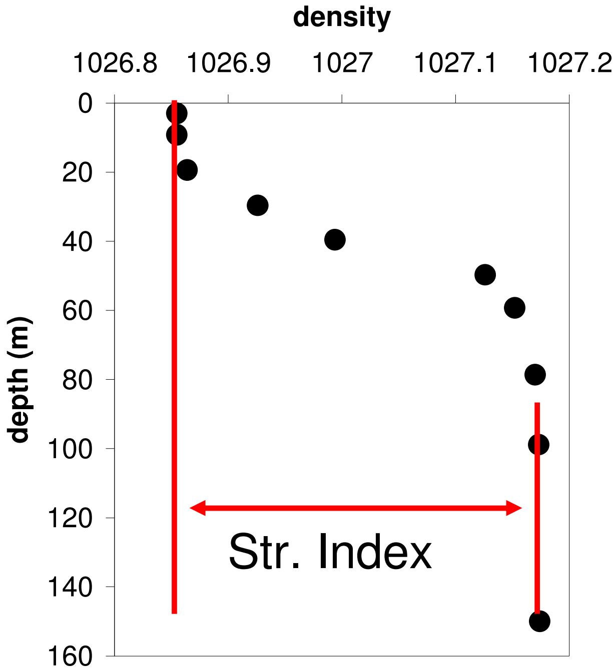


Stratification index



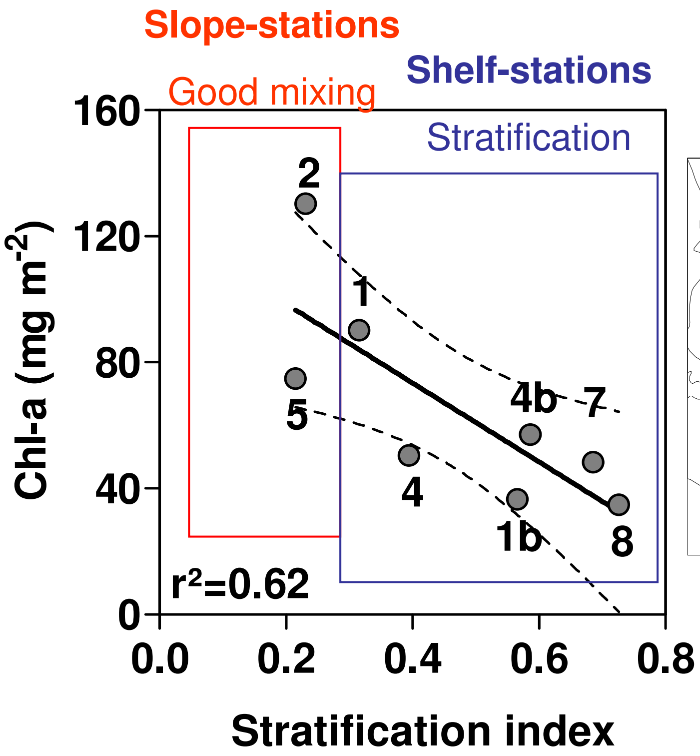
Higher index corresponds to more stratified conditions

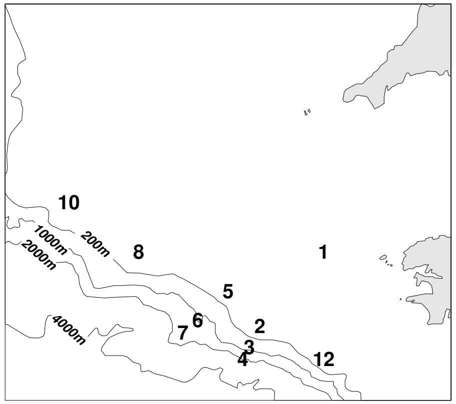
Stratification index



Higher index corresponds to more stratified conditions

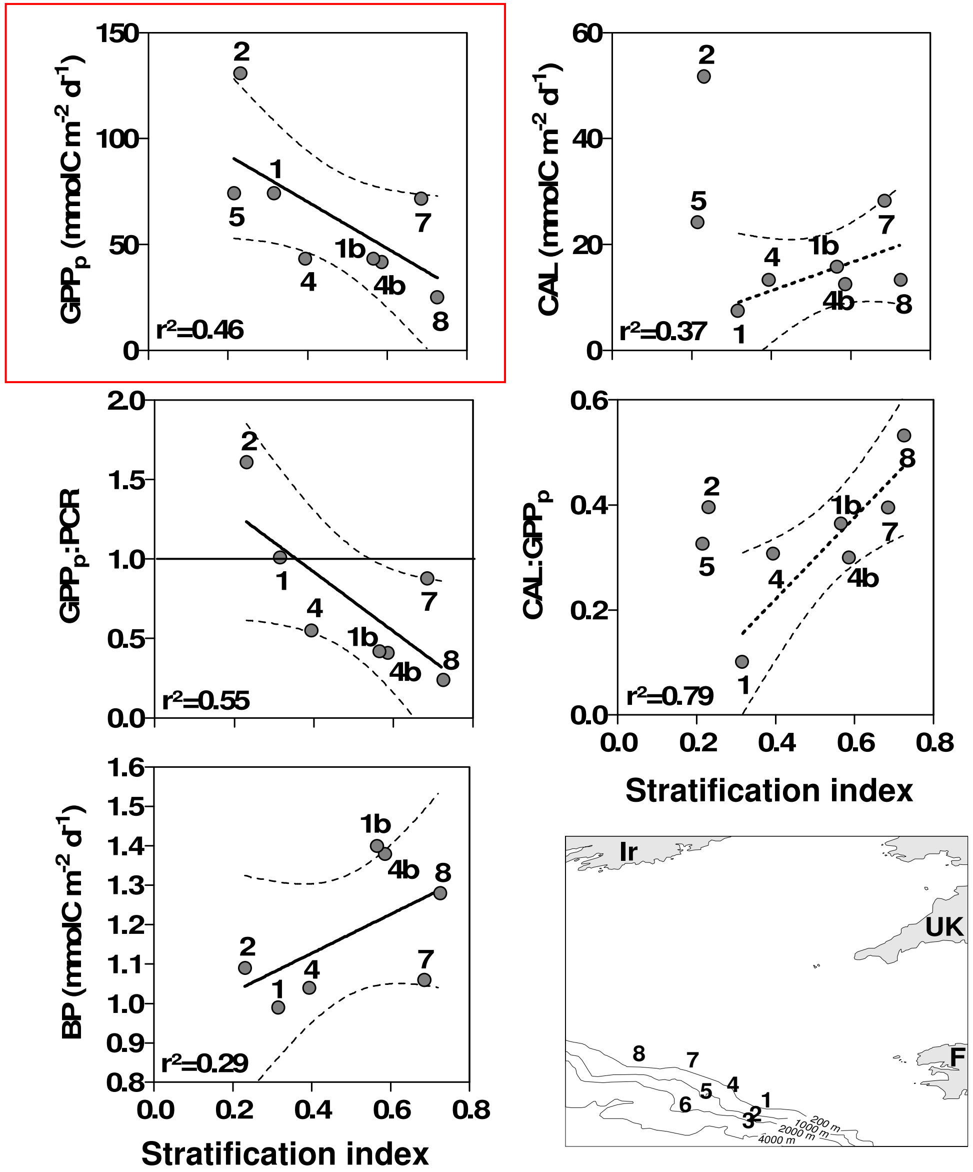
Example: Integrated Chl-a concentration





Stratification index

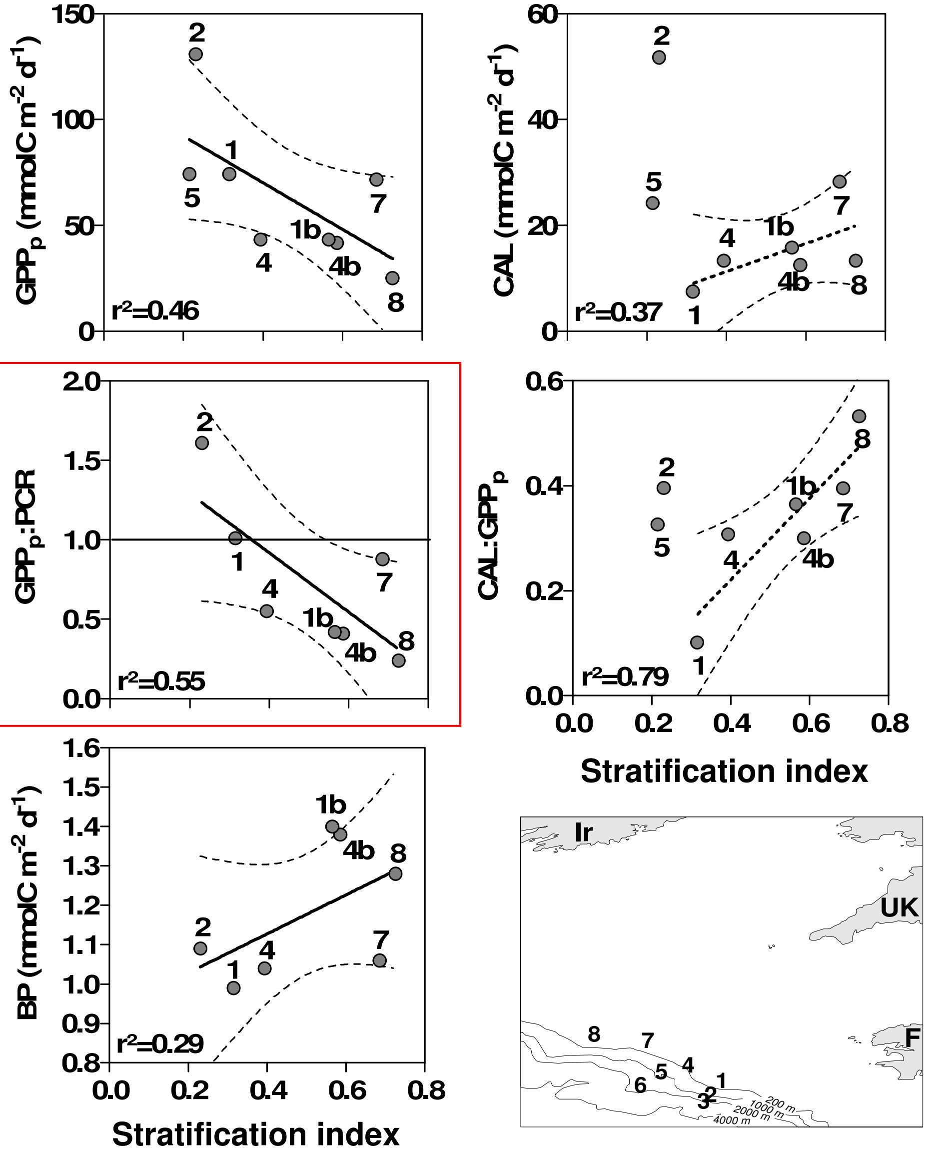
Primary production decreases with increasing stratification



Stratification index

Primary production decreases with increasing stratification

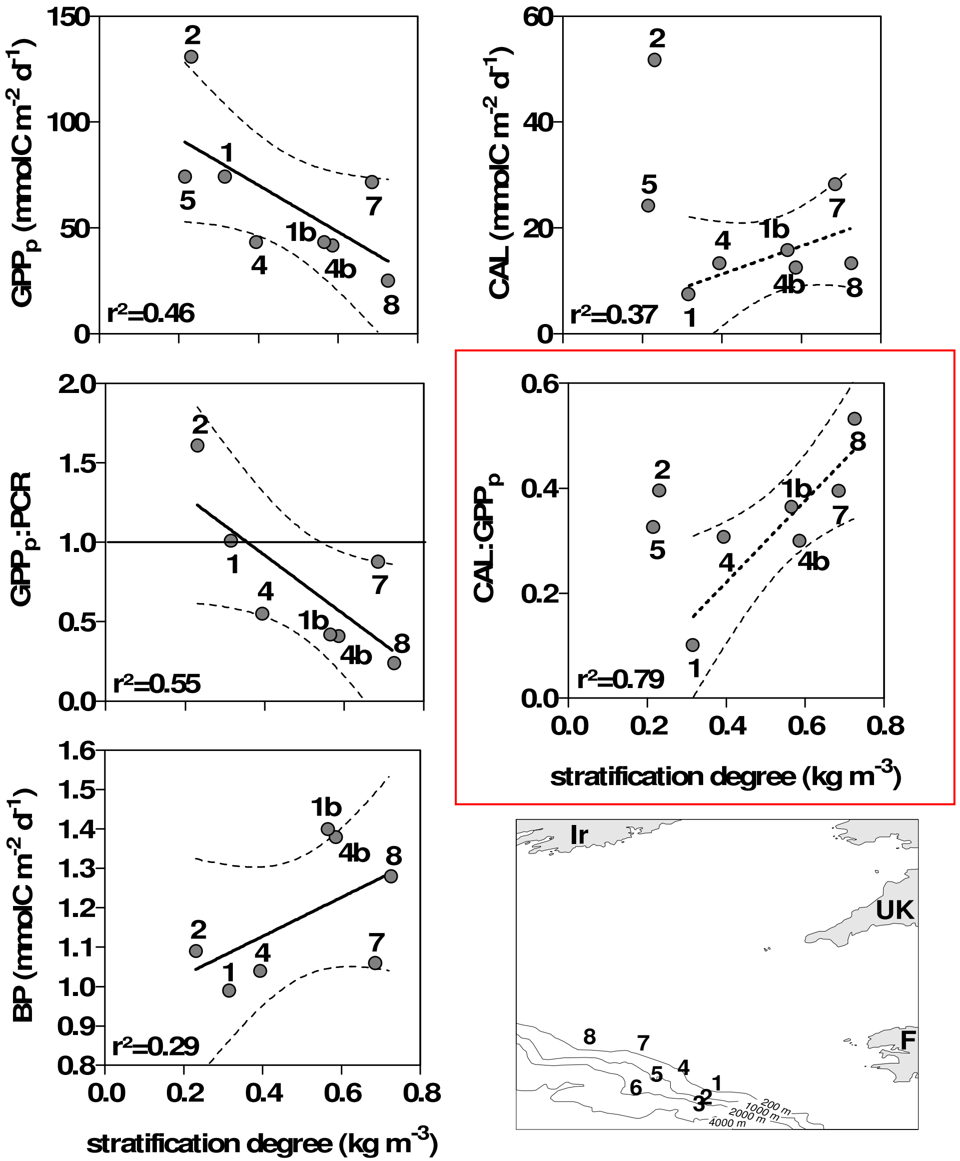
The system evolves towards heterotrophy with increasing stratification



Stratification index

Primary production decreases with increasing stratification

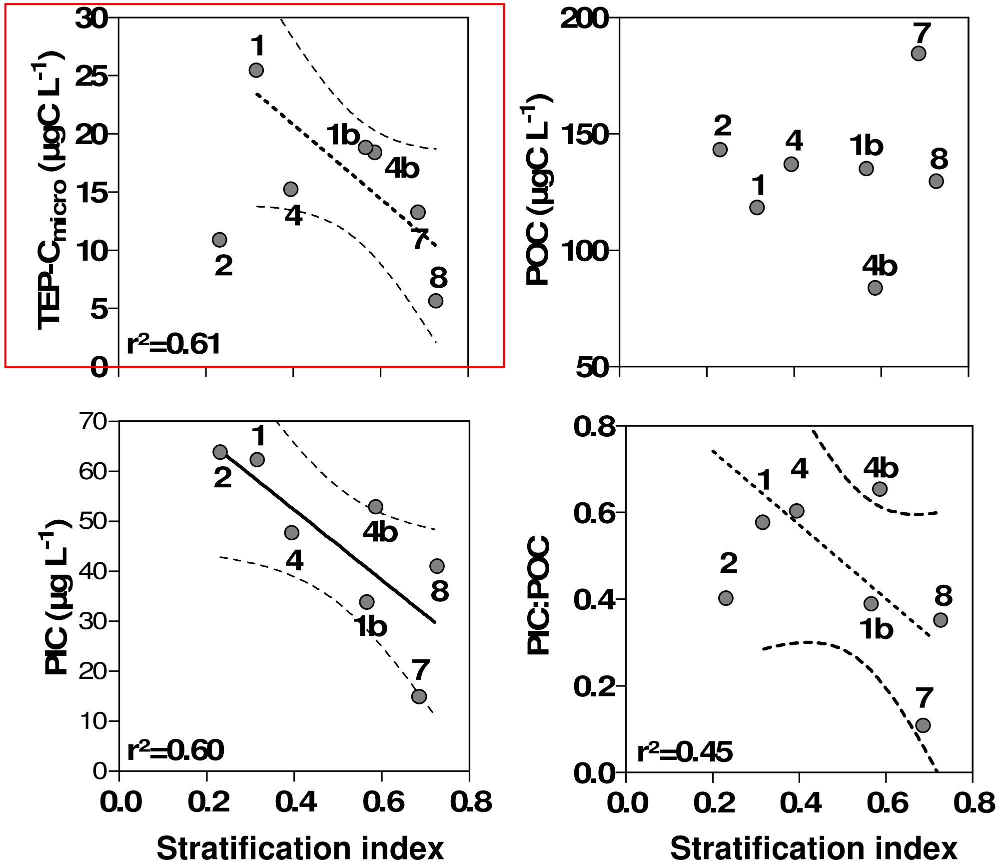
The system evolves towards heterotrophy with increasing stratification



C:P ratio increases with increasing stratification

Stratification index

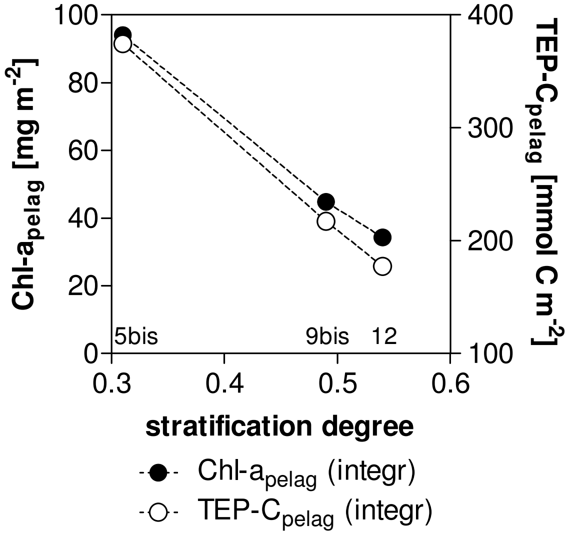
The system evolves towards heterotrophy with increasing stratification



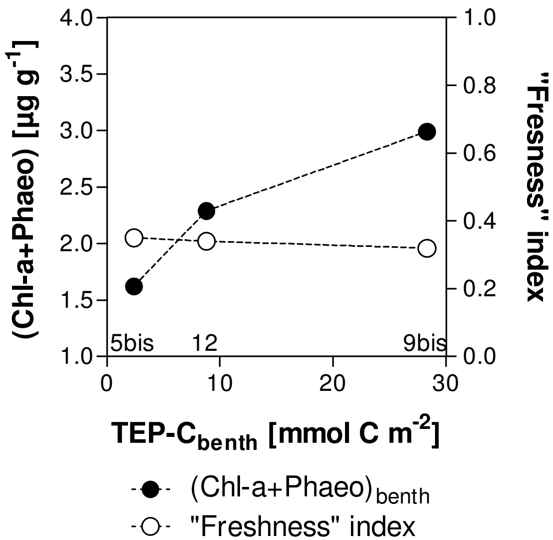
TEP_{color} and sediment (Cruise 2008)

The abundance of **TEP-C** and **Chl-a** in the **water column** decreases as water stratifies.

Integrated TEP-C value is of the same magnitude as the C- content of the deposited fluffy layer (de Wilde *et al.*, 1998).



More **TEP-C** is observed on the **bottom**, where phytoplankton detritus are more abundant and degraded (« Freshness index »:Chl-a:(Chl-a+Phaeo)=0.35).



Scientific background

"Traps on 8 to 9 May contained large aggregates (Fig. 2) consisting almost exclusively of intact *Emiliana huxleyi* cells, embedded in mucoid material. These occurred following the peak of abundance of this coccolithophorid in surface waters (1.45 x 10^6 cells dm^{-3})." (Cadée, 1985)

Vol. 24: 193–196, 1985 | MARINE ECOLOGY – PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published July 11

NOTE

Macroaggregates of *Emiliana huxleyi* in sediment traps

G. C. Cadée

"Sedimentation of coccoliths on the seabottom can probably only take place when they are transported in macroaggregates or faecal pellets (Honjo & Roman 1978). Loose coccoliths (sinking rate ~ 10 cm d^{-1}, Honjo 1976) will probably never reach the seabottom, intact cells (sinking rate ~ 1 m d^{-1}, Smayda 1971) also need a much longer time than macroaggregates (sinking rate ~ 100 m d^{-1}, Smayda 1971) to reach the bottom."

Scientific background

PERGAMON

Deep-Sea Research II 48 (2001) 3107–3139

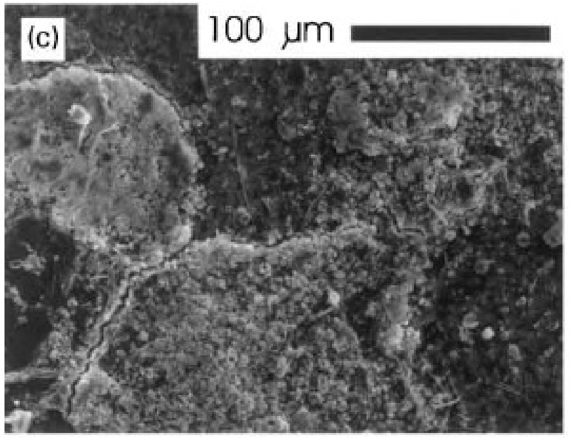
DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

Distribution, composition and flux of particulate material over the European margin at 47°–50°N

I.N. McCave[a,*], I.R. Hall[a,1], A.N. Antia[b], L. Chou[c], F. Dehairs[d], R.S. Lampitt[e], L. Thomsen[f], T.C.E. van Weering[g], R. Wollast[c]

(June, 1995). (c) Depth 500 m, station OM-7. This is below the SNL but within the depth range of generally enhanced SPM concentrations. In this case the filter is blocked with large organic patches of mucus some several hundred micrometres in diameter, which on closer examination show embedded particles of coccoliths, silt and clay. The



(McCave *et al.*, 2001)

Fig. 4. SEM image of mucus layer at st. E showing the solid remains of a typical coccolithophorid assemblage.

Pergamon Progress in Oceanography 42 (1998) 165–187

Progress in Oceanography

Late-summer mass deposition of gelatinous phytodetritus along the slope of the N.W. European Continental Margin

P.A.W.J. de Wilde*, G.C.A. Duineveld, E.M. Berghuis, M.S.S. Lavaleye, A. Kok

a carbon load of 250 mmol C m^{-2} over an area of 50,000 km^2. The recent state of the mucus allowed us to search for its origin. Characteristic pigment composition and the presence of coccoliths pointed to prymnesiophytes (coccolithophorids) as a major contributor, but dinoflagellates (peridinin) and green algae (chlorophyll-b, lutein) must have contributed as well. Sim-

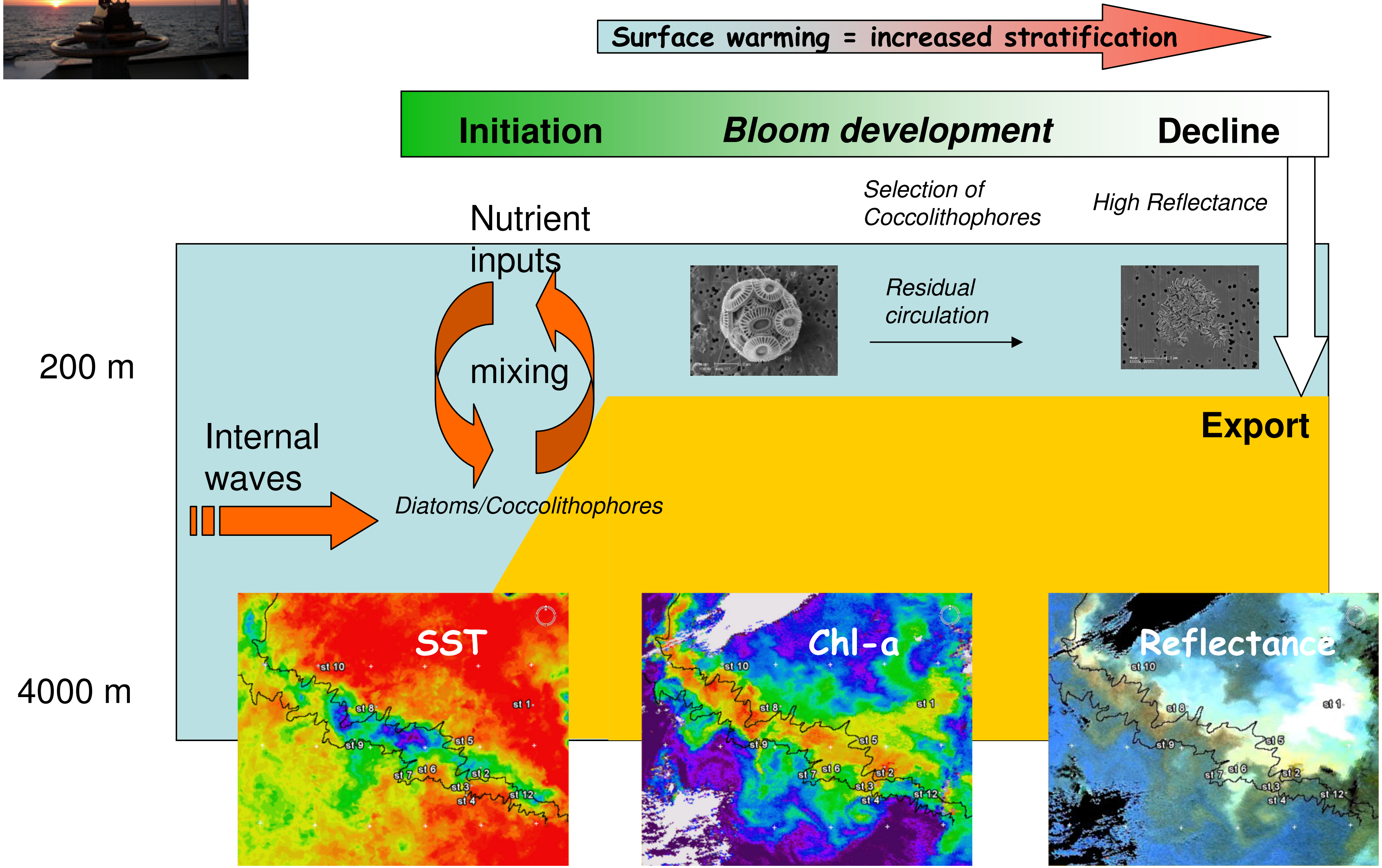
Outline

- Preambule:
  - Problematic of coccolithophorid studies
  - Internal calcification
  - Lessons from the cultures
  - Ecological niche
- Results:
  - Bay of Biscay
  - Multidisciplinary cruises
  - 2004
  - 2006
  - 2008
- Perspectives:
  - Synthesis of field data
  - Mechanism of bloom development in the Bay of Biscay
  - Conceptual model for coccolithophorid calcification

Synthesis of field data

PARAMETERS	SHELF **Biscay** April-May 2002 this study	SHELF **Biscay** April-May 2003 this study	SHELF **Biscay** early June 2004 this study	SHELF **Biscay** early June 2006 this study
Nutrients and Chl-a				
T°	12-13°	11.5-12.5°	12-15° (up to 17°)	13-14°
DSi (µM)	~1.0	<2.0	<2.0	<2.0
PO4 (µM)	0.01		< 0.2	<0.1
Chl-a (µg L^{-1})	<0.1 to (3.0-4.0)	2.0-2.3	0.25 and <1.0 (up to 1.5)	0.5 to 2.0
Int Chl-a (mg m^{-2})	up to 121	up to 127	up to 87	up to 130
UML depth (m)	20 to 40	<40	30 to 50	10 to 40
Z_0 (PAR) (m)	22 to 44	20 to 30	20 to 35	26 to 37
Suspended matter				
POC (µM)	7.5 to 20.0	8.9 to 19.3	7.7 to 15.5	4.8 to 17.3
POC (µg L^{-1})	90 to 240	107 to 231	92 to 186	58 to 208
PIC (µM)	4.2 to 8.3	7.5 to 63.5	<4.0 (up to 8.2)	3.5 to 7.5 (up to 10.6)
PIC (µg L^{-1})	50 to 100	90 to 462	<48 (up to 98.4)	42 to 90 (up to 127.2)
PIC:POC (standing stock ratio)	0.54	0.6 (up to 3.3)	0.20 to 0.30	0.30 to 0.66
Coccolithophores				
Cell density (ml^{-1})			2 000 to 8 000	
Liths density (ml^{-1})			2 000 to 53 000	
Liths:cell			3 to 10:1	
Metabolism				
PP (µMPOC h^{-1})	0.66	0.25-1.23	0.15-0.20 (up to 0.30)	0.25 (0.08-0.61)
PP (mg C m^{-3} h^{-1})				
CAL µMPIC h^{-1})	0.07 to 0.42	up to 0.18	0.05 (up to 0.22)	0.01 to 0.14
CAL (mg C m^{-3} h^{-1})				
C:P (instantaneous production ratio)	<0.35±0.15> (0.04-0.81)	<0.12±0.11> (0.01-0.34)	<0.11±0.16> (0.01-0.84)	<0.24±0.15> (0.01-0.49)
Int PP (gPOC m^{-2} d^{-1})	0.02 to 1.06	<1.21±0.44> (0.3-1.69)	0.21 to 0.68	0.30 (up to 1.57)
Int PP (mmol m^{-2} d^{-1})				
Int CAL (gPIC m^{-2} d^{-1})	0.1 to 0.52	<0.13±0.07> 0.04-0.26	up to 0.14 (st 2)	0.09 to 0.62
Int CAL (mmol m^{-2} d^{-1})				
C:P (integrated production ratio)	<0.45±0.31>	<0.12±0.06> (0.03-0.21)	0.02-0.31	<0.34±0.12> (0.10-0.53)
GP (O_2) (µM O_2 m^{-3} d^{-1})				
GP (O_2) (mmol O_2 m^{-2} d^{-1})				
DCR (O_2) (µM O_2 m^{-3} d^{-1})				2.0-5.2
DCR (O_2)(mmol O_2 m^{-2} d^{-1})				73.7 to 104.3
carbonate chemistry				
ΔTA (µmol kg^{-1})	-23.7 <-6.1>		-5 to -47	up to -26
pCO_2	< atm equ.	< atm equ.	263 to 325	265 to 325
ΔpCO_2 (µatm)	-15	-10	-30 to -40	-26
O_2 Sat % (surf)				110%

Mechanism of bloom development



Conceptual representation

Why do they calcify?

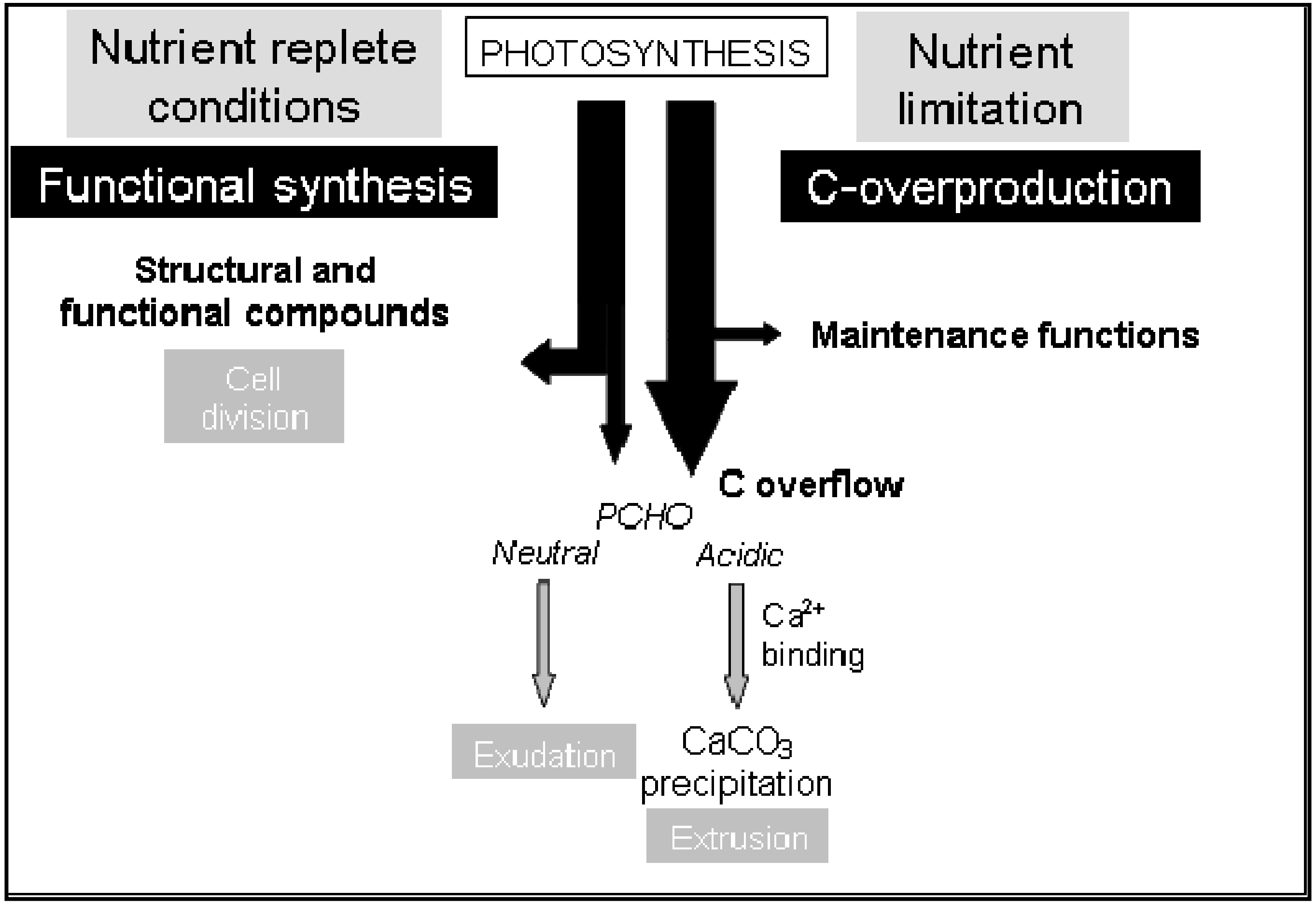
For coccolithophores, calcification is:

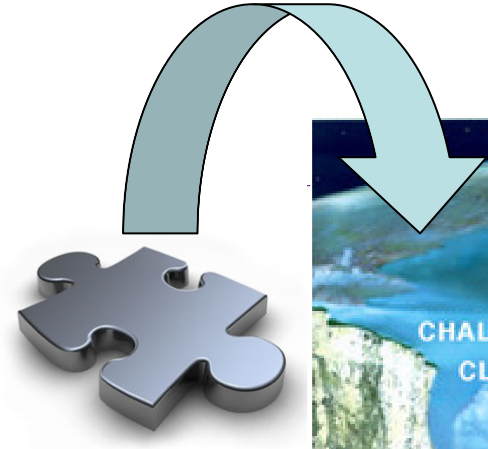
- Not a protection against grazers/viruses
- Not a way to modulate buoyancy
- Not a way to modulate the incoming light
- Cost effective mechanism
- Associated to the production of pôlysaccharides
- Also taking place when cell division has stopped

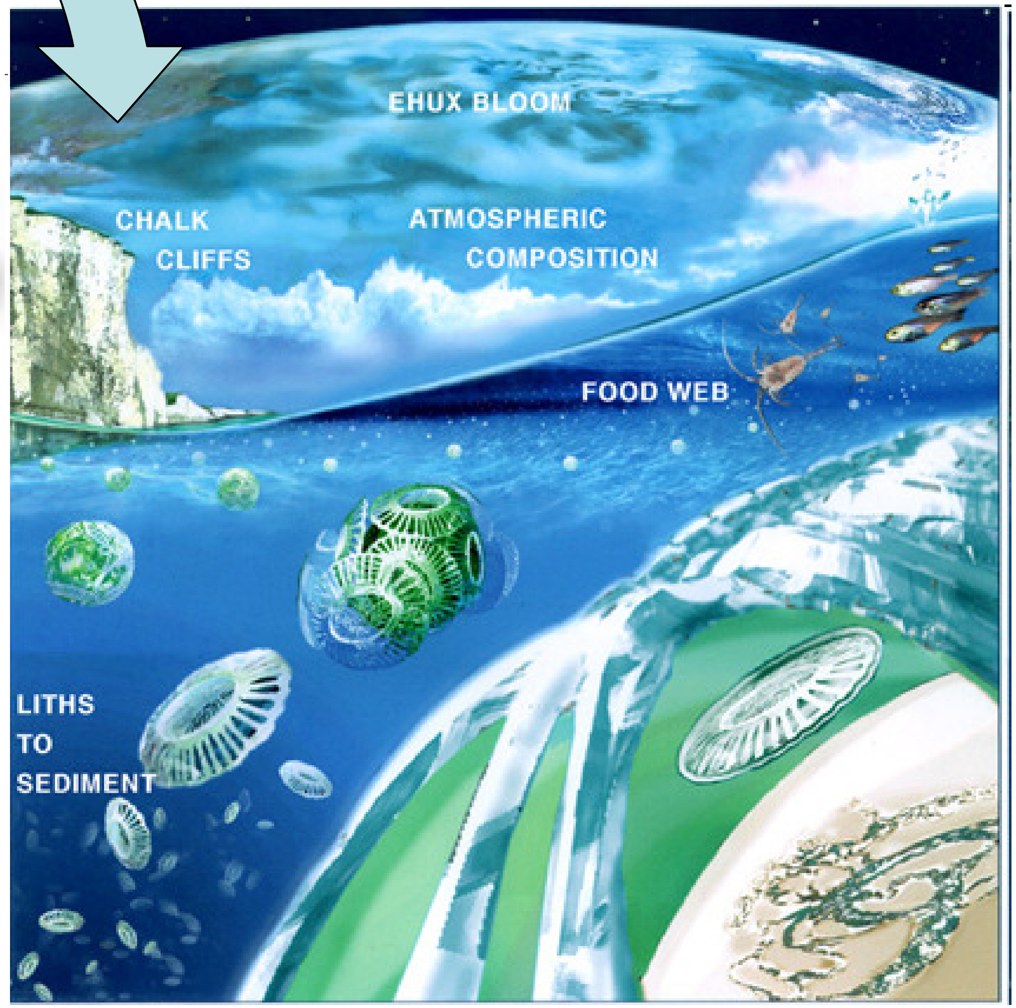
Carbon concentration mechanism, « Trash can function » ?

Conceptual representation

Internal calcification represents an energetic investment compatible with a **"Trash-can function"** and a **"C-overflow function"**.



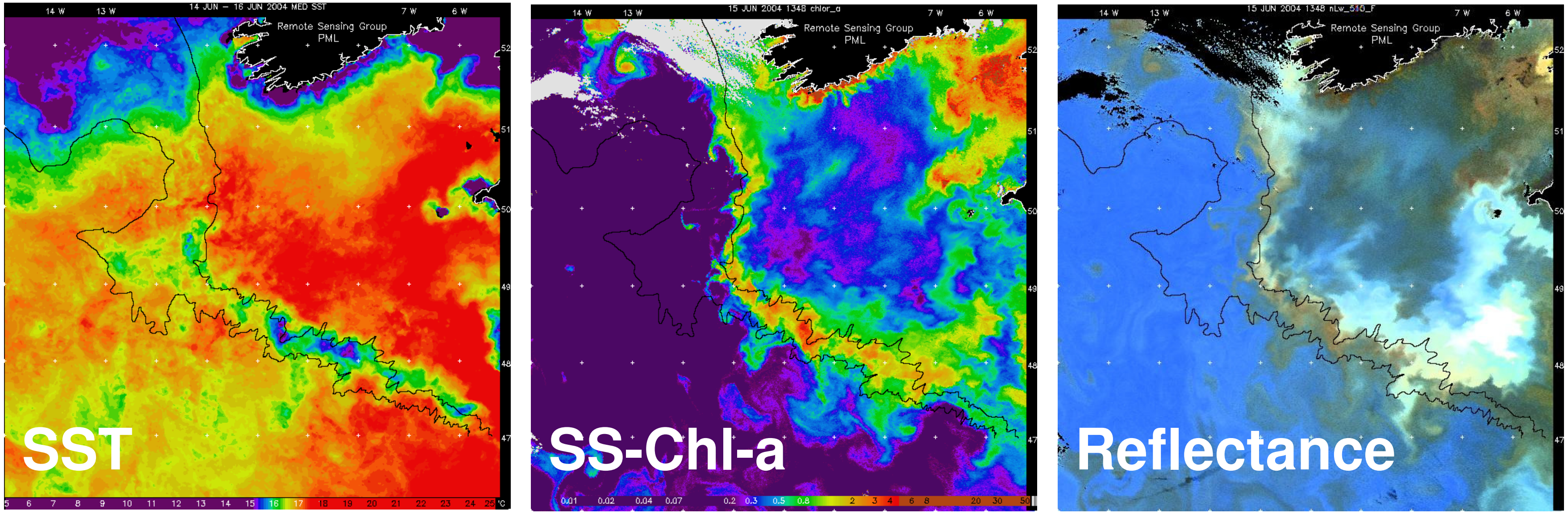




Jess & Glynn Gorick

Thank you for your attention

The northern Bay of Biscay



Composite image (14-16 June 2004)