The seasonality of primary production and phytoplankton composition in the Celtic Sea

Work module 3 - The Autotrophs: *focuses on the uptake of inorganic C, N, P, Si by the autotrophs, and the partitioning of organic matter into dissolved and particulate forms.*

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WM-3 Key Hypotheses & Deliverables

Supports Objective 2 (Determine the relative importance of external nutrient sources and *internal biogeochemical cycling* in maintaining the shelf pump).

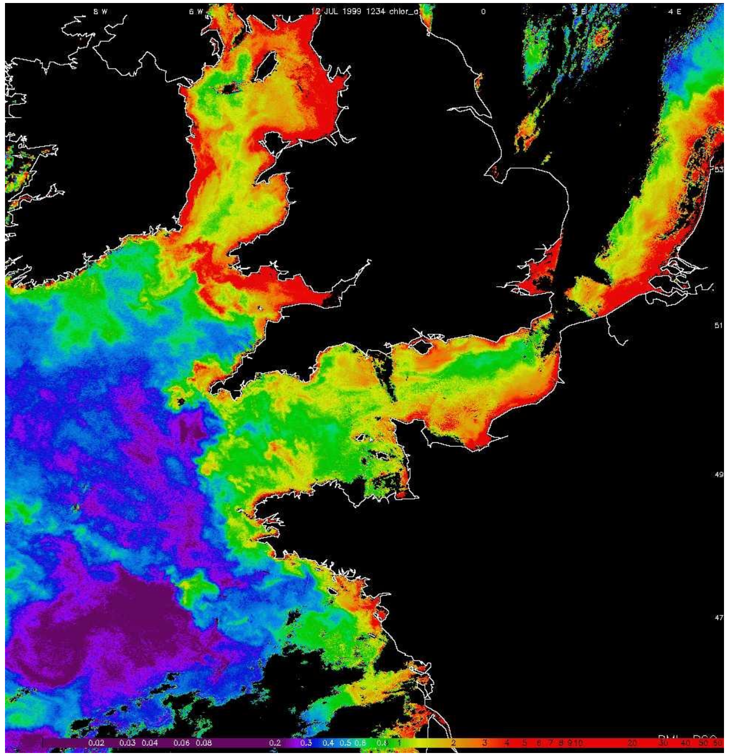
Hypothesis - 3: Autotrophic community structure and resource availability influence the stoichiometry of organic matter through increasing C:N:Si:P ratios under nutrient depleted conditions.

H3i: The spring bloom uses C and nutrients (N, P, Si) at close to canonical Redfield ratios.

H3ii: Departures from spring stoichiometry occur in response to available resources; C:N within autotrophs will increase as N becomes limiting, accompanied by release of C-rich DOM.

H3iii: Gradients in phytoplankton community structure drive shifts in the stoichiometry of POM and DOM.

WM-3 Deliverables



Deliverables (Talk outline):

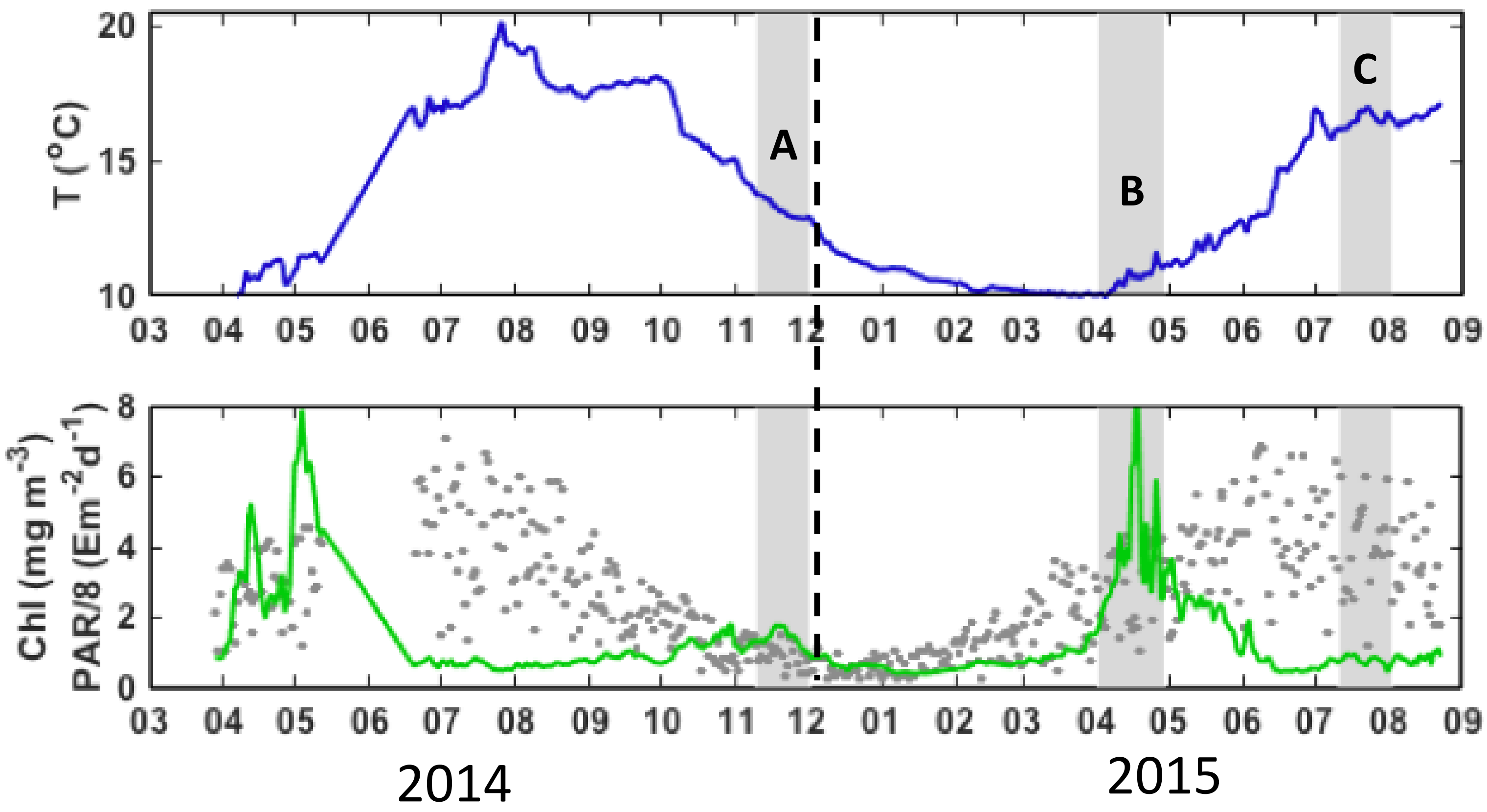
1. Spatially and seasonally-resolved primary production & community structure
2. Quantification of calcification and nitrogen fixation, maps of PIC distribution
3. Spatially & seasonally resolved measurements of the stoichiometry of C, N, P & Si uptake
4. Production of dissolved organic carbon (DOC) and phosphorus (DOP)
5. Community structure and uptake stoichiometry

Replicating seasonal irradiances

Percentage Light Depth	LED Panels	Neutral density type (% transmission)	Measured Irradiance (µmol quanta m^{-2} s^{-1})	Target Photon flux (mol quanta m^{-2} d^{-1})	Actual Photon flux (mol quanta m^{-2} d^{-1})	Actual Photon flux (mol quanta m^{-2} h^{-1})
November 2015 (photoperiod = 9 h; E_0 = 8.7 mol quanta m^{-2} d^{-1})						
60%	2	2 x 0.15 ND (69%)	167	5.2	5.4	0.60
40%	1	None	147	3.5	4.8	0.53
20%	1	0.30 ND (51%)	70	1.7	2.3	0.25
10%	1	0.15 ND (69%)	26	0.9	0.8	0.09
5%	1	0.9 ND (14%)	15	0.4	0.5	0.05
s1%	1	1.2 ND (7%)	7	0.1	0.2	0.03
April 2015 (photoperiod = 14 h; E_0 = 33.9 mol quanta m^{-2} d^{-1})						
60%	3	None	440	20.3	22.2	1.58
40%	3	1 x 0.15 ND (69%)	260	13.5	13.1	0.94
20%	3	3 x 0.3 ND (51%)	120	6.8	6.0	0.43
10%	1	0.3 ND (51%)	68	3.4	3.4	0.24
5%	2	2 x 0.9 ND (14%)	21	1.7	1.1	0.08
1%	1	1.2 ND (7%)	7	0.3	0.4	0.03
July 2015 (photoperiod = 16 h; E_0 = 39.8 mol quanta m^{-2} d^{-1})						
60%	3	None	440	23.9	25.3	1.58
40%	3	1 x 0.15 ND (69%)	260	15.9	15.0	0.94
20%	3	3 x 0.3 ND (51%)	120	8.0	6.9	0.43
10%	1	0.3 ND (51%)	68	4.0	3.9	0.24
5%	2	2 x 0.9 ND (14%)	21	2.0	1.2	0.08
1%	1	1.2 ND (7%)	7	0.4	0.4	0.03

Poulton et al., (submitted to Prog. Oceanogr.)

Seasonal context – CCS mooring data



Hickman, Sivyier et al., (unpublished data)

A. November 2014 – Autumn

(low light, cooling, mixing?)

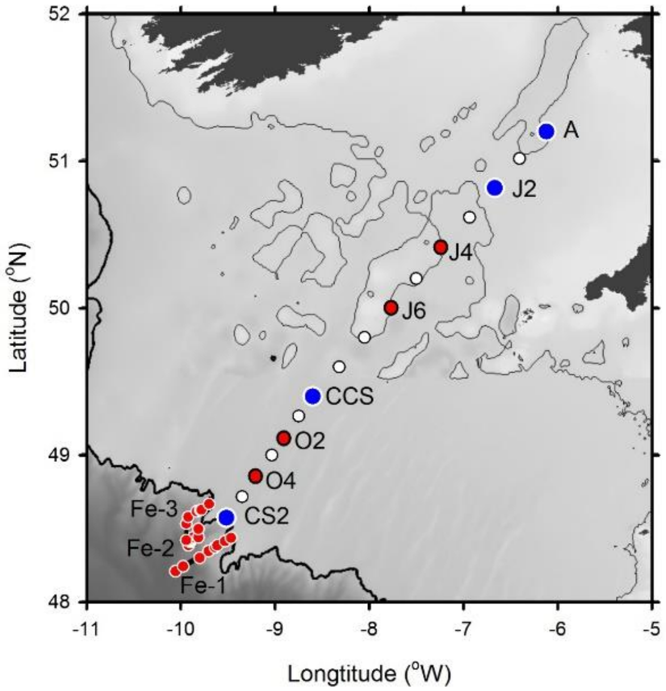
B. Spring 2015 – April

(increasing light, stratification, spring bloom)

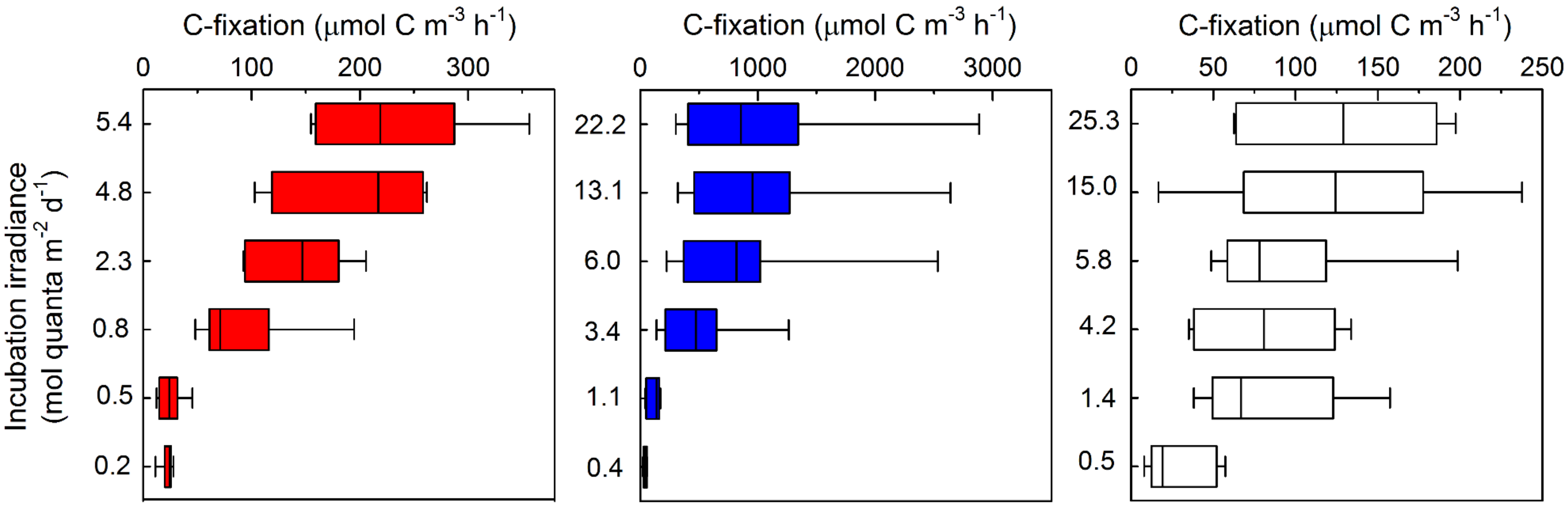
C. Summer - July

(stratified, high light, low nutrients, low biomass)

Spatially & seasonally resolved primary production



- Numerous measures of C-fixation:
  - Short-term C-fixation (6-8 hr) (DOP production, ‘gross production’)
  - Net primary production (24 hr) (*cf.* Calcite Production)
  - Size-fractionated primary production (24 hr)
  - Photosynthesis vs Irradiance (2-6 hr) [Kieran Curran PhD]
  - Electron Transport Rates (ETR, FRRf) [James Fox PhD]



Poulton, Daniels & Mayers (unpublished)

Seasonality - Euphotic zone integrals

Season / Date	Site	Chl-*a* (mg m^{-2})	C_{phyto} (mmol C m^{-2})	C_{bact} (mmol C m^{-2})	NPP (mmol C m^{-2} d^{-1})
10 Nov	CCS	59.7	91	28	37.0
12 Nov	CCS	37.4	36	-	18.5
18 Nov	CS2	54.4	78	24	22.5
20 Nov	CS2	57.6	73	24	26.3
22 Nov	CCS	68.7	91	32	42.9
25 Nov	CCS	70.8	93	32	46.9
Mean		**58.1**	**77**	**28**	**32.4**
04 April	CCS	49.6	153	49	117.6
06 April	CCS	61.4	162	57	59.1
10 April	CS2	37.8	106	27	87.8
11 April	CCS	94.9	221	142	154.0
15 April	CCS	152.6	180	162	532.1
20 April	CCS	92.3	168	182	206.2
24 April	CS2	57.4	202	44	132.8
25 April	CCS	110.4	247	142	321.0
Mean		**82.1**	**180**	**101**	**201.3**
14 July	CCS	19.3	200	30	58.5
15 July	CCS	28.5	121	23	43.7
19 July	CS2	18.4	66	32	32.5
20 July	CS2	17.2	-	-	18.3
24 July	CCS	35.7	86	33	38.3
29 July	CCS	26.4	79	27	19.7
30 July	CCS	28.0	-	-	36.8
Mean		**24.8**	**110**	**29**	**35.4**

Poulton et al., (submitted to Prog. Oceanogr.)

Autumn (low light)

- Moderate Chl-*a*, low C_{phyto} & C_{bact} biomass & NPP
- **late Autumn bloom**

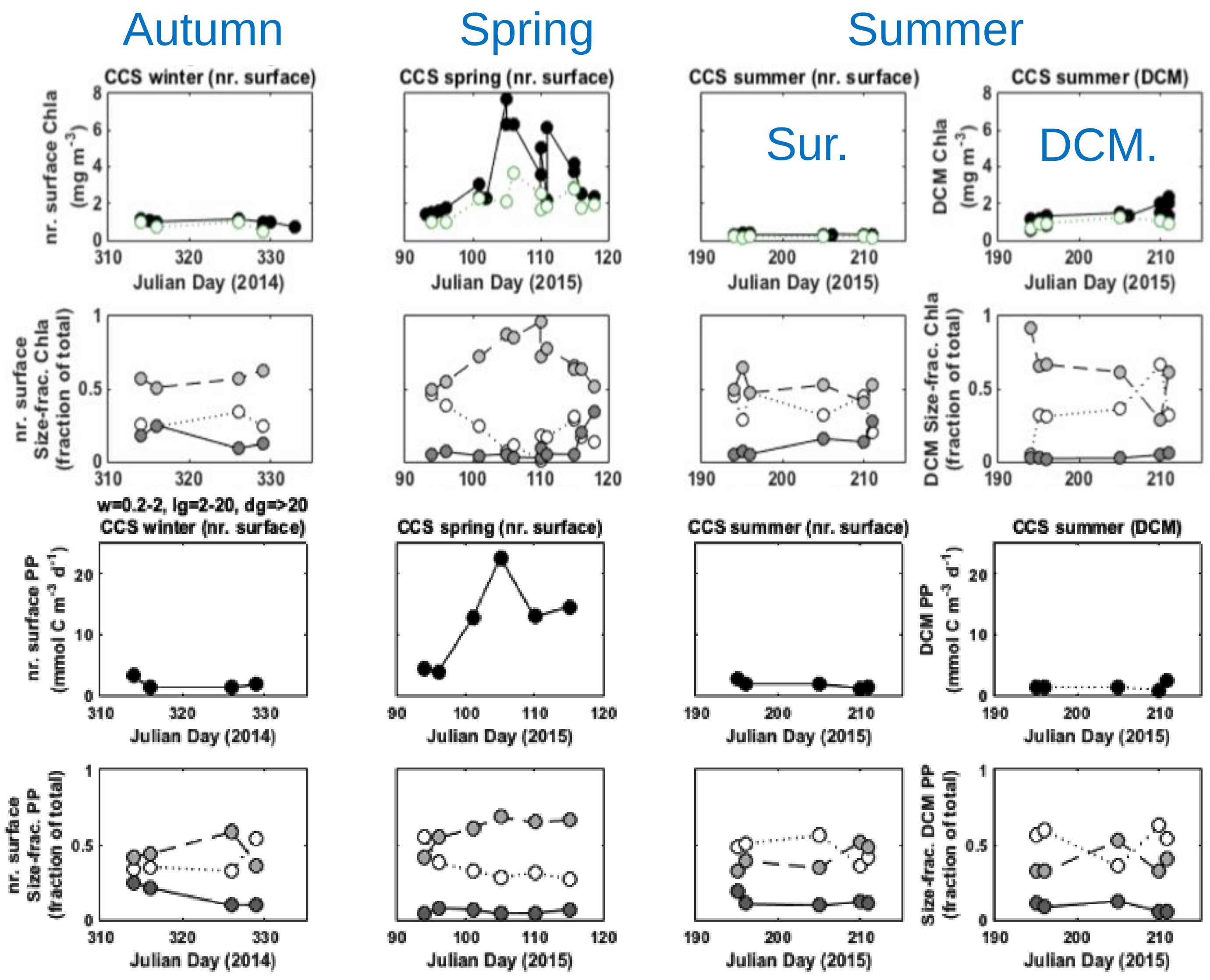
Spring (**transitional**)

- First half: increasing biomass and NPP (peaks ~15-18th April)
- Second half: post-peak, decline in Chl-*a* but not C_{phyto} or NPP

Summer (low nitrate+nitrite and phosphate)

- Low Chl-*a* but high C_{phyto} (**variable C:Chl-*a***)
- NPP similar to autumn despite low nutrients (**nutrient recycling**)

Size-fractionated Chl-*a* and Net Primary Production



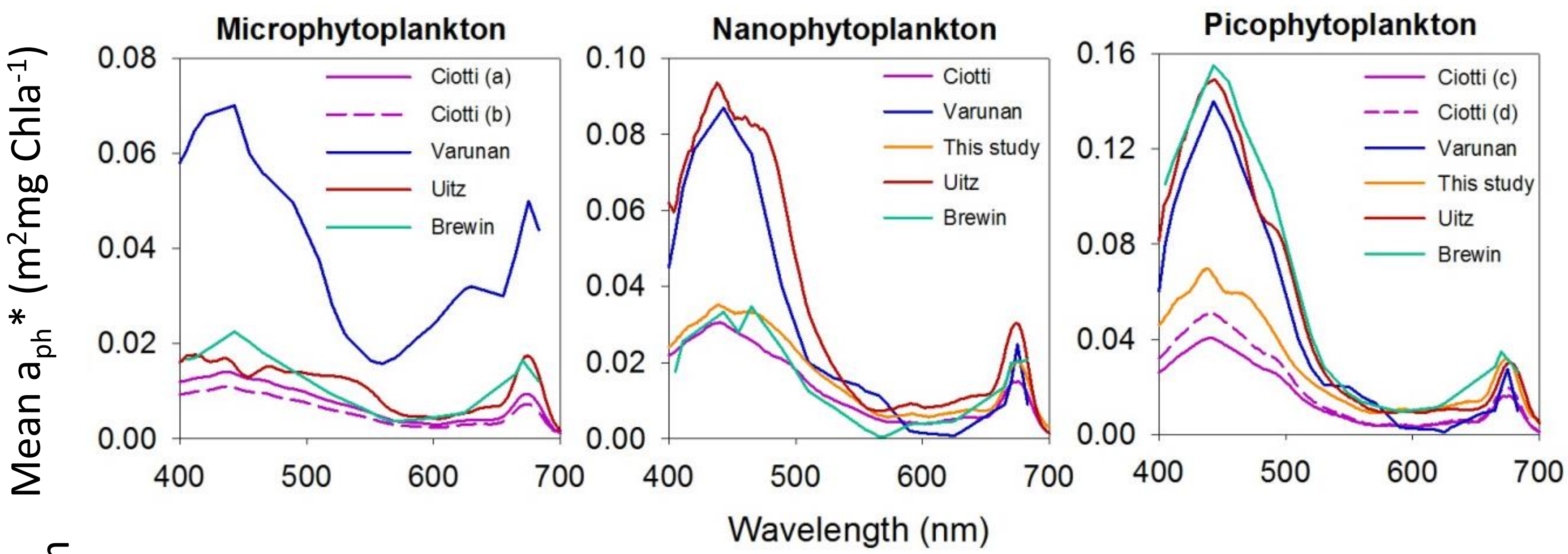
<2 um (white), 2-20 um (grey), >20 um (dark grey)

- Consistent btwn Chl-*a* and NPP
- Dominance of nanoplankton (2-20 µm) in autumn, spring and summer
- Microplankton (>20 µm) low
- Nanoplankton dominated biomass and NPP in 2015 spring bloom (few diatoms)

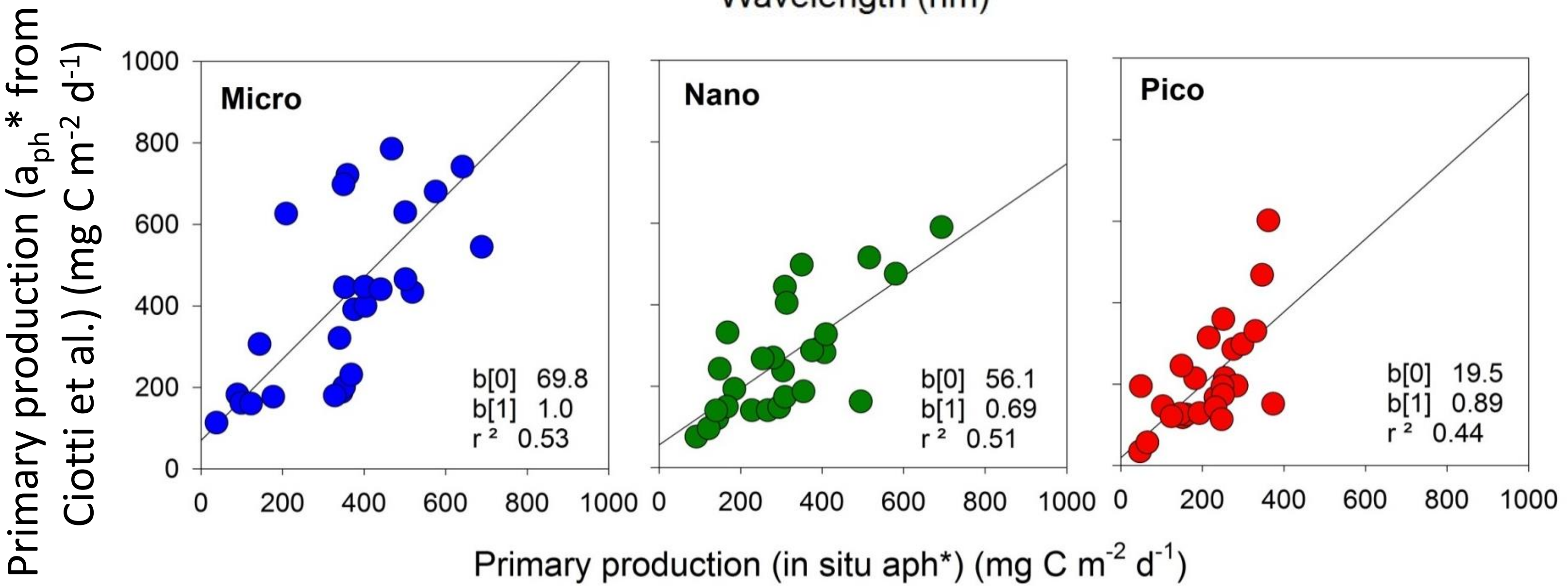
Hickman et al., (in prep. for Prog. Oceanogr.)

Models of size-fractionated phytoplankton absorption coefficient in the Celtic Sea

K Curran
(PhD, G Tilstone)



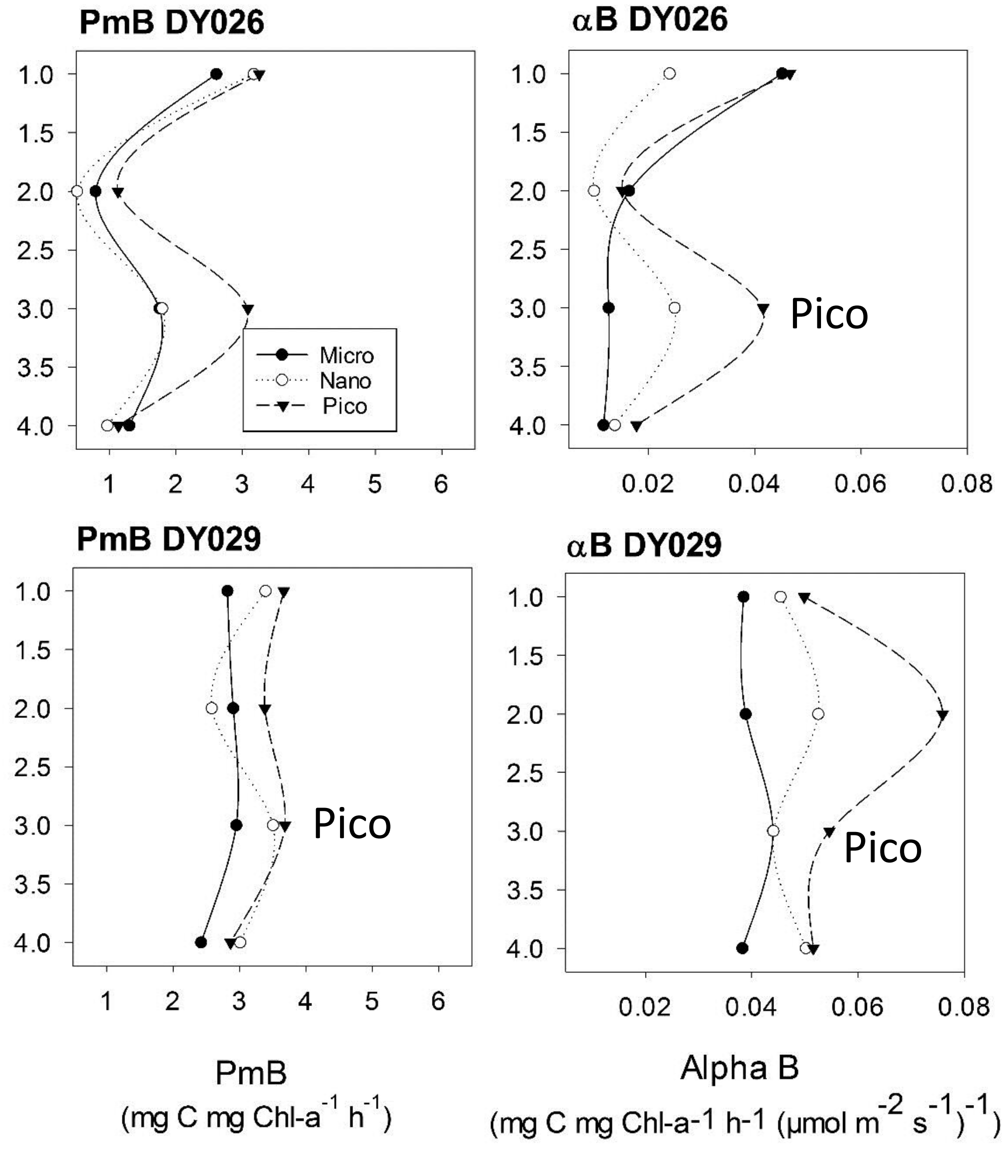
Comparison of 5 models with in situ a_{ph}: Ciotti et al. model is the most accurate.



Sensitivity of primary production to Ciotti et al. modelled a_{ph} : good fit for 3 size-classes.

Comparison of size-fractionated (SF) photosynthetic rates for the Celtic Sea with a global satellite model

DY026 & DY029 in situ photosynthetic rates.

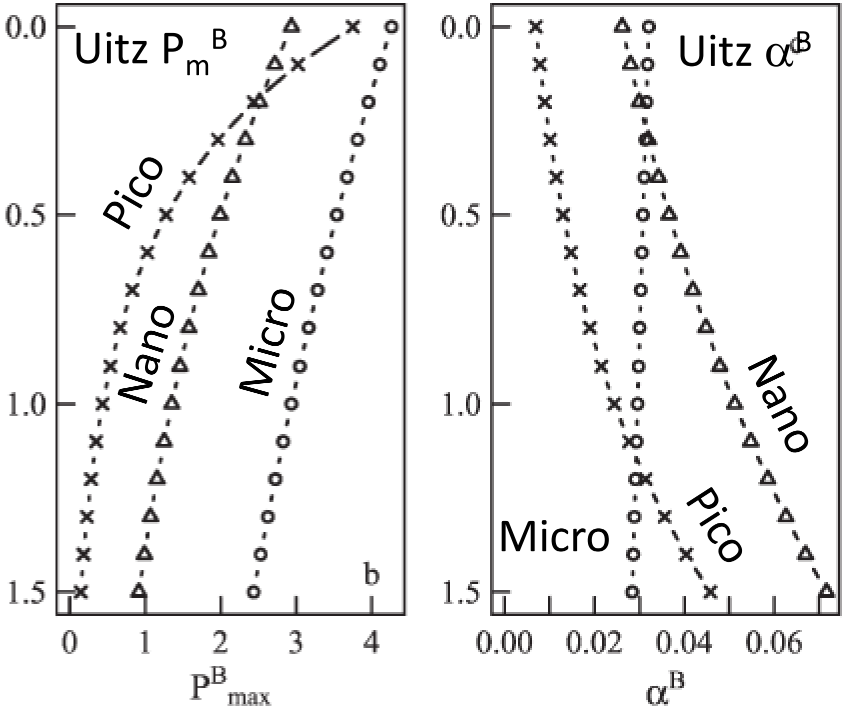


K Curran (PhD, G Tilstone)

<u>BOTTOM:</u> photosynthetic rates used in satellite model of SF primary production indicate that micro- have highest and pico- lowest C-fix rates

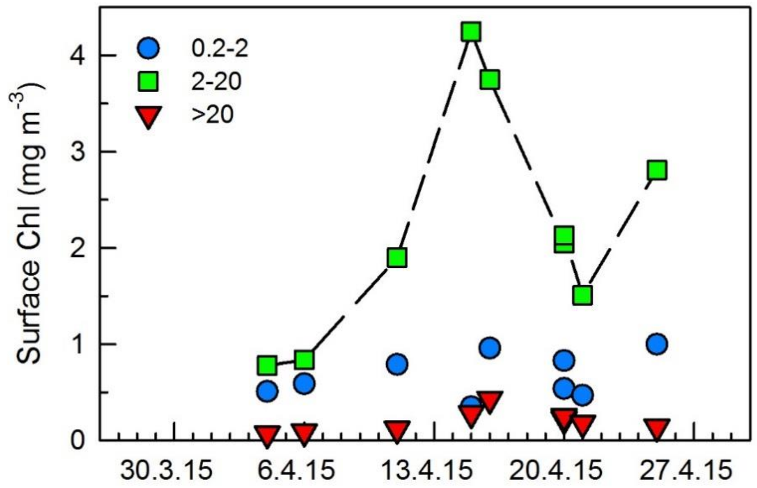
<u>LEFT:</u> In situ measurements indicate opposite trend in spring & summer.

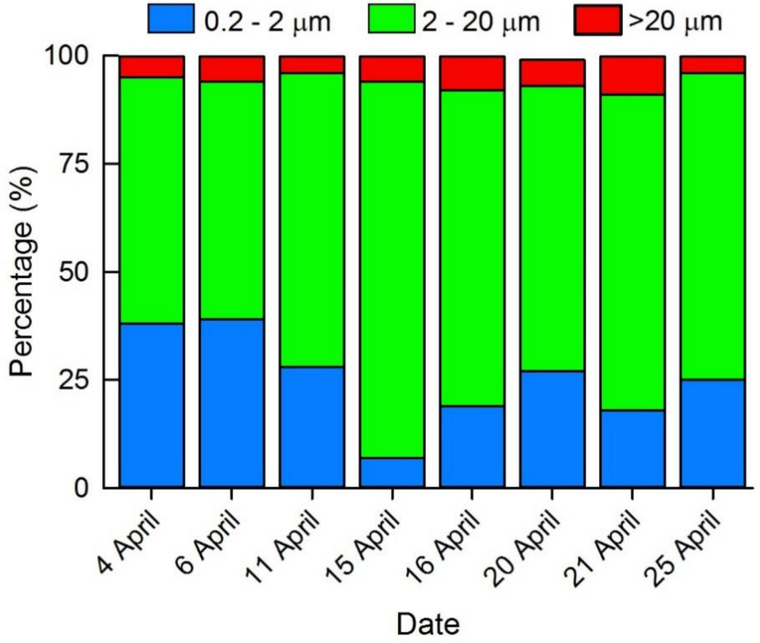
Uitz (2008) modelled photosynthetic rates.



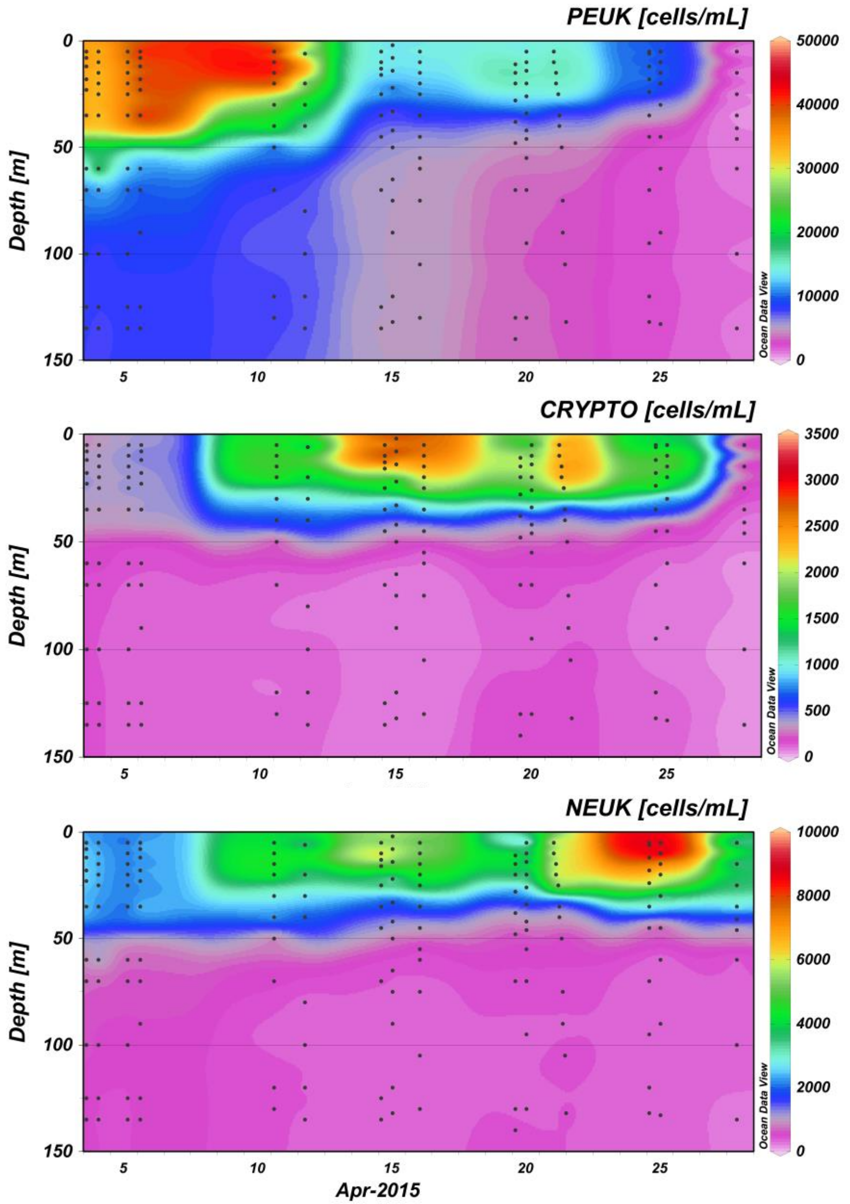
Micro- circles; nano- triangles; pico- crosses

Celtic Sea Spring Bloom 2015 (April)





Poulton et al., (unpublished)



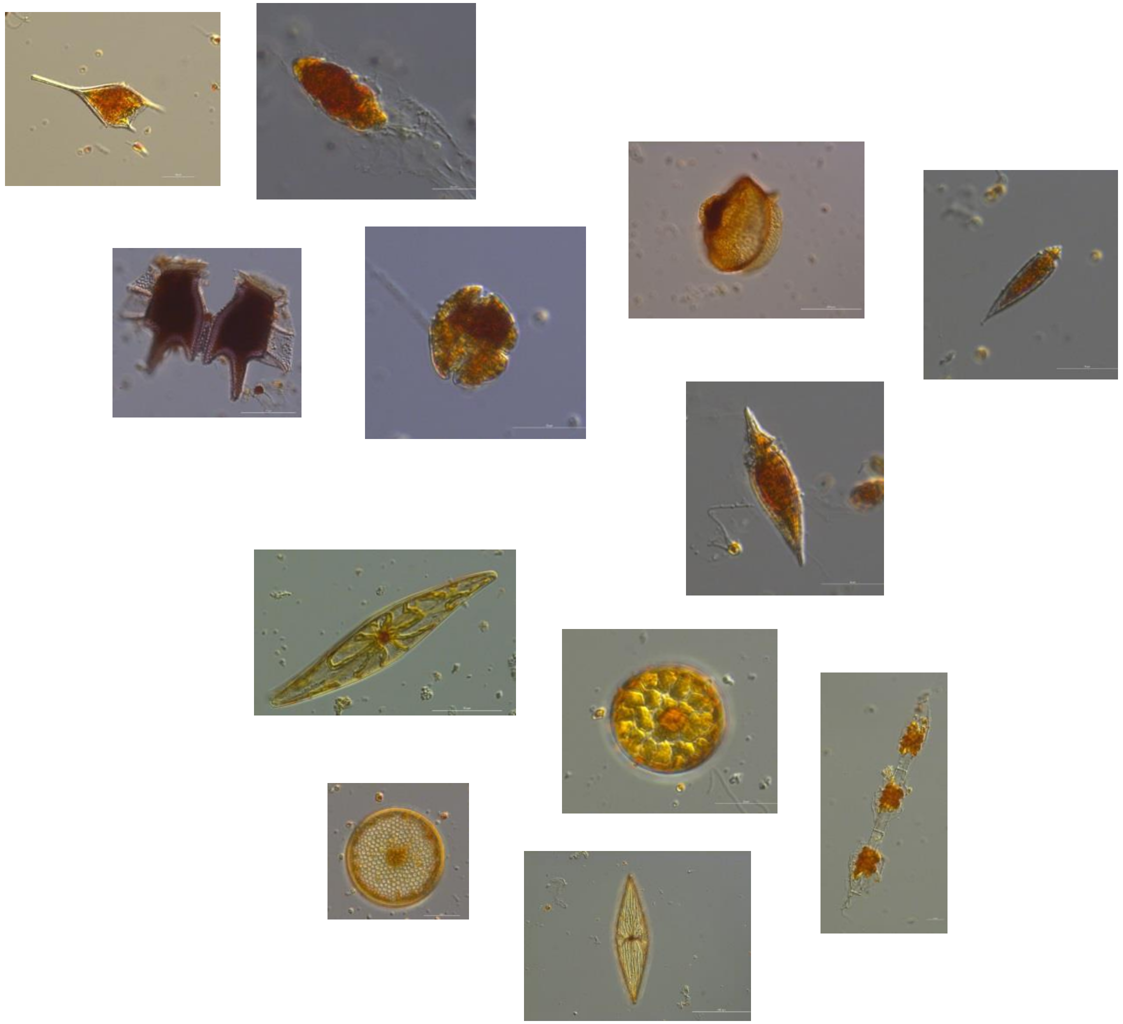
Tarran et al., (in prep.)

- Nanoplankton dominated biomass, production & cell abundances
- Succession: picoeukaryotes first 1/3, cryptophytes 2/3, nanoeukaryotes last 1/3
- Large (>20 µm) diatoms only at end, but nano-diatoms (*Minidiscus* sp., up to 8000 cells mL^{-1}, <10% Chl-*a*, C_{phyto}, NPP: Poulton & Gore, unpublished results)
- Main grazers? Micro-zooplankton? Trophic transfer?

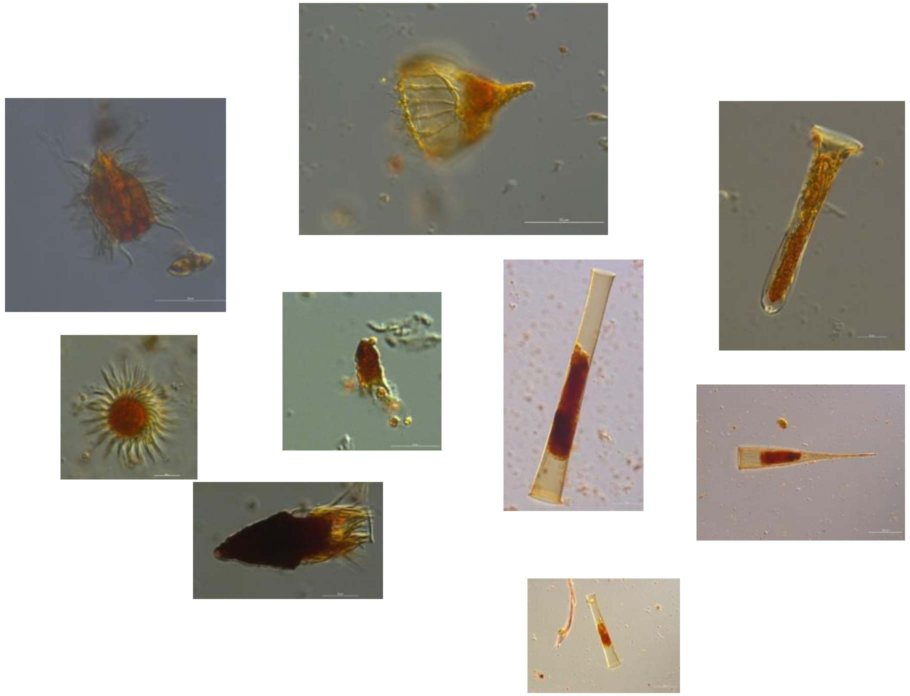
Spatially & seasonally resolved micro-plankton

DY018, DY029 & DY033 – Lugol's microscopy counts, data available at BODC, SSB Dropbox,

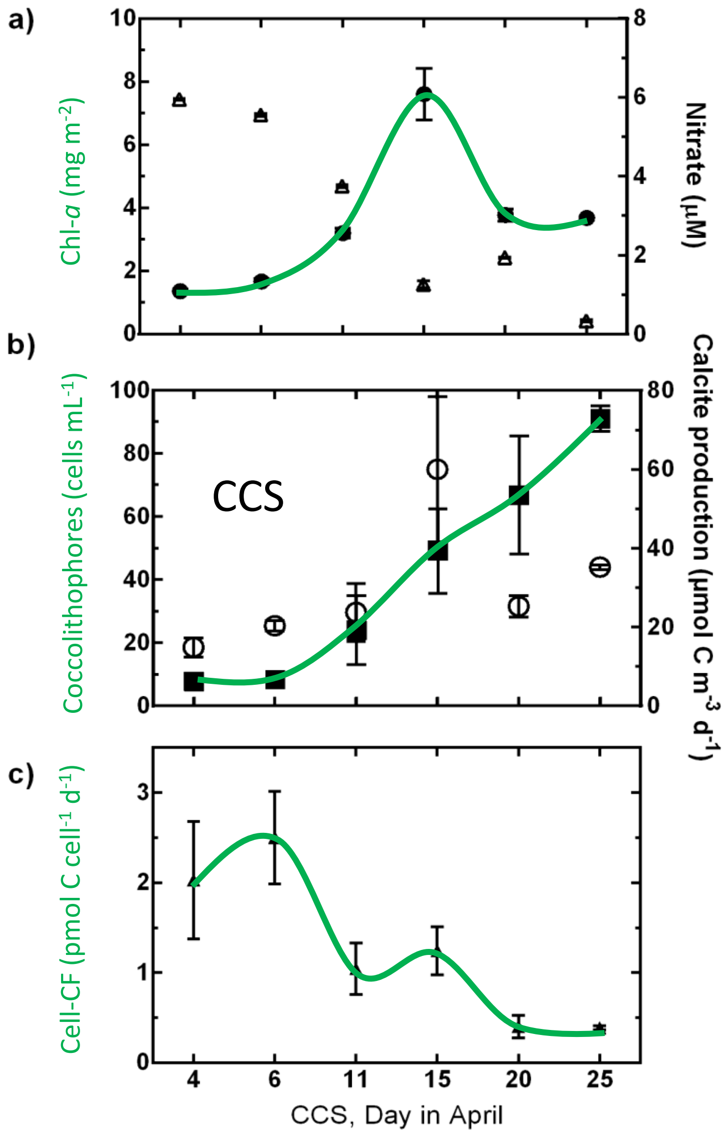
Claire Widdicombe (clst@pml.ac.uk)



- Ca. 140 taxa/species >15µm within five functional groups (inc. 'mixotrophic taxa')
- Abundance (cells ml^{-1}) and biomass (mg C m^{-3})

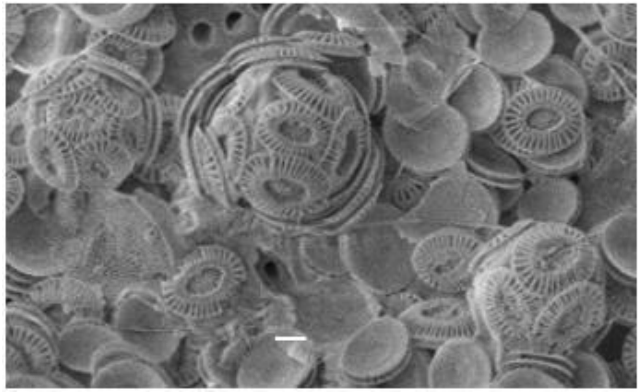


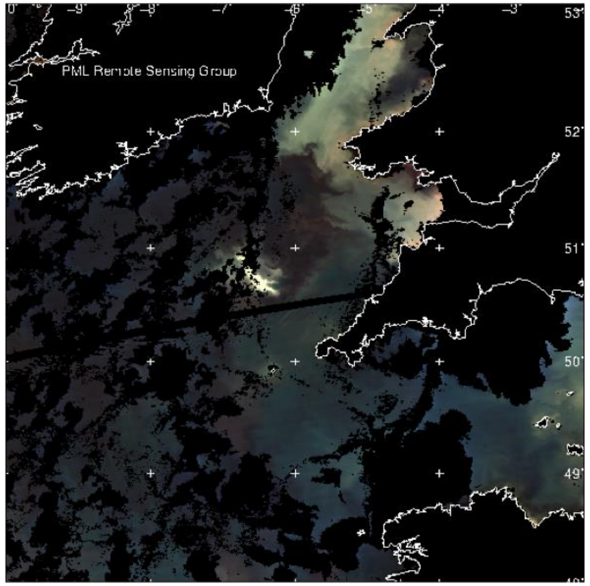
Coccolithophores & calcite production in Celtic Sea



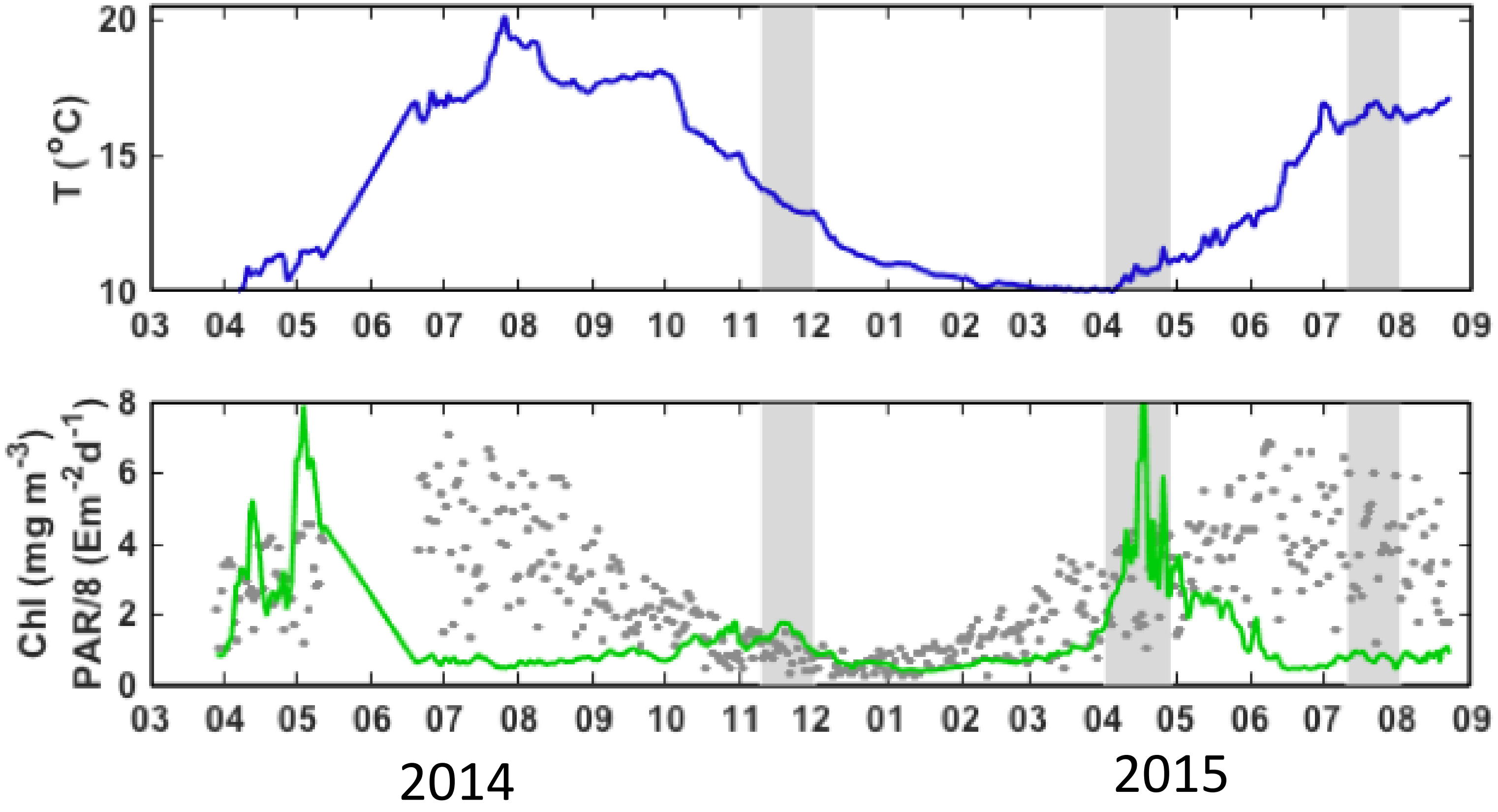
Mayers et al., (submitted Prog. Oceanogr.)

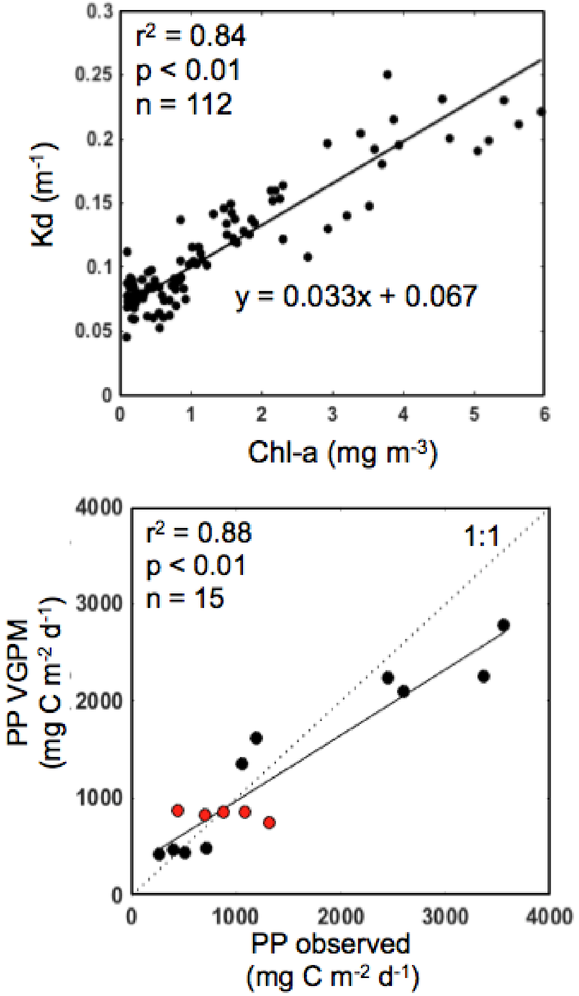
- Coccolithophore counts, species & calcite production for 3 cruises (+ mortality rates)
- Coccolithophores present in spring bloom at CCS and J2 *E huxleyi* bloom (highest calcite production measured ever!)
- High mortality losses by microzooplankton (Mayers et al., submitted to Prog. Oceanogr.)
- Seasonal patterns in species composition, calcite production, cell-CF & environmental drivers (Mayers et al., in prep.)





Seasonally resolved primary production CCS (Mooring data)

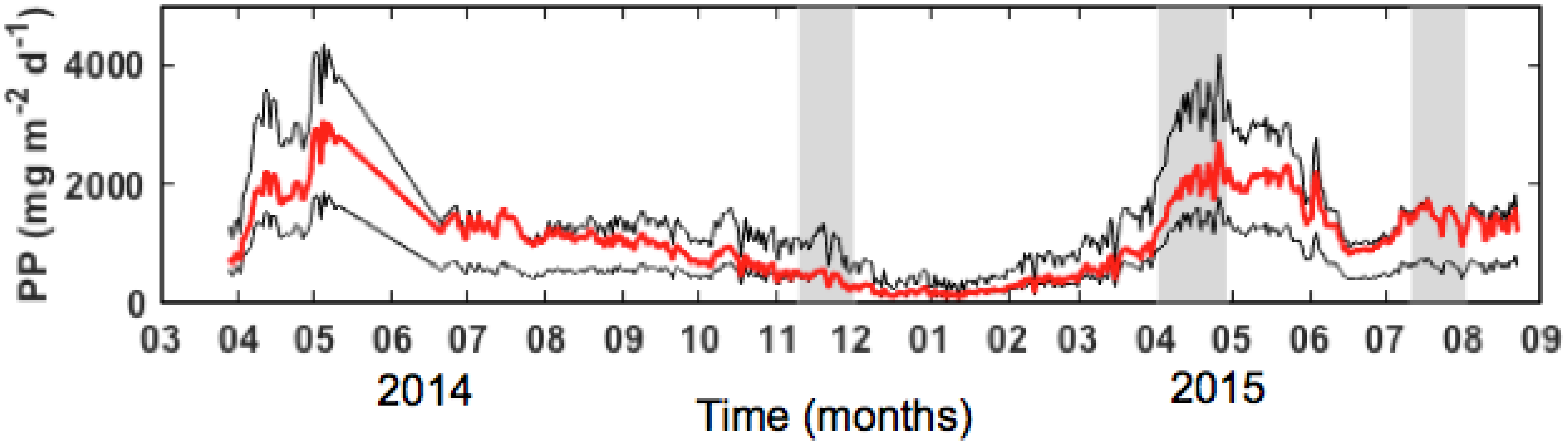




Hickman et al.,
(in prep. for Prog. Oceanogr.)

- Depth-integrated Primary Production via 'VGPM' model (Behrenfeld & Falowski, '97)
- Uses Surface Chl-*a* (Smartbuoy), Euphotic zone depth (Chl-*a* and Kd vs Chl-a relationship from ship), day-length (Smartbuoy), total daily PAR (Smartbuoy), maximum photosynthetic rate (ship, 14C)
- Shows good agreement with ship-derived primary production

Seasonally resolved primary production CCS (Mooring data)



- Annual NPP (VGM): ~30 mol C m^{-2} yr^{-1} (± 40%, depending on model parameterisation)
- Spring bloom: ~5 mol C m^{-2} yr^{-1} (14% annual NPP, >3 mg m^{-3} Chl-*a*)
- Summer: ~23 mol C m^{-2} yr^{-1} (70% annual NPP, spring to Autumn/end Nov)
- Winter: ~2 mol C m^{-2} yr^{-1}

Uptake stoichiometry: Particulate Nitrogen

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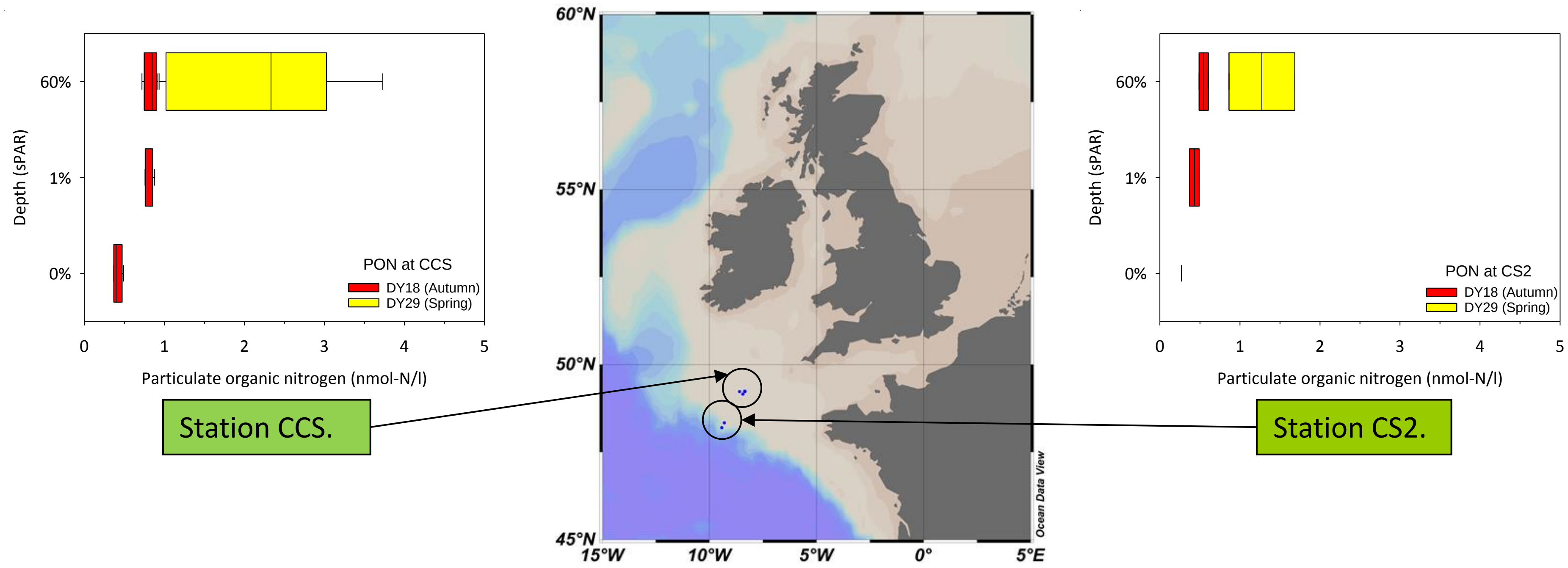
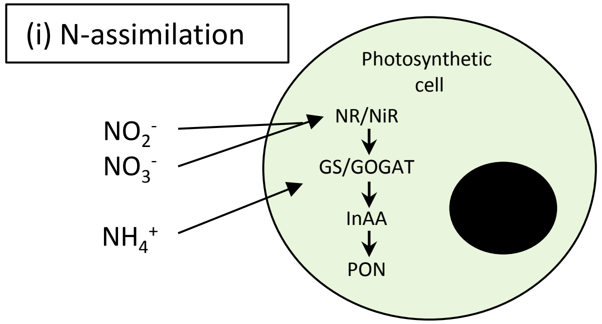
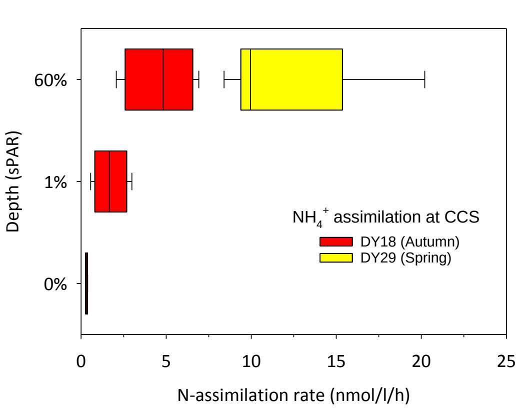


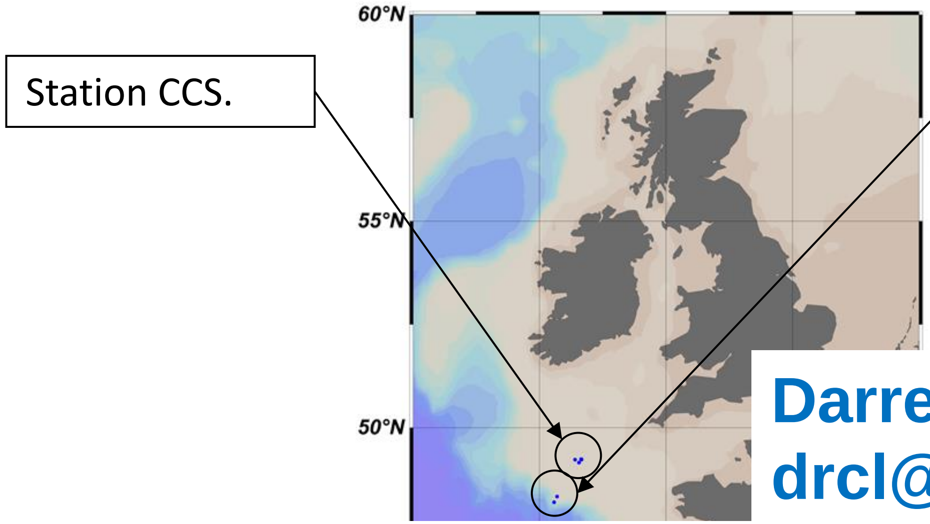


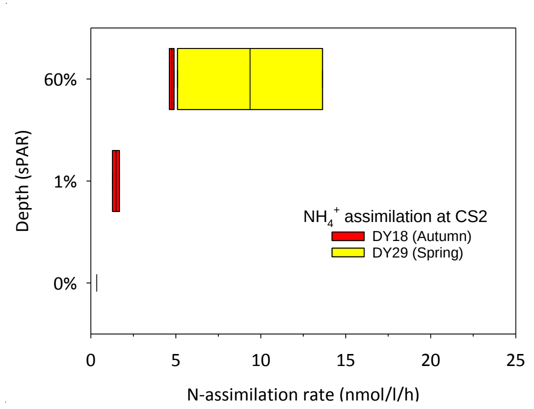
- Particulate Organic Nitrogen (PON – predominantly the nitrogen associated with phytoplankton cells) concentration at CCS and CS2 demonstrating (i) a link with light depth, (ii) a seasonal influence, and (iii) a distinction between stations (higher at CCS).

- Processes investigated at these stations; (i) the assimilation of nitrogen by phytoplankton (WM3) and (ii) the regeneration of nitrogen by various (mostly) microbial processes (WM5).

Uptake stoichiometry: Nitrogen uptake







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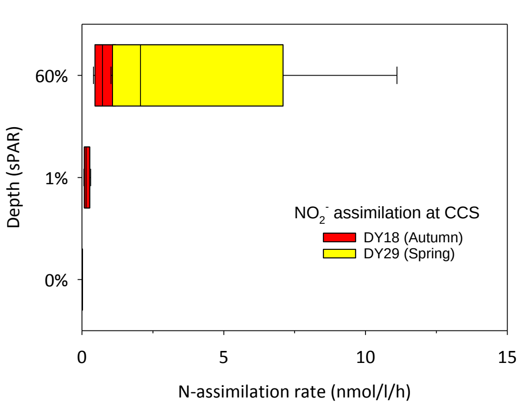
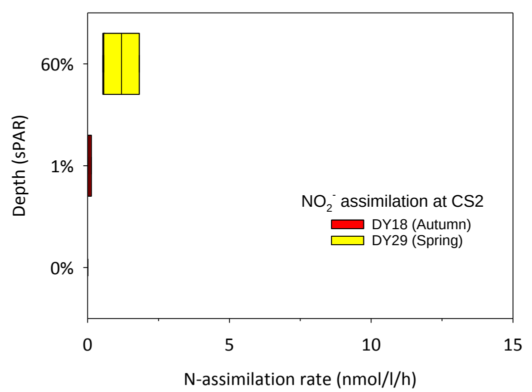
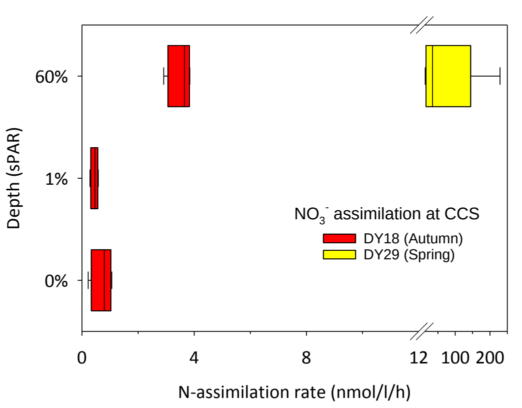


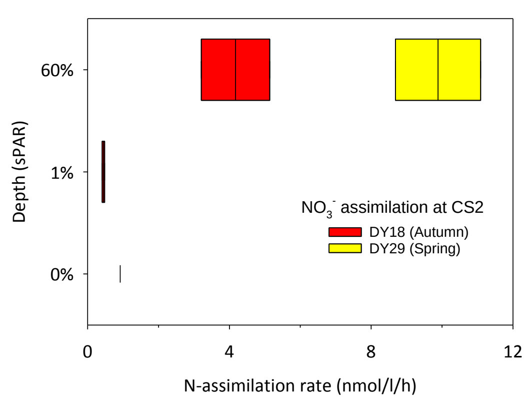
- The rate of N-assimilation by marine phytoplankton decreased as depth increased (~light).

- Nitrate assimilation dominated N-assimilation in the spring. In the autumn nitrate and ammonium assimilation were comparable.

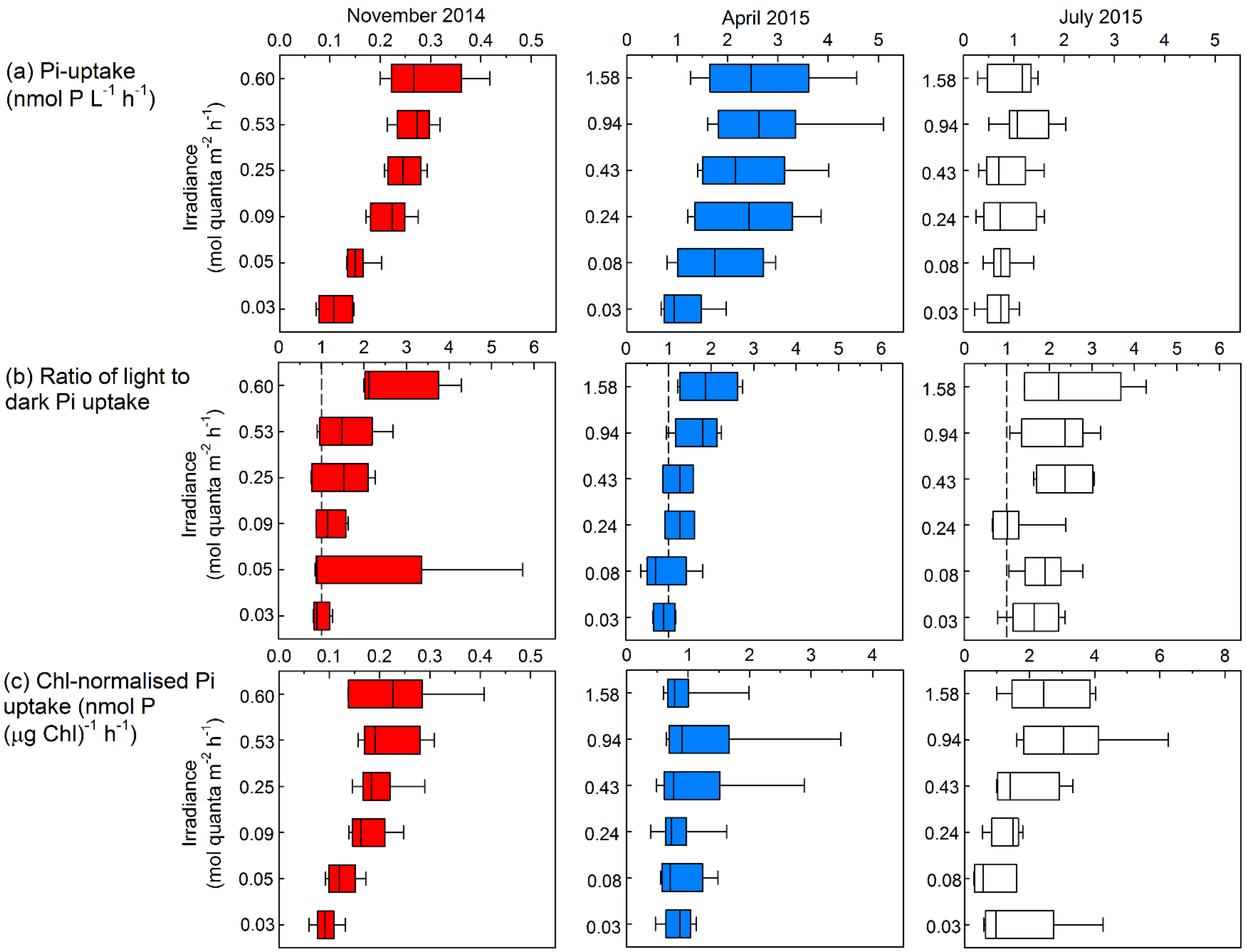
- Generally, the highest N-assimilation activity was associated with station CCS; nitrate assimilation during spring at this location was noteworthy (higher than NW African upwelling).







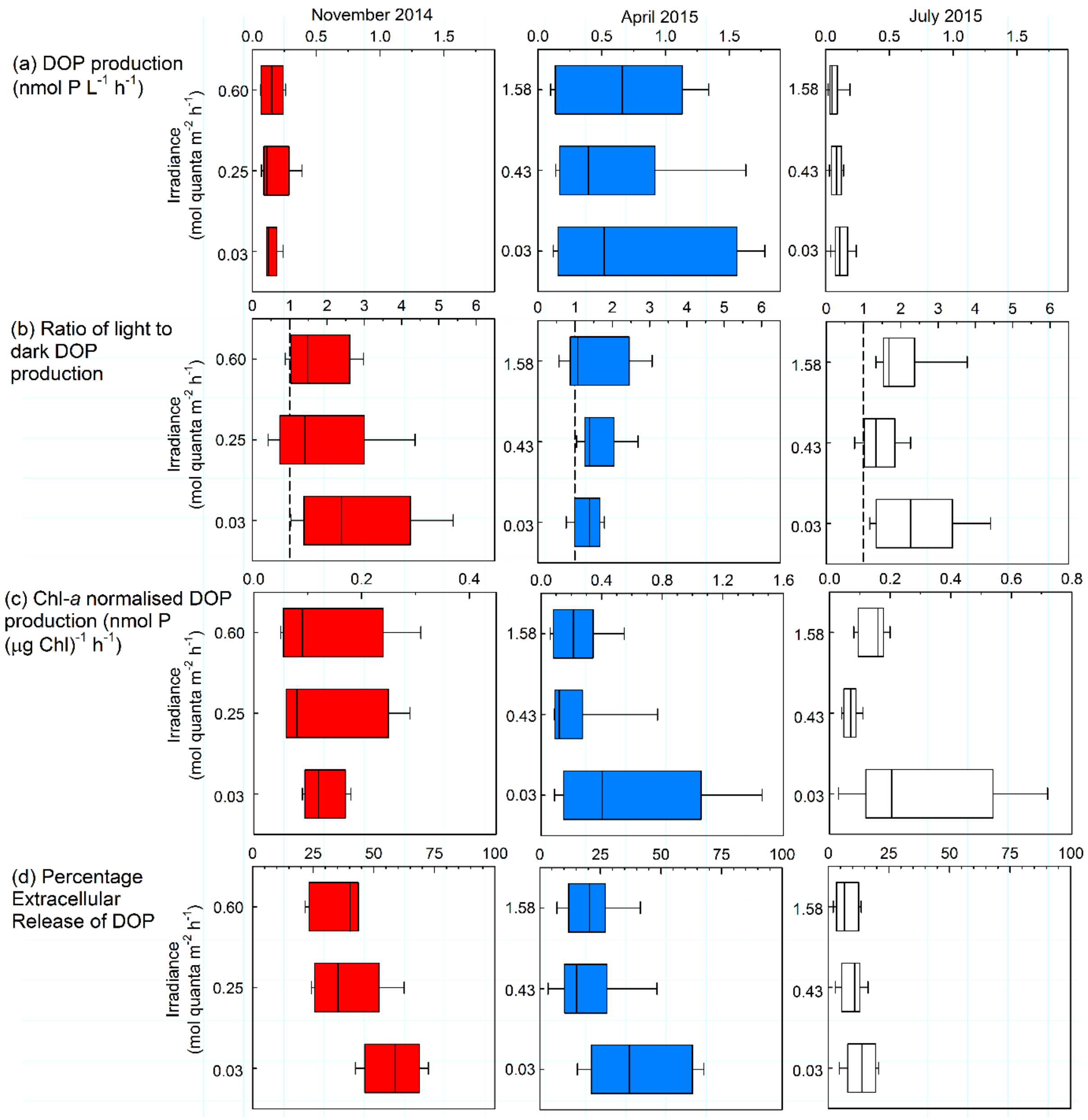
Uptake stoichiometry: Phosphorus uptake & release as DOP



- Depth (light) related variability, as well as seasonal (light, P) related variability
- Low rates in November; low biomass-normalised (Chl-*a*, POP) rates (**low affinity**)
- High rates in April, as well as summer
- Highest biomass-normalised (Chl-*a*, POP) rates in summer (**high affinity**)

Poulton et al., (submitted to Prog. Oceanogr.)

Uptake stoichiometry: DOP Production



- No variability with depth (light), but clear seasonal patterns with high rates in spring and low in summer (**P-retention**)
- High biomass-normalised (Chl-*a*) rates in autumn and spring but generally similar between cruises
- High %PER in Autumn, similar in spring BUT really low in summer (despite moderate rates of uptake) (**P-retention**)

Poulton et al.,
(submitted to Prog. Oceanogr.)

Summary of C:P uptake stoichiometry

Autumn

- Light limited, slow phytoplankton growth and low bacterial growth efficiency (Garcia-Martin et al., submitted)
- Low P_i -uptake, high % DOP release (low affinity, poor retention)
- C:P uptake (81-188) generally similar to Redfield ratio (106:1)

Early spring

- Increasing light / stratification stimulates rapid phytoplankton growth (see Hopkins et al., in prep.)
- High P_i -uptake, low % DOP release (high affinity & retention)
- C:P uptake (58-96) P-rich (*cf.* growth rate hypothesis): strong influence of phytoplankton on P-dynamics

Late spring

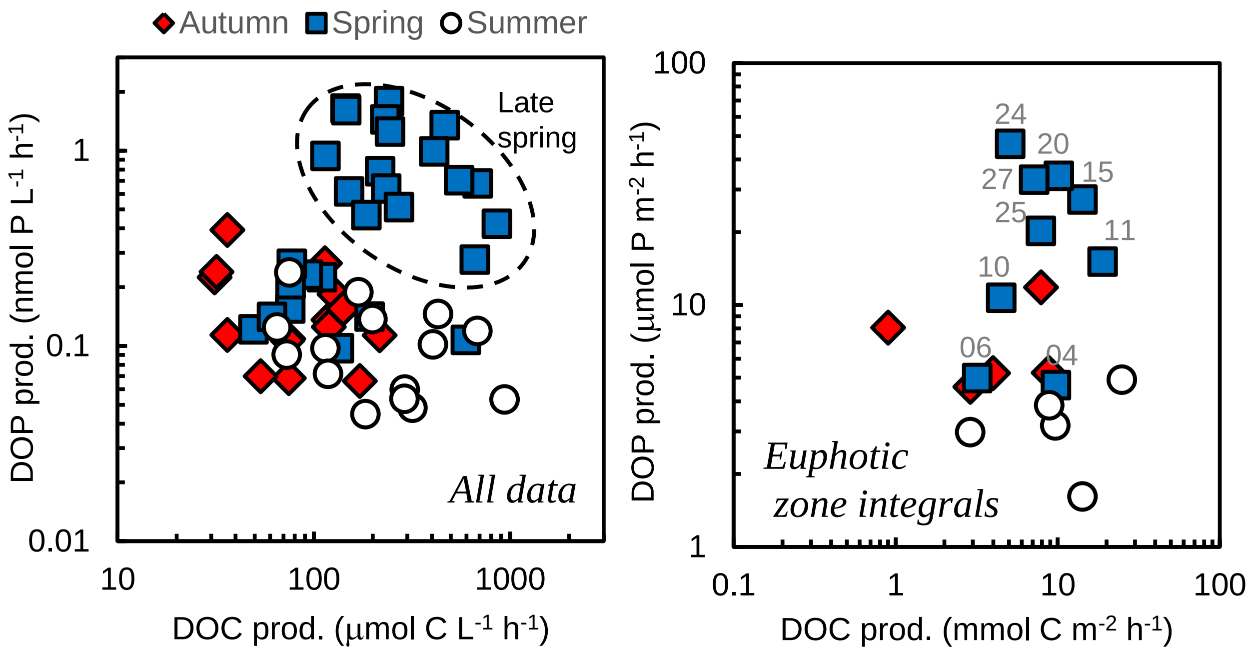
- Declining nutrients slows phytoplankton growth rates, low bacterial growth efficiency (Garcia-Martin et al., submitted)
- P_i -uptake remains high, but increasing % DOP release (high affinity, poor retention)
- C:P uptake (117-156) close to Redfield as bloom peaks and depletes nutrients

Summer

- Low (limiting) nutrients, slow phytoplankton growth, high bacterial growth efficiency (Garcia-Martin et al., submitted)
- P_i -uptake high (esp. biomass-normalised), very low % DOP release (high affinity & retention)
- C:P uptake (12-62) very P-rich, bacterial (cell C:P ~50?) dominance of P-dynamics

Poulton et al., (submitted to Prog. Oceanogr.)

Seasonality of C:P of DOM production



- Seasonal patterns to DOC and DOP production (also as bloom progresses to deplete phosphate in spring)
- Clearest separation via variability in DOP production (leads to variable C:P ratio of DOM)
- **DOP production drives C:P of DOM**

	Autumn		Spring		Summer		Units
DOC prod.	4.9	(0.9 - 8.8)	9.0	(3.2 - 19.0)	12.2	(2.9 - 25.0)	mmol C m^{-2} h^{-1}
PER-DOC	42	(24 - 61)	32	(20 - 51)	75	(54 - 86)	%
DOP prod.	7.0	(4.6 - 11.8)	20.6	(8.8 - 54.9)	3.0	(1.3 - 4.9)	µmol P m^{-2} h^{-1}
PER-DOP	18	(13 - 27)	9	(3 - 23)	4	(2 - 8)	%
DOC:DOP	**939**	**(635 - 1679)**	**667**	**(110 - 2120)**	**4063**	**(970 - 8878)**	**mol mol^{-1}**

- **DOM C-rich, especially in summer** (due to efficient retention/recycling)

Poulton et al., (in prep.)

Annual scaling of observations (work in progress)

	Spring	Summer	Autumn	Winter	Annual	
NPP (VPGM)	(5)	(23)	-	(2)	30	mol C m^{-2}
NPP (*Ship*)	19	3	3	3	28	mol C m^{-2}
DOC prod.	12	17	4	3	36	mol C m^{-2}
% PER	38 (32)	84 (75)	55 (42)	55 (-)	56	
Pi-uptake	149	79	22	21	271	mmol P m^{-2}
DOP prod.	27	4	5	5	41	mmol P m^{-2}
NPP:Pi-uptake	125	42	135	135	103	mol mol^{-1}
± Redfield	+18%	-60%	+29%	+29%	-3%	
DOC:DOP*	437	4067	700	700	875	mol mol^{-1}
± Redfield	+312%	+3737%	+560%	+560%	+725%	

Poulton et al. (in prep.)

- Good agreement between scaling-up ship measurements and VPGM (sorry..)
- Annual estimate of DOC prod ~ 36 mol C m^{-2} or 56% of total C-fixation
- Annual estimate of DOP prod ~ 41 mmol P m^{-2} or ~14% of total Pi-uptake

- C:P uptake, though seasonal variability, on annual scale is Redfield (Winter+Spring cancel out Summer)
- But the C:P of DOM is extremely non-Redfield and very C-rich (esp. in summer)
- (*Please note: possible to made C:P uptake and DOM slightly more P-rich depending on day-light or day)

Addressing the original WM-3 hypotheses

<u>H3:</u> Autotroph community structure and resource availability influence the stoichiometry of organic matter through increasing C:P ratios under nutrient depleted conditions

Actually, <u>microbial plankton composition</u> and resource availability (N, P <u>and light</u>) influenced stoichiometry, though low light (Redfield uptake) and low nutrients (P-rich uptake, C-rich DOM) had different C:P stoichiometry.

H3i: Optimal growth conditions of the spring bloom lead to C and P being used at ratios close to the canonical Redfield ratio;

No, rapid growth rates of phytoplankton in spring bloom led to P-rich uptake (with DOM production becoming more P-rich as nutrients declined).

H3ii: Departures from Redfield ratio occur in response to changes in resource (light, nutrient) availability: C:P will increase as P becomes limiting, with release of C-rich DOM.

Kinda; non-Redfield C:P uptake occurred under low nutrients (<u>not low light</u>), but due to bacterial dominance of P-dynamics in summer (not phytoplankton).

DOM was very C-rich during summer but <u>due to low DOP release not high DOC production</u>.

WM-3 Data sets

C = collected										
A = Analysed										
D = Delivered to BODC					WP1		WP1		WP1	
	DY008	**JC105**	**DY026**	**DY017**	**DY018**	**DY021**	**DY029**	**DY030**	**DY033**	**DY034**
Chlorophyll	C,A,D	C,A,D	C,A,D	C,A,D	C,A,D	C,A,D	C,A,D	C,A,D	C,A,D	C,A,D
Chlorophyll Size-fractions			C,A,D	C,A,D	C.A.D	C,A,D	C.A.D	C,A,D	C.A.D	C,A,D
Taxonomiy (small)					C,A,D		C,A,D		C,A,D	
Taxonomy (large)					C,A,D		C,A,D		C,A,D	
Taxonomy (Coccolithophores)					C,A		C,A		C,A	
C-fixation Size fractions					C,A		C,A		C,A	
C-fixation total					C,A		C,A		C,A	
DOC production					C,A		C,A		C,A	
P-uptake					C,A		C,A		C,A	
DOP production					C,A		C,A		C,A	
Calcification					C,A		C,A		C,A	
N assimilation and regeneration					C,A		C,A		C	
N2 fixation (summer)									C,A	
PIC										
BiSi					C,A	C,A	C,A	C,A	C,A	C,A
Fe uptake							C,A		C,A	
Si uptake					C,A					
NO3 assimilation and regeneration					C,A		C,A		C	
NH4 asimilation and regeneration					C,A		C,A		C	
NO2 asimilation and regeneration					C,A		C,A		C	

Conclusions (or ‘the questions we need to start asking’)

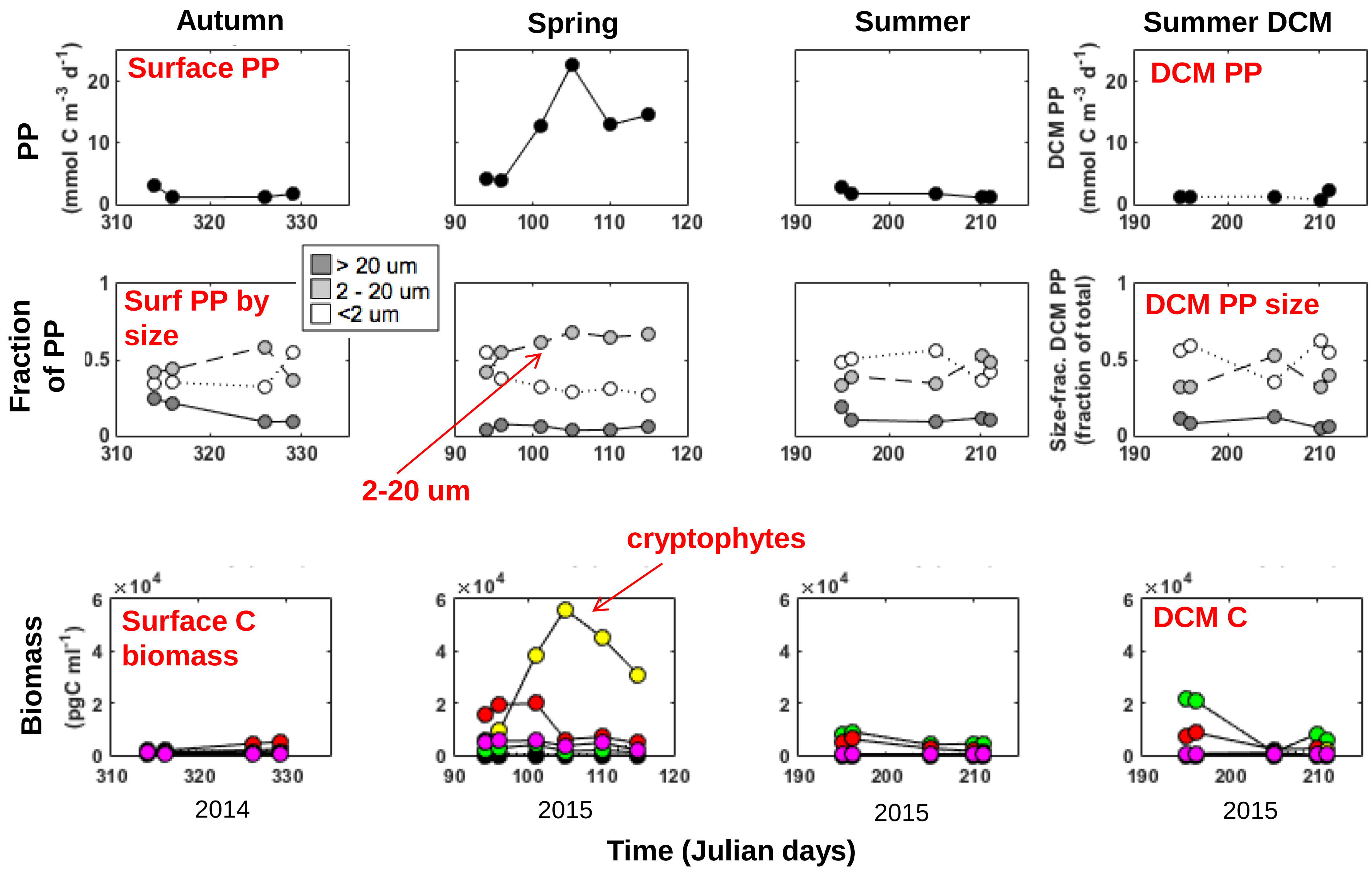
- Have large number of measurements, showing consistent patterns and new paradigms as they are combined together to address original hypotheses and objectives;
- Nanoplankton rule (CCS during 2015): what does this mean for the ecosystem or the Celtic Sea?
- Is this normal (at CCS vs Celtic Deep)? What are we missing if it is, or isn’t?
- Where have all the (big) diatoms gone? (or ‘why where the small ones so successful’?)
- Strong succession patterns within ‘functional’ or size-based groups: what implications does this have for the biogeochemistry or ecosystem function (i.e. does diversity matter?)
- Stoichiometry (C:P) does vary seasonally, but not necessarily as expected, and have yet (but soon) to fully combine C-N-P uptake dynamics
- DOM is where the C is, though P-dynamics strongly influence its C:P stoichiometry (what about N?)
- How far and wide do these stoichiometric insights apply (open-ocean?)

THANKS FOR LISTENING

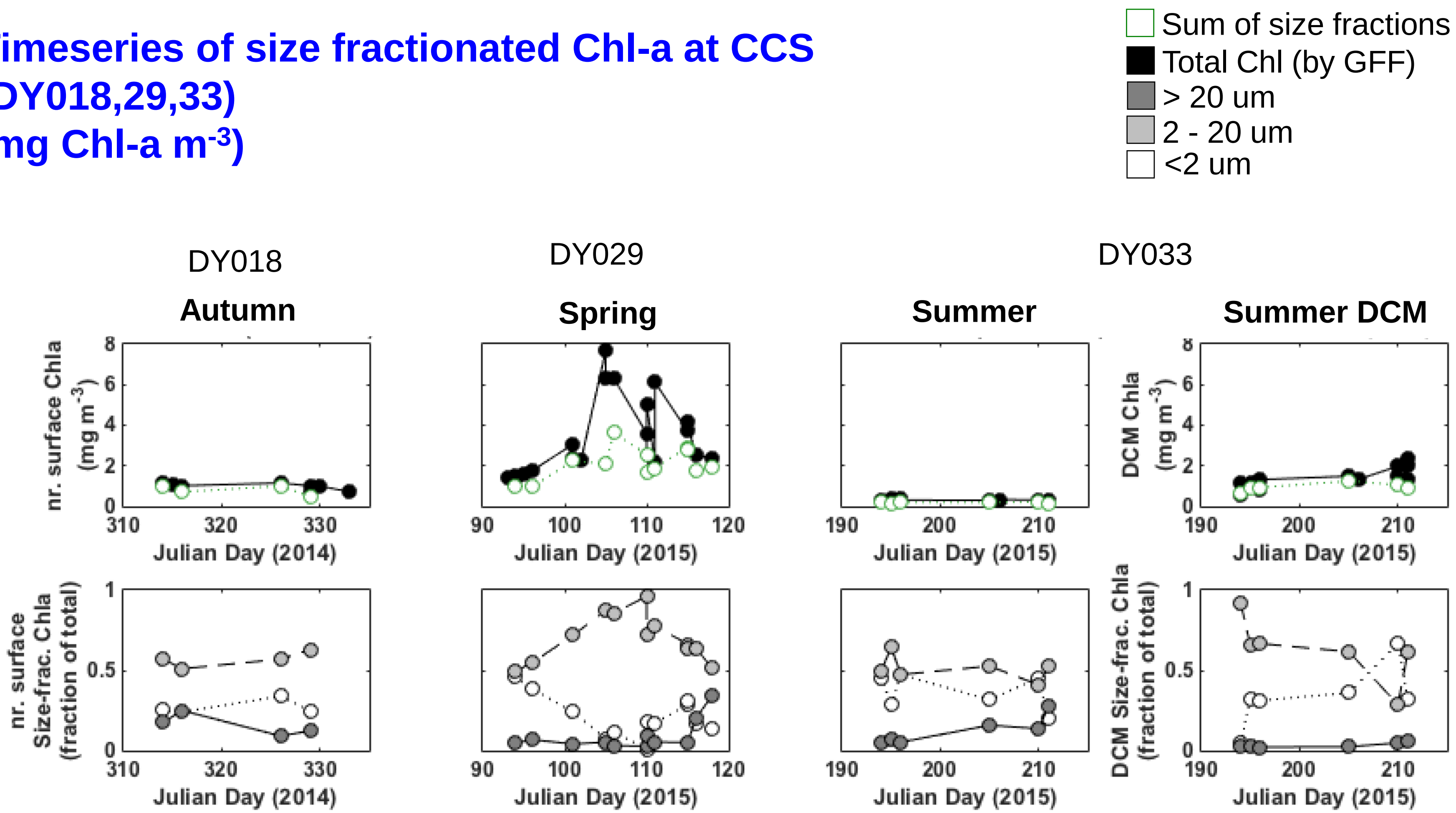
Timeseries of size fractionated 24hr 14C uptake at Central Celtic Sea (CCS) station (DY018,29,33)

CCS: PP dominated by cells <20um, even during bloom

Bloom dominated by cryptophytes and mixotrophic ciliates (*Tarran, Widdecombe*)



Timeseries of size fractionated Chl-a at CCS (DY018,29,33) (mg Chl-a m^{-3})



Chl-a not dominated by large cells (>20um), even during bloom

Average depth-integrated PP for each cruise (at CCS and CS2), from 24hr PP experiments:

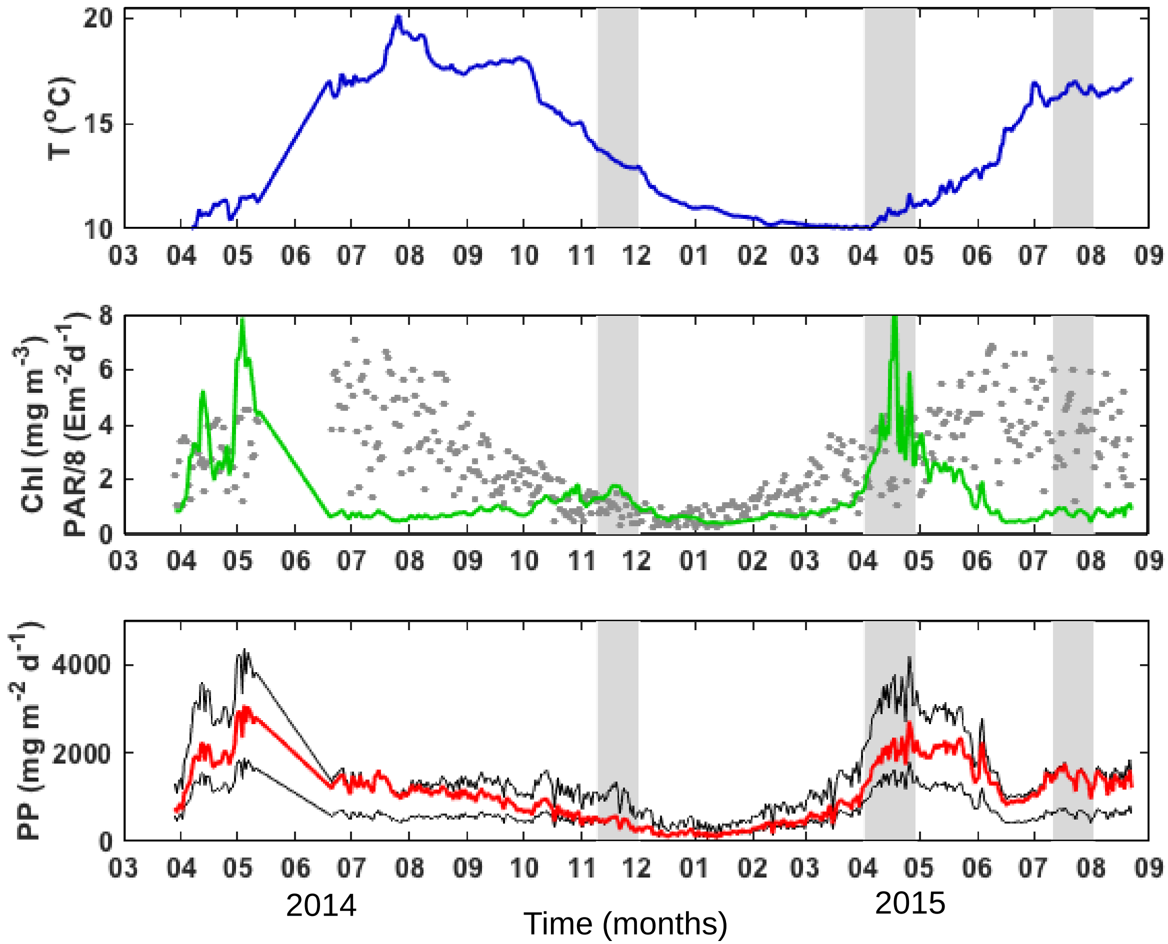
		DY018	DY029	DY033
Depth-integrated PP (mmol C m-2 d-1)	CCS	39 +/- 1.9 n = 4	198 +/- 8.2 n = 6	74 +/- 2.4 n = 5
	CS2	29 +/- 1.4 n = 2	180 +/- 6 n = 1	48 +/- 1.1 n = 2
Depth-integrated Chl-a (mg m-2)	CCS	47 +/- 10 n = 10	115 +/- 39 n = 21	37 +/- 7 n = 15
	CS2	45 +/- 7 n = 10	60 +/- 19 n = 4	39 +/- 22 n = 4

Same but PP in g:

Kieran comparison: rough estimate of range taken from "Slides_forAlex_Kcurran_PhD.pptx":
Sum of SFs: min 50+100+50 = 200 mg m-2 d-1
max 700+700+400 = 1800 mg m-2 d-1
K's range in total PP slightly lower

SFs: >20 lowest
0.2-2 and 2-20 roughly similar contributions.
It'd be good to check if K sees slightly higher contribution of 2-20um fraction in the surface during summer.

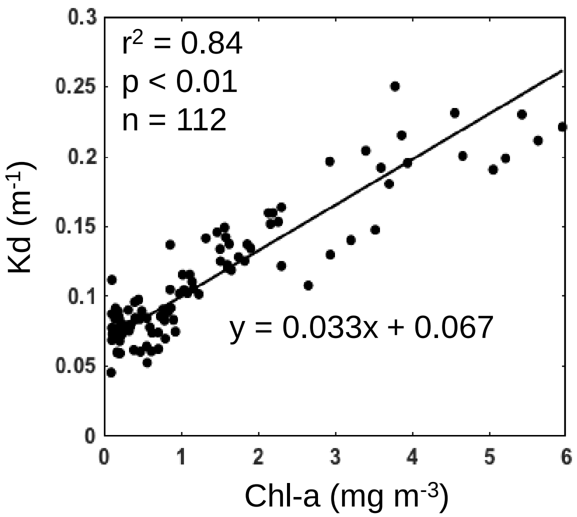
		DY018	DY029	DY033
Depth-integrated PP (mg C m-2 d-1)	CCS	468 +/- 23 n = 4	2376 +/- 98 n = 6	888 +/- 29 n = 5
	CS2	348 +/- 27 n = 2	2160 +/- 72 n = 1	576 +/- 13 n = 2
Depth-integrated Chl-a (mg m-2)	CCS	47 +/- 10 n = 10	115 +/- 39 n = 21	37 +/- 7 n = 15
	CS2	45 +/- 7 n = 10	60 +/- 19 n = 4	39 +/- 22 n = 4



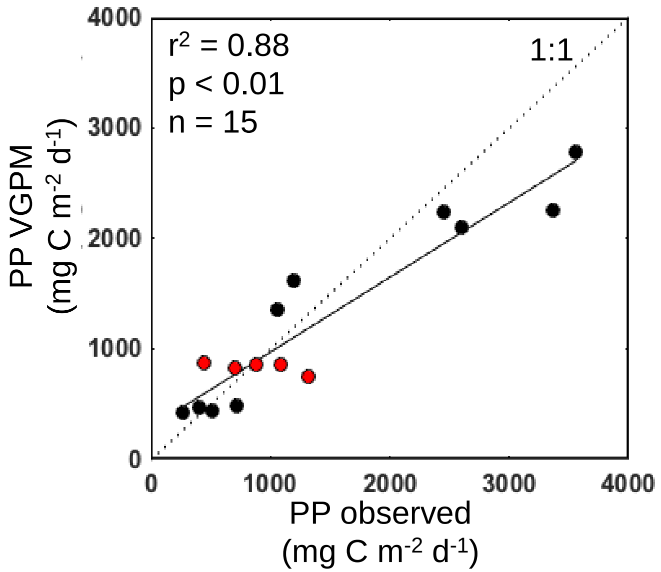
Top: CEFAS Smartbuoy Temp (blue), daily average
Middle: Smartbuoy Chl (green), daily average; Smartbuoy PAR (dots), daily sum
Bottom: Depth-integrated Primary Production via “VGPM” model (Behrenfeld & Falkowski 1997, Eq 10). The VGPM model estimates depth-integrated PP every day using the following:

- Surface Chl (from Smartbuoy)
- euphotic zone depth (from Smartbuoy Chl and kd vs Chl relationship observed during cruises, fig attached),
- day length (from Smartbuoy)
- total daily PAR (from Smartbouy),
- maximum photsynthetic rate (measured via 14C uptake experiments during DY018, DY029, DY033 and averaged for each cruise). The red and black lines are calculated using different assumptions for how these cruise-mean P*max values are interpolated between cruises: Red line is assuming a linear interpolation between the cruise-mean values, the upper and lower black lines are assuming the highest and lowest cruise-mean values are constant all year. In other words, upper and lower bounds based on highest and lowest observed values.

Vertical grey bands are times of DY018, DY029, DY033 where the data were collected.



Kd vs Chl observed during DY018, DY029, DY033 used to calculate euphotic zone depth for VGPM.

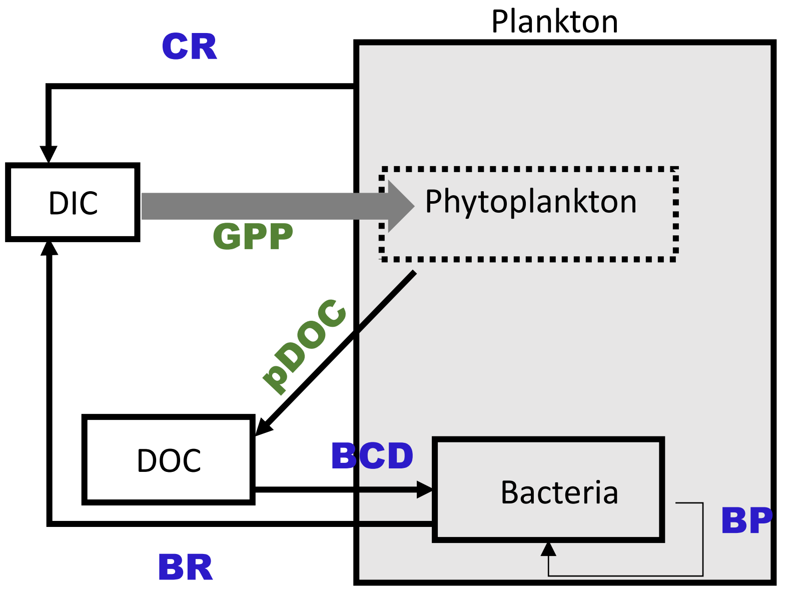


Depth-integrated PP estimated via VGPM compared to observed (integral of 6 depths) during DY018, DY029, DY033 (red dots are summertime when DCM may mean VGPM is less accurate).

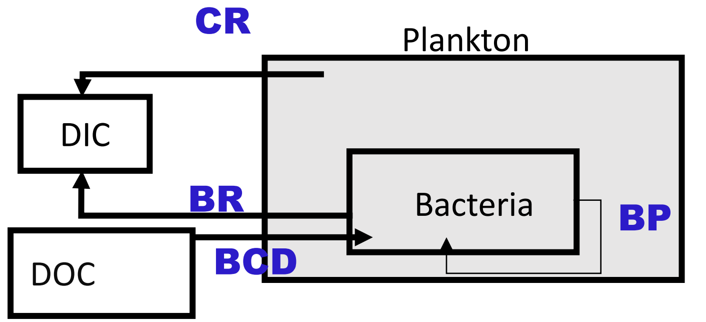
------ Annual and seasonal PP from Smartbuoy+VGPM
- Annual:
394 g C m-2 y-1 (range 210-490 g C m-2 y-1). The first value being the integration of the red line in the figure (also re-attached) and range is based on integration of the upper and lower black lines (reminder - the different lines reflect different ways the observed ‘physiology’ is extrapolated between cruises and effectively quantify the error resulting from not measuring physiology through time).
- Spring Bloom:
55 g C m-2 season-1 (range 34-79 g C m-2 season-1).
Where the bloom is between the first and last time Chl is above 3 mg m-3 during 2015 (24 days).
- Summer:
276 g C m-2 season-1 (range 135-314 g C m-2 season-1).
Where summer is from the end of 2015 spring bloom to end of smartbuoy deployment in 2015 (23rd Aug) and added to that the period between 24th August 2014 to the end of summer 2014 (210 days). I assumed the end of summer was November 30th, given the wc was still stratified and we caught tail end of autumn bloom during DY018.

** If anyone has preference/concensus of timespan for spring and summer let me know and I’ll adjust! **

Conceptual model



UML

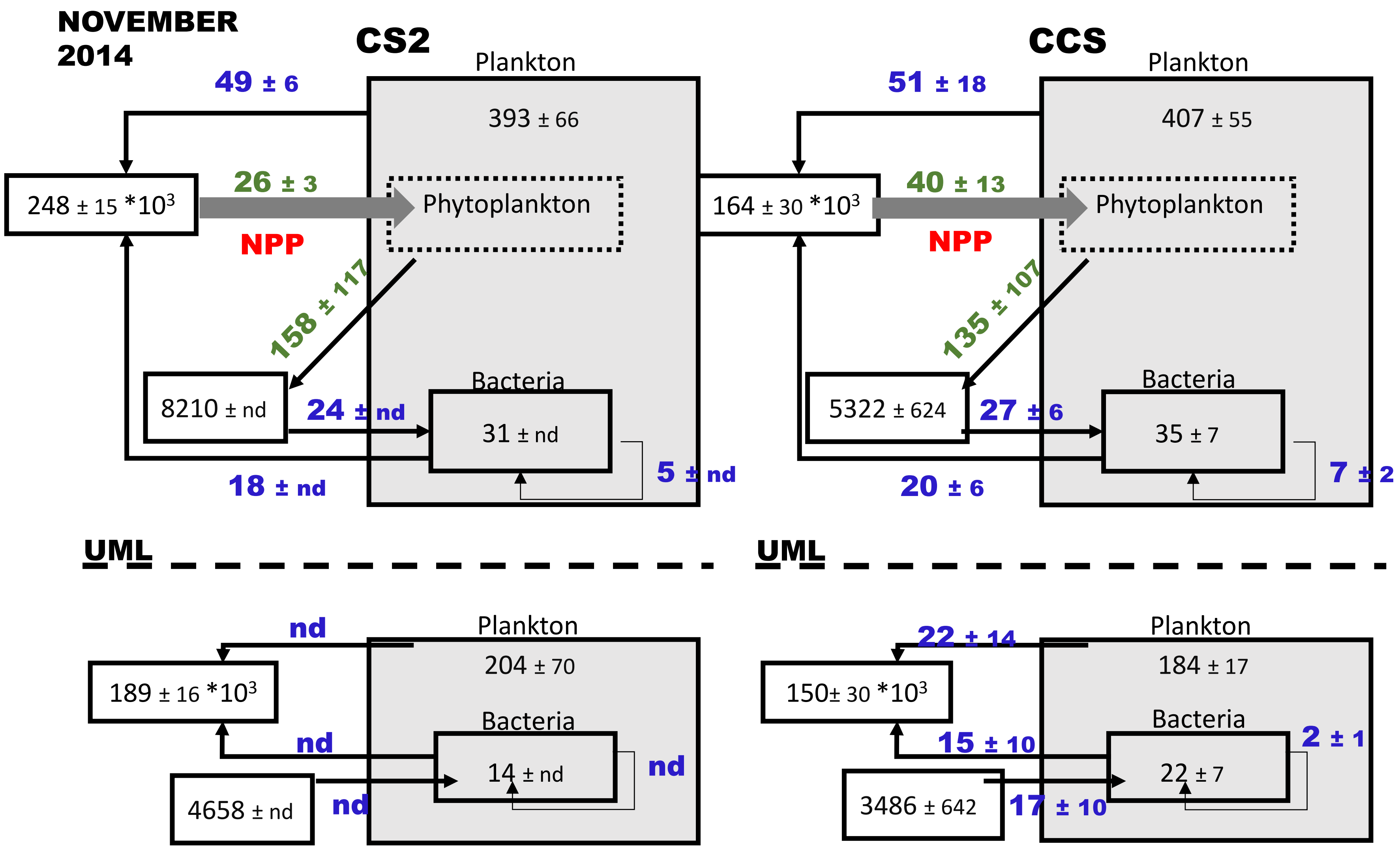


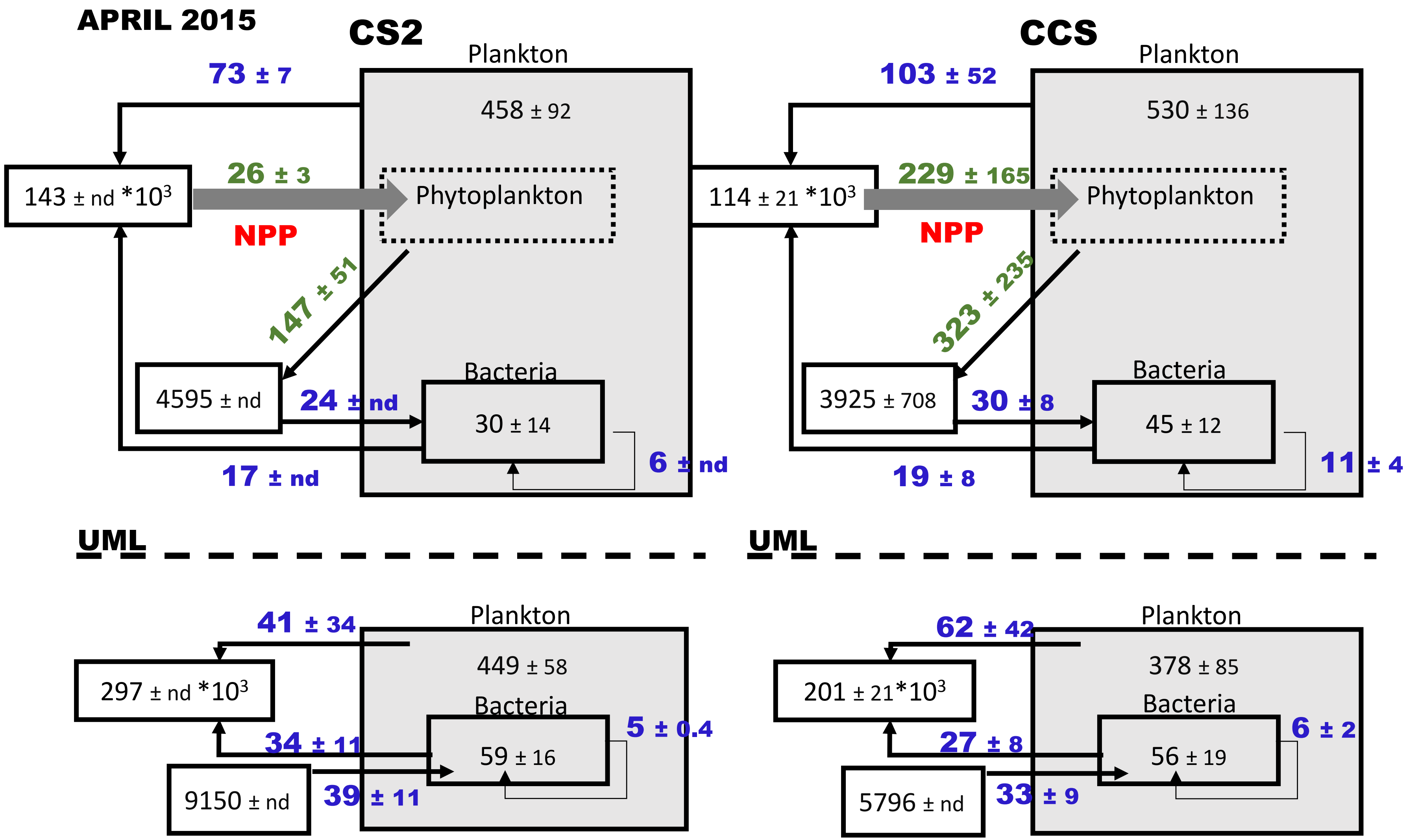
Units:
DIC, POC, DOC, bacterial biomass: mmol C m^{-2}

GPP, pDOC, CR, BR, BCD and BP: mmol C m^{-2} d^{-1}
The GPP is (GPP+pDOC)

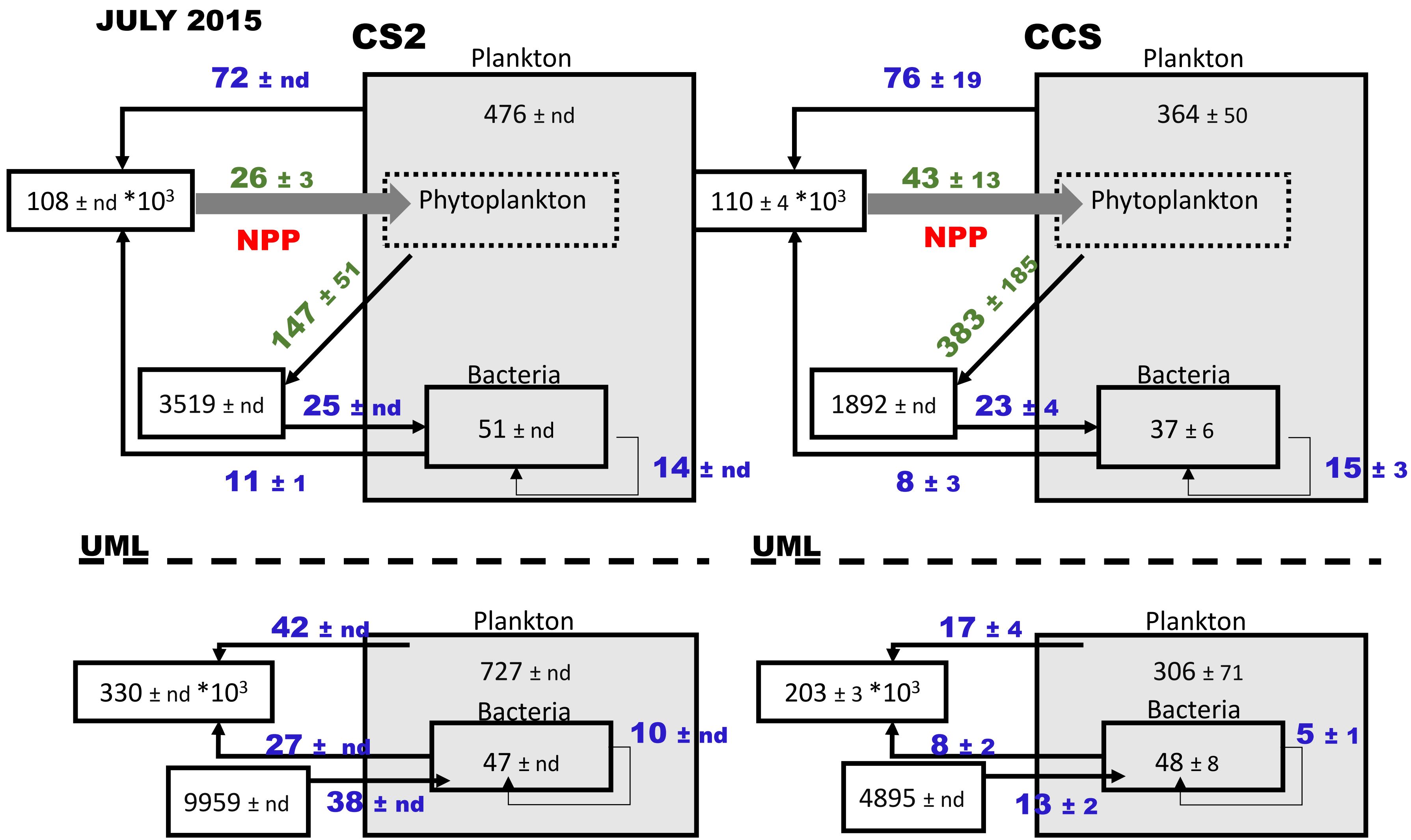
Data from:
A Poulton, M. Humphrey, C. Mahaffey, C. Davis, K. Davidson, D. Purdie, C. Robinson and EE Garcia-Martín

**Need to correct the data with the latest Changes*
(if there are any in POC and DOC)


NOVEMBER 2014
CS2
Plankton
393 ± 66
49 ± 6
248 ± 15 *10³
26 ± 3
NPP
Phytoplankton
158 ± 117
8210 ± nd
24 ± nd
Bacteria
31 ± nd
5 ± nd
18 ± nd
CCS
Plankton
407 ± 55
51 ± 18
164 ± 30 *10³
40 ± 13
NPP
Phytoplankton
135 ± 107
5322 ± 624
27 ± 6
Bacteria
35 ± 7
7 ± 2
20 ± 6
UML
UML
nd
Plankton
204 ± 70
189 ± 16 *10³
Bacteria
nd
14 ± nd
nd
4658 ± nd
nd
22 ± 14
Plankton
184 ± 17
150± 30 *10³
Bacteria
2 ± 1
15 ± 10
22 ± 7
3486 ± 642
17 ± 10



APRIL 2015
CS2
Plankton
73 ± 7
458 ± 92
143 ± nd *10³
26 ± 3
Phytoplankton
NPP
147 ± 51
4595 ± nd
24 ± nd
Bacteria
30 ± 14
6 ± nd
17 ± nd
CCS
Plankton
103 ± 52
530 ± 136
114 ± 21 *10³
229 ± 165
Phytoplankton
NPP
323 ± 235
3925 ± 708
30 ± 8
Bacteria
45 ± 12
11 ± 4
19 ± 8
UML
UML
41 ± 34
Plankton
449 ± 58
297 ± nd *10³
Bacteria
5 ± 0.4
34 ± 11
59 ± 16
9150 ± nd
39 ± 11
62 ± 42
Plankton
378 ± 85
201 ± 21*10³
Bacteria
6 ± 2
27 ± 8
56 ± 19
5796 ± nd
33 ± 9



JULY 2015
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72 ± nd
476 ± nd
108 ± nd *10^3
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NPP
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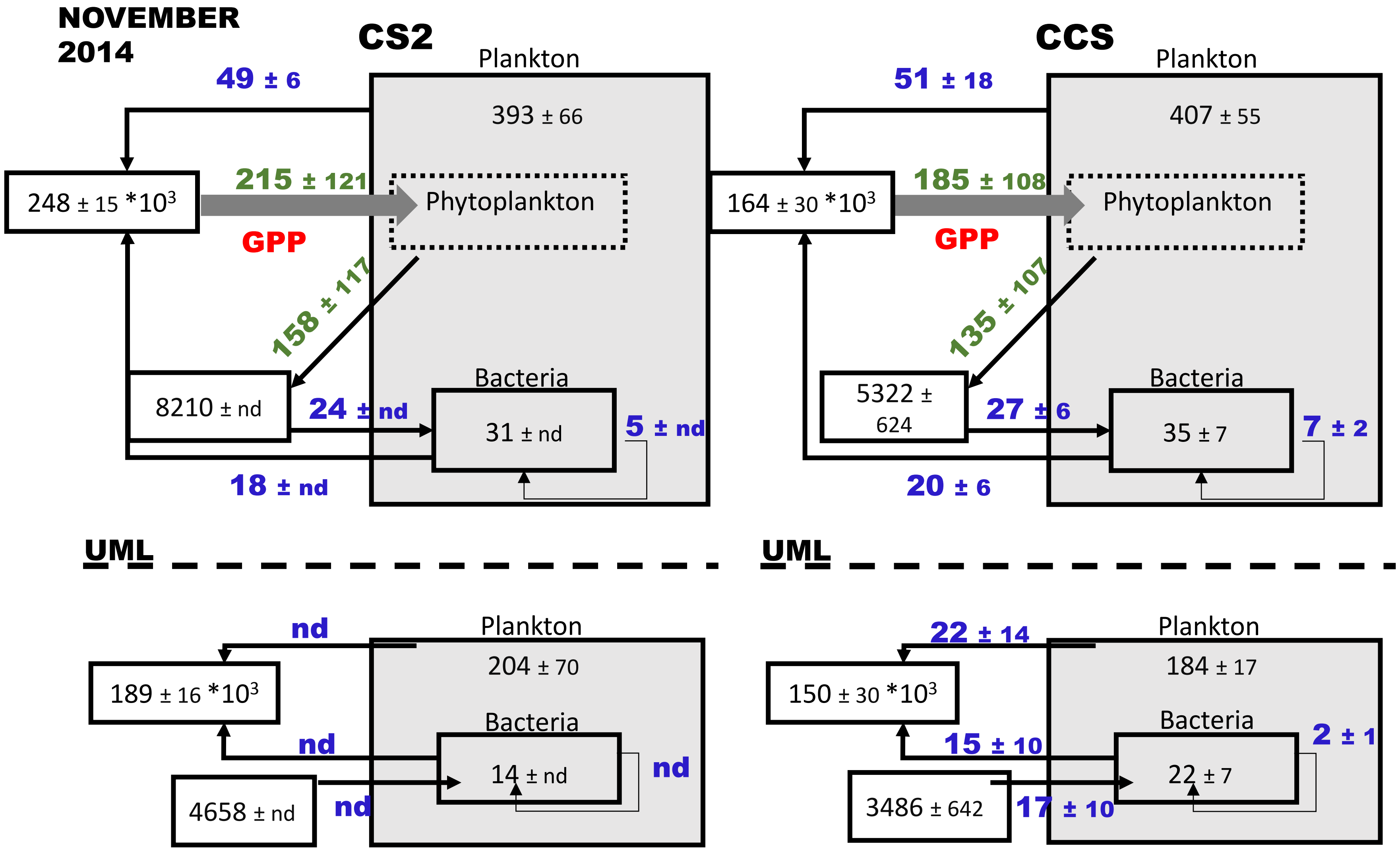
3519 ± nd
25 ± nd
Bacteria
51 ± nd
14 ± nd
11 ± 1
CCS
Plankton
76 ± 19
364 ± 50
110 ± 4 *10^3
43 ± 13
Phytoplankton
NPP
383 ± 185
1892 ± nd
23 ± 4
Bacteria
37 ± 6
15 ± 3
8 ± 3
UML
UML
42 ± nd
Plankton
727 ± nd
330 ± nd *10^3
Bacteria
27 ± nd
10 ± nd
47 ± nd
9959 ± nd
38 ± nd
17 ± 4
Plankton
306 ± 71
203 ± 3 *10^3
Bacteria
8 ± 2
5 ± 1
48 ± 8
4895 ± nd
13 ± 2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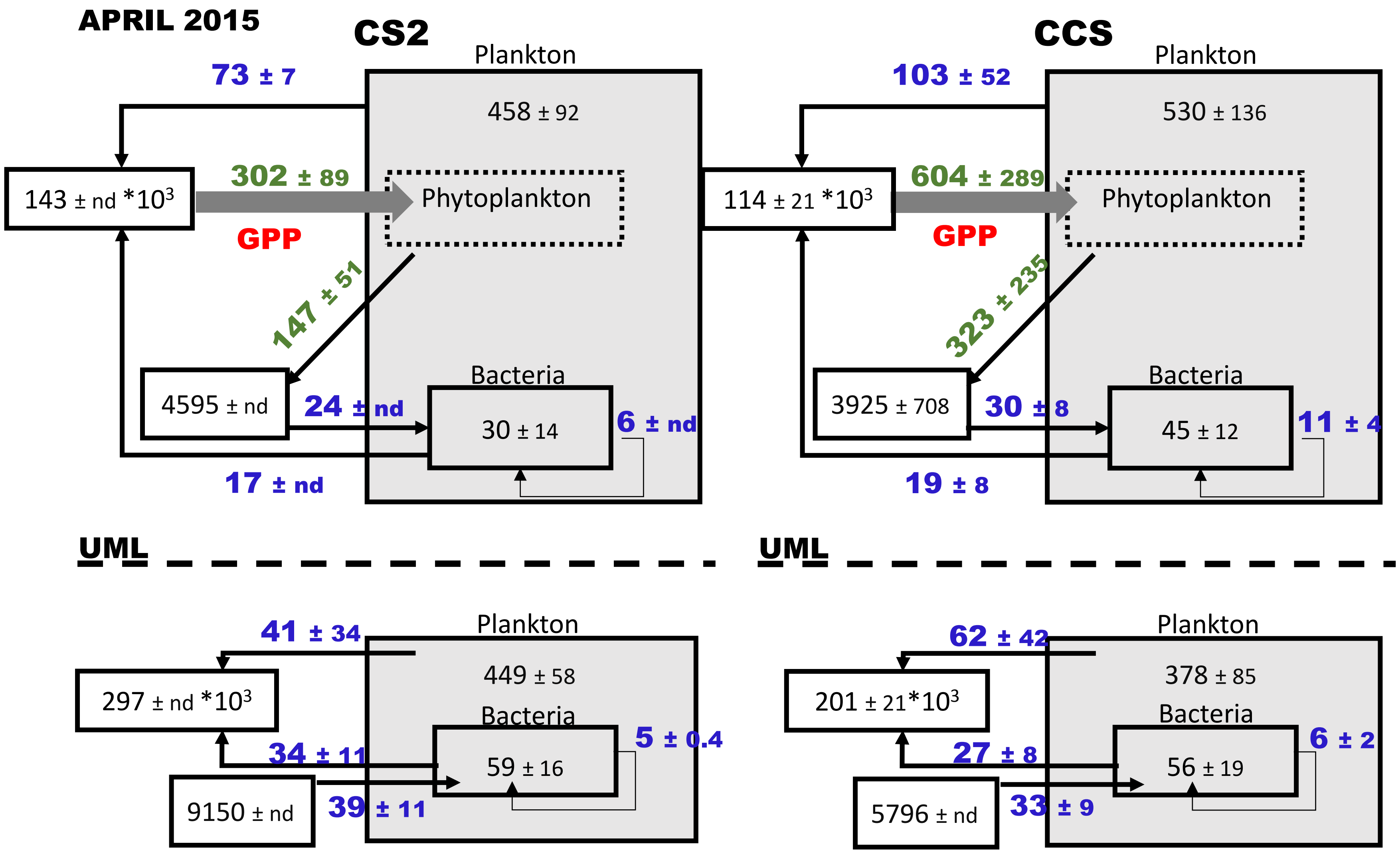

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Plankton
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378 ± 85
Bacteria
6 ± 2
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5796 ± nd
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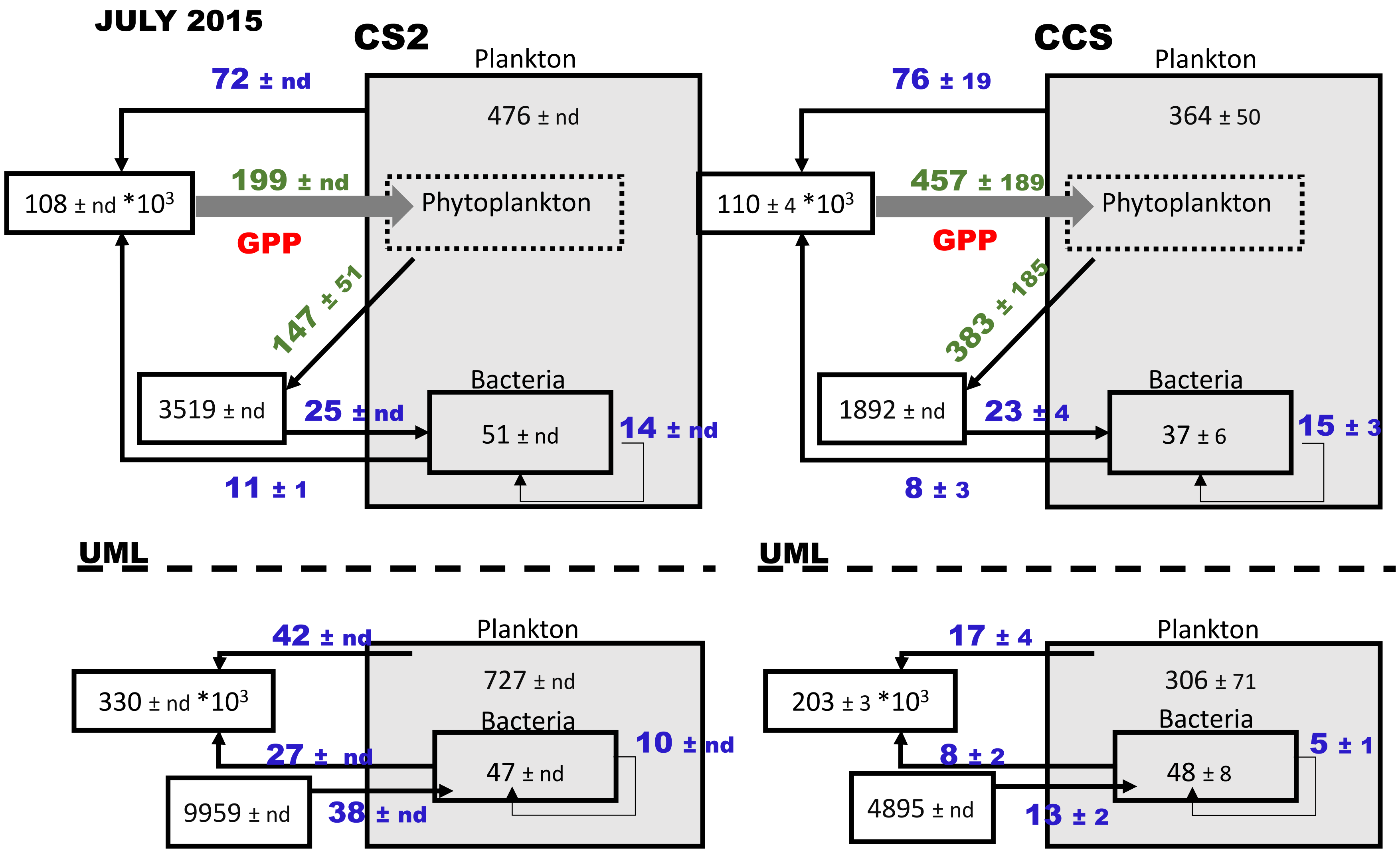

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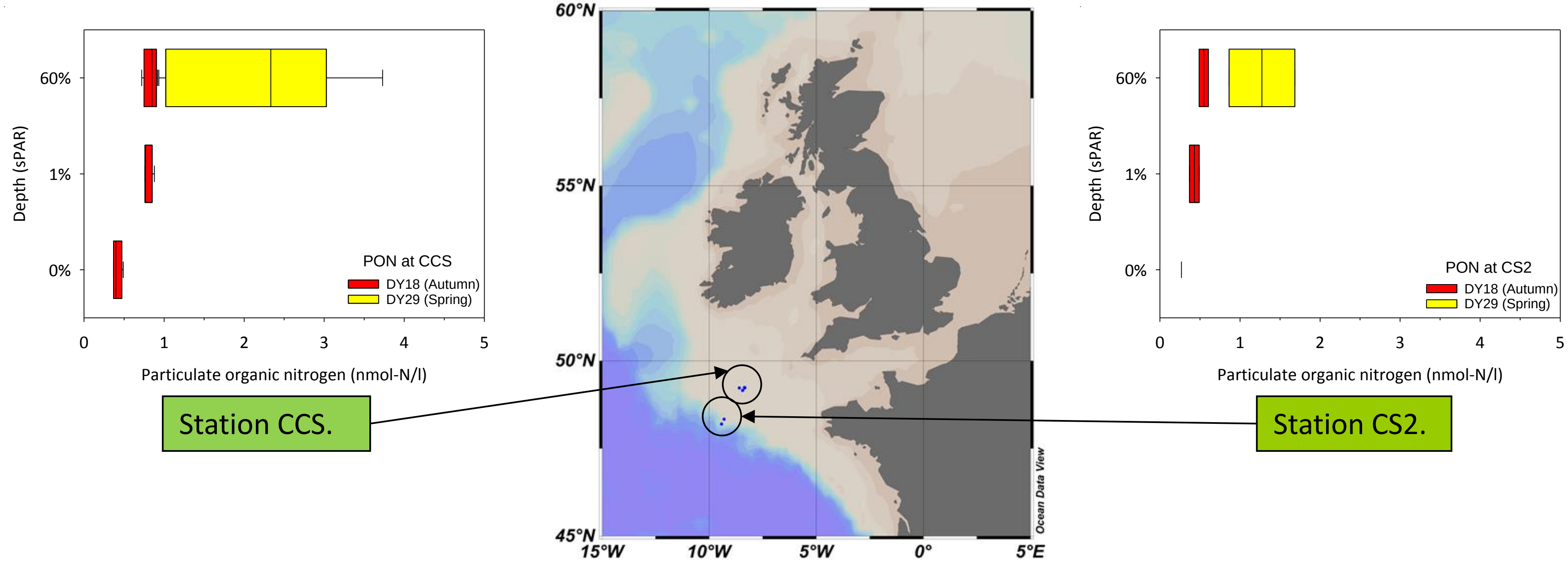
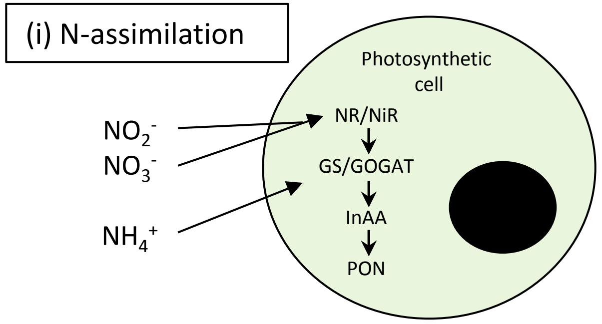
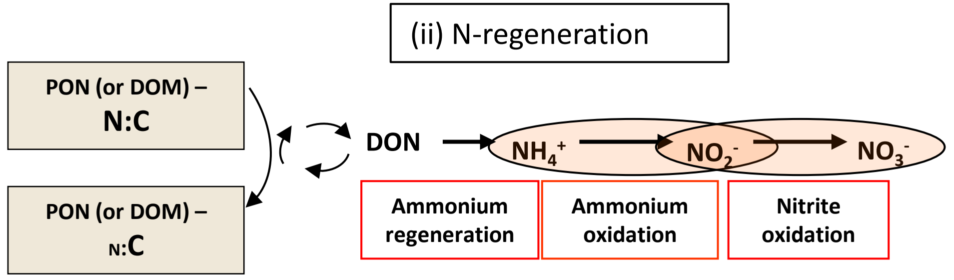


- Particulate Organic Nitrogen (PON – predominantly the nitrogen associated with phytoplankton cells) concentration at CCS and CS2 demonstrating (i) a link with light depth (ii) a seasonal influence (iii) a distinction between stations.

- Processes investigated at these stations; (i) the assimilation of nitrogen by phytoplankton and (ii) the regeneration of nitrogen by various (mostly) microbial processes.





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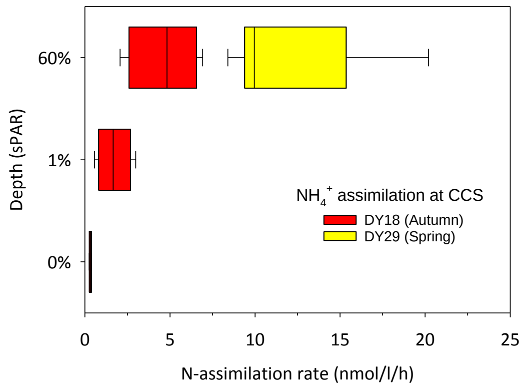

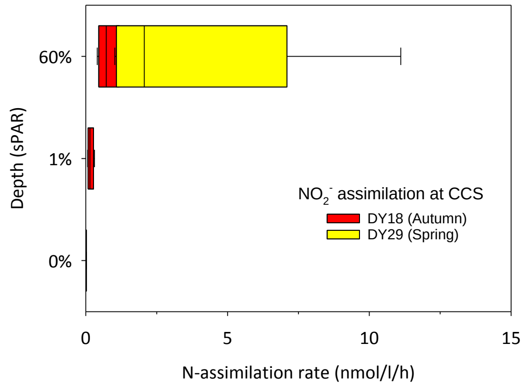

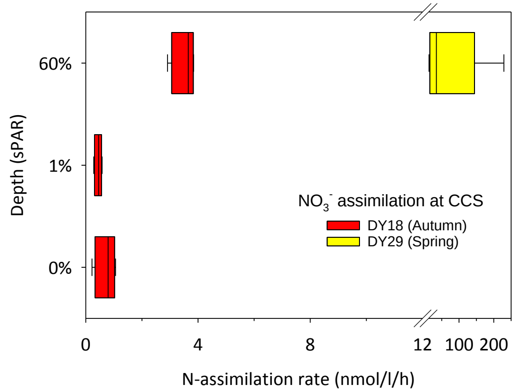

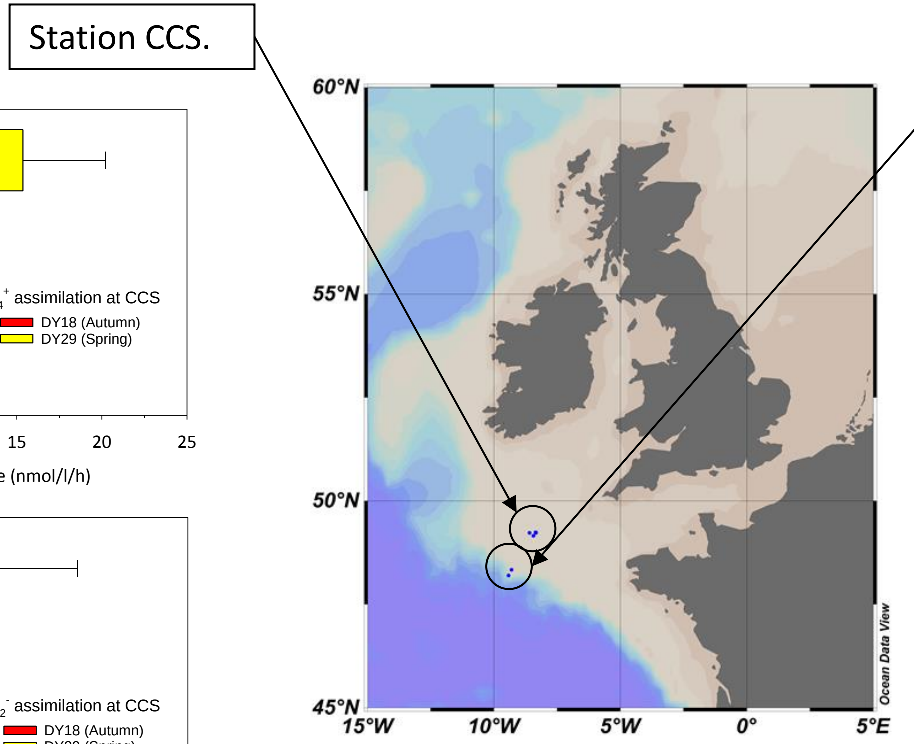

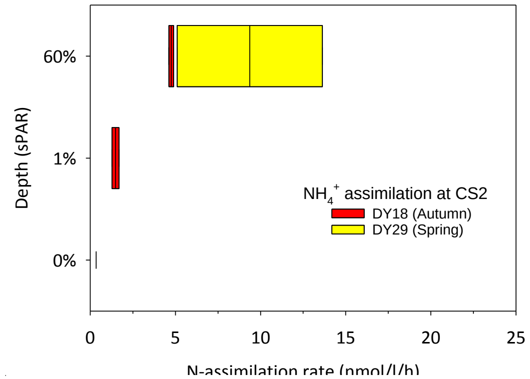

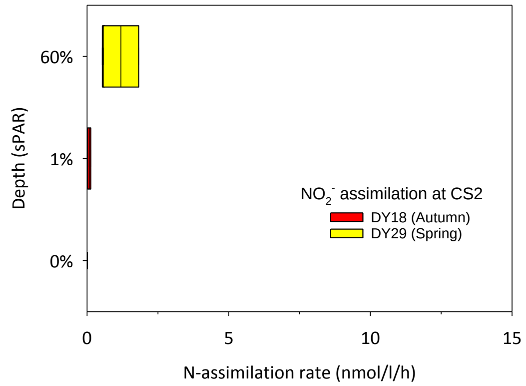

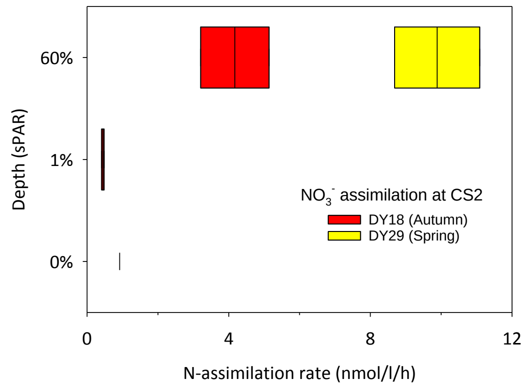

- The rate of N-assimilation by marine phytoplankton decreased as depth increased.
- Nitrate assimilation dominated N-assimilation in the spring. In the autumn nitrate and ammonium assimilation were comparable.
- Generally, the highest N-assimilation activity was associated with station CCS; nitrate assimilation during spring at this location was noteworthy.

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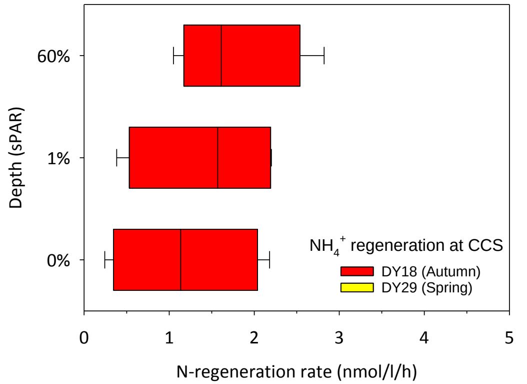
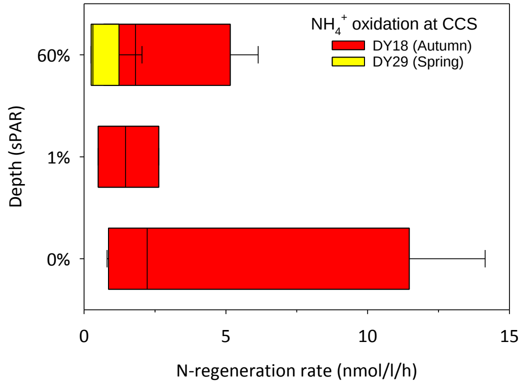
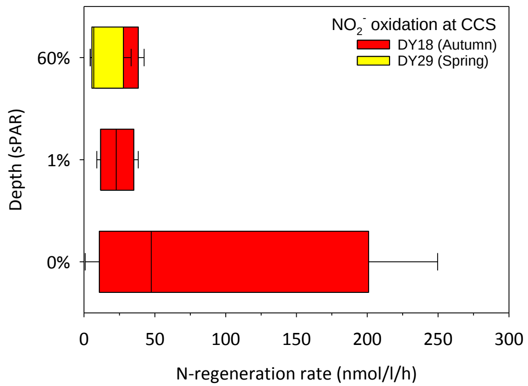
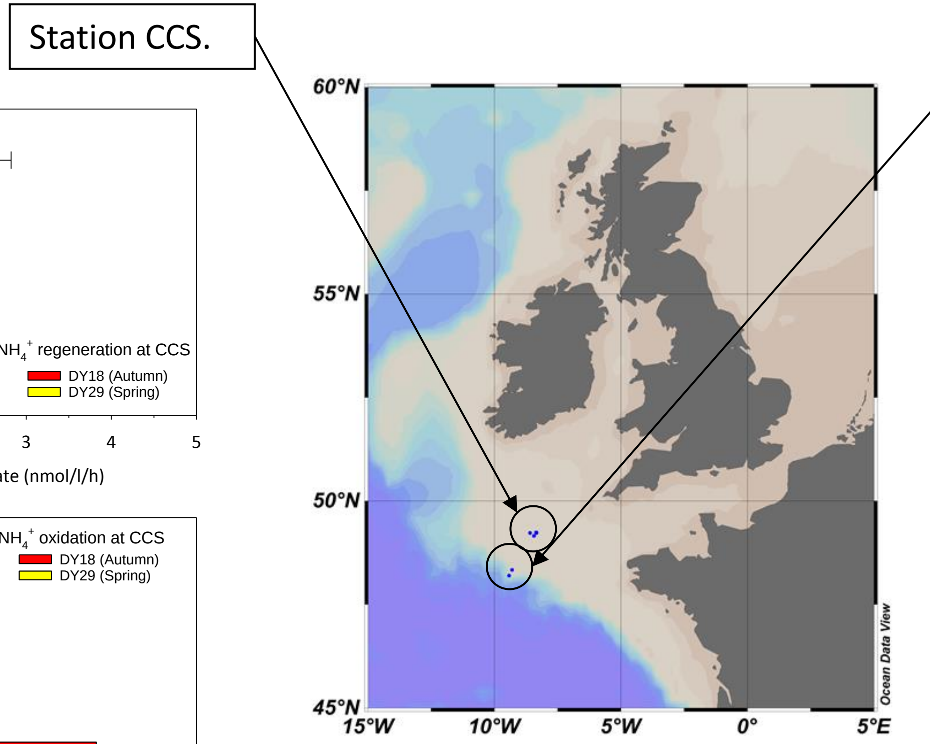
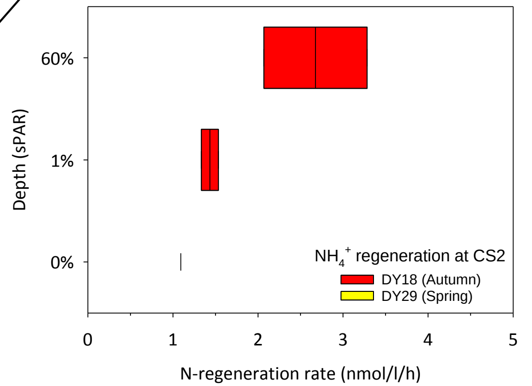


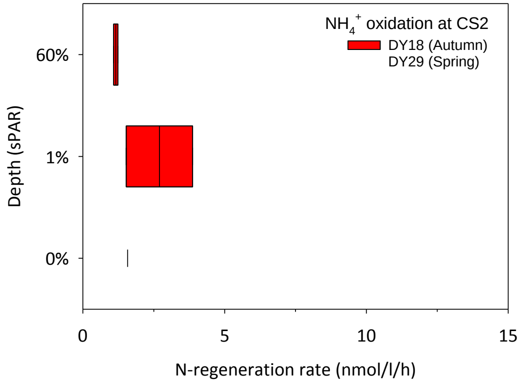


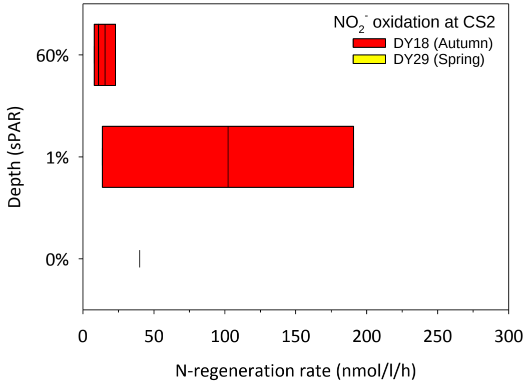




- N-regeneration rates were generally higher in the autumn.
- Very high rates of nitrification were measured in the aphotic zone during autumn.
- Generally, the highest N-regeneration activity was associated with station CCS.







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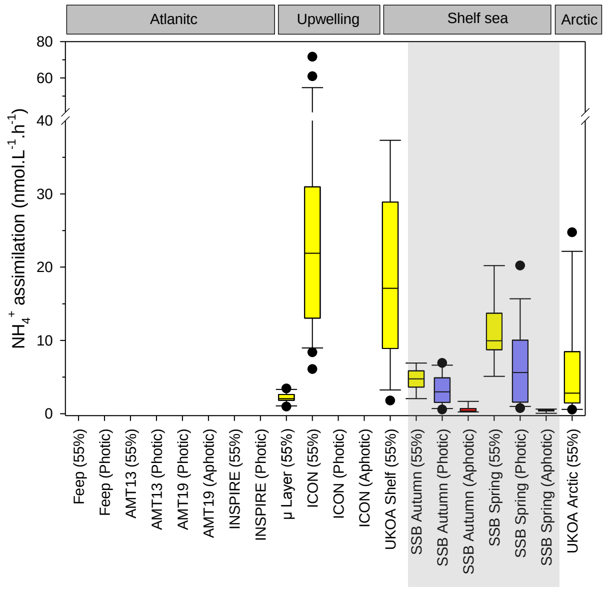

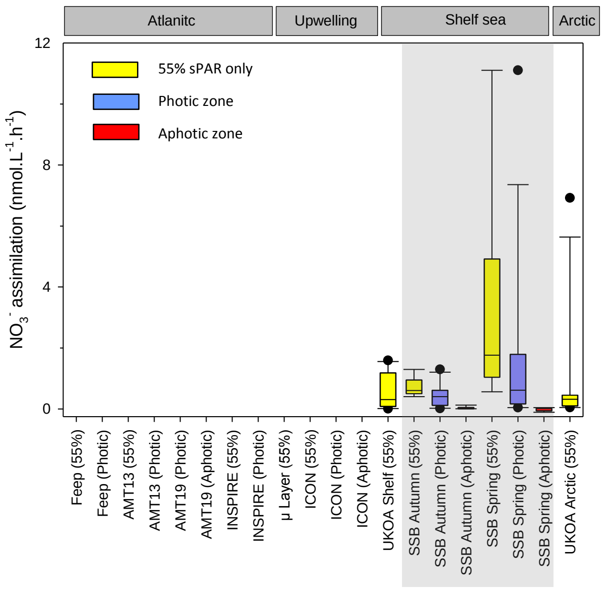

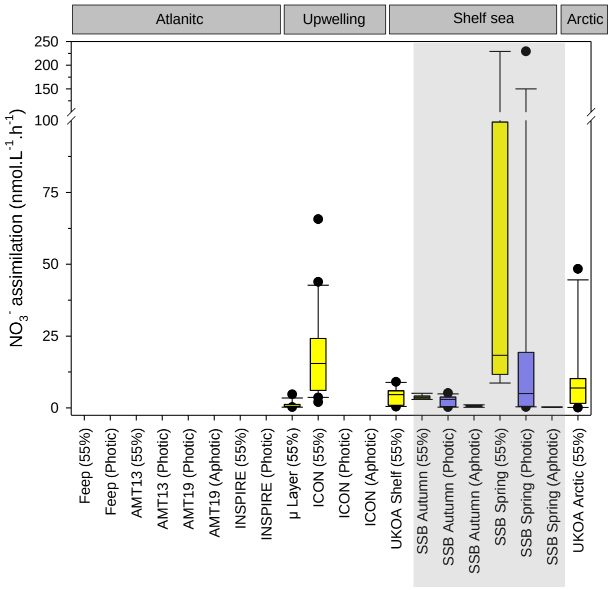

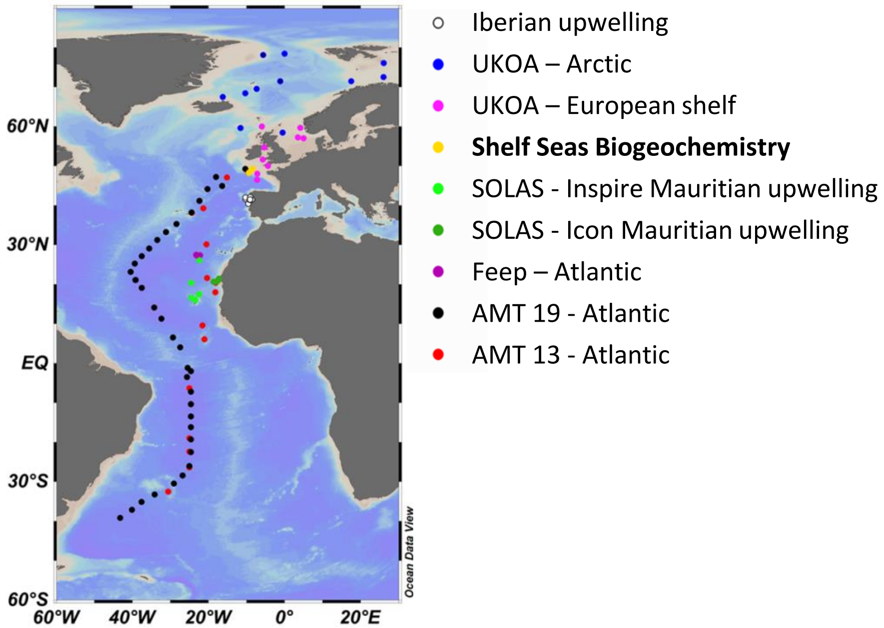

Process rates from SSB wer compared to other studies including the oligotrophic Atlantic, upwelling regions, the Arctic and European shelf.

- Rates of ammonium assimilation by phytoplankton were comparable to the Arctic, but lower than measured during the summer in UK waters.
- Unusually, nitrite was a significant source of inorganic nitrogen for phytoplankton in contrast to other locations.
- Springtime rates of nitrate assimilation by phytoplankton (transiently) exceeded those measured in the Mauritanian upwelling, one of the globes most productive marine ecosystems.

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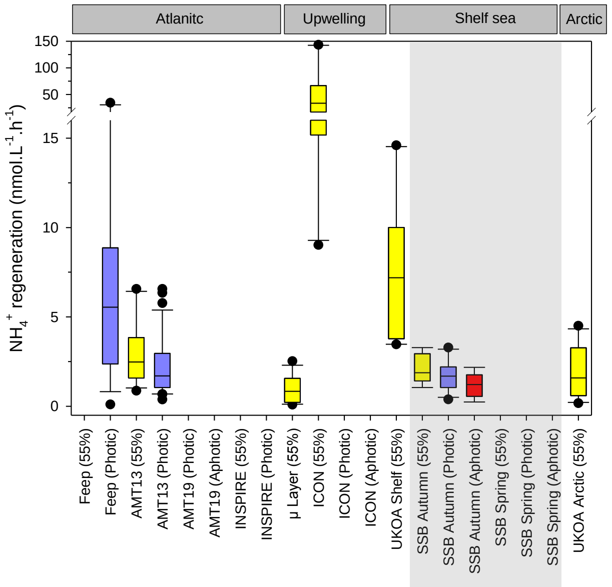

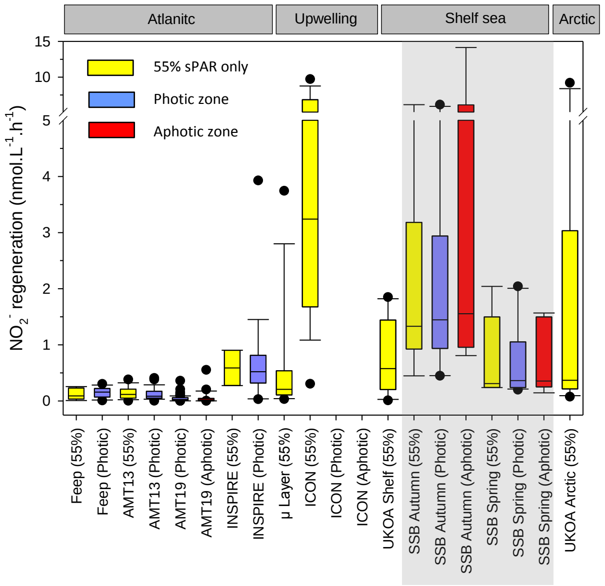

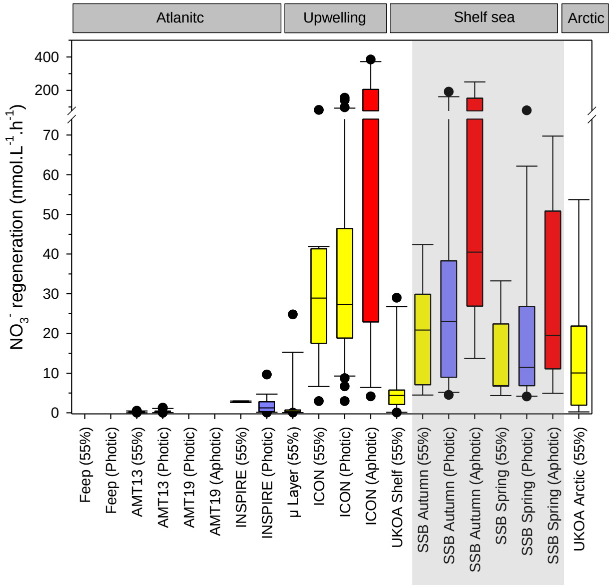

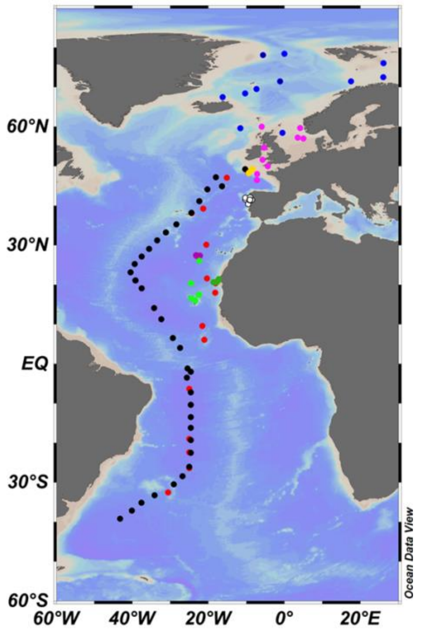

Iberian upwelling

UKOA – Arctic

UKOA – European shelf

Shelf Seas Biogeochemistry

SOLAS - Inspire Mauritian upwelling

SOLAS - Icon Mauritian upwelling

Feep – Atlantic

AMT 19 - Atlantic

AMT 13 - Atlantic

Process rates from SSB were compared to other studies including the oligotrophic Atlantic, upwelling regions, the Arctic and European shelf.

- Rates of ammonium regeneration were towards the lower end of the range measured in other locations.
- A broad range of nitrification rates were measured during SSB reflecting strong depth and seasonal variability.
- Decoupling between these rates implies that nitrogen recycling in association with particles may be important (close physical/chemical association between processes; intermediate steps underestimated with tracer methods).

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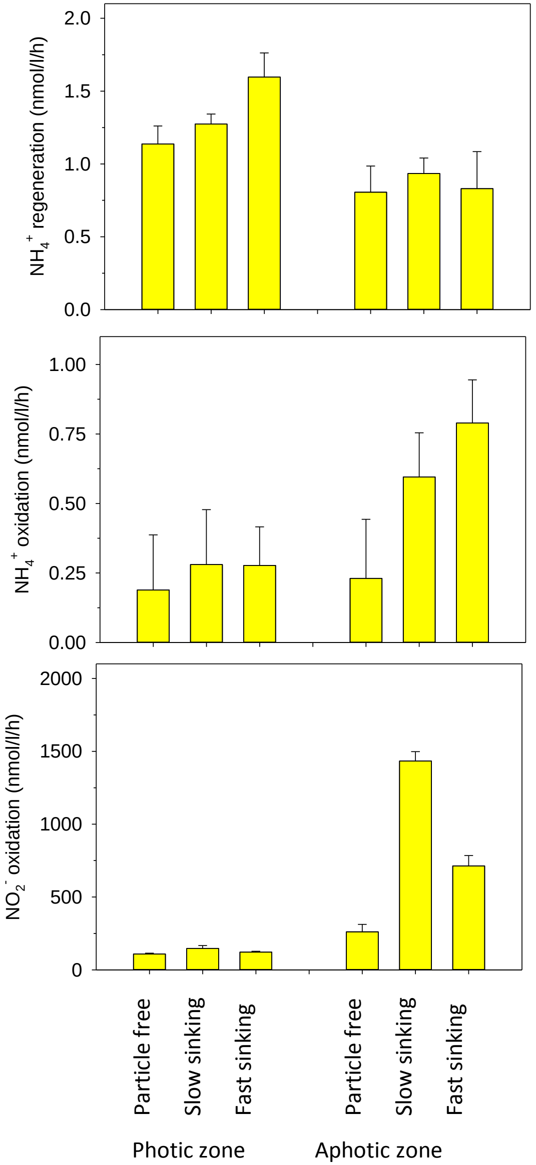

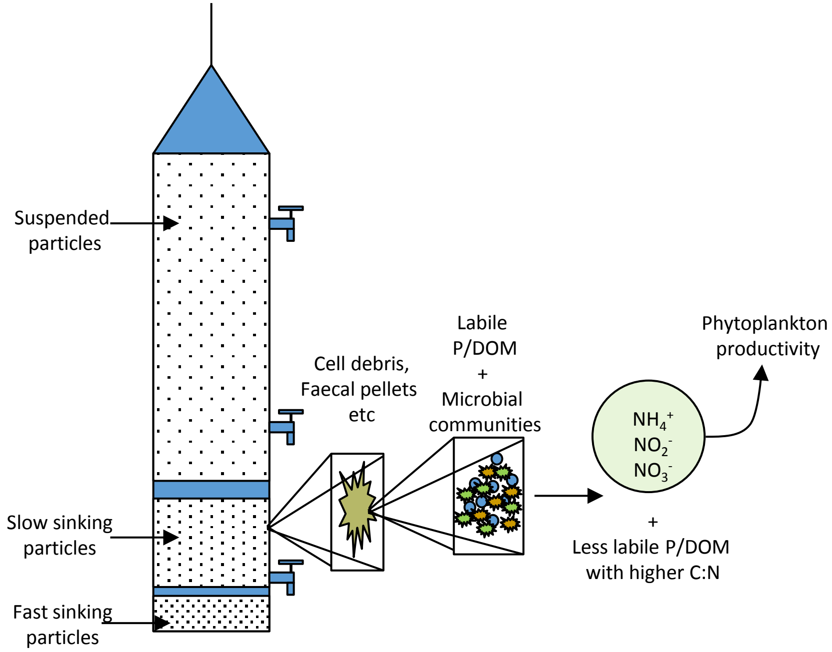

Snow-catcher samples (DY018; Autumn; station CCS)

Comparing process rates measured in the ‘particle free’ (or neutrally buoyant particles) fraction with ‘Slow’ and ‘Fast’ sinking fractions;

Evidence for the release of ammonium from particles in the photic zone.

A clear association between elevated rates of nitrification and marine particles was evident in the aphotic zone.

Microbes associated with marine particles very actively recycle inorganic nitrogen.

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Results from N-cycle studies, which are perhaps intuitive, may be summarised as:

- Highest N-cycle activity associated with on-shelf station CCS. The highest rates of N-assimilation took place in the surface waters during spring. The highest rates of N-regeneration took place in the autumn at aphotic depths.

- N-regeneration activity was associated with marine particles, especially nitrification at aphotic depth.

- Seasonal and depth related variability in assimilation and regeneration will have implications for the stoichiometry of DOM and POM.

To fully address specific hypothesis, synthesis with related data sets is needed;

H5: Remineralisation of POM and DOM creates a carbon-rich residual organic matter pool.

H5(ii) The characteristics of particles (size, source, mineral and organic content) sets their sinking rate and dictates if particles are remineralised in surface or bottom waters (or sediments).

- N-regeneration activity differed between particle type (fast/slow sinking) and retrieval depth (photic/aphotic) implying that particle composition influenced remineralisation characteristics. Associated process activity is likely to increase particulate C:N (to be verified with elemental analysis).

H5(iv) Remineralisation of organic N to nitrate via nitrification results in a sea-to-air flux of N2O.

- Results demonstrated active nitrification throughout the water column and between seasons. If the shelf seas region was to be a source of atmosphere N_2O, this would be most likely in the autumn.