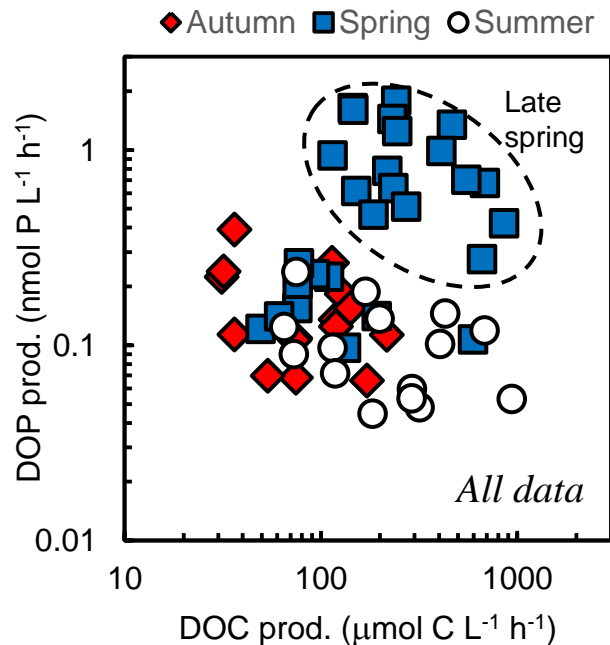
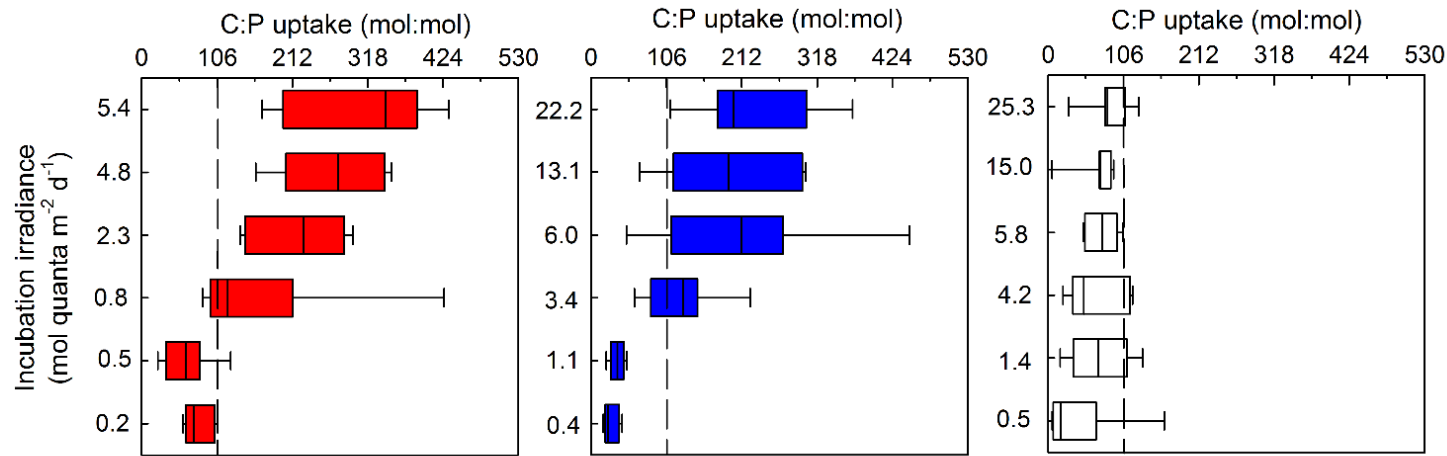


Stoichiometry of Phytoplankton Carbon to Phosphorus Uptake in a Shelf Sea from Spring to Fall



Poulton, A.J.^{1,2}, Davis, C.³,
Daniels, C.J.², Mayers, K.M.J.⁴,
Harris, C.⁵, & Woodward, E.M.S.⁵

¹ The Lyell Centre, Heriot-Watt University,
Edinburgh, UK

² National Oceanography Centre,
Southampton, UK

³ University of Liverpool, UK

⁴ University of Southampton, UK

⁵ Plymouth Marine Laboratory, UK

Summary of C:P uptake stoichiometry

Autumn

- **Light limited**, slow phytoplankton growth and low bacterial growth efficiency
- 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**
- 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
- 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**
- 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**



Summary

- The seasonal cycle of resource availability in temperate shelf seas has a strong selective pressure on phytoplankton diversity and the biogeochemical cycling of key elements, such as carbon (C), nitrogen (N) and phosphorus (P).
- We made parallel measurements of P-uptake and C-fixation, plus the release of dissolved organic phosphorus (DOP) and dissolved organic carbon (DOC), seasonally during spring-summer-fall cruises to the central Celtic Sea (Box 1).
- Particulate P-uptake and C-fixation varied seasonally and with irradiance: relative to the Redfield ratio (106:1), upper waters were C-rich and deep waters P-rich in spring and autumn, while all light levels were P-rich in summer (Box 2).
- The release of DOC and DOP varied seasonally, with DOP release high in spring and DOC release high in summer. Relative to the Redfield ratio, dissolved release was P-rich in spring and C-rich in summer (Box 3).
- Water-column daily integrals of particulate uptake were close to the Redfield ratio in spring and autumn, and P-rich in summer (Box 4).
- Particulate and dissolved C:P stoichiometry varied seasonally: (a) spring particulates changed from P-rich to C-rich, while dissolved phases showed the reverse; (b) summer particulates were P-rich while dissolved phases were C-rich; and (c) autumn particulates and dissolved phases were both C-rich.

2. Vertical Profiles of C-fixation and P-uptake

- The rates of P-uptake (Fig. 2a) and C-fixation (Fig. 2b) varied both seasonally and across the light gradient used to replicate seasonal and vertical changes in irradiance. The vertical decline in P-uptake and C-fixation was steepest in autumn and spring, and weakened in summer, which resulted in higher light levels being C-rich and lower light levels being P-rich (Fig. 2c).
- The ratio of C:P uptake (Fig. 2d) was <106 throughout the water-column in summer, meaning that particulates were extremely P-rich. Turnover times of the inorganic phosphorus pool (Fig. 2d) also showed a strong gradient related to irradiance level, with turnover times being shortest in summer.

Figure 2: Box and whisker plots of P-uptake (a), C-fixation (b), C:P uptake ratios (c), and inorganic P (Pi) turnover times (d) at different light levels. Dashed line on (c) indicates Redfield ratio. Turnover calculated after Bjorkman & Karl (1984; MEPS 111).

1. The Shelf Sea Biogeochemistry (SSB) Programme

- The SSB programme examined P-uptake, C-fixation, DOC and DOP release in the Celtic Sea (Fig. 1) during fall (November, 2014), spring (April, 2015) and summer (July, 2015).
- Short-term (6 h) P-uptake and DOP release measured using P-33 following Reynolds et al. (2014, Global Biogeochem. Cycl. 28) and Karl & Tien (1992, Limnol. Oceanogr. 37).
- Short-term (6 h) C-fixation, daily (24 h) rates of primary production and DOC release measured using C-14 following Poulton et al. (2014, Biogeochemistry 11) and Lopez-Sandoval et al. (2011, Biogeochemistry 8).
- Uptake rates made in temperature-controlled incubator with seasonal irradiance levels reconstructed using LED light panels, neutral density light filters and adjusted for varying day lengths.
- Irradiance depths sampled and replicated were 60%, 40%, 20%, 10%, 5% and 1% of surface incident irradiance.

Figure 1: Celtic Sea, with sampling sites - Central Celtic Sea (CCS) and Shelf Edge (CS2), (SW of UK).

3. Dissolved Organic Phosphorus and Carbon Release

- The release of dissolved organic carbon (DOC) and dissolved organic phosphorus (DOP) on short time-scales (6 h) varied seasonally (Fig. 3), but showed no vertical changes (data not shown).
- Rates of DOP release were highest during spring and lowest in summer, whereas rates of DOC showed the opposite pattern (Fig. 3). Autumn rates of DOC and DOP release were most similar to the rates seen in spring.
- The stoichiometry of the dissolved phases were nearest to the Redfield ratio (106:1) during autumn, while spring rates were P-rich and summer rates were C-rich (Fig. 3).
- DOC and DOP release varied considerably during spring, with dissolved phases going from being C-rich to P-rich (relative to Redfield) as the spring bloom developed in the central Celtic Sea.

Figure 3: DOP and DOC release scatter plot. Legend: Autumn (red), Spring (blue), Summer (grey). Redfield ratio (106:1) is shown as a dashed line.

4. Integrated Water Column Measurements

- Rates across the six light levels were integrated over a 50 m water column, with daily rates of primary production (PP) compared to 24 h rates of P-uptake (Table 1). Average ratios across the water-column of DOC to DOP release (h⁻¹) are also presented. Seasonal patterns of integrated C:P stoichiometry differed in absolute values but showed the same general pattern to individual irradiance levels (Fig. 2): close to Redfield ratios in autumn and spring, P-rich in summer (Table 1).

Season	Site	Chl	PP	P uptake	C:P	Avg DOC:DOP
		(mg m ⁻³)	(mmol P m ⁻² d ⁻¹)	(mmol C m ⁻² d ⁻¹)	(mmol C mmol P ⁻¹)	(mol mol ⁻¹)
Autumn (November 2014) - Autumn bloom?						
10 Nov	CCS	75	0.3	53	170	ND
12 Nov	CCS	67	0.3	29	125	127
18 Nov	CS2	42	0.3	21	81	670
20 Nov	CS2	53	0.2	26	112	728
22 Nov	CCS	60	0.3	46	165	763
25 Nov	CCS	71	0.3	47	188	1824
MEAN		65	0.3	37	140	821
Spring (April 2015) - Chl and PP peak on 15 April						
04 April	CCS	67	2.1	164	78	1558
06 April	CCS	82	1.4	92	64	480
10 April	CCS	40	1.8	104	58	228
11 April	CCS	153	2.7	282	96	377
15 April	CCS	300	3.9	1006	259	108
20 April	CCS	173	3.5	428	121	58
24 April	CCS	99	2.2	259	117	24
25 April	CCS	168	3.5	537	156	66
MEAN		135	2.6	396	118	382
Summer (July 2015)						
04 July	CCS	42	1.0	61	54	ND
15 July	CCS	30	1.0	39	39	ND
18 July	CS2	45	1.7	75	42	806
20 July	CCS	36	1.9	40	39	ND
24 July	CCS	31	0.8	36	45	4741
28 July	CCS	53	1.5	16	12	1694
31 July	CCS	37	0.7	43	43	2573
MEAN		34	1.1	43	42	1783

Table 1: Inventories of Chlorophyll-a (Chl), P-uptake, Primary Production (PP), C:P uptake ratio, and the average ratio of DOC to DOP release during spring, summer and fall in the Celtic Sea.

Clear spring transition - particulate material P-rich prior to Chl and PP peak and C-rich thereafter; dissolved phases opposite. C-rich prior to Chl peak and P-rich thereafter.

Summer low Chl and PP, particulates P-rich and dissolved phases (very) C-rich.