Phosphorus cycling in the sea: new stories and enduring questions

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Please note this has been edited to remove unpublished examples, feel free to contact me with any questions.

The take home message

- The basics:
  - P is important
  - It is rapidly cycled
  - It comes in organic forms - that are poorly characterized
- Tech advances
  - Magic tells us that the inorganic form is at very low levels
  - Distribution of bond classes in high molecular weight DOP
- Adaptation to low P is common
  - Frequency and expression of *pstS*
  - The emerging importance of polyphosphate
  - Losing your phospholipids
  - Metabolism of phosphonates
- Enduring mysteries
  - Low molecular weight DOP composition
  - P machinery in the agal viruses
  - Microbial metabolism of reduced P

Why phosphorus?

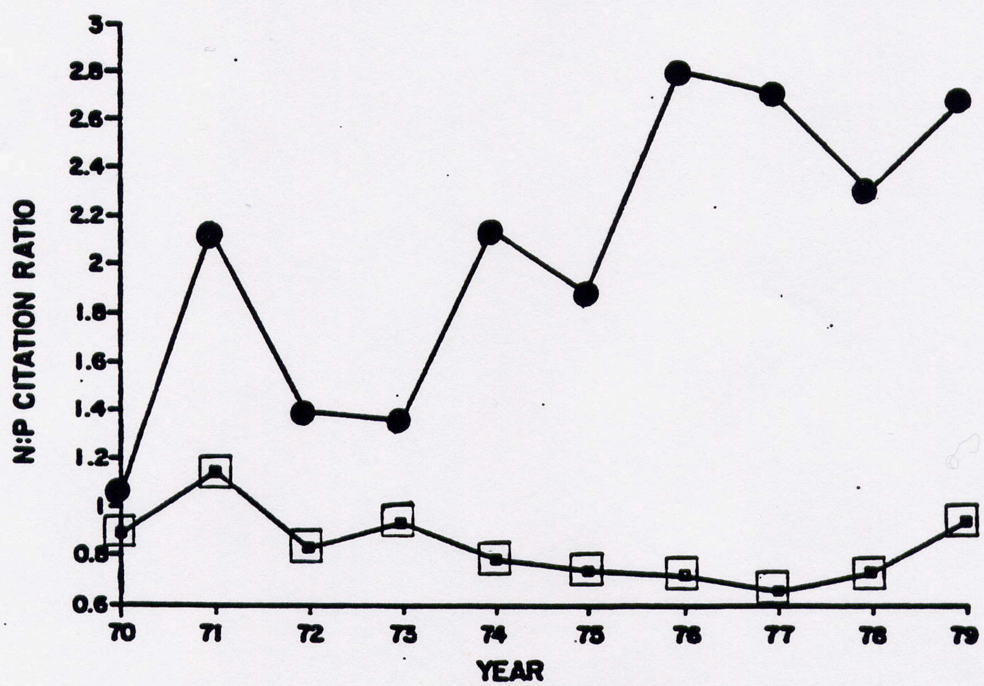


Fig. 16. Ratio of nitrogen citations to phosphorus citations in freshwater (□) and brackish and marine waters (●) from 1970 to 1979, based on citations in the Bibliographic Retrieval Services Biosis Data Base.

In 1970, equal numbers of N and P citations. By 1980, 4-fold increase in N versus P

The importance of P broadly appreciated

articles

The relative influen

Nature of Phosphorus Limitation
in the Ultraoligotrophic

Phosphorus Deficiency in the Atlantic: An Emerging Paradigm in Oceanography

By James W. Ammerman, Raleigh R. Hood,
Darin A. Case, and James B. Cotner

Eos, Vol. 84, No. 18, 6 May 2003

news and views

Aquatic ecology

Phosphorus, the staff of life

David M. Karl

The P cycle basics

Major P fluxes

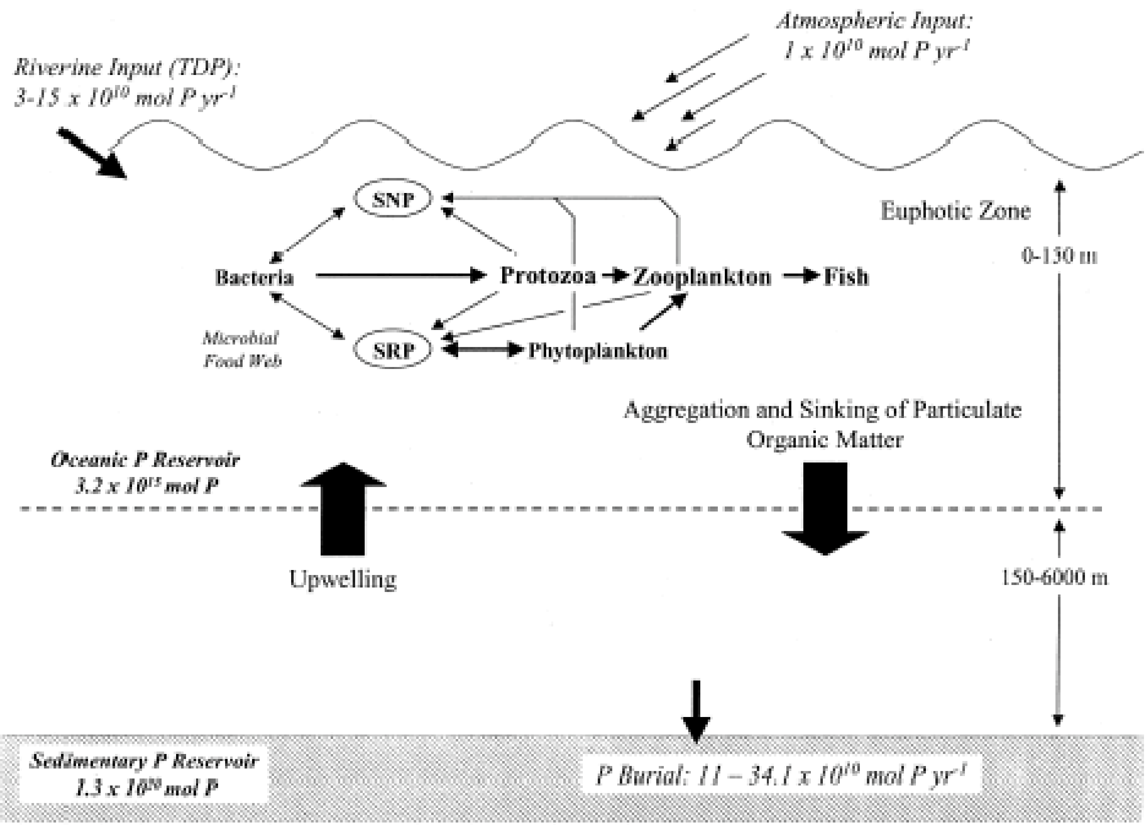


Fig. 3. The pre-anthropogenic marine P cycle. See text for details on fluxes.

Benitez-Nelson 2000

P turnover - can be fast

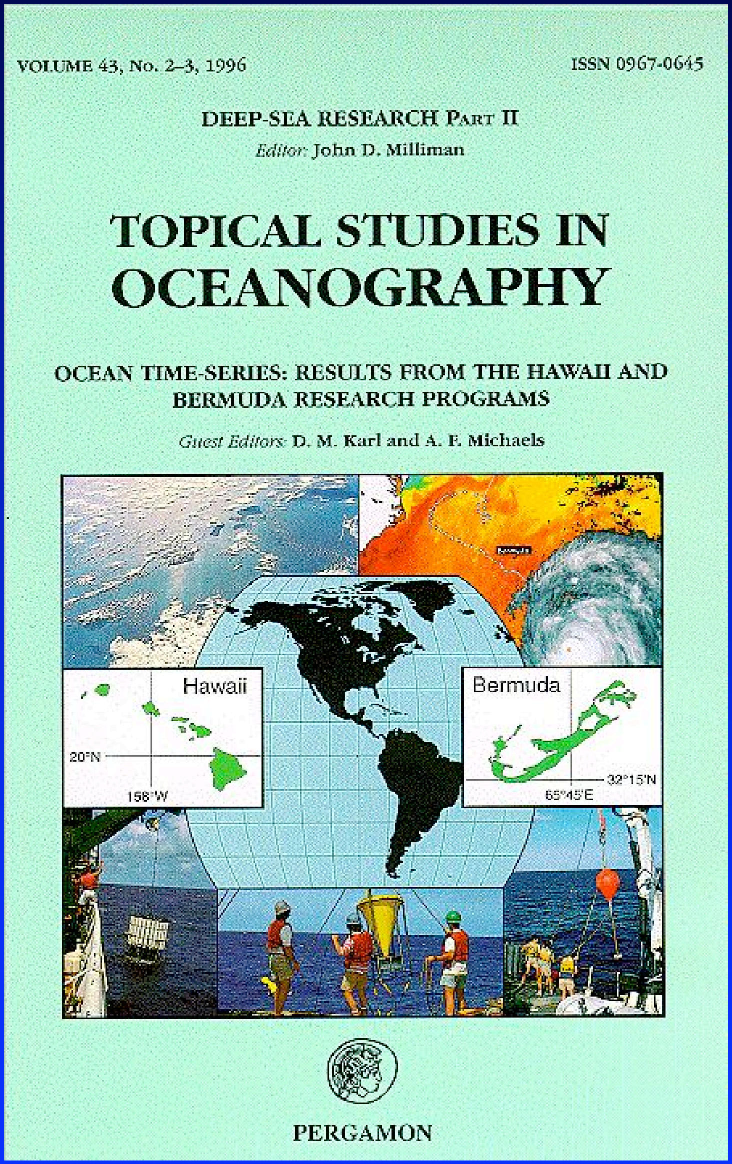
Table 3
SRP and SNP turnover rates

P turnover rates	Coastal	Open ocean	References
SRP	< 1 h–10 days (> 1000 days in Bedford Basin)	Week to several months	Pomeroy, 1960; Duerden, 1973; Taft et al., 1975; Harrison et al., 1977; Perry and Eppley 1981; Smith et al., 1985;Sorokin, 1985; Harrison and Harris, 1986; Björkman and Karl, 1994; Björkman et al., 1999; Benitez-Nelson and Buesseler, 1999a
Total SNP	3–> 90 days	50–300 days	Jackson and Williams, 1985; Orrett and Karl, 1987; Lal and Lee, 1988; Lee et al., 1992; Karl and Yanagi, 1997; Björkman et al., 1999; Benitez-Nelson and Buesseler, 1999a
Bioavailable SNP (model compounds)	2–30 days	1–4 days	Ammerman and Azam, 1985; Nawrocki and Karl, 1989; Björkman and Karl, 1994; Björkman and Karl, 1999
Microplankton (< 1 μm)	> 1–3 days	NA	Benitez-Nelson and Buesseler, 1999a
Phytoplankton (> 1 μm)	< 1–8 days	< 1 week	Waser et al., 1996; Benitez-Nelson and Buesseler, 1999a
Macrozooplankton (> 280 μm)	14–40 days	30–80 days	Lal and Lee, 1988; Lee et al.,1991, 1992; Waser et al., 1996; Benitez-Nelson and Buesseler, 1999a

P pools and their analysis

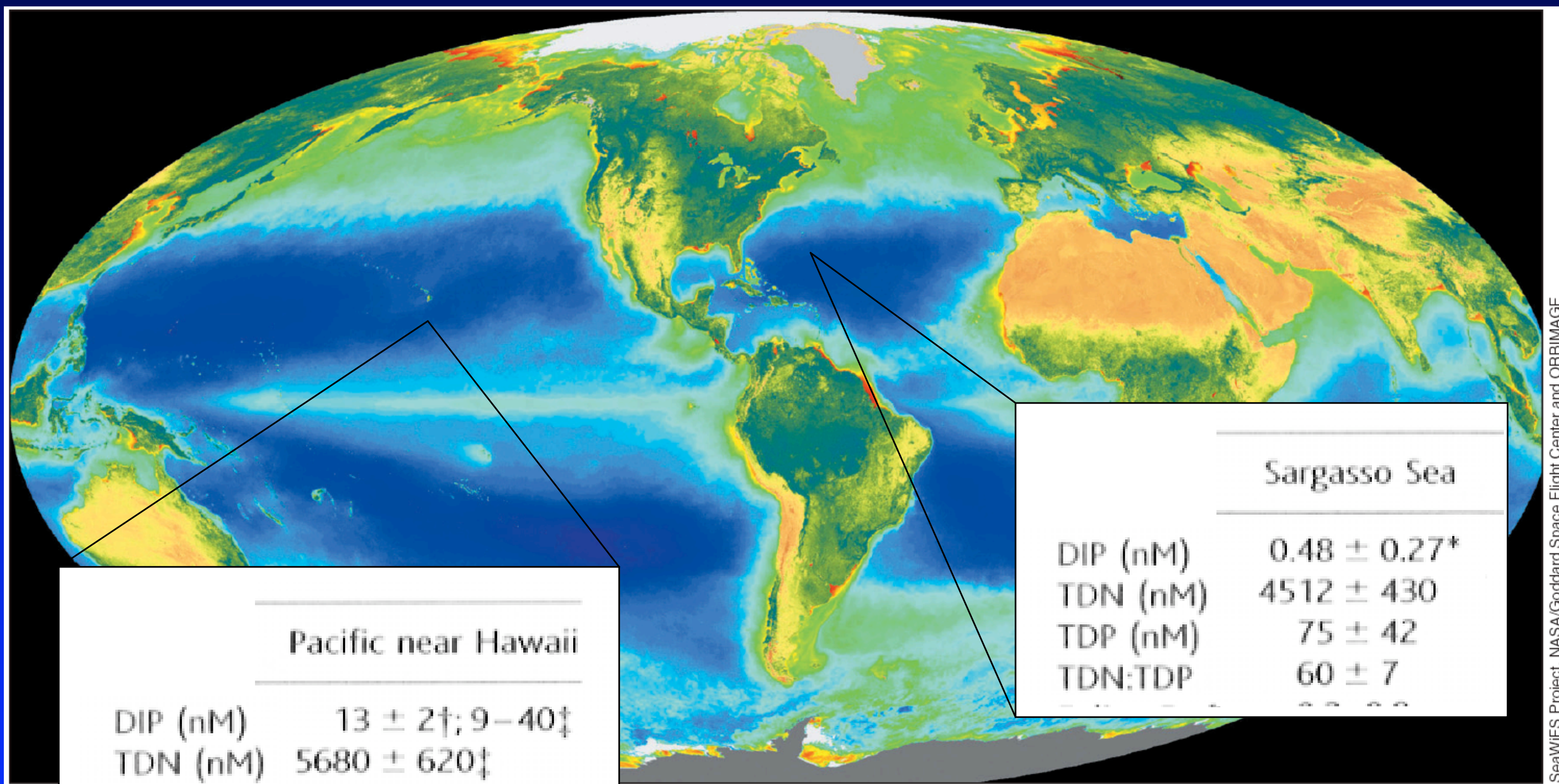
Time series observations pave the way

HOT



BATS

Low P in many ocean biomes

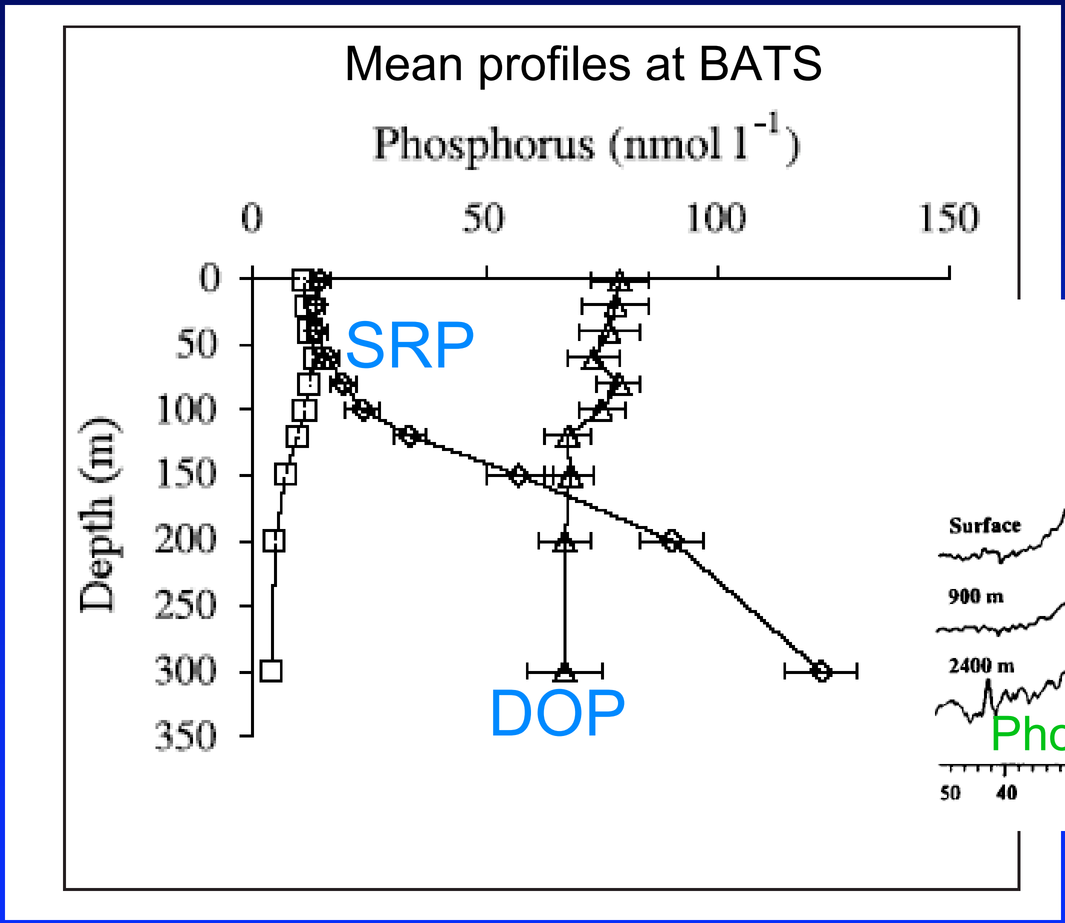


	Sargasso Sea
DIP (nM)	0.48 ± 0.27*
TDN (nM)	4512 ± 430
TDP (nM)	75 ± 42
TDN:TDP	60 ± 7

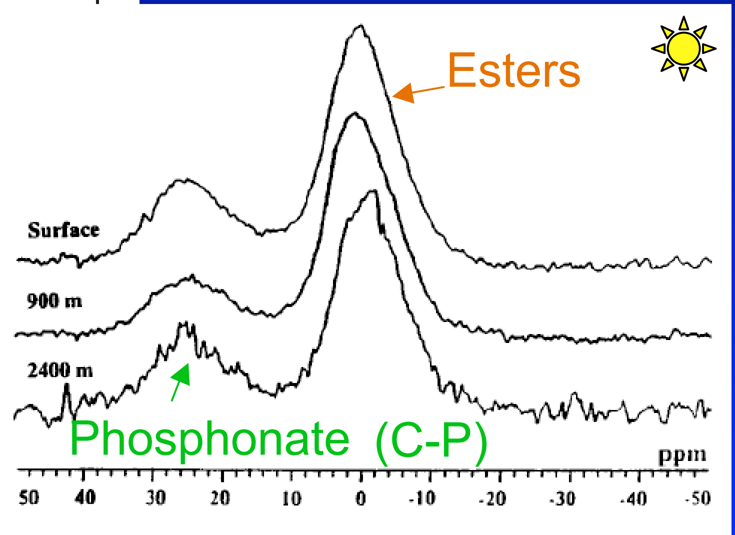
	Pacific near Hawaii
DIP (nM)	13 ± 2†; 9–40‡
TDN (nM)	5680 ± 620‡
TDP (nM)	222 ± 14‡
TDN:TDP	26 ± 3

Wu et al. 2000

Phosphorus profiles in the Sargasso Sea



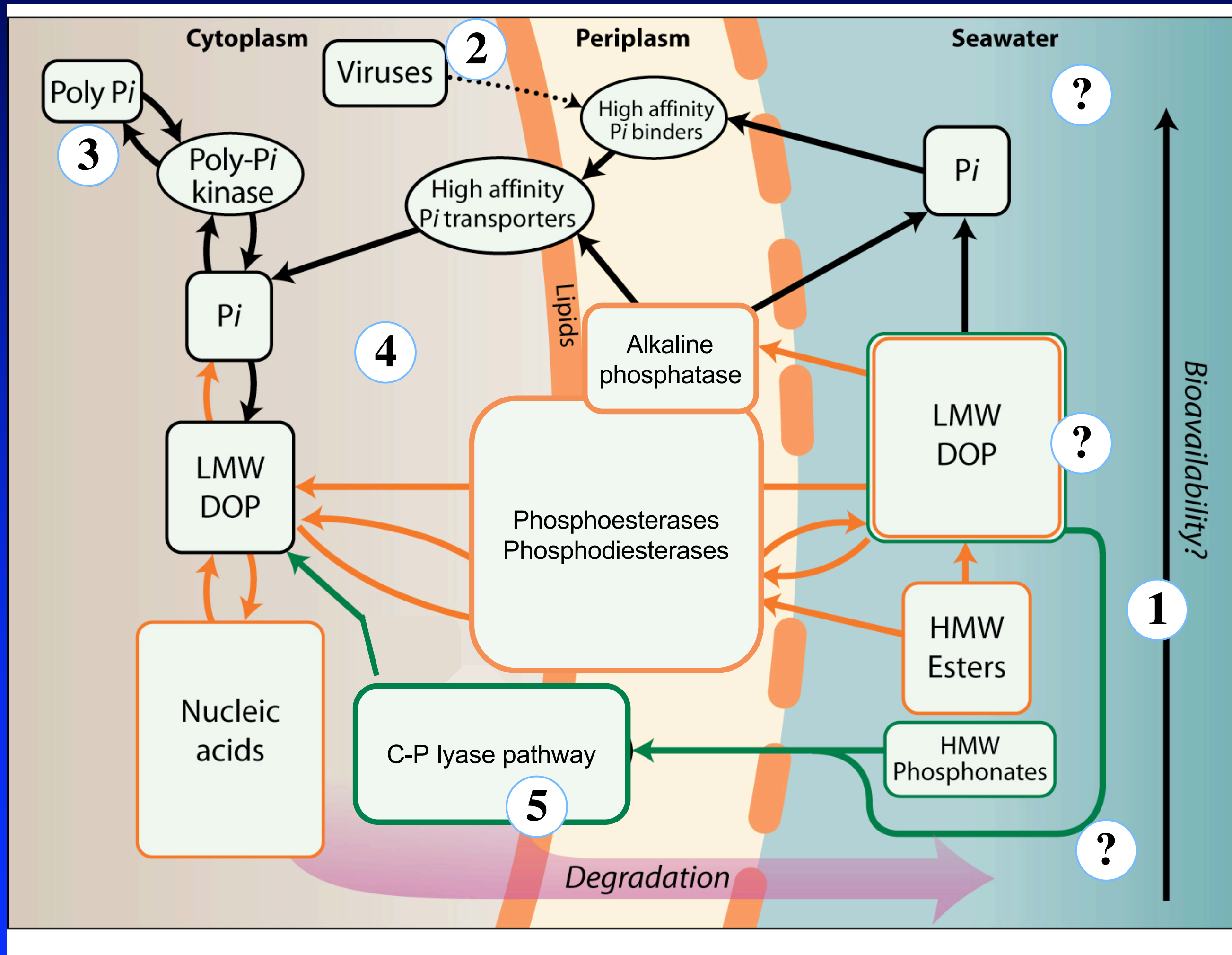
Ammerman et al. 2003



Kolowith et al. 2001

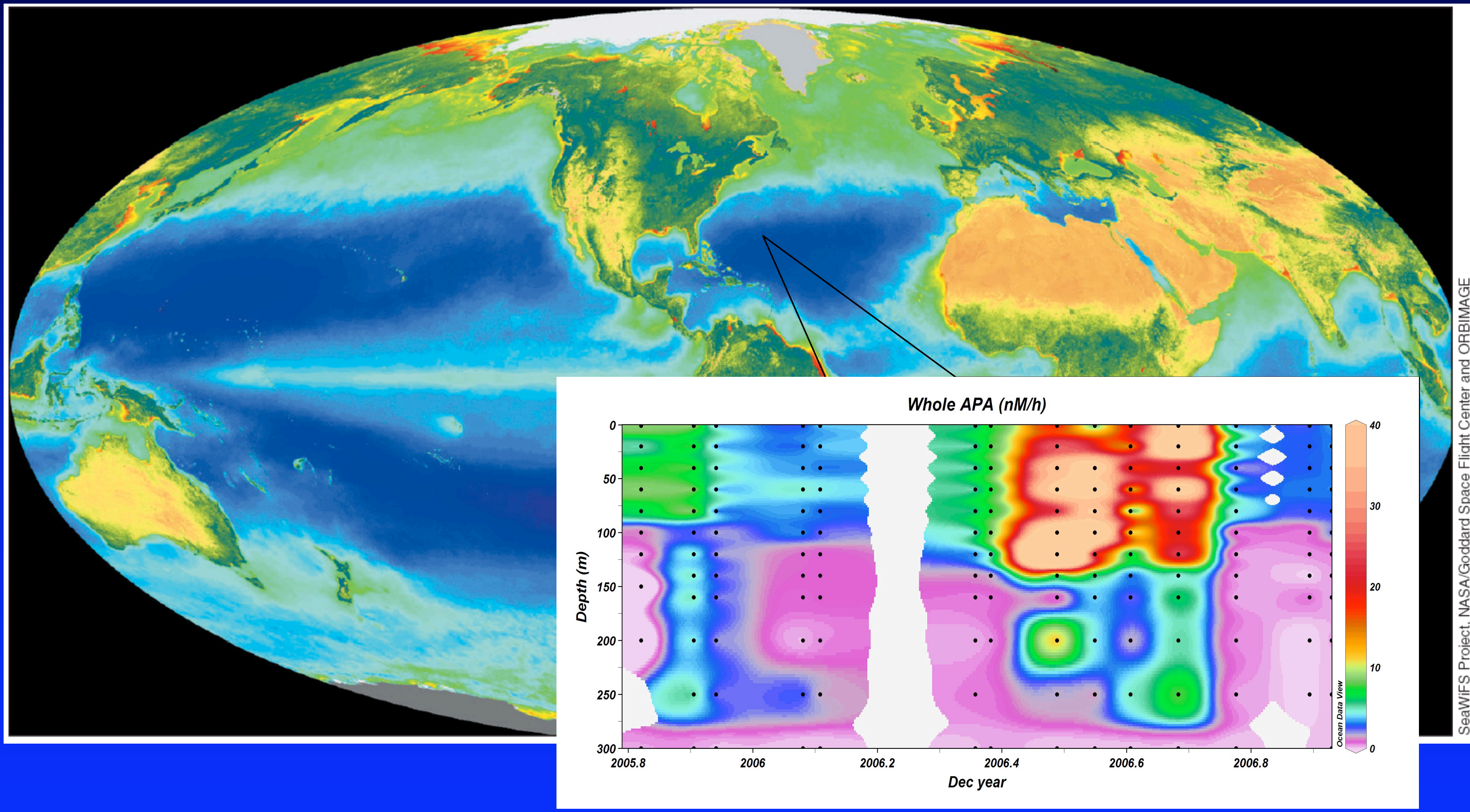
The DOP revolution

A conceptual diagram of marine microbial interactions with phosphorus



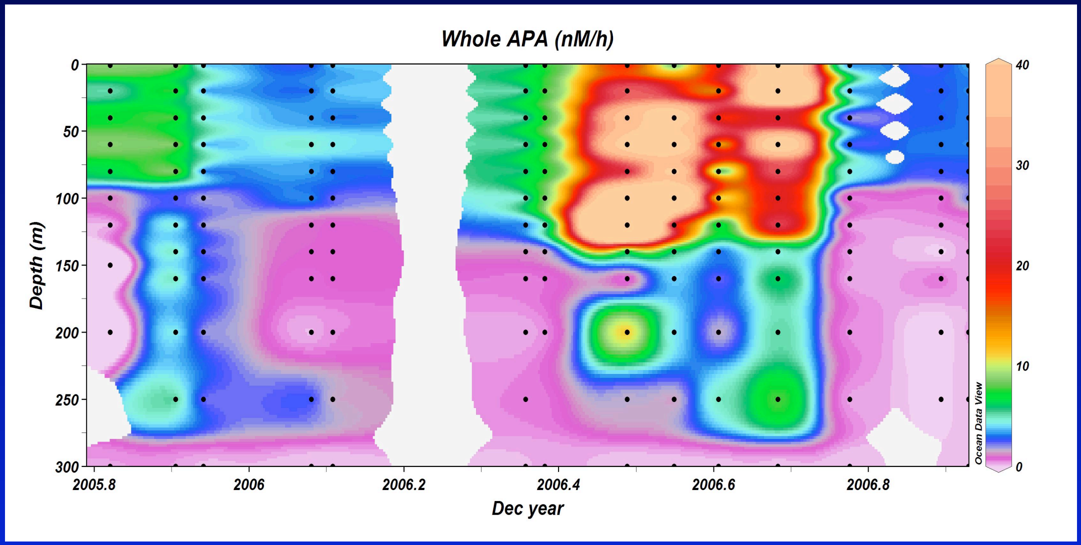
Dyhrman et al. 2007

Alkaline phosphatase in the Sargasso Sea

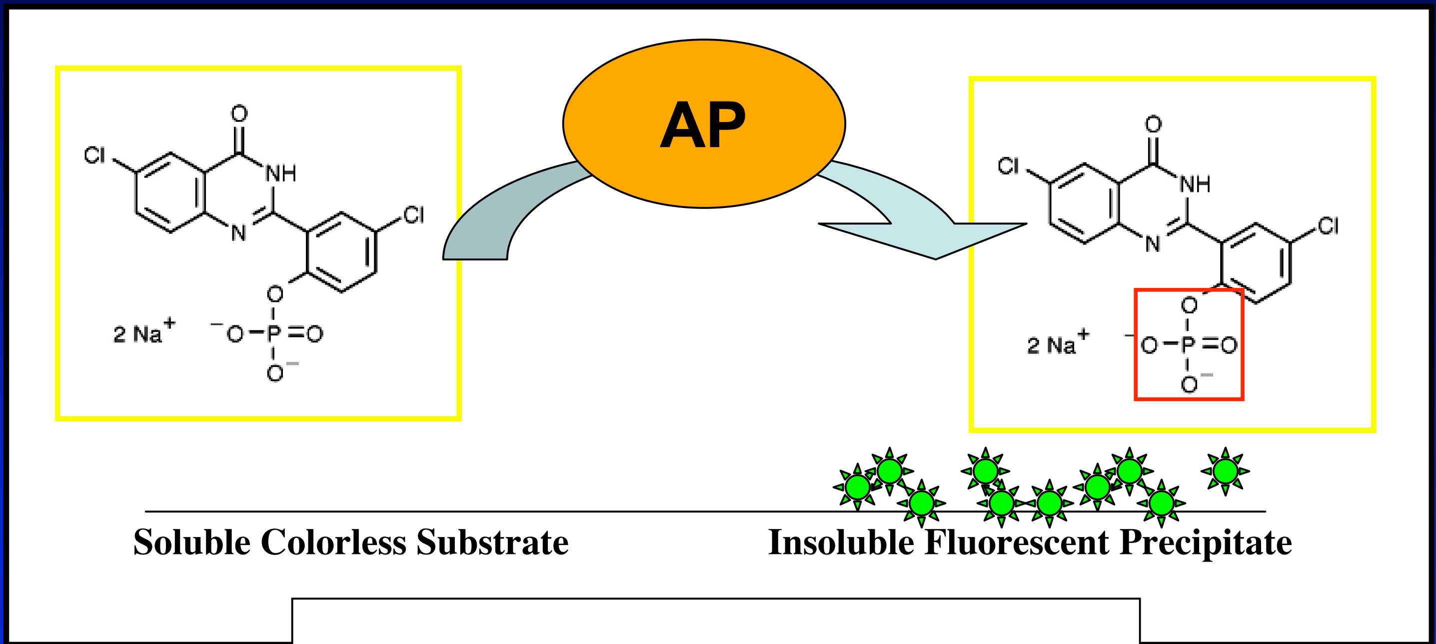


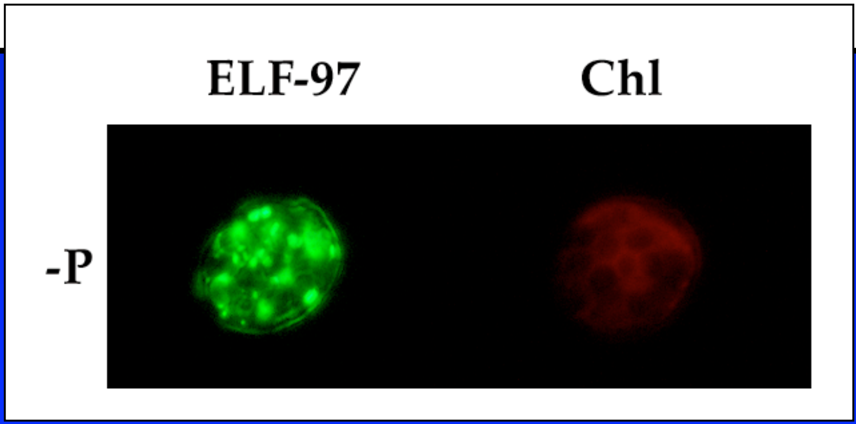
Does DOP support primary production?

Seasonal DOP inventory declines at BATS



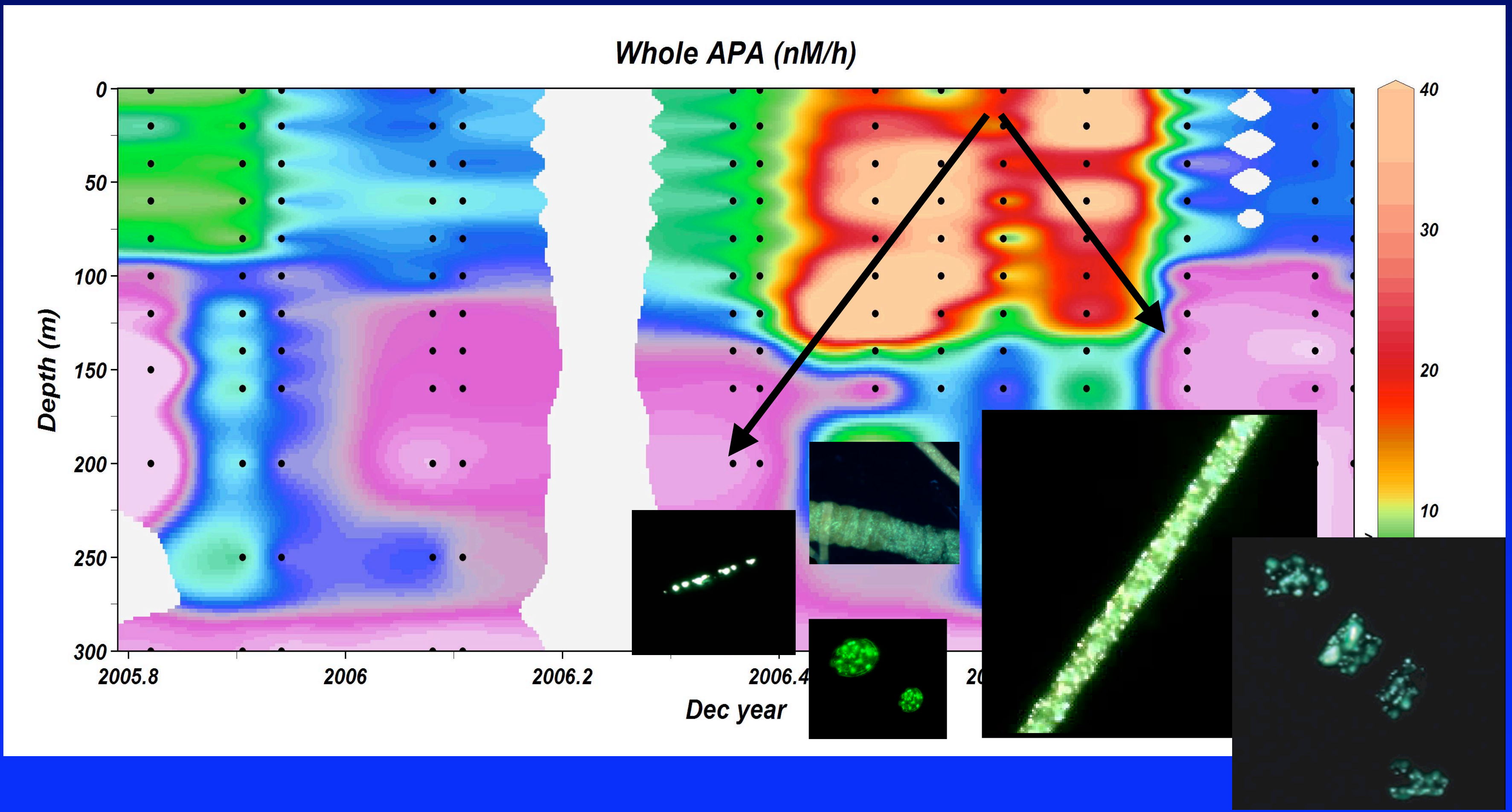
Enzyme labeled fluorescence

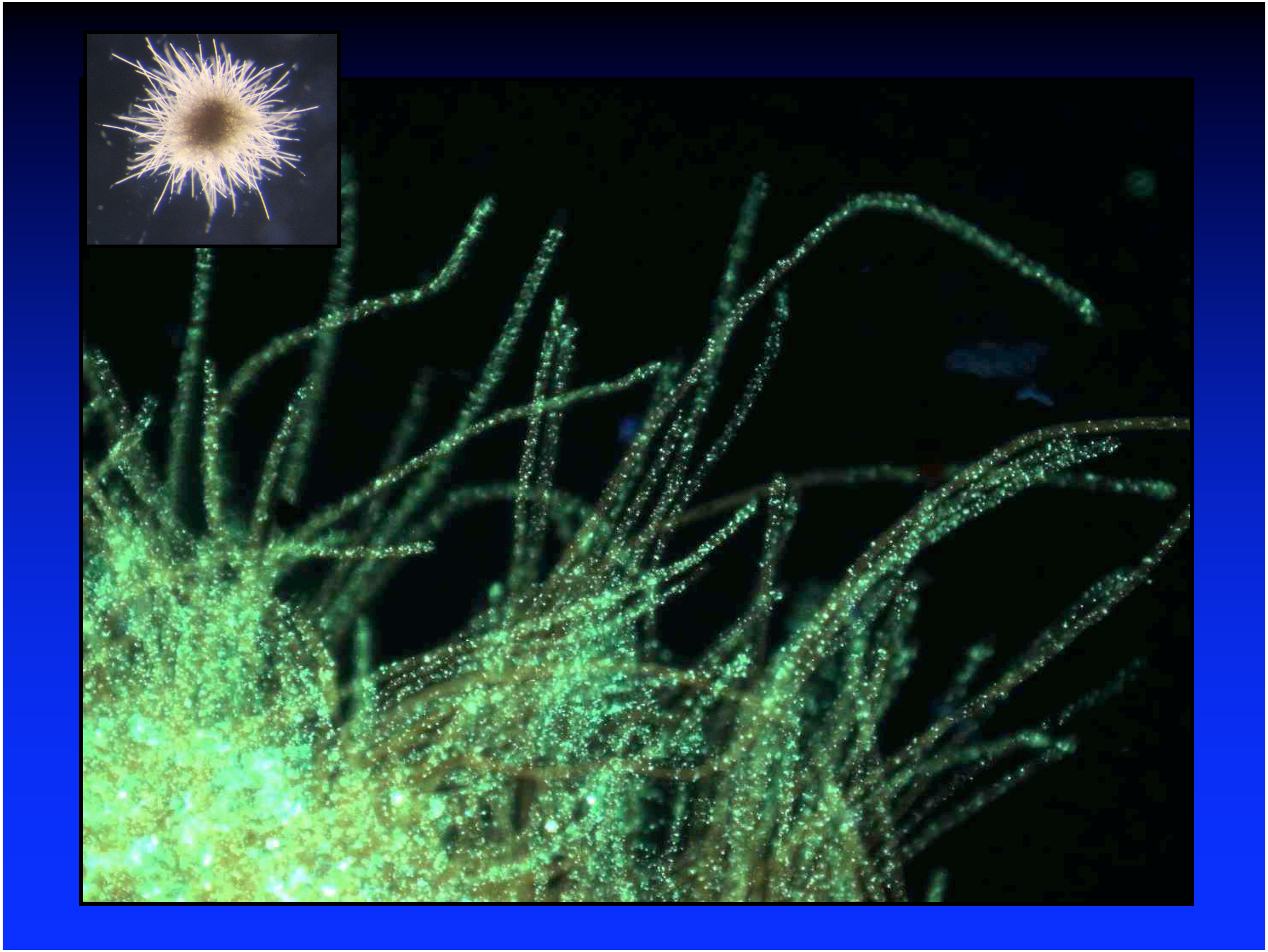




Dyhrman and Palenik 1999

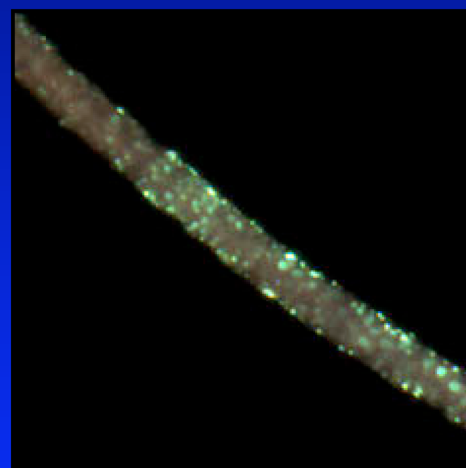
Many microbes contributing to APA

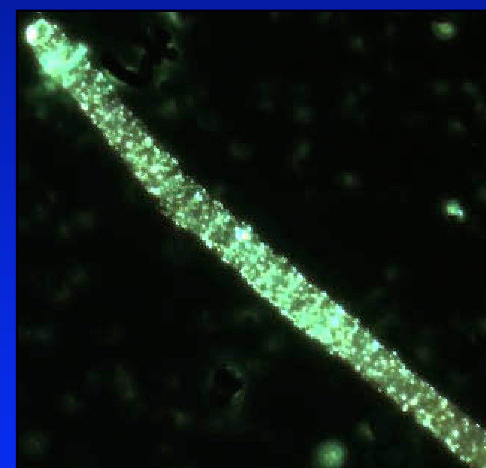




Seasonal APA in the Sargasso Sea

June	August	October
DIP: 10.2 nM	DIP: 25.0 nM	DIP: 9.8 nM





P dynamics in the NASG

- **DIP and DOP depletion in the NASG**
- **During the Spring up to 30% of the production in the NASG may be supported by DOP - corresponds to APA**
- **The bioavailability of DOP is important!!**

LETTERS

Phosphorus cycling in the North and South Atlantic Ocean subtropical gyres

RHIANNON L. MATHER[1], SARAH E. REYNOLDS[1*], GEORGE A. WOLFF[1†], RICHARD G. WILLIAMS[1], SINHUE TORRES-VALDES[2], E. MALCOLM S. WOODWARD[3], ANGELA LANDOLFI[2*], XI PAN[2], RICHARD SANDERS[2] AND ERIC P. ACHTERBERG[2]

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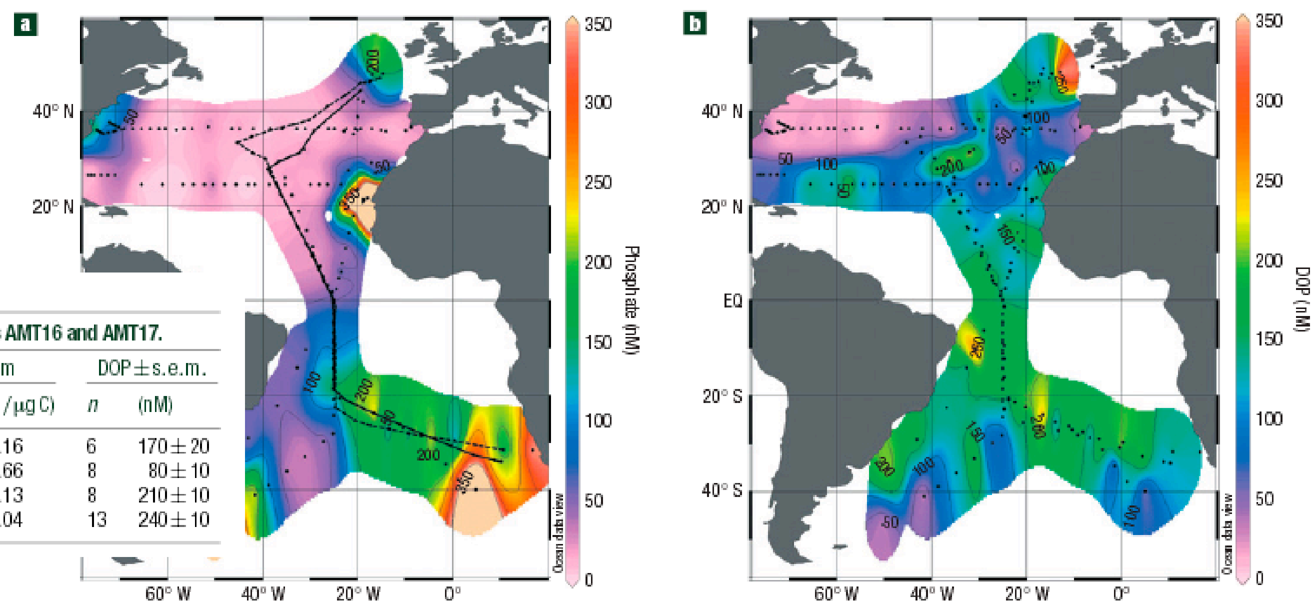
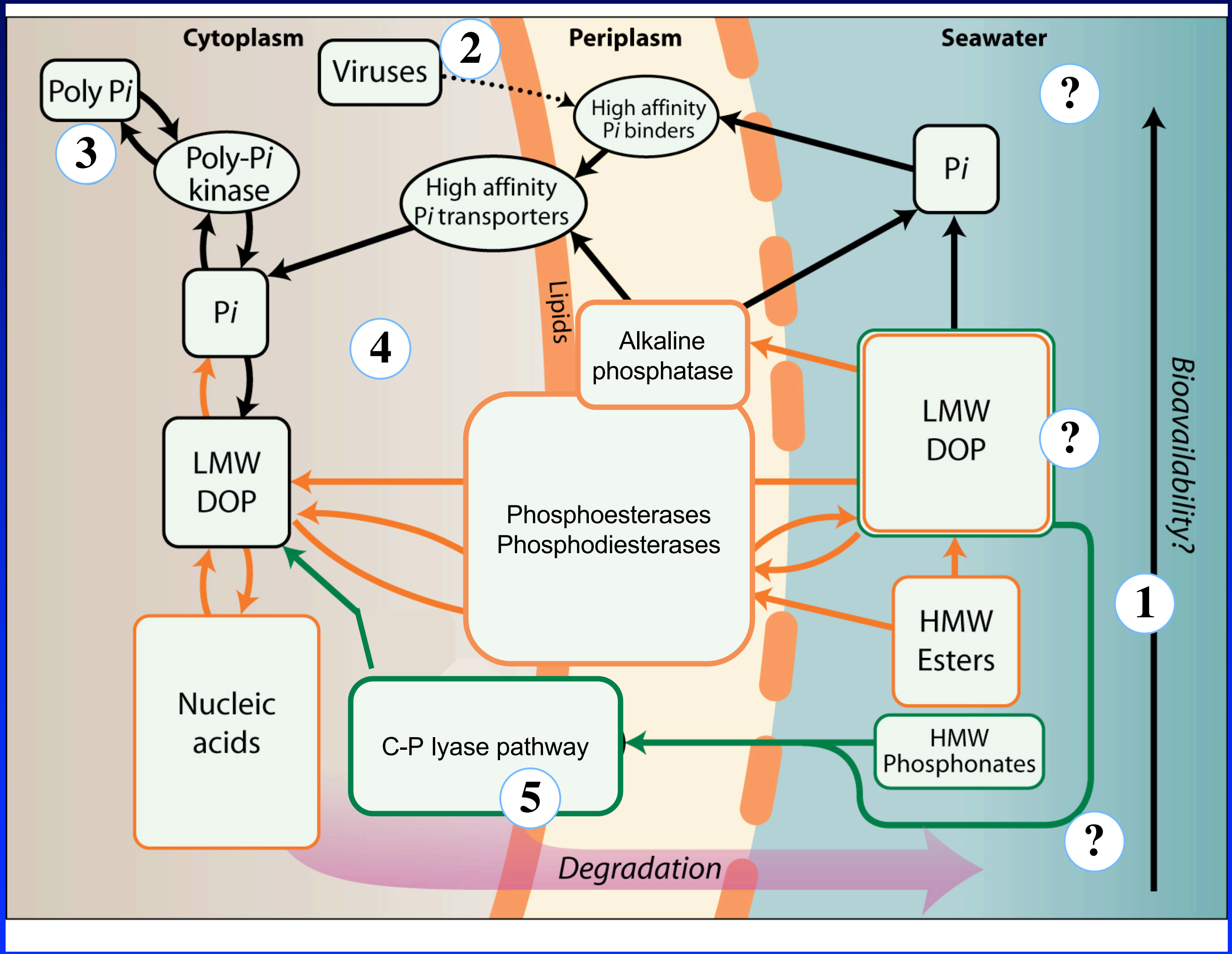


Table 1 APA and DOP ± their standard errors for cruises AMT16 and AMT17.

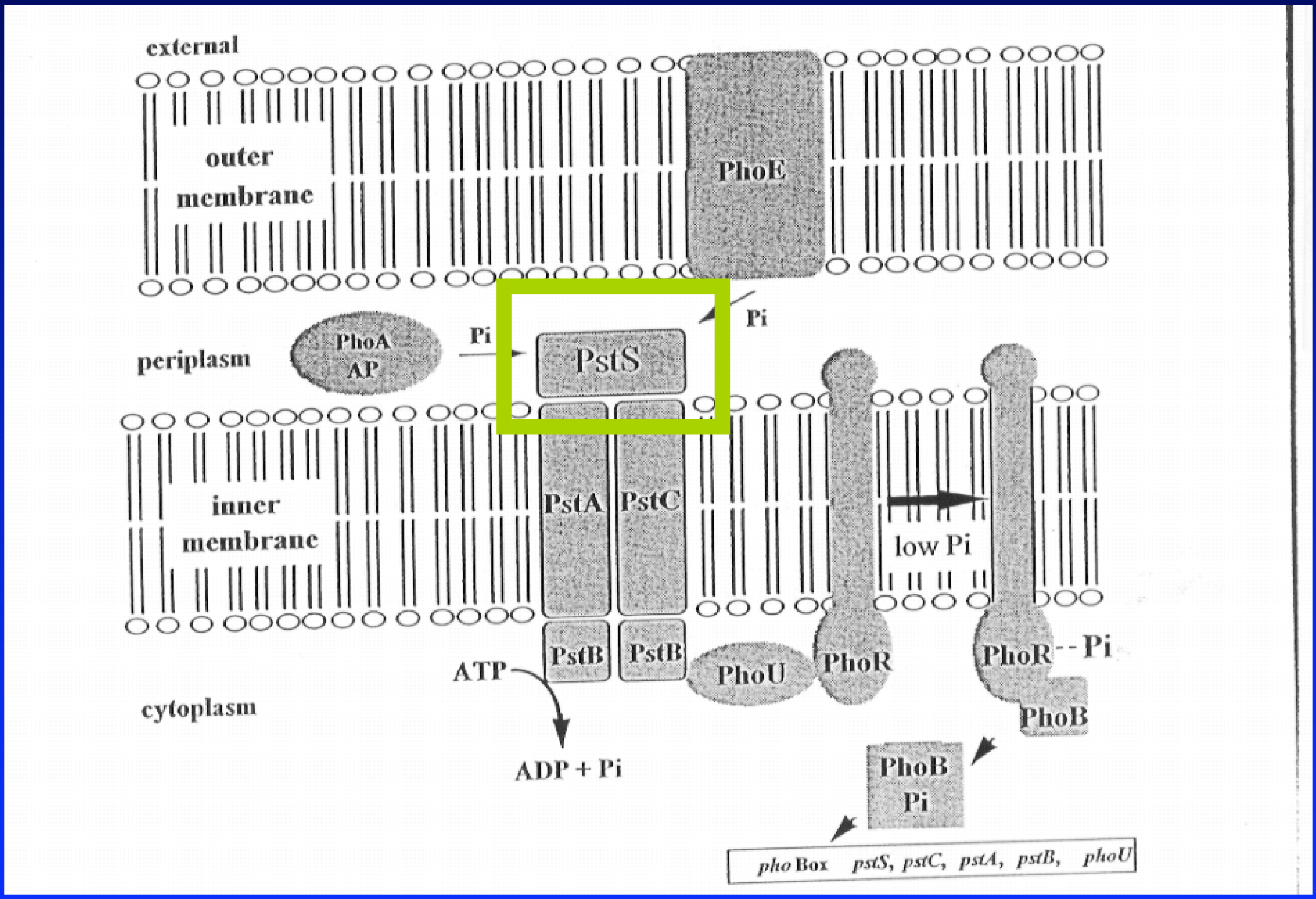
Province/Month	Season	Cruise	APA ± s.e.m		DOP ± s.e.m.	
			n	(nM P h^{-1}/μg C)	n	(nM)
SASG June	Autumn	AMT16	4	0.84 ± 0.16	6	170 ± 20
NASG June	Spring	AMT16	7	2.44 ± 0.66	8	80 ± 10
NASG Nov	Autumn	AMT17	5	0.84 ± 0.13	8	210 ± 10
SASG Nov	Spring	AMT17	10	0.20 ± 0.04	13	240 ± 10

A conceptual diagram of marine microbial interactions with phosphorus



Dyhrman et al. 2007

High affinity phosphate binding (*pstS*)

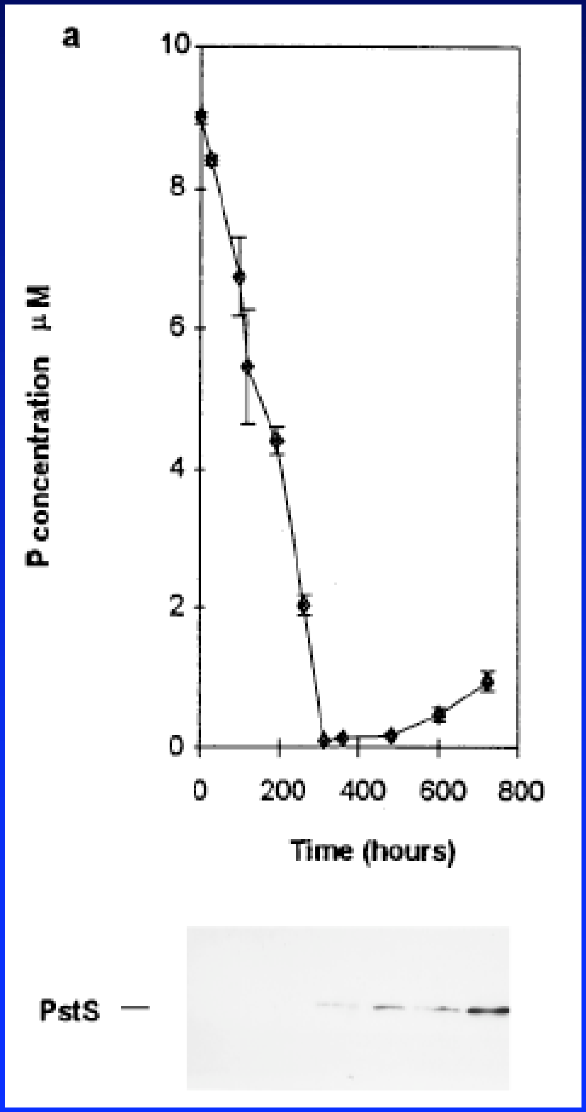


Scanlan and Wilson 2000

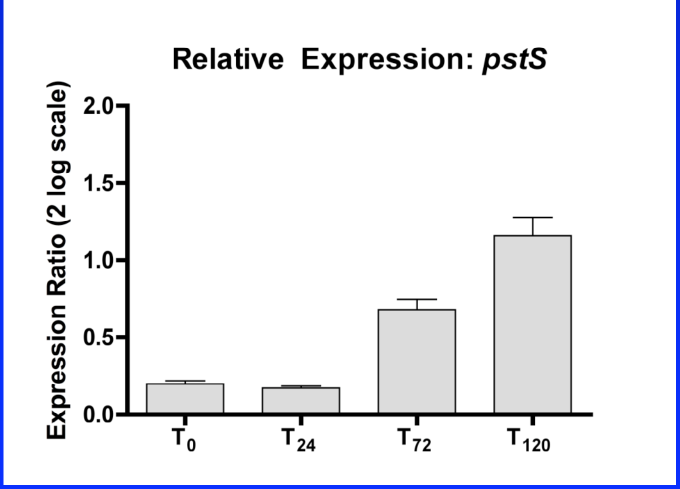
PstS - *Synechococcus* and *Crocosphaera*

- Multiple copies of *pstS* are present in many of the cyanobacterial genomes
- In most - but not all cases it is part of the the *pstSCAB* system for the high affinity transport of phosphate
- The gene and protein are typically up-regulated by P deficiency as a part of the pho regulon

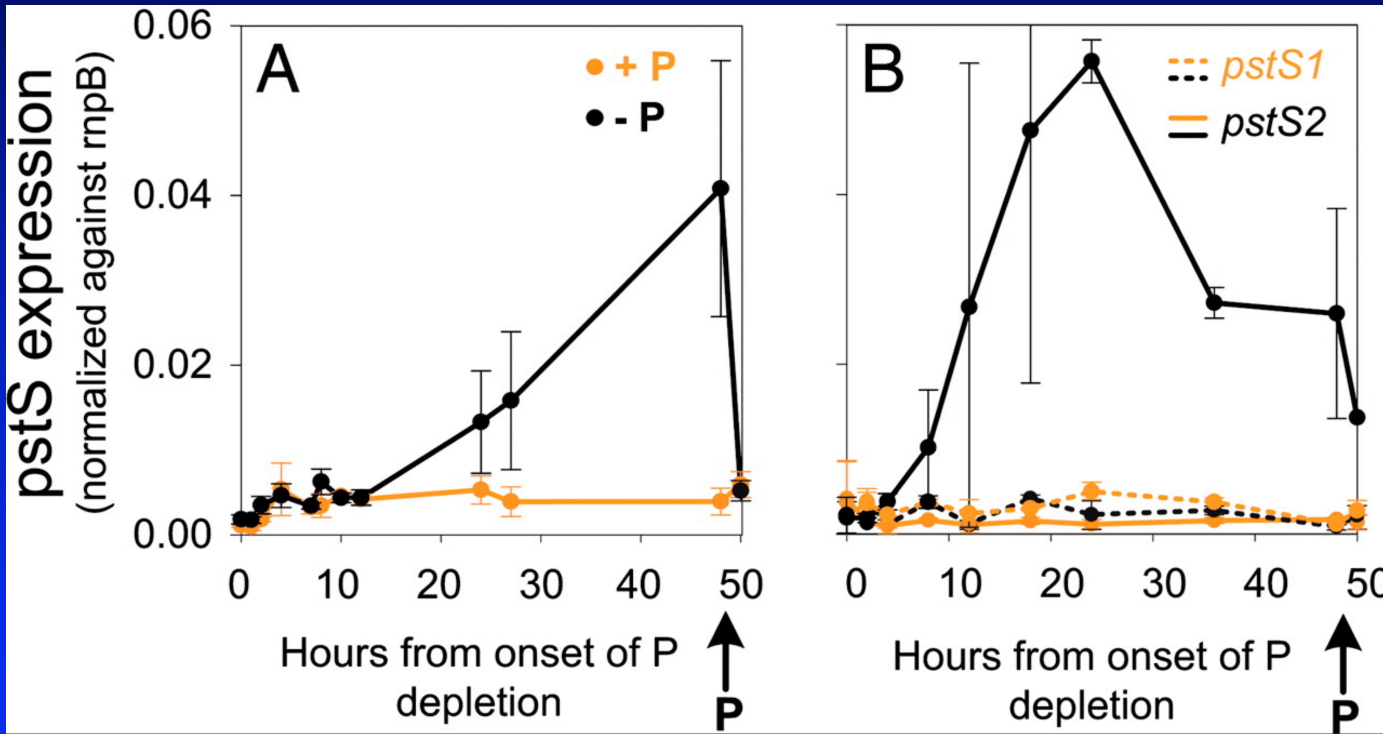
Synechococcus



Crocosphaera



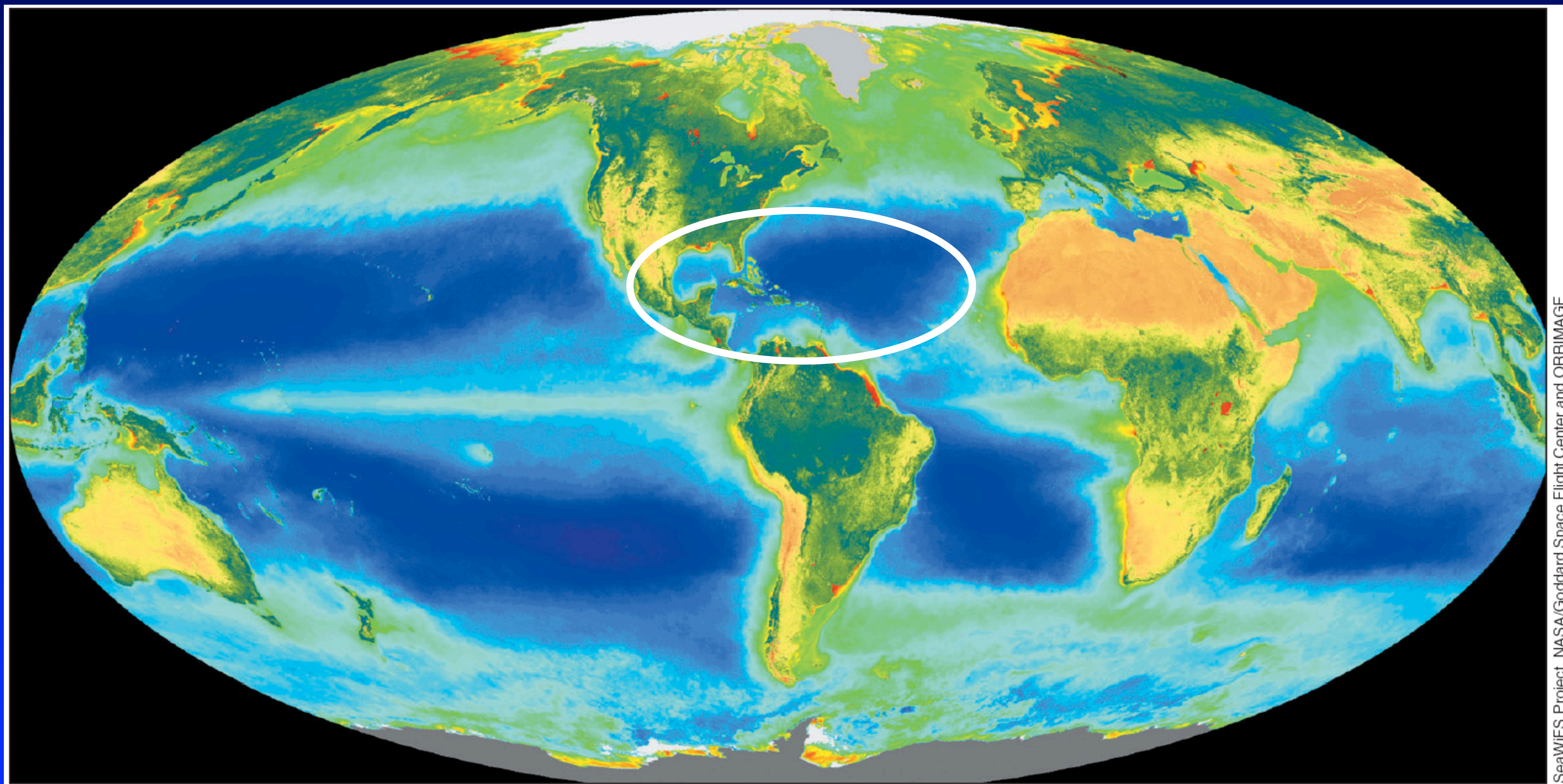
pstS - Prochlorochoccus



Martiny, Adam C. et al. (2006) Proc. Natl. Acad. Sci. USA 103, 12552-12557

PNAS

NASG: SAR11 *pstS*



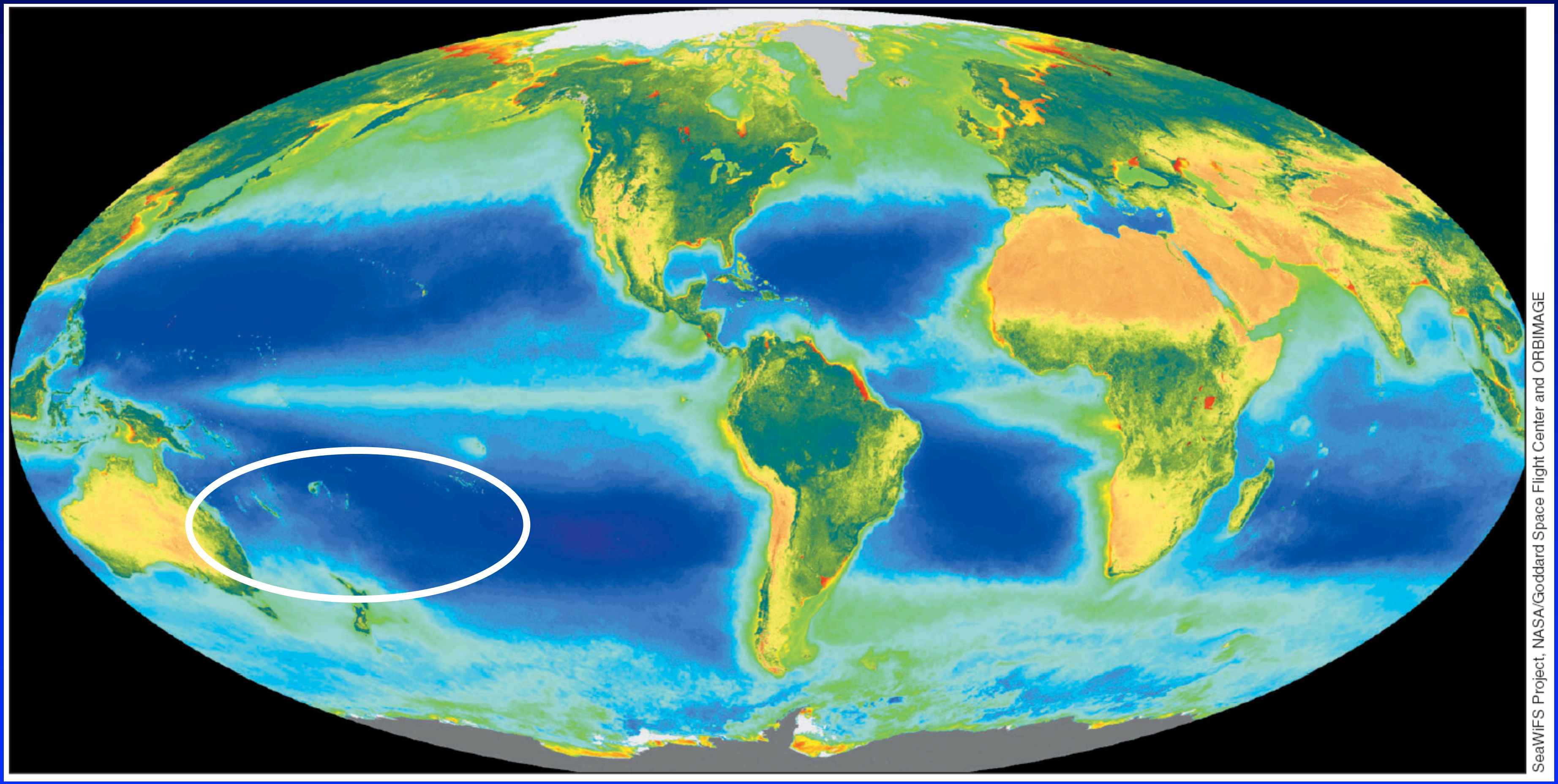
PstS - in the Sargasso Sea

Sowell et al. 2008 ASM General Meeting

PstS - dominant in the Sargasso Sea

Sowell et al. 2008 ASM General Meeting

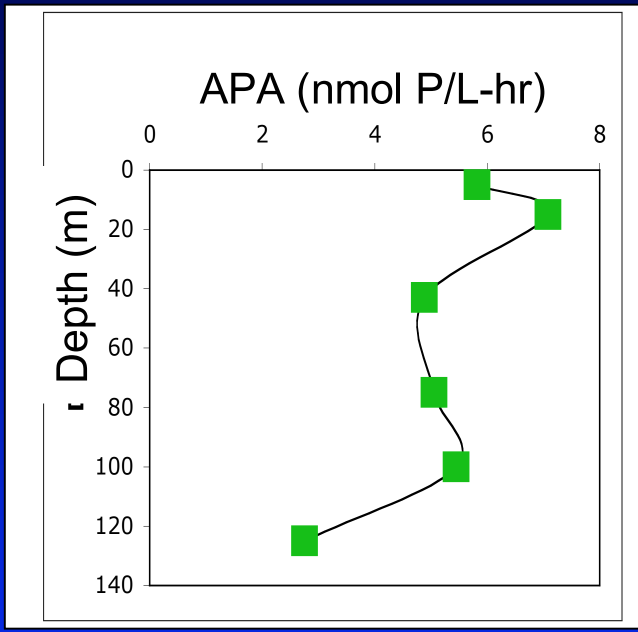
South Pacific: *Crocosphaera pstS*

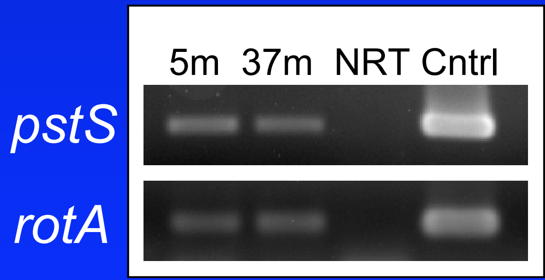


Thanks to Jon Zehr for supporting our cruise participation and for samples!

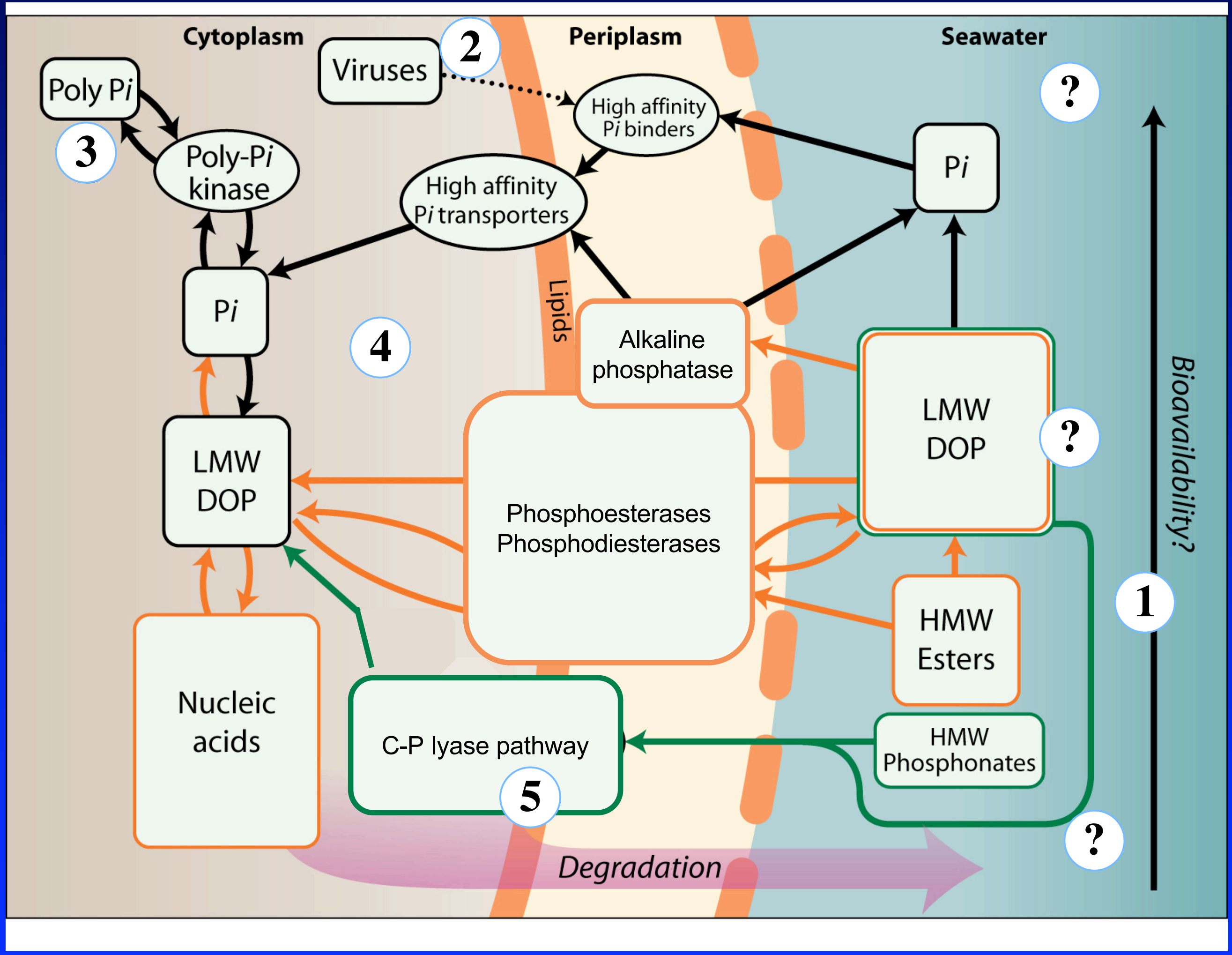
Crocosphaera pstS expression

- St. 25 depth profile:
  - Alkaline phosphatase activity indicates P-monoester hydrolysis
  - Expression of *pstS*
  - Both are possible markers of P physiology





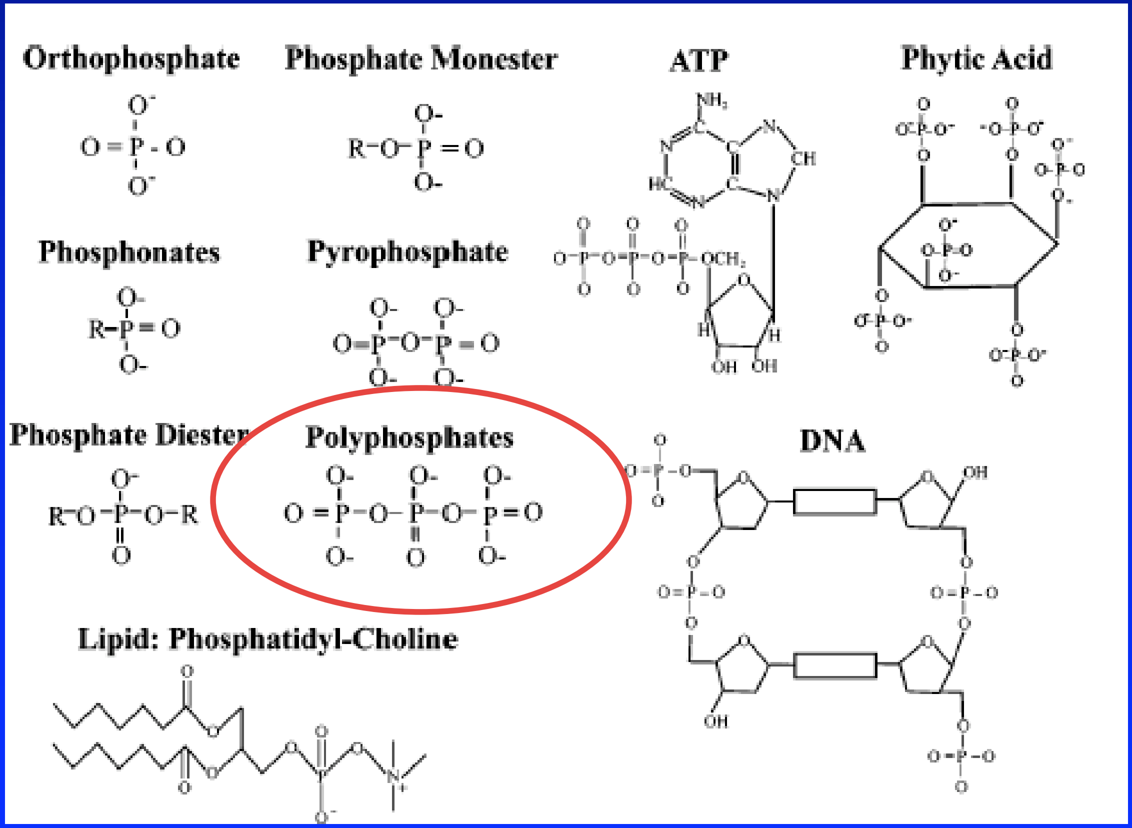
A conceptual diagram of marine microbial interactions with phosphorus



Dyhrman et al. 2007

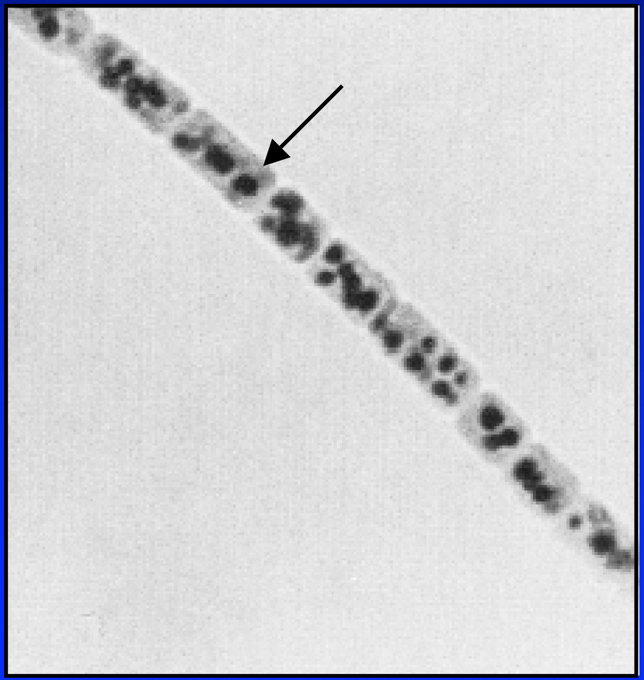
Importance of polyphosphate in P cycling

- Is polyphosphate (polyP) common?
- How is polyphosphate accumulation and degradation regulated?
- Is polyphosphate important to overall P cycling?



Polyphosphate (polyP)

PolyP granules in *Anabaena* spp.



(Bolier et al 1992)

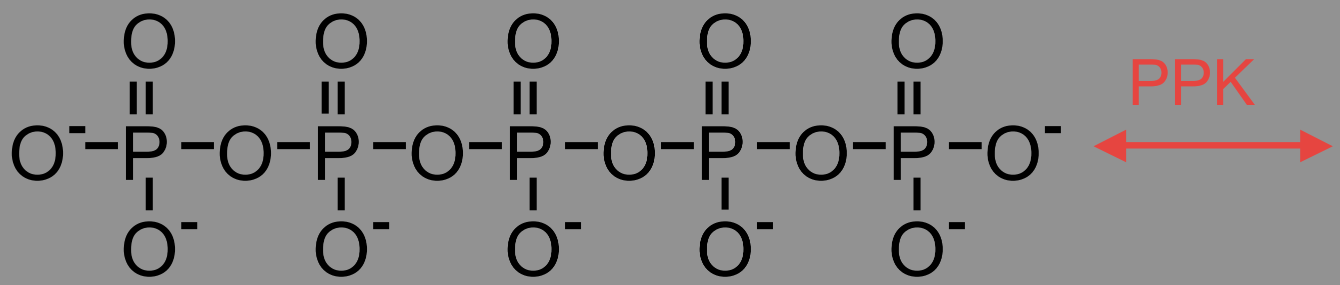
- Linear chains of P_i ranging in length from 3-1000s residues
- Can form large granules
- Functions:
  - energy reserve
  - ballasting
  - metal chelator
  - osmotic regulation
  - short and long term reservoir for P
- PolyP relatively understudied in marine systems

Key questions

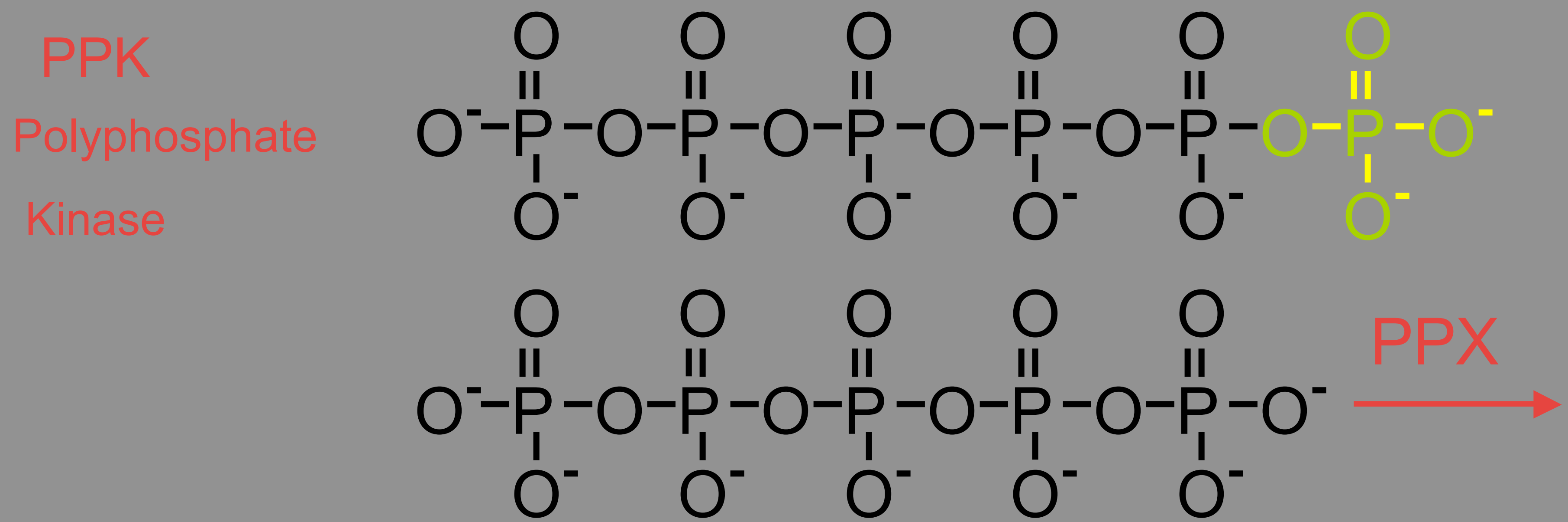
- PolyP dynamics not comprehensively addressed in marine models
- Do *Trichodesmium* and *Crocosphaera* have the capacity to synthesize and degrade PolyP?
- Do *Trichodesmium* and *Crocosphaera* metabolize PolyP in culture?
- Does *Trichodesmium* produce PolyP *in situ?*
  - Luxury uptake, P overplus, P mining?

Thanks to Liz Orchard

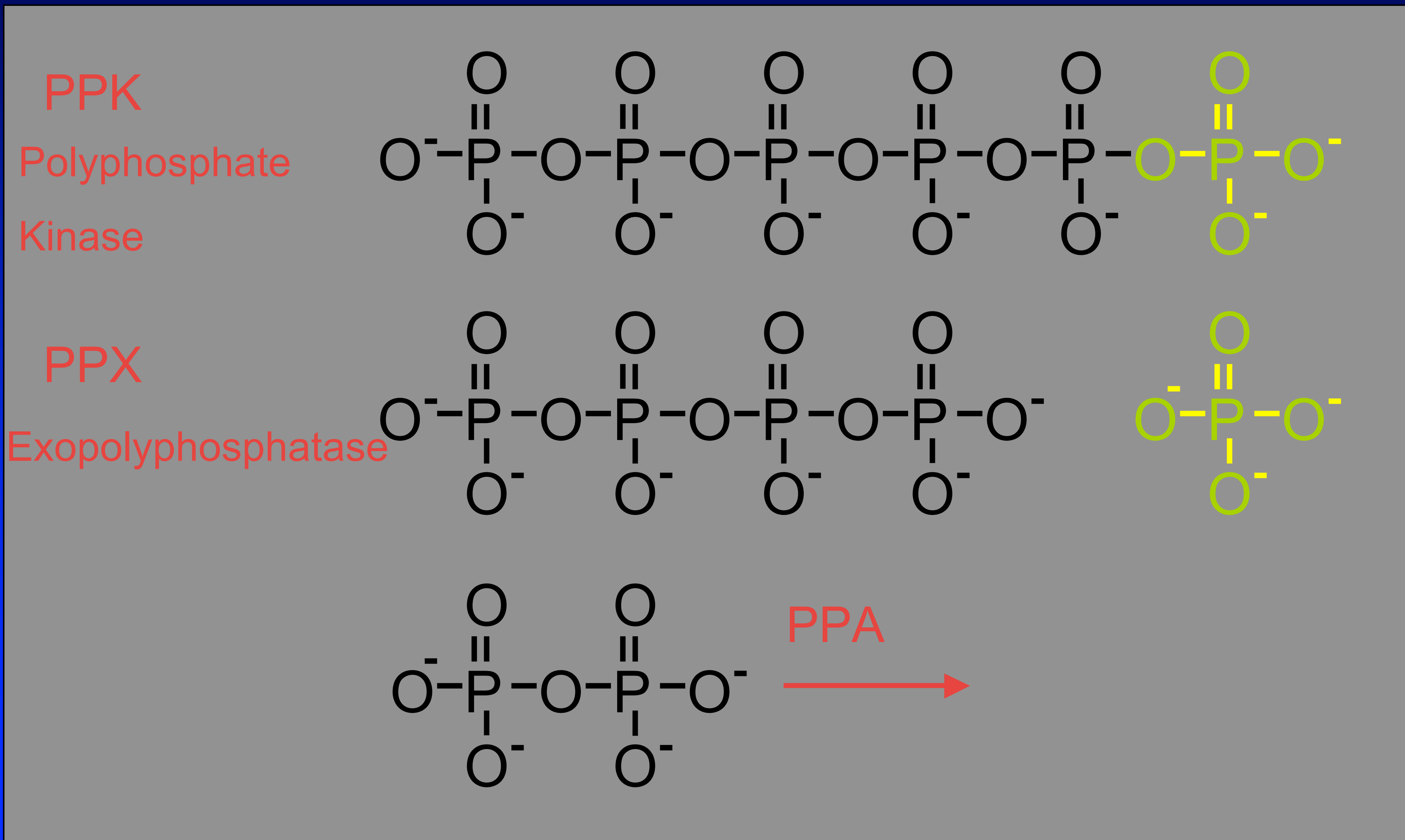
ppK



ppX



ppA

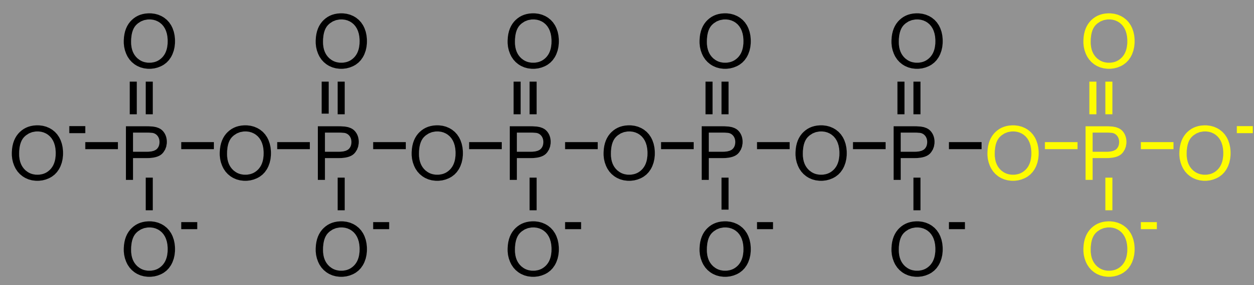


polyP

PPK

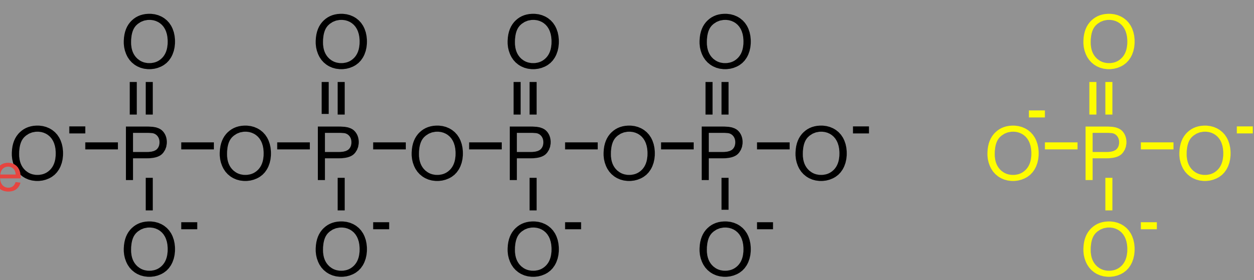
Polyphosphate

Kinase



PPX

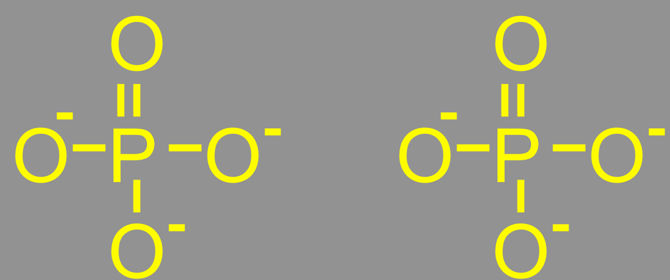
Exopolyphosphatase



PPA

Inorganic

Pyrophosphatase



Presence of genes in cultured models

Extract DNA

↓

Look for presence of gene with PCR

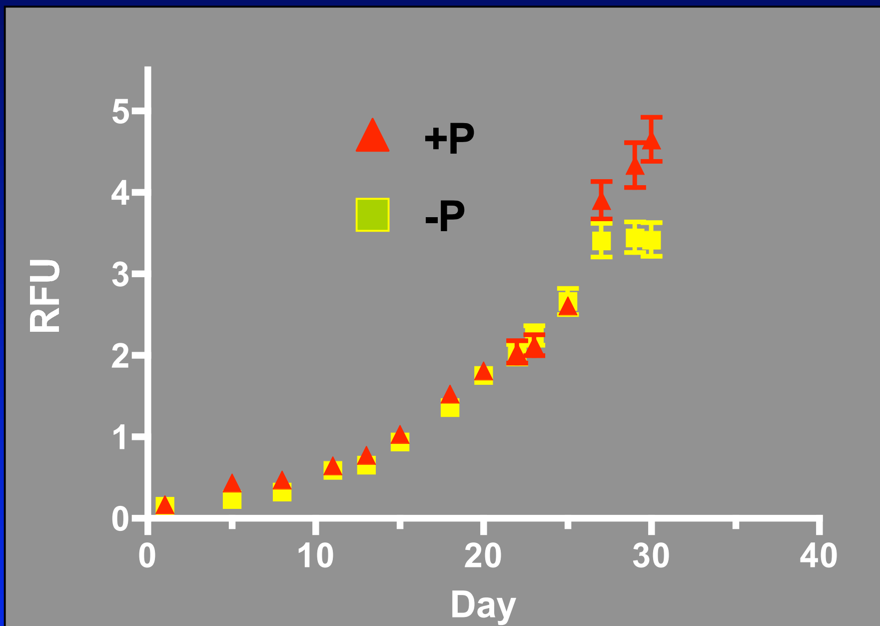
↓

Sequence gene products

	ppK	*ppA*	*ppX*
Crocosphaera watsonii WH8501	✔	✔	✔
Trichodesmium erythraeum IMS101	✔	✔	✔
T. spiralis	✔	94%*	93%
T. tenue	✔	94%	93%
T. thiebautii	✔	95%	94%

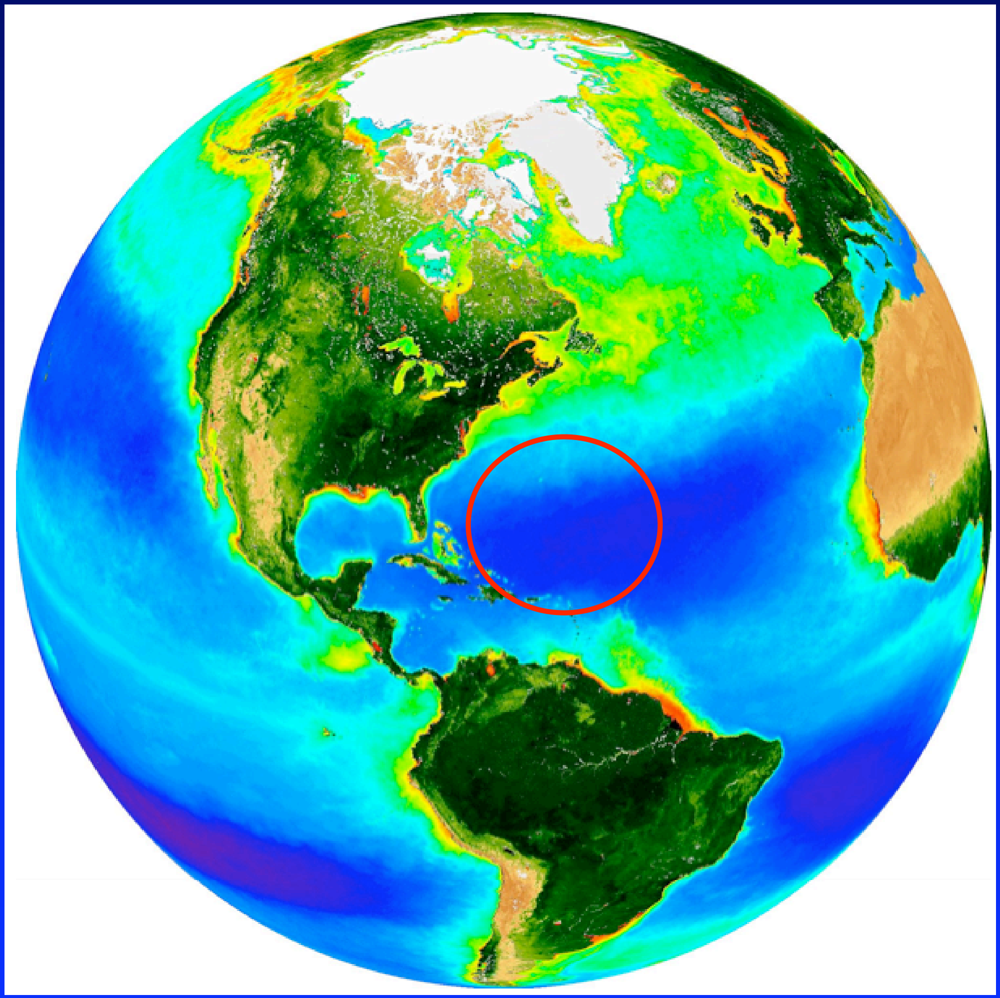
Trichodesmium and *Crocosphaera* have the molecular machinery to produce and degrade PolyP

Detecting PolyP in cultures



Harvest Cells → Solid-State ^{31}P-NMR → Relative Abundance of PolyP

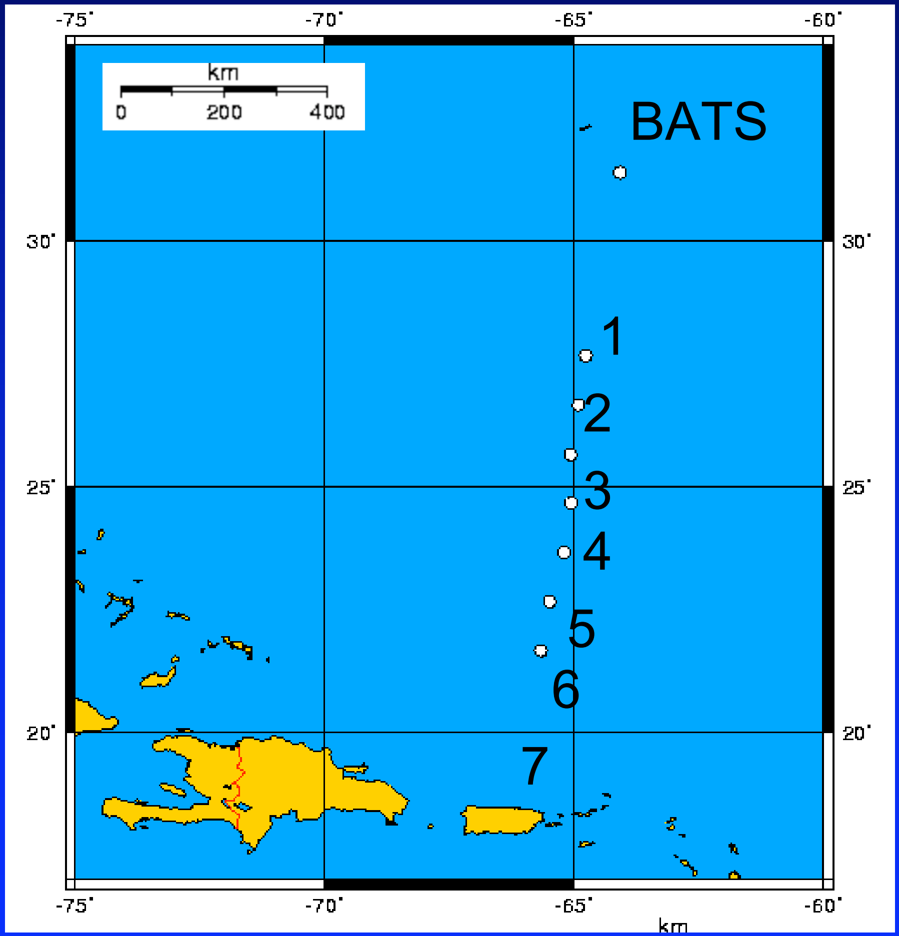
PolyP in oligotrophic systems



http://oceancolor.gsfc.nasa.gov/SeaWiFS/

- Few studies have looked at PolyP in oligotrophic environments
- NASG is a very low P environment
- Is PolyP detectable in this environment?

PolyP in oligotrophic systems



Net Tow

↓

Pick and Wash *Trichodesmium* Colonies

↓

^{31}P-NMR

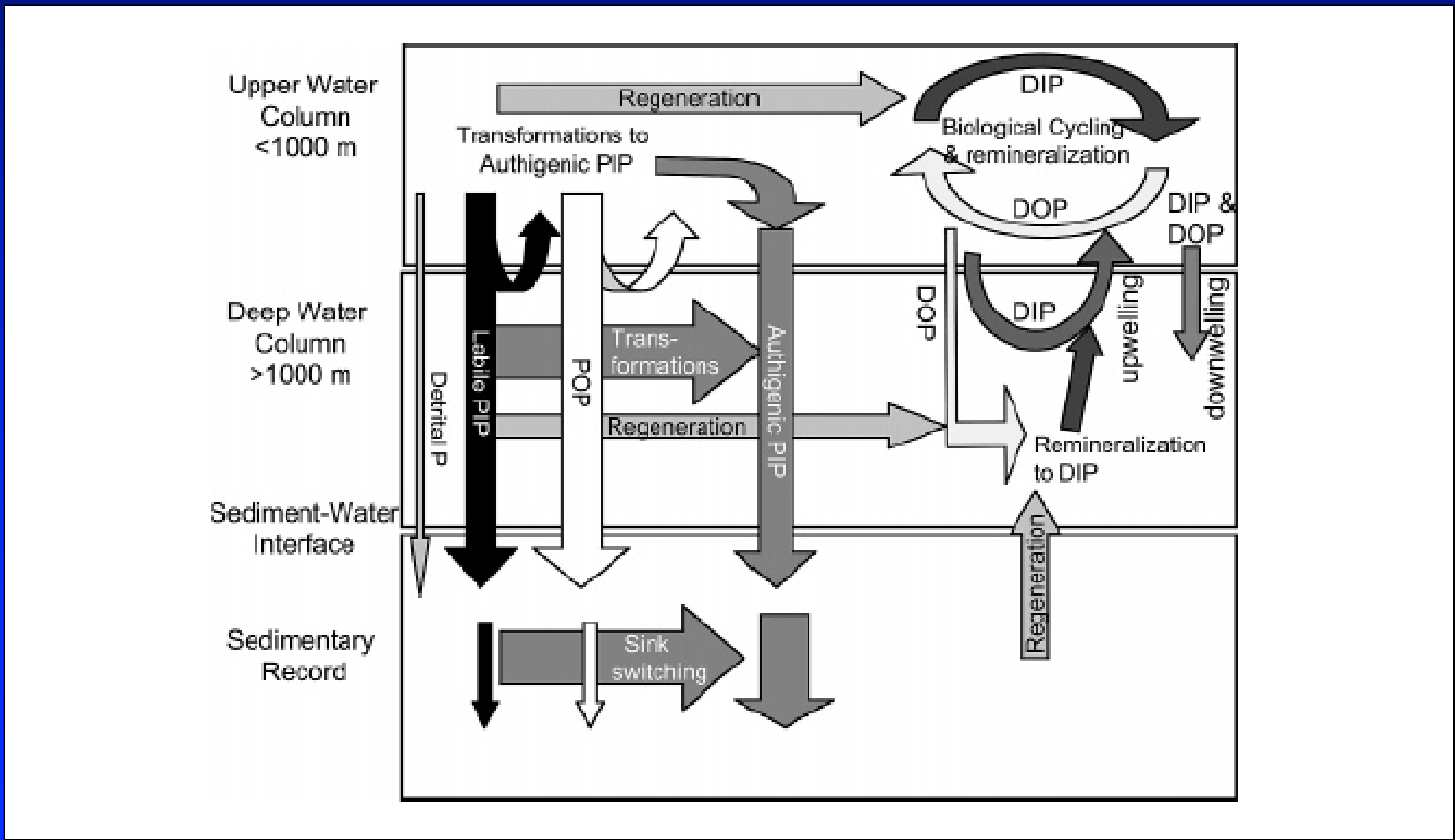
PolyP in oligotrophic systems

PolyP in oligotrophic systems

PolyP may be more important to P cycling and bioavailability - even in oligotrophic environments than previously thought

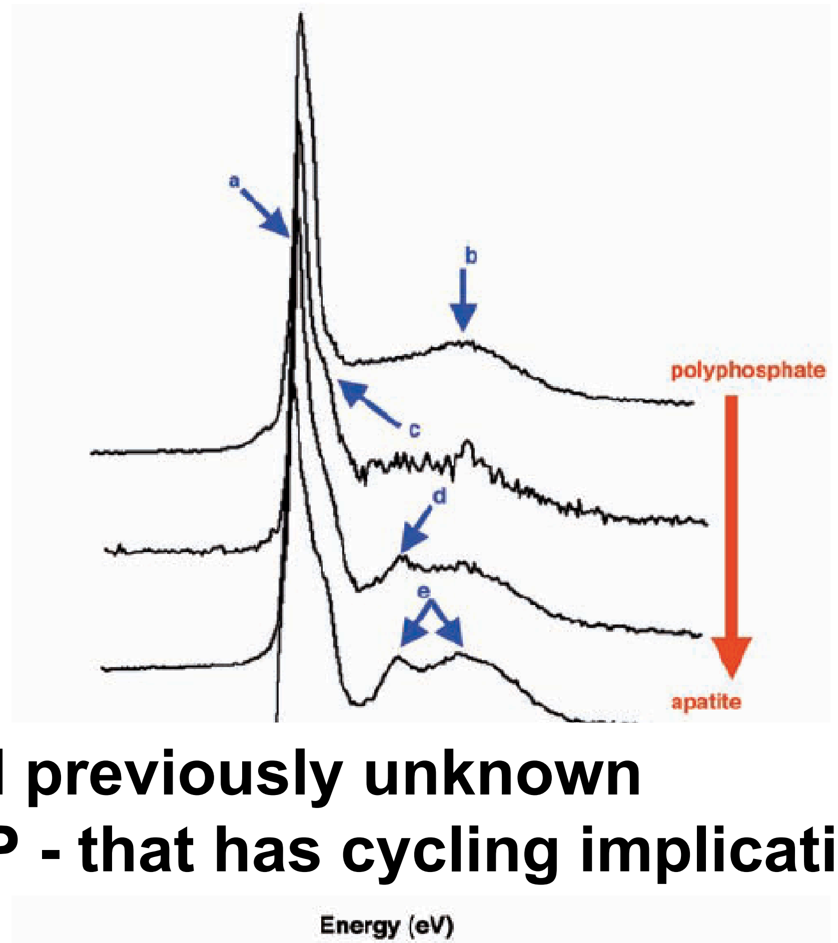
Geologic P sequestration

- Calcium phosphate minerals (e.g. apatite) are common in marine sediments, and a major P sink
-
-



Diagenic transformation of polyP to apatite

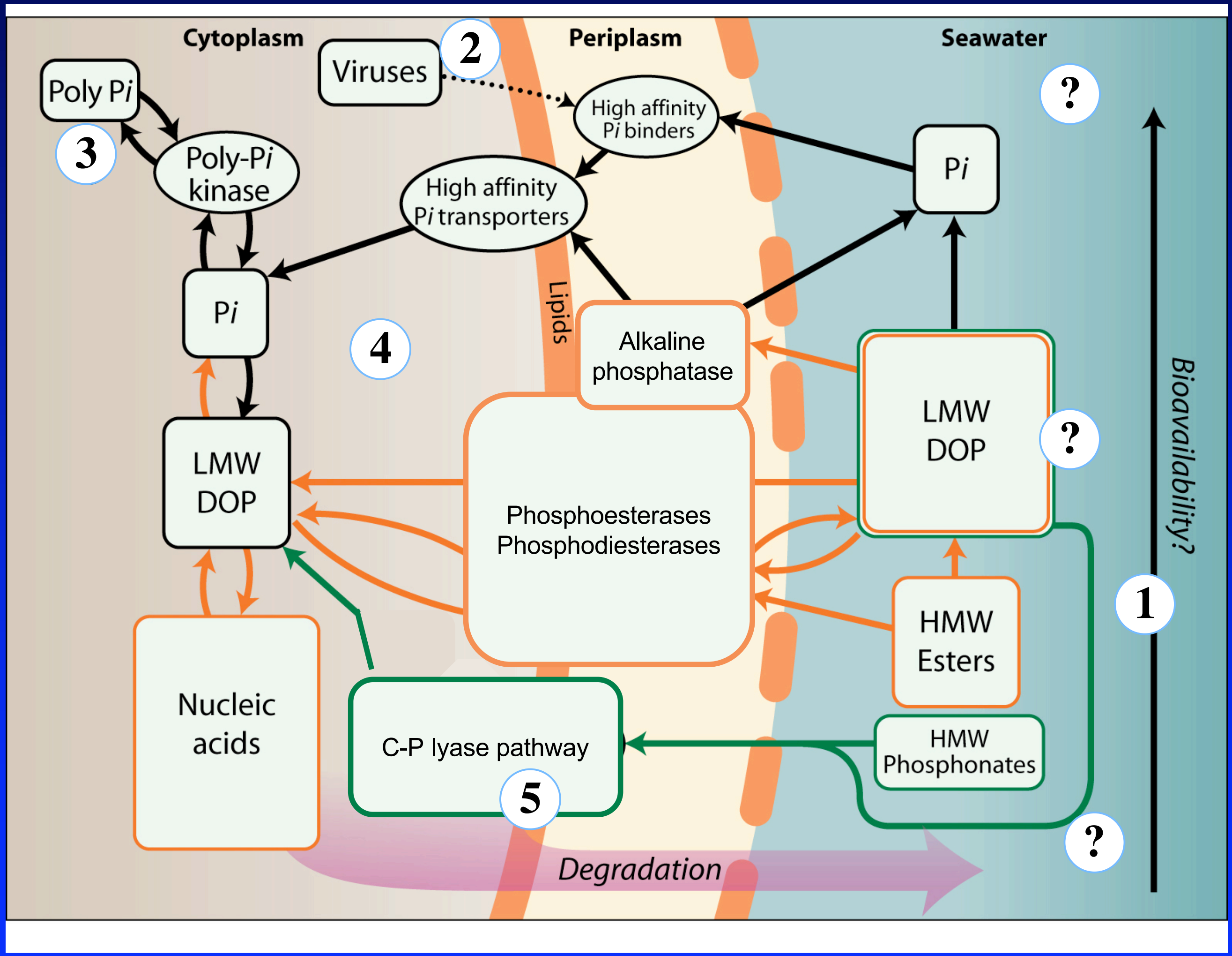
Fig. 2. Diagenetic transformation of polyphosphate to apatite. An overlay of phosphorus x-ray fluorescence spectra collected from micrometer-sized phosphorus-rich regions in Effingham Inlet sediment illustrates the diagenetic transition from polyphosphate (**top**) to apatite (**bottom**). The primary phosphorus fluorescence peak occurs at 2150 eV (a). Spectral features above the primary peak reflect the local bonding environment of phosphorus. Polyphosphate, a simple linear polymer associated with calcium in cells, is characterized by a single peak 18 eV above the primary



A very recent - and previously unknown transformation of P - that has cycling implications.

crystalline, which may account for the appearance of a primary peak "shoulder" (c). As the crystalline mineral matrix develops further, a peak 11 eV above of the primary peak appears (d), and secondary peaks become more defined (e). The spectra presented in this figure were collected from a single Effingham Inlet sediment sample <3 years of age. Thus, the relative ages of the particles that yielded these spectra are not known.

A conceptual diagram of marine microbial interactions with phosphorus



Dyhrman et al. 2007

Intracellular P distribution in microbes

Table II. *Percentage of P in Different Chemical Pools in Some Marine Organisms and* E. coli

For *E. coli*, content of the components was from Neihardt (Neidhardt, 1987), while total P was estimated as 3.2% of dry weight from Luria (Luria, 1960); average mol wts were from Neihardt for all calculations. Data for *Synechococcus* are from Cuhel and Waterbury (1984). For *Isochrysis* (T-ISO), the carbon (8.09 pg cell^{-1}) and DNA (0.28 pg cell^{-1}) content was obtained from Veldhuis et al., 1997; a Redfield ratio of 106:1 was used to calculate P content. RNA was estimated as three times DNA on a weight basis; lipid at 5.9 pg cell^{-1} was from Brown, 1991, and 20% (12–25% range) was estimated to be phospholipid (Ben-Amotz et al., 1985). Data for *Chaetoceros* are from Oku and Kamatani (1995).

Component	*E. coli*	*Synechococcus*	*Isochrysis*	*Chaetoceros*
DNA	9.7	3.2	14	16.4
RNA	61.0	43.8	41	*
Lipid	12.5	0.4	26	1.1
Other				
LPS	5.7			
LMW		51.4		19 (sugar-P)
ATP, NADPH	1.8			1.9
Orthophosphate				45.0
Undescribed	9.2	1.2	19	16.6
Total P/cell	0.29 fm	0.21 fm	6.36 fm	180.3 fm

* Nucleic acid pool is 16.4% and is assumed to be RNA and DNA.

Redfield - an average

Living organism (particulate debris) in seawater have similar overall compositions

Average plankton compositions determined by Redfield et al., 1963
⇒ "famous" Redfield-ratio for the production of **generic** marine organic matter:

$$106\ CO_2 + 16\ HNO_3 + H_3PO_4 + 122\ H_2O \Rightarrow \Rightarrow \Rightarrow$$
$$(CH_2O)_{106}\ (NH_3)_{16}\ H_3PO_4 + 138\ O_2$$

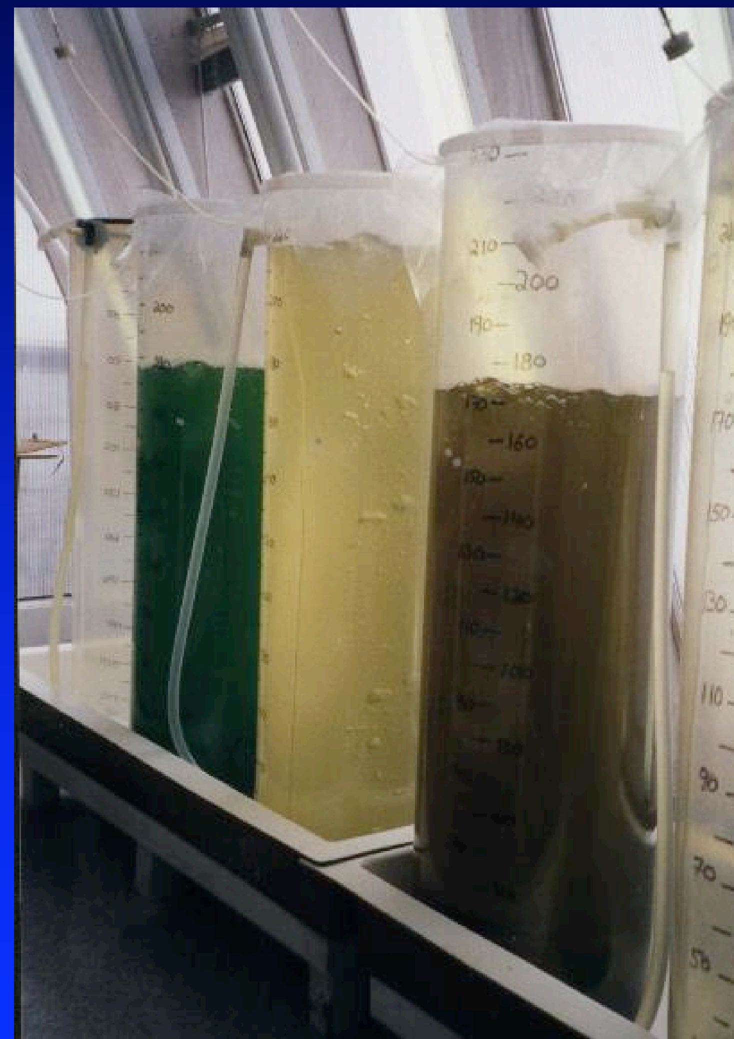
Atomic Ratios of the Principal Elements Present in Plankton

	C	N	P
Zooplankton	103	16.5	1
Phytoplankton	108	15.5	1
Average	106	16	1

Considerable plasticity among the phytoplankton

Table 4. Optimum N:P atomic ratios for some freshwater and marine phytoplankton (from Smith 1982 and Kilham and Kilham 1984).

N:P	Species
87	*Scenedesmus quadricauda*
39	*Cryptomonas erosa*
30	*Scenedesmus obliquus*
28	*Oscillatoria agardhii*
25	*Fragilaria crotonensis*
24	*Chaetoceros affinis*
23	*Selenastrum capricornutum*
21	*Ankistrodesmus falcatus*
21	*Pseudoanabaena catenata*
12	*Skeletonema costatum*
12	*Asterionella formosa*
10	*Synedra ulna*
9	*Microcystis* sp.
7	*Melosira binderana*



Redfield plasticity

RKR is an “average” value

Many phytoplankton are not average and show considerable C:N:P placticity

For example: C:N:P Ratios of *Chlorella* growing under different nutrient regimes (Ketchum and Redfield, 1949)

	C	N	P	N:P
Normal	**47**	**5.6**	**1**	**6**
P-deficient	**231**	**30.9**	**1**	**31**
N-deficient	**75**	**2.9**	**1**	**3**

Flexible stoichiometry in *Trichodesmium*

Limnol. Oceanogr., 51(4), 2006, 1777–17

Flexible elementa

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Vol. 42: 243–253, 2006 | AQUATIC MICROBIAL ECOLOGY Aquat Microb Ecol | Published March 29

Plasticity of N:P ratios in laboratory and field populations of *Trichodesmium* spp.

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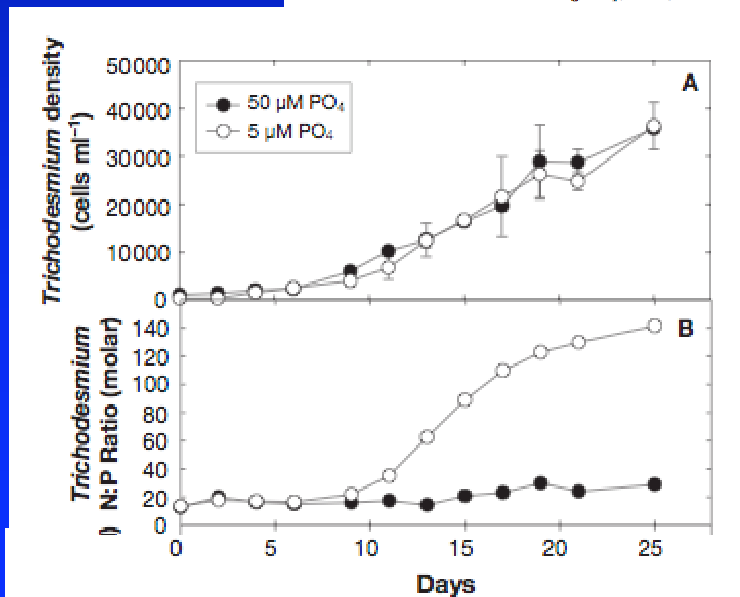


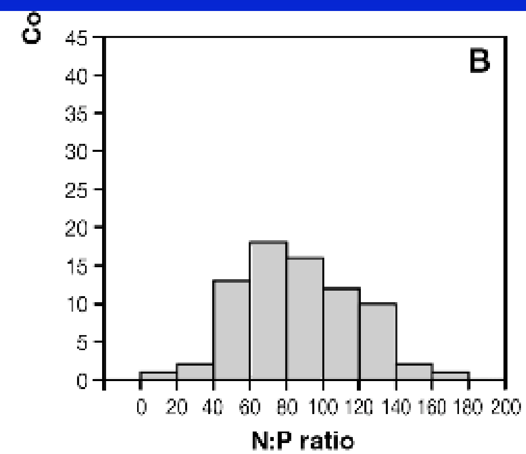


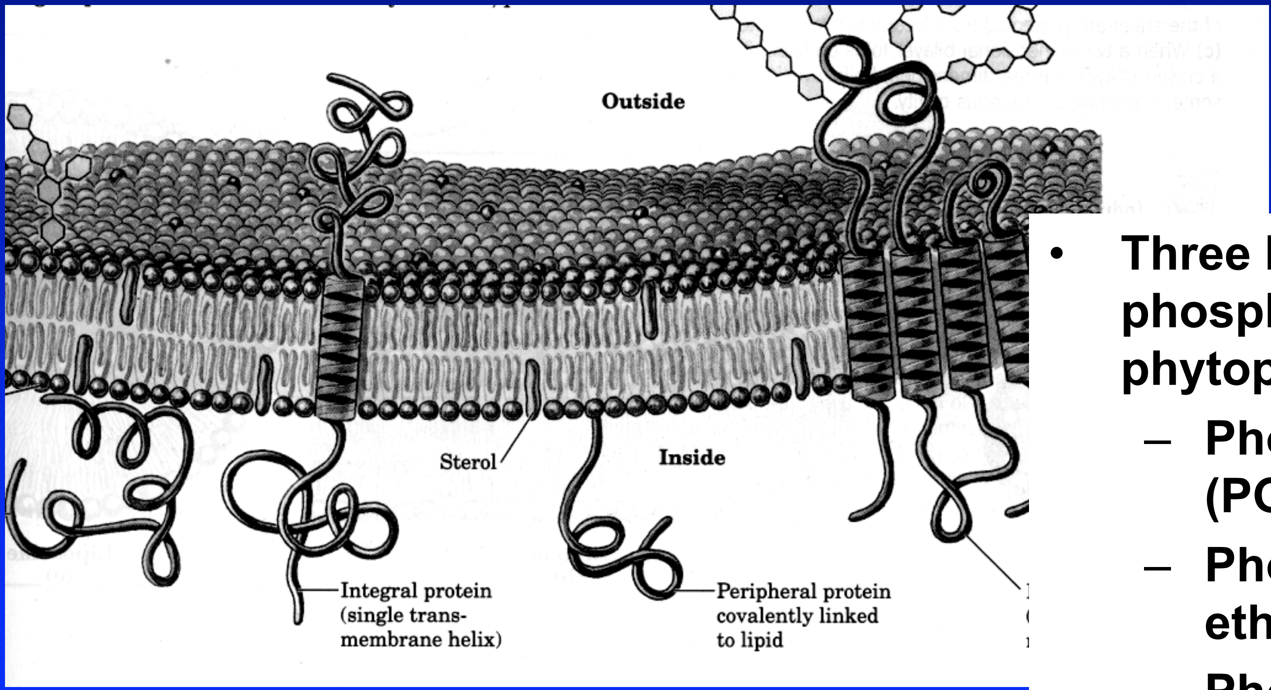
Fig. 5. *Trichodesmium* spp.. N:P ratios of (A) floating and (B) sinking colonies (Gulf of Mexico)

Flexible stoichiometry - how?

- P is locked up in DNA, RNA, lipids, and other molecules which may or may not be flexible
- One long term strategy would be to have a small genome, given the P locked up in nucleic acids
- But that doesn’t explain short-term physiological plasticity
- Variable stores of polyP are a possibility
- Another possibility is alternative molecules - serving to conserve P

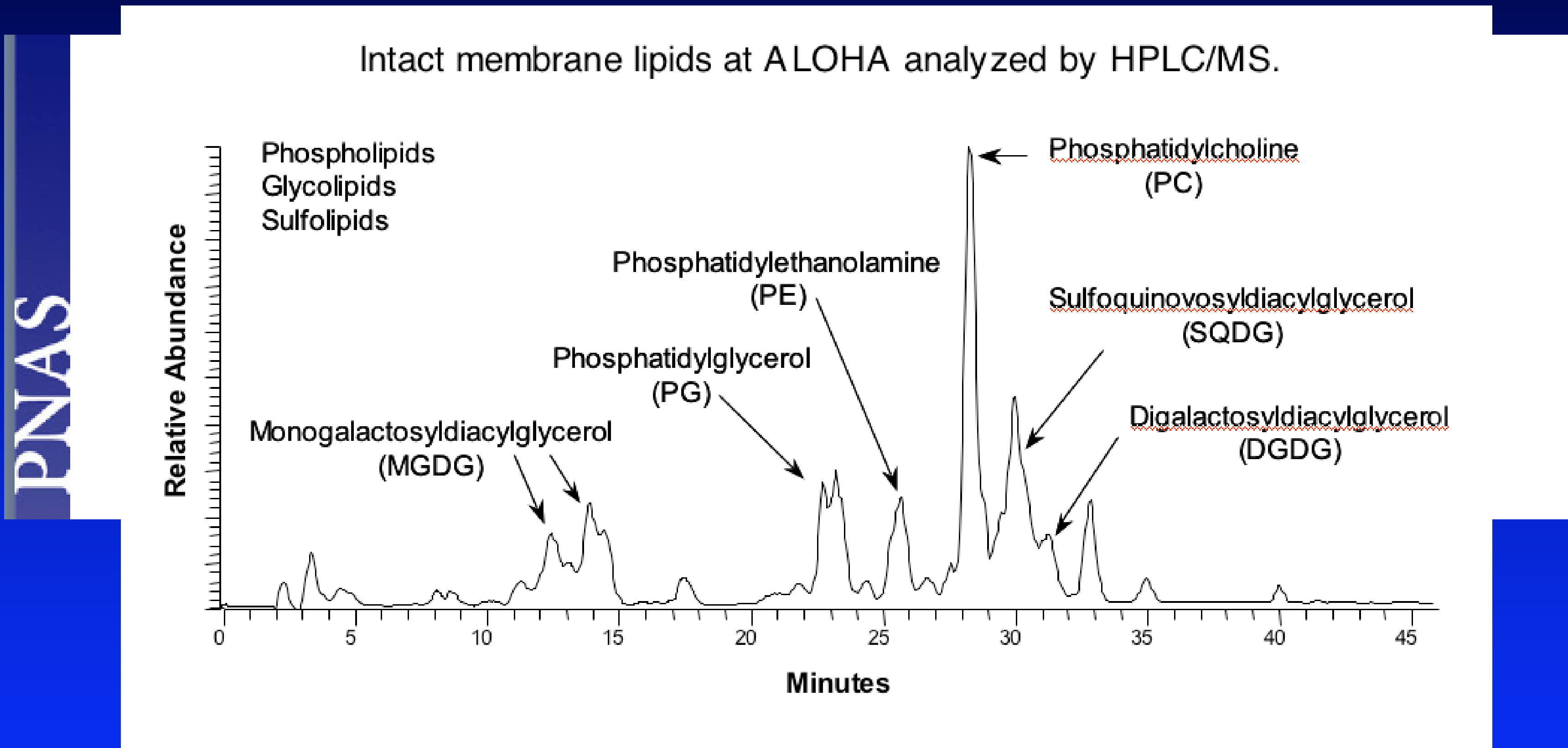
Flexible stoichiometry - how?

- Phospholipids
  - Are found primarily in cell membranes.
  - Composed of a polar “head” group and a nonpolar “tail” group.



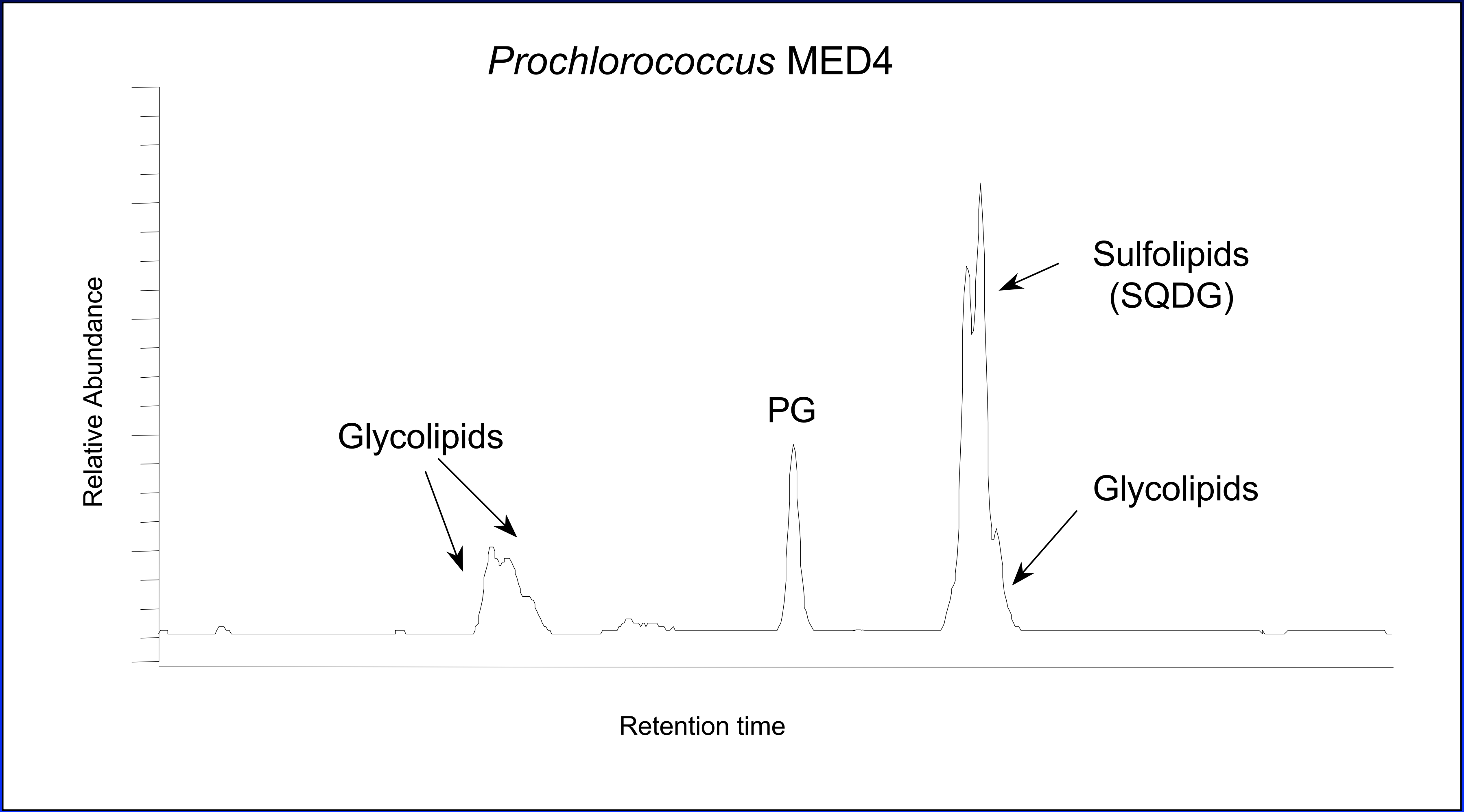
- **Three basic types of phospholipids in phytoplankton.**
  - **Phosphatidylglycerol (PG).**
  - **Phosphatidyl-ethanolamine (PE).**
  - **Phosphatidylcholine (PC).**

Phospholipids and some alternatives



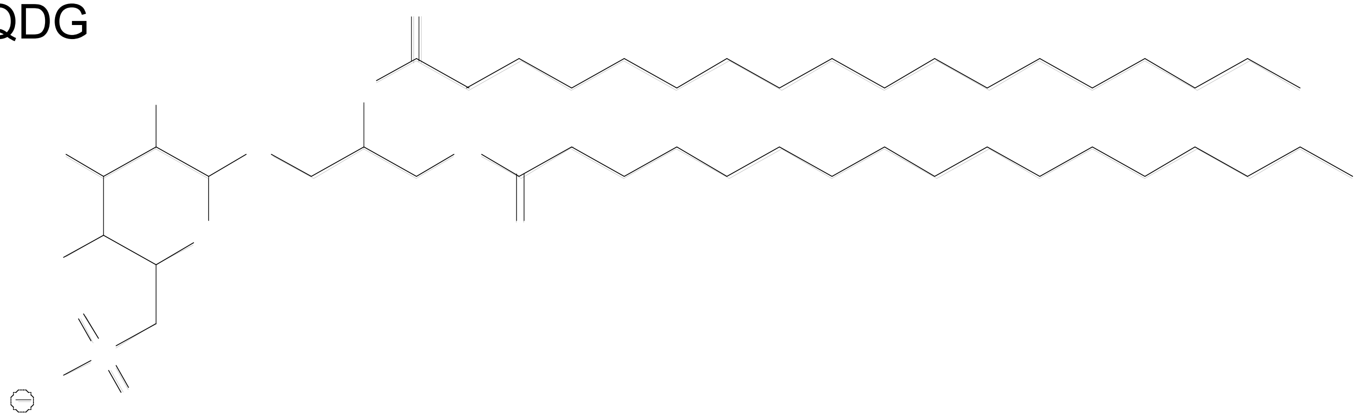
Seawater was filtered on 0.2μm anodisc membrane, which was then extracted by Bligh and Dyer. Intact polar lipids were identified and quantified by HPLC/MS.

Phospholipid alternatives in *Prochlorococcus*

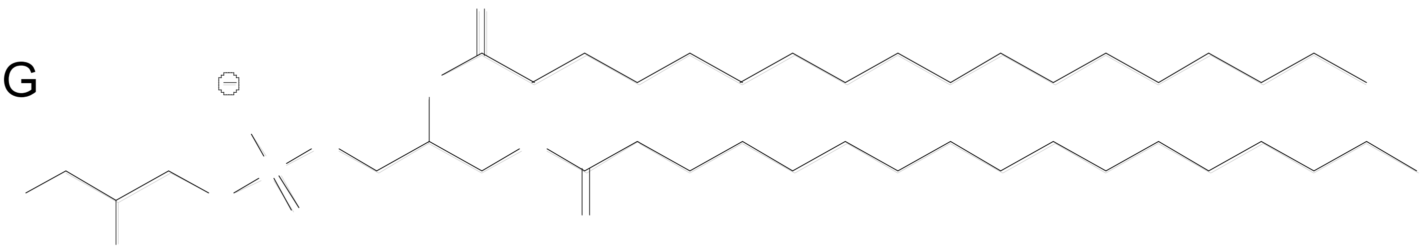


SQDG can be used as a “substitute” for PG…

SQDG



PG



SQDG and PG are the only anionic lipids in photosynthetic membranes, and may, in principal, serve the same functions (Benning et al., *Proc. Natl. Acad. Sci.*, 1993).

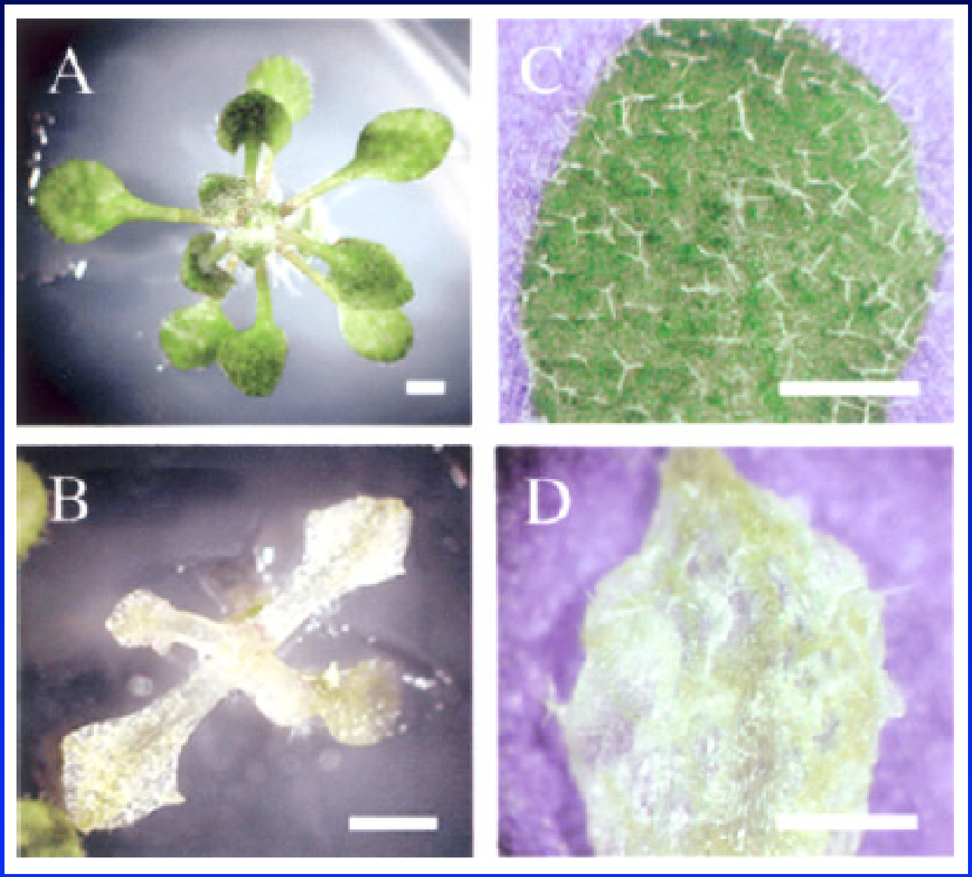
…but there are costs for using SQDG instead of PG

• The recognition of PG/SQDG interchangeability led to burst of basic research with cyanobacteria and plants in the 1990's.

•PG composes >30% of total P in corn.

•10-20 papers describing numerous mutants defective in PG and/or SQDG.

• Substituting SQDG for PG negatively impacts both PS I and PS II because PG is slightly more effective at stabilizing chlorophyll and pigments than SQDG (e.g. the substitution incurs costs).



Hagio et al., *Plant Cell Physiol.,* 2002.

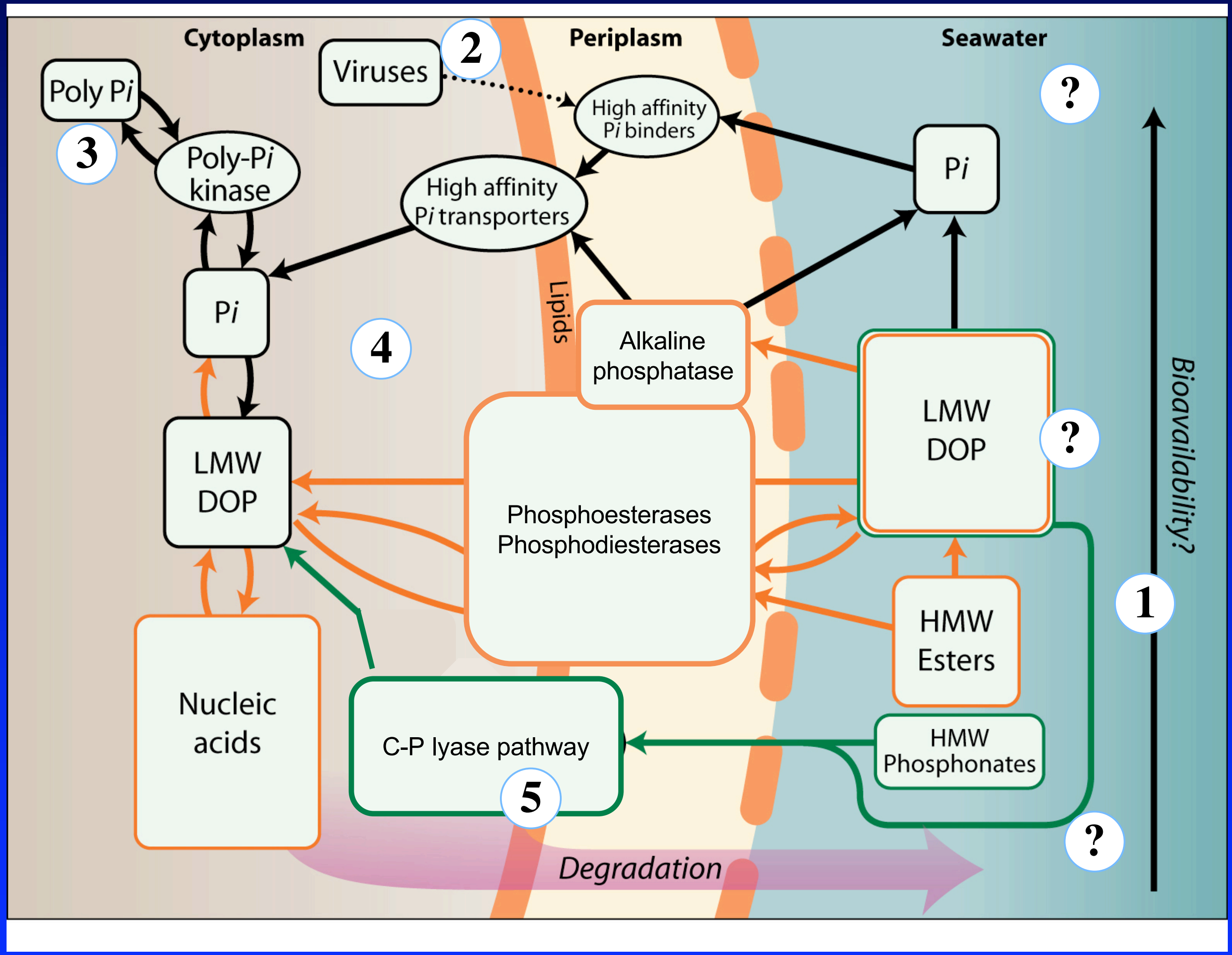
Lipid substitution in *Synechococcus*

Lipid substitution in Diatoms

Lipid substitution in coccolithophores too!

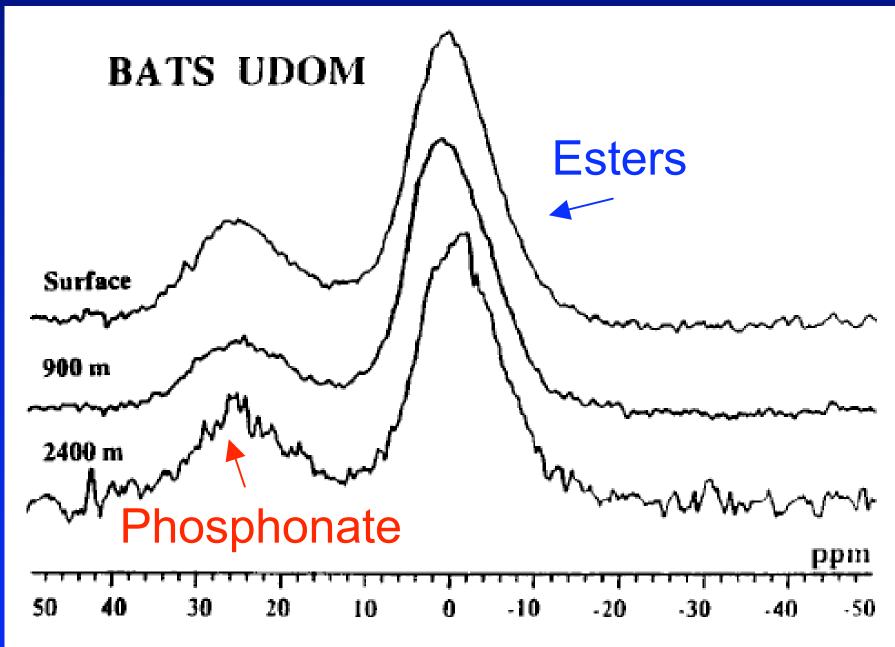
SQDG in the field

A conceptual diagram of marine microbial interactions with phosphorus



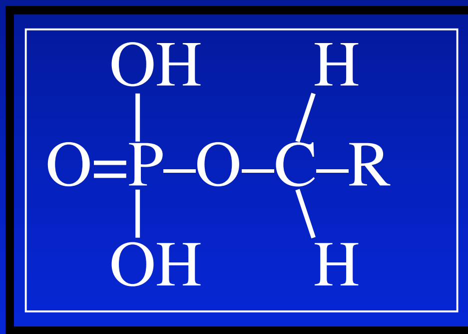
Dyhrman et al. 2007

^{31}P NMR of UDOM in the Sargasso Sea

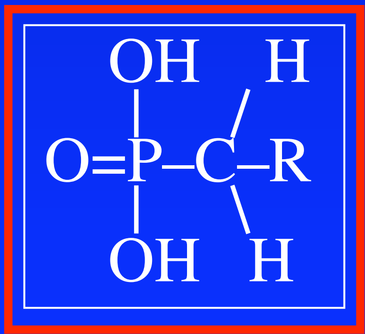


Kolowith et al. 2001

- Phosphomonoesters

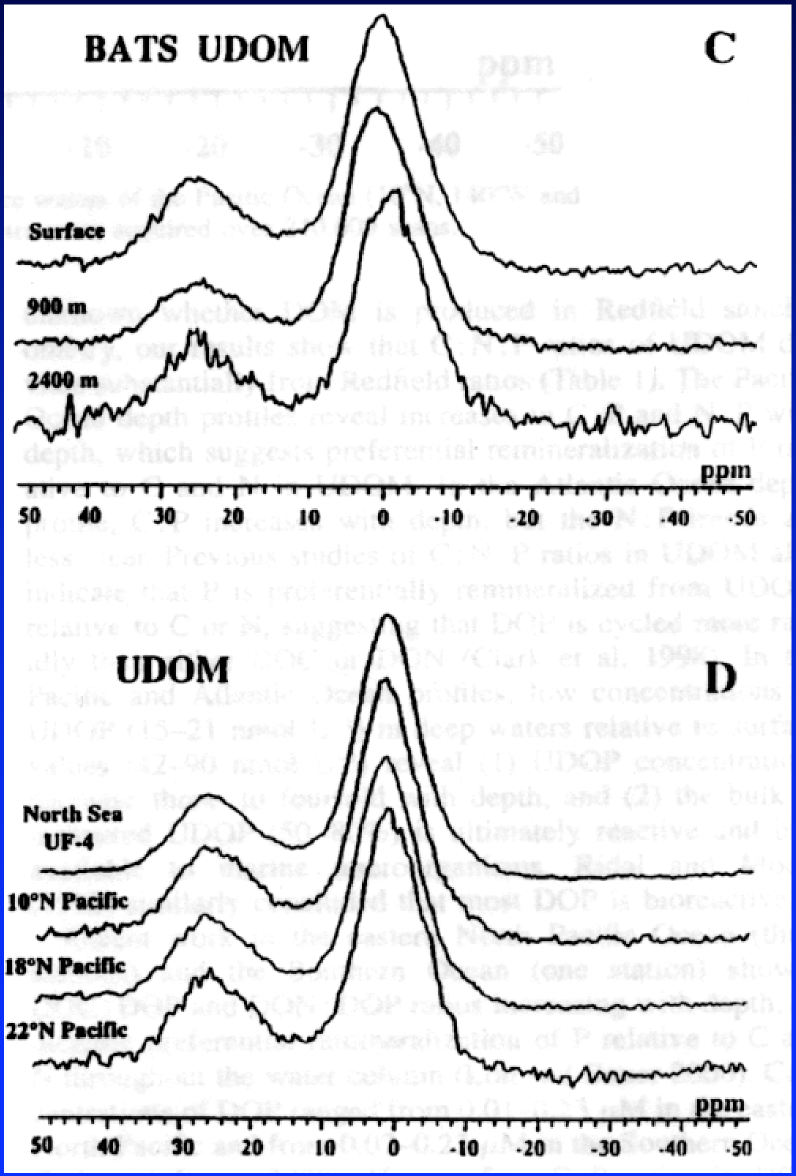


- Phosphonates



P bond class distribution

- DOP by solid state ^{31}P NMR of UDOM (high molecular weight only)
  - DOP is composed of primarily of phosphoesters (75%).
  - Also, phosphonates (25%).
  - The ratio of phosphoesters to phosphonates is fairly constant regardless or environment or depth
  - Esters (C-O-P) are thought to be much more labile then phosphonates (C-P)



Pathways of phosphonate metabolism

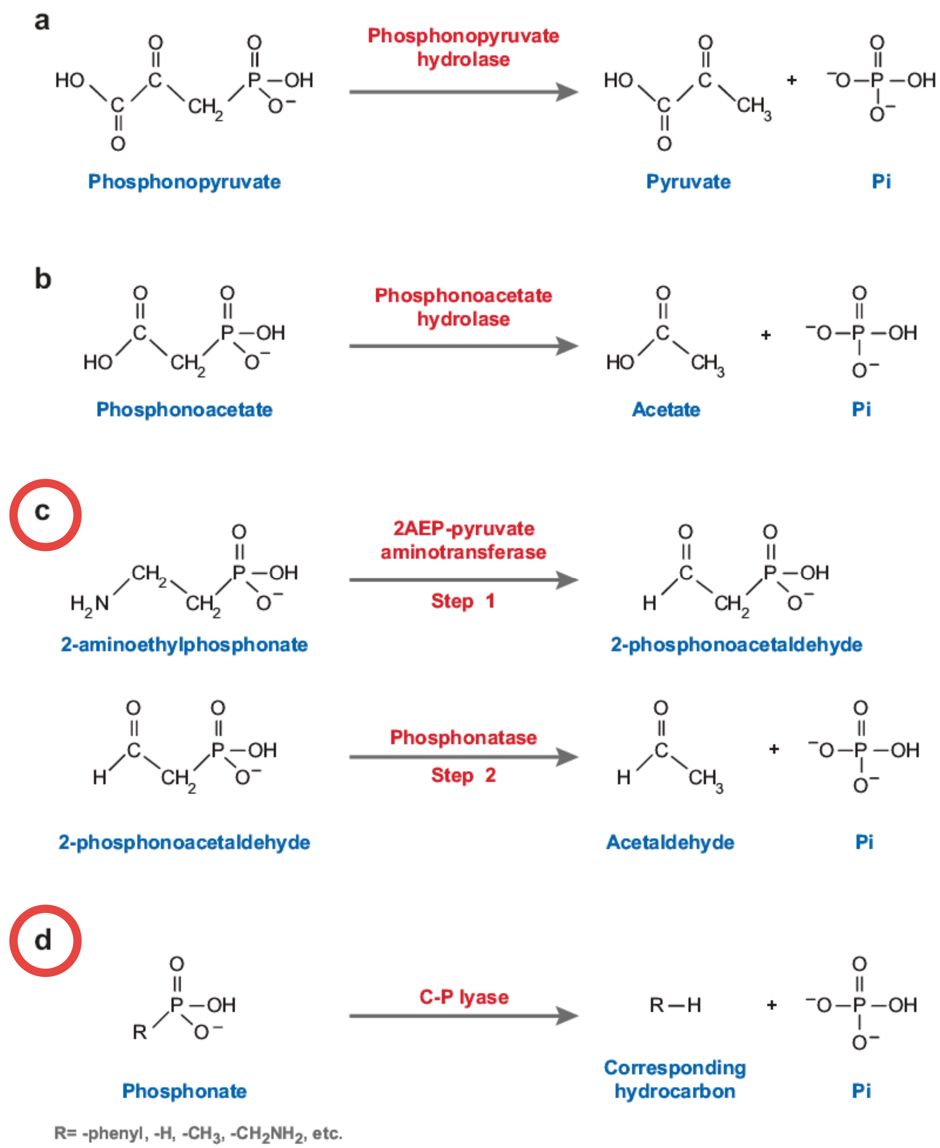


Figure 4

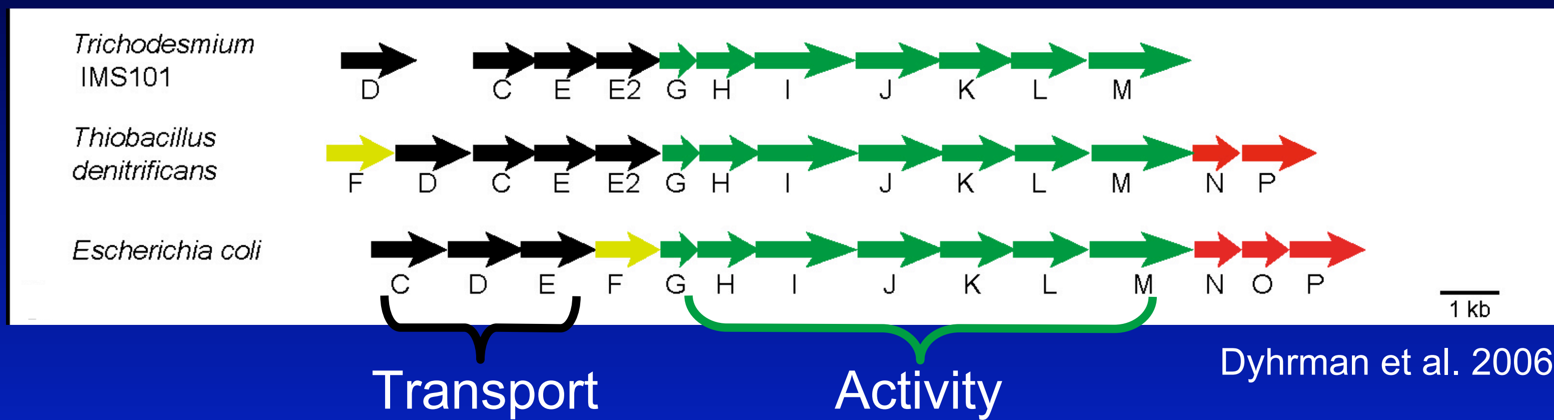
Pathways for the degradation of phosphonate compounds. (*a*) Phosphonopyruvate hydrolase pathway. (*b*) Phosphonoacetate hydrolase pathway. (*c*) Phosphonoacetaldehyde (phosphonatase) pathway. (*d*) C-P lyase pathway.

phnA

phnX/W

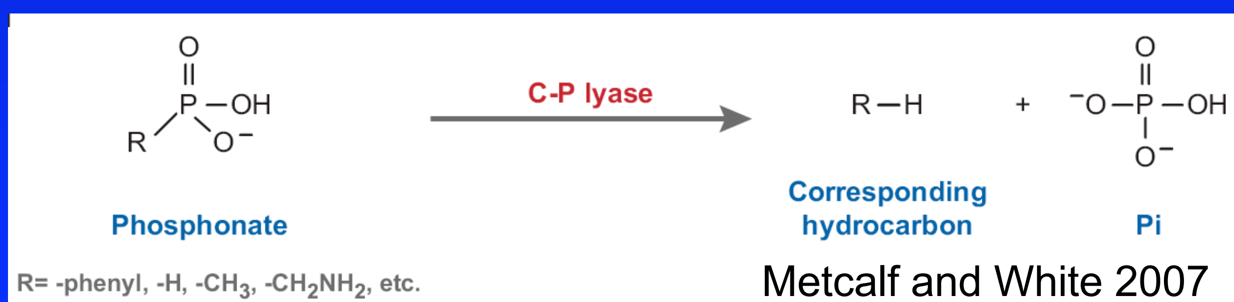
phnG-M

P acquisition genes in *Trichodesmuim erythraeum*



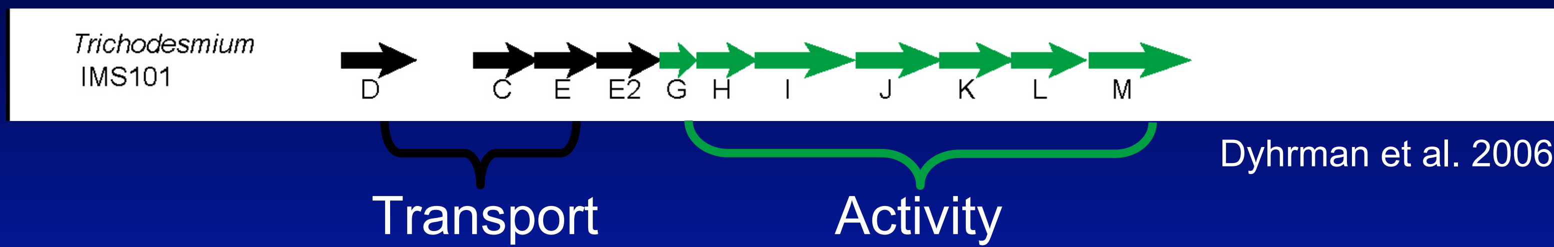
Dyhrman et al. 2006

- All *phn* genes required for C-P lyase mediated phosphonate metabolism are present in the IMS101 genome



Metcalf and White 2007

P acquisition genes in *Trichodesmuim*



Dyhrman et al. 2006

- The *phnD* and *phnJ* genes are present in other *Trichodesmium* species.

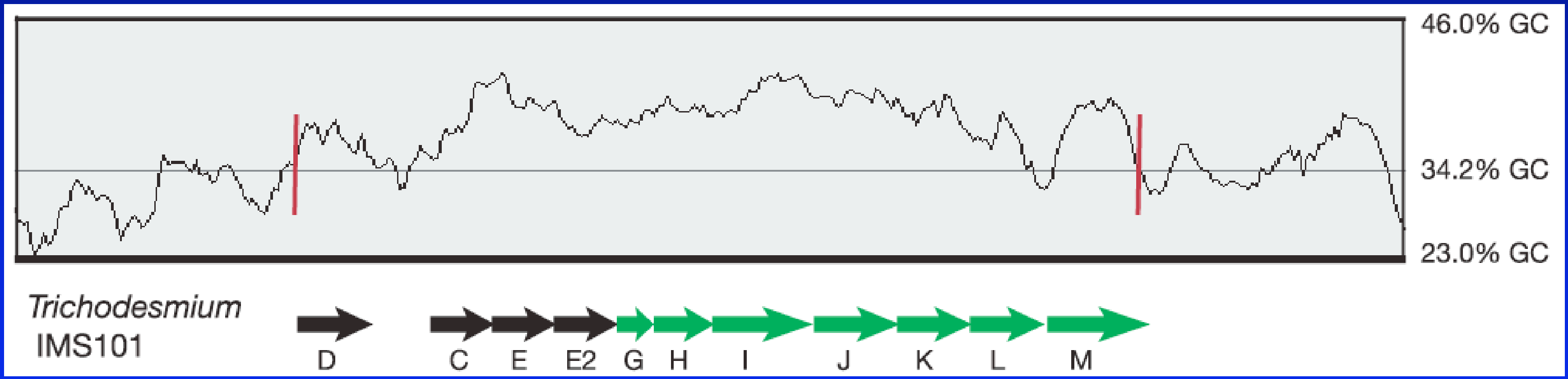
Species	pstS	phoA	ppX	phnD	phnJ
T. erythraeum	X	X	X	X	X
T. theibautii	X	X	X	X	X
T. tenue	X	X	X	X	X

* 98-100% identical

- C-P lyase gene cluster is not represented in any of the marine *Syn, Pro* or *Croco* genomes examined to date.

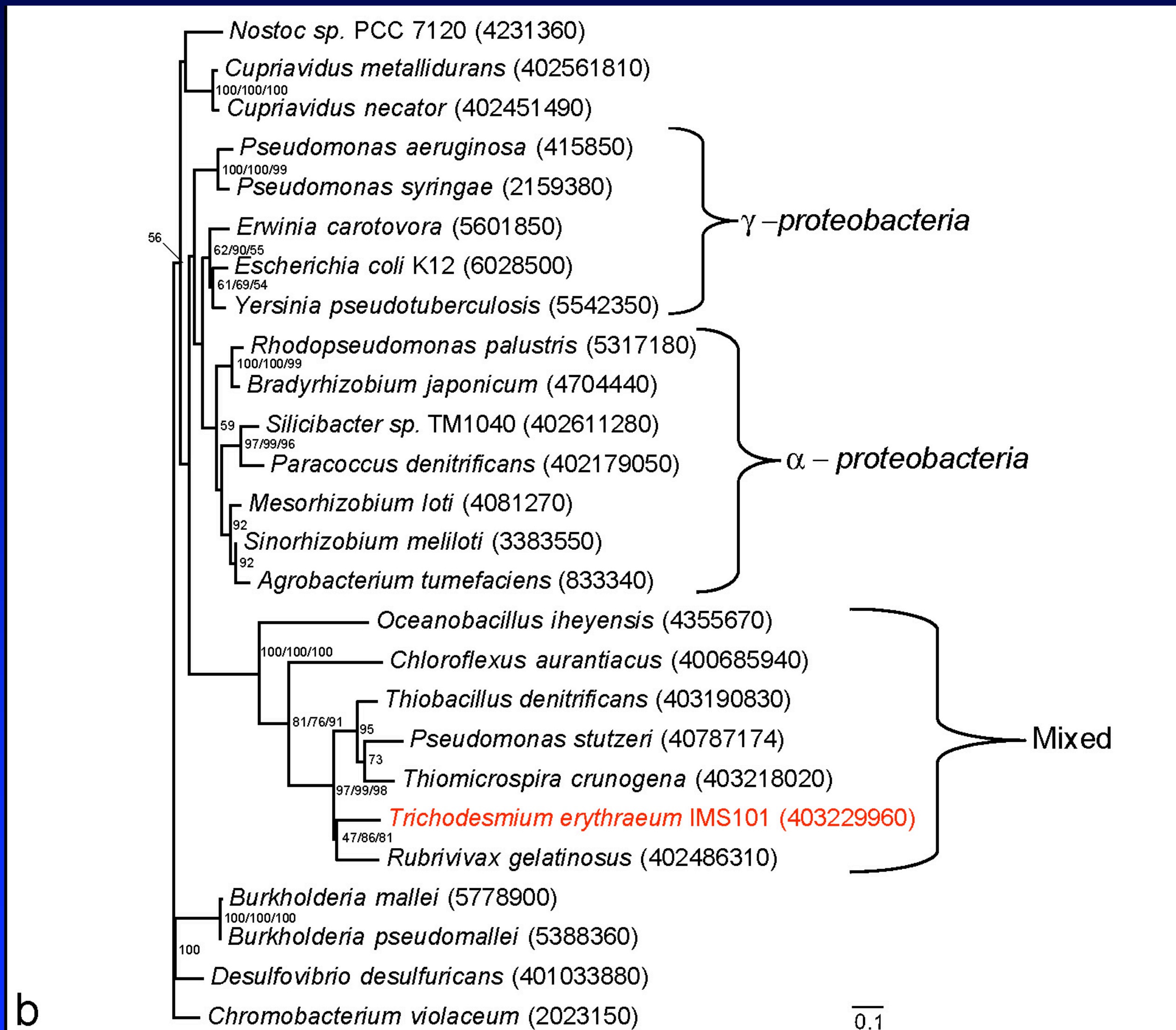
Possible gene transfer…?

- The GC content is elevated in the *phn* cluster relative to the rest of the genome



- The *phnJ* gene clusters with distantly related bacteria.

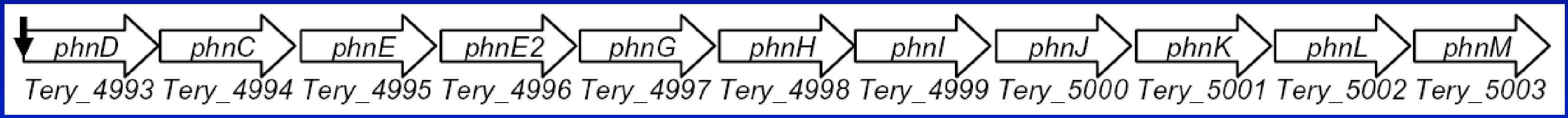
phnJ phylogeny



(Dyhrman et al. 2006 - Thanks to Dr. Eric Webb!)

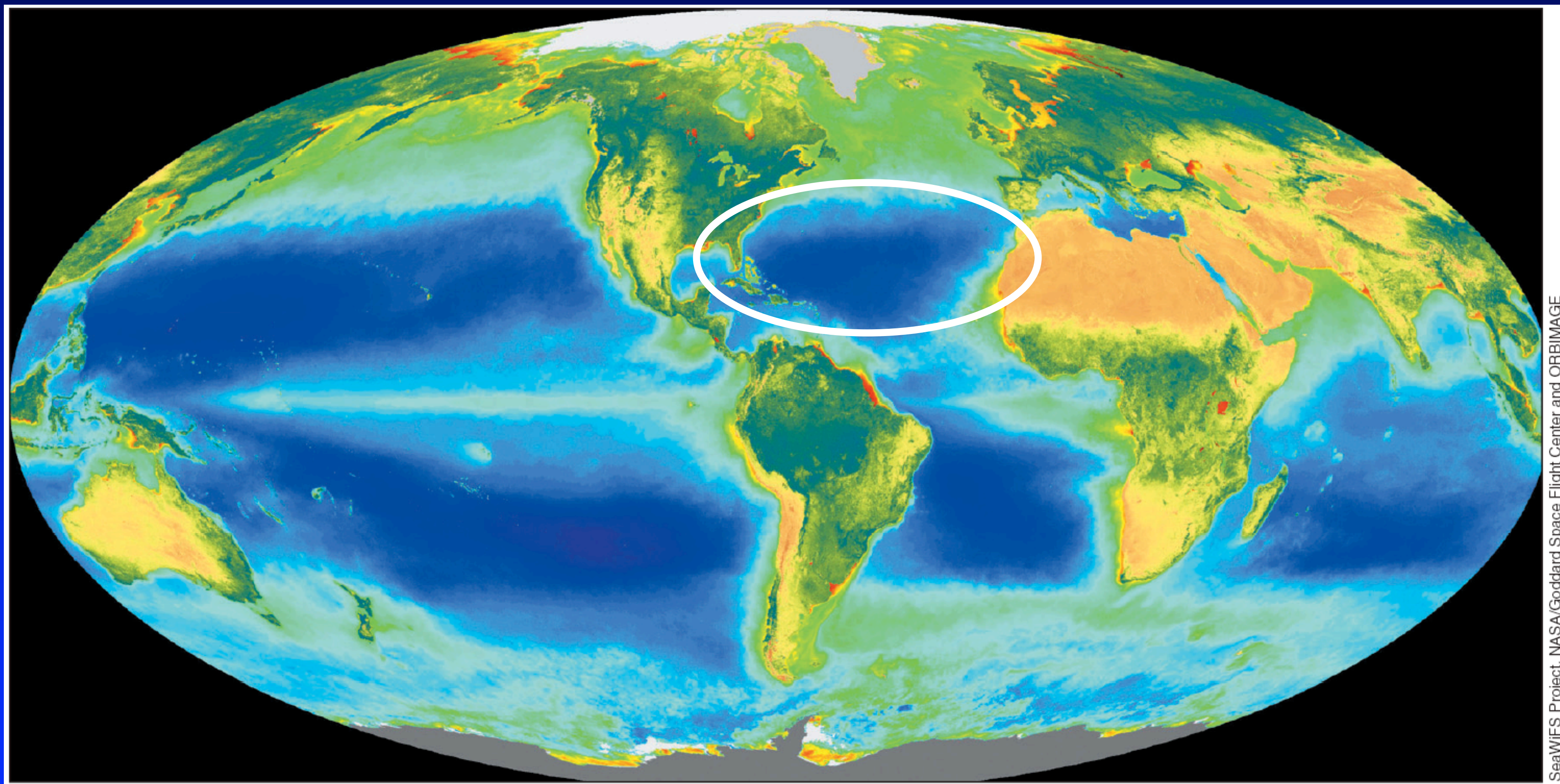
P regulation

- Expression studies
  - Su et al. 2007 identify pho boxes for the *phn* and *pstS* gene clusters.

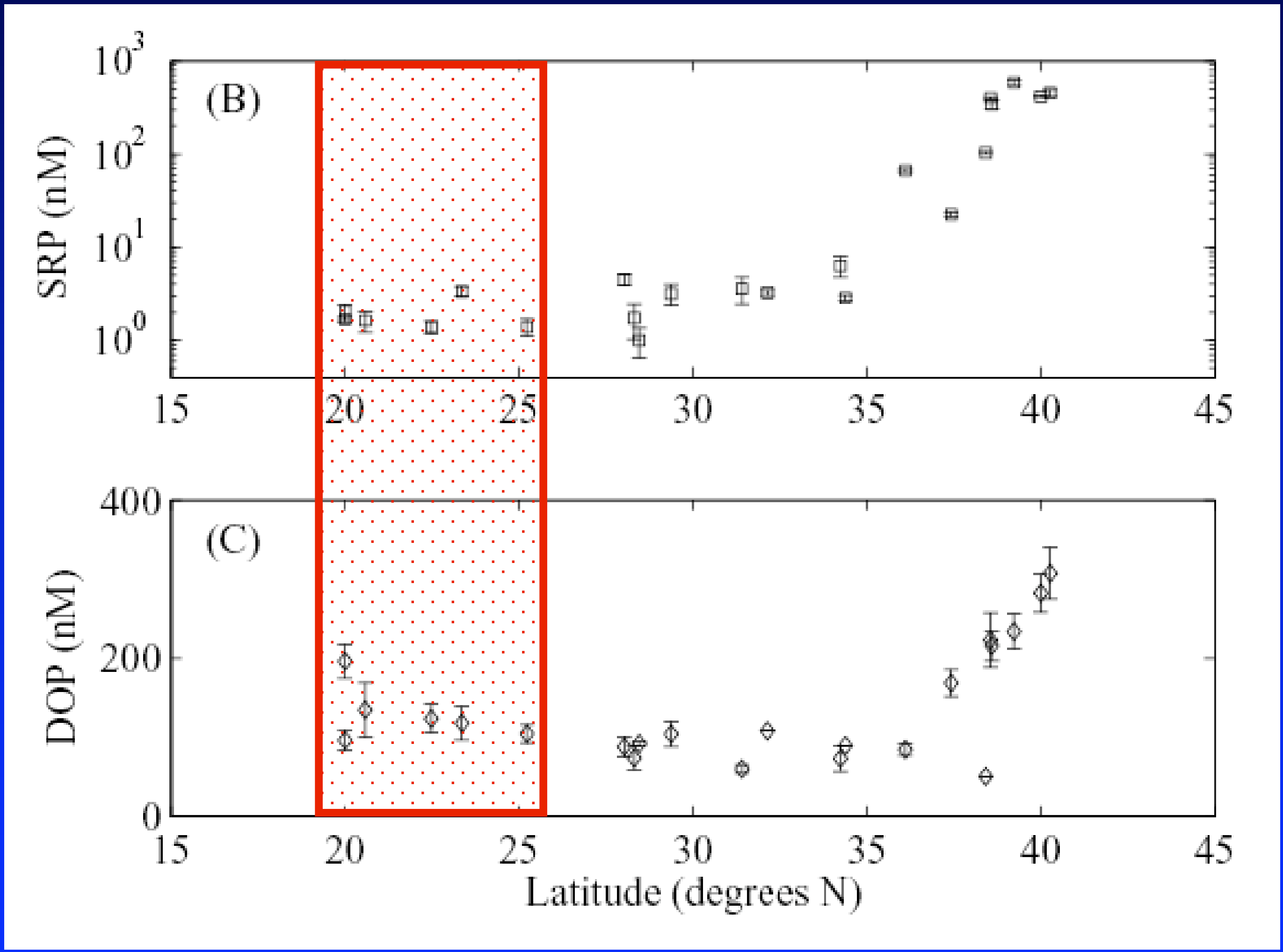


- Target genes appear P-regulated.
- Quantitative approaches under development to examine the timing of the response.

Sargasso Sea: *Trichodesmium* P acquisition

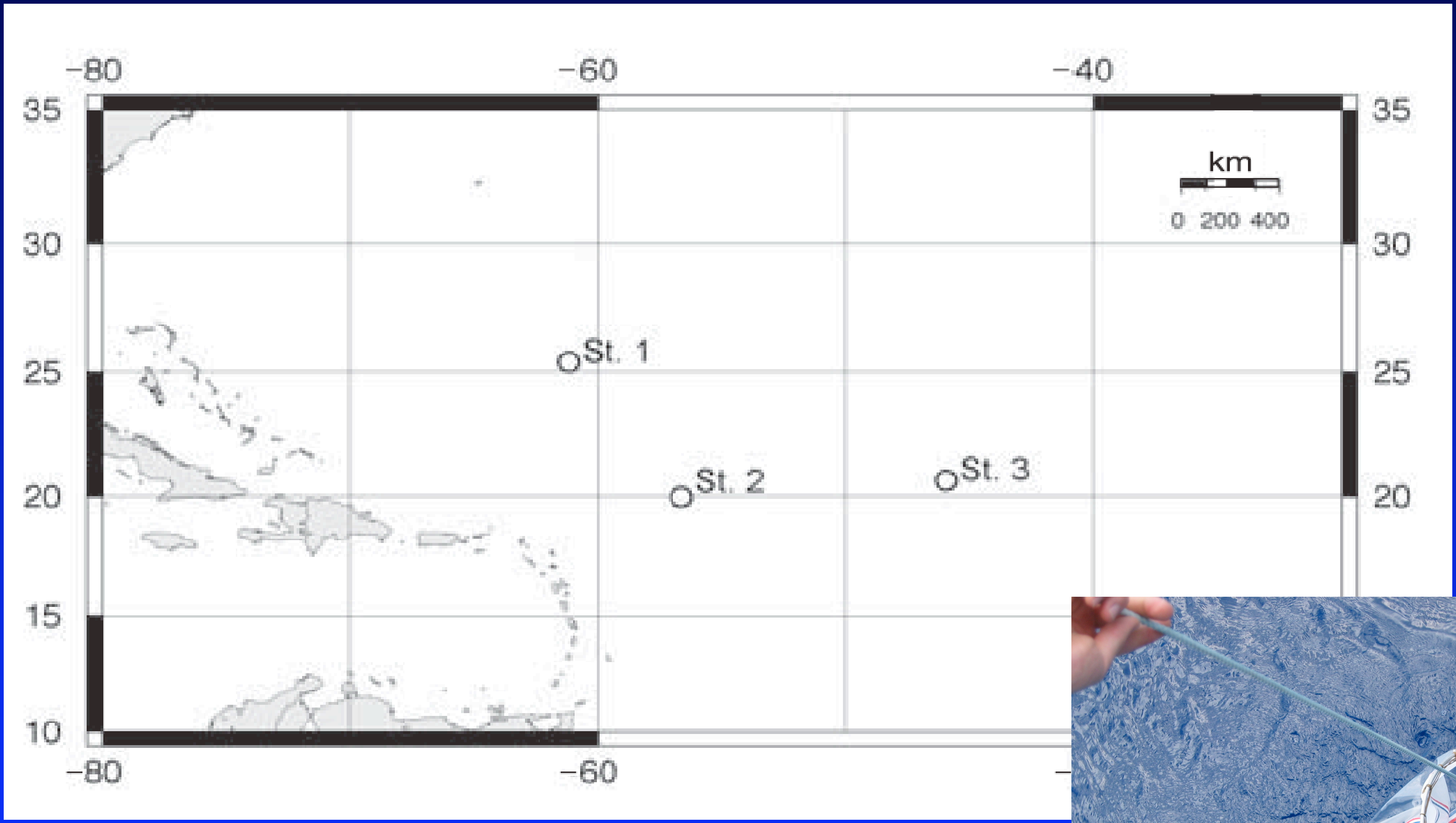


Sargasso Sea: P biogeochemistry

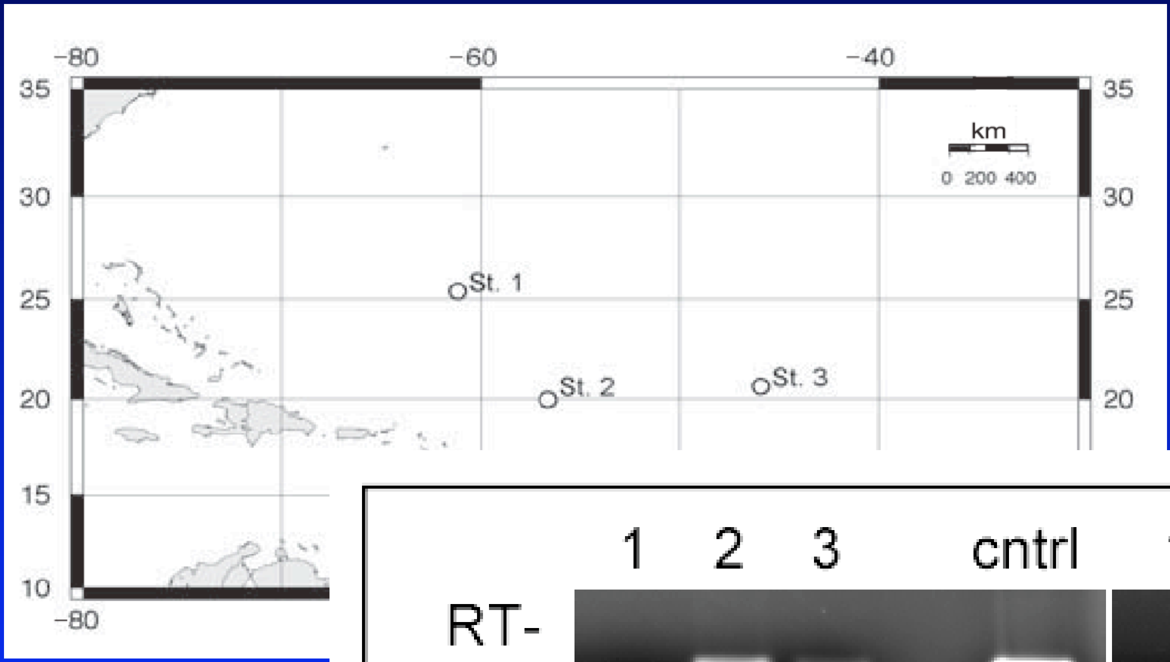


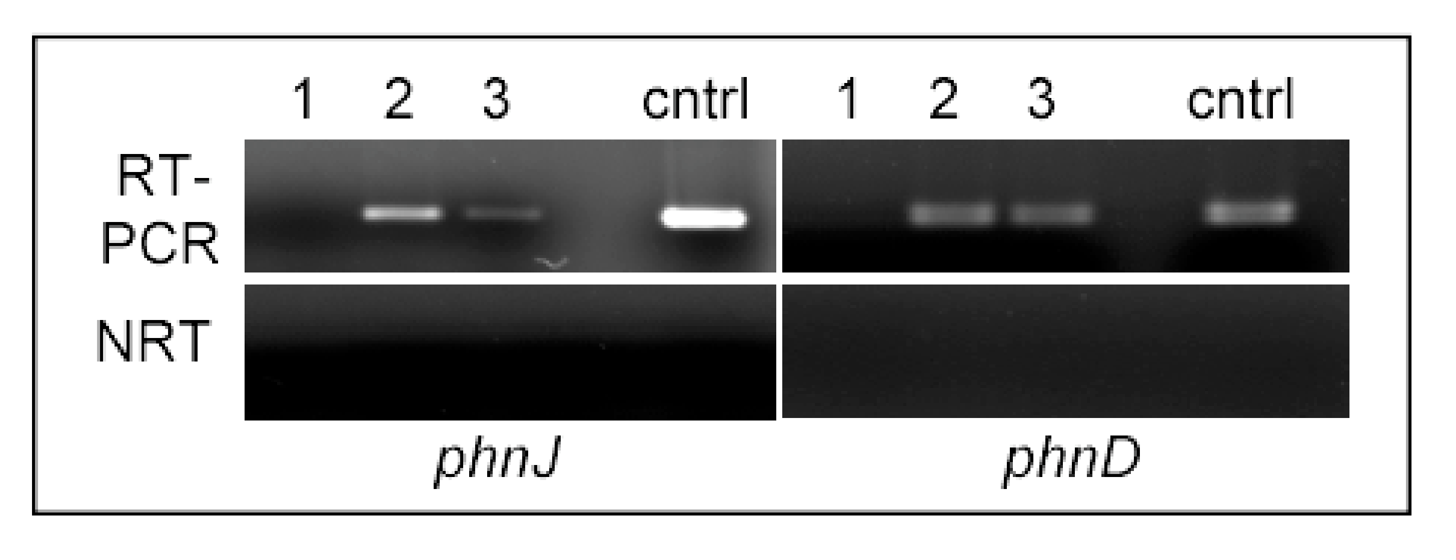
Wisniewski Jakuba et al. In press

Does *Trichodesmium* express phosphonate metabolism genes in the field?

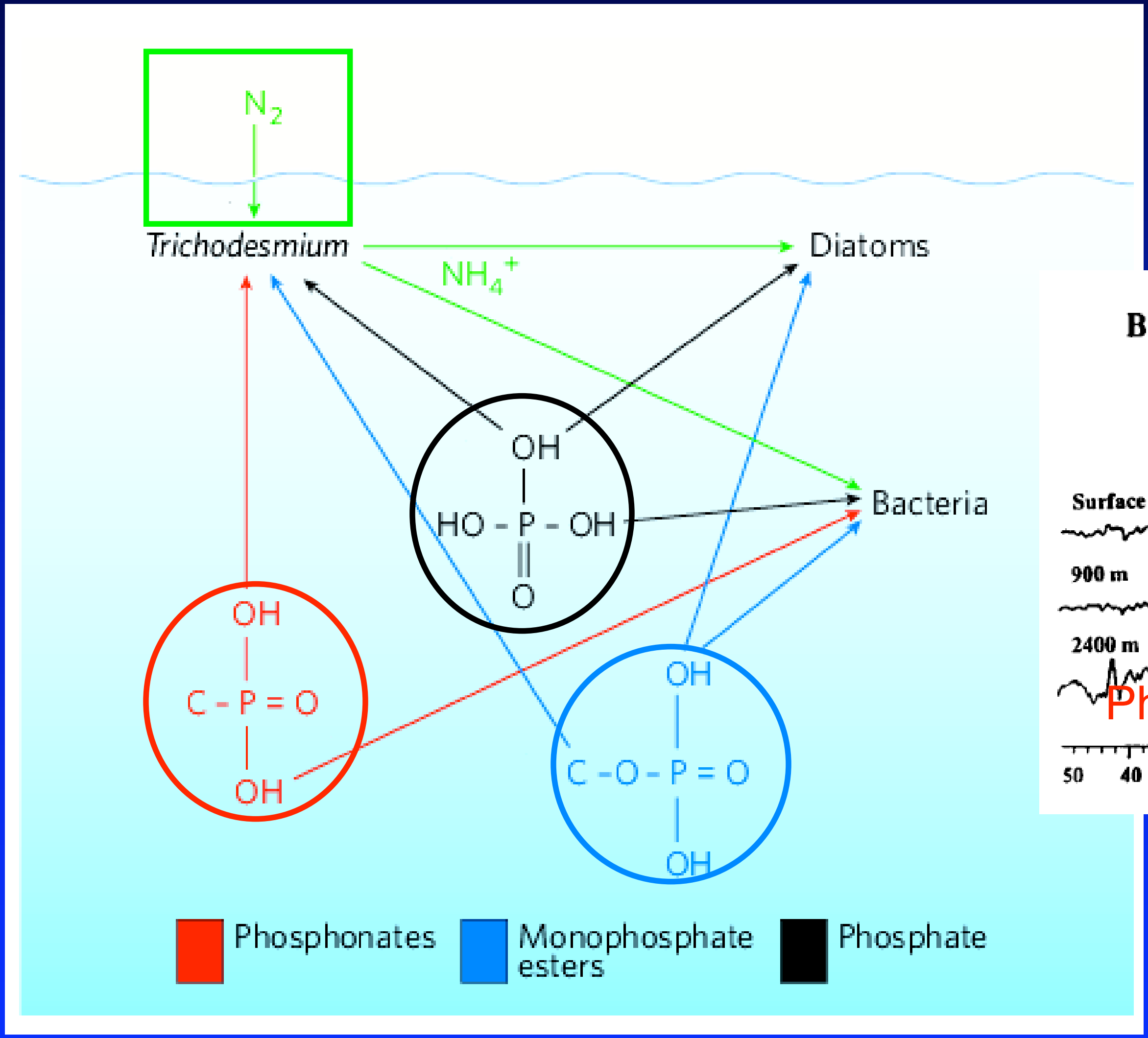


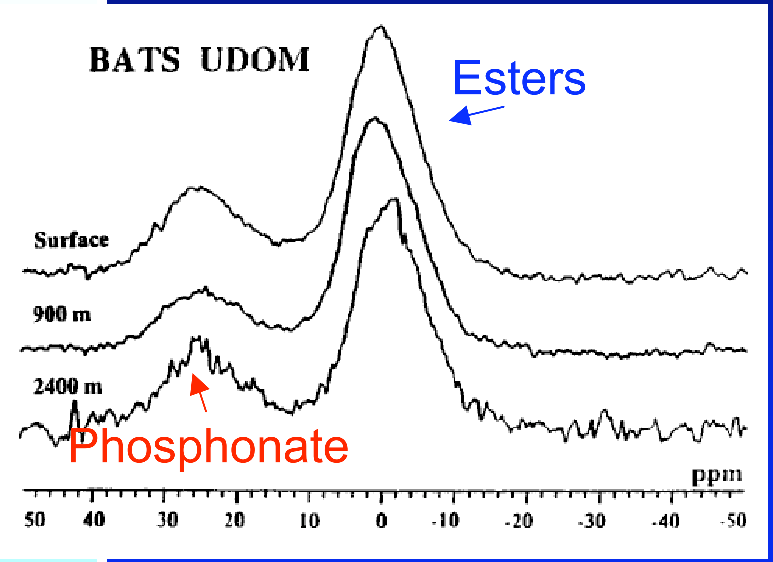
phnJ and *phnD* are differentially expressed in field populations





Geochemical niche adaptation in *Trichodesmium*

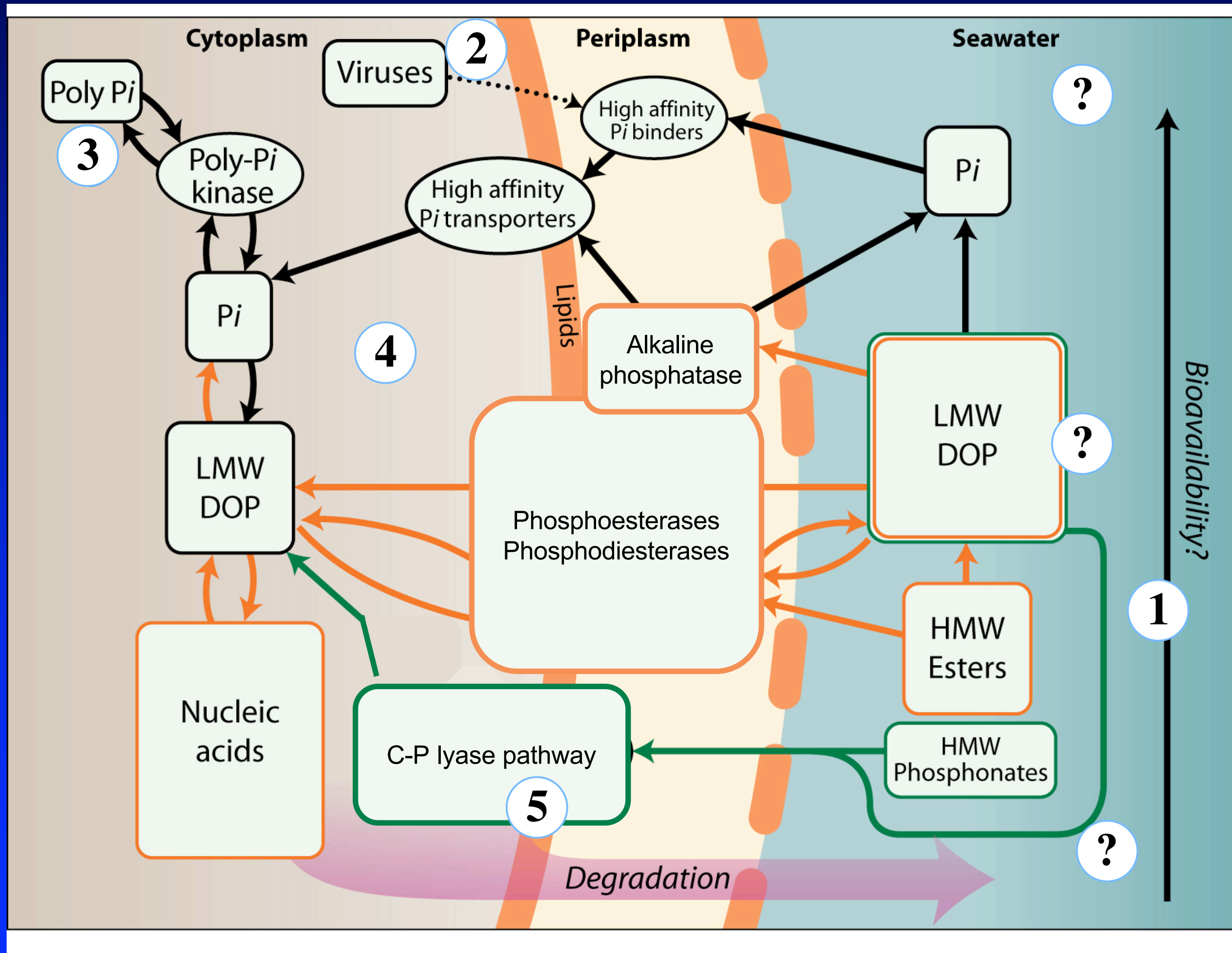




Kolowith et al. 2001

Sañudo-Wilhelmey 2006

A conceptual diagram of marine microbial interactions with phosphorus



Dyhrman et al. 2007

Enduring mysteries…

- The composition of low molecular weight DOP?

Table 2
Composition of SNP in the marine environment

SNP compound class	%Composition (method)[a]	Reference
Bulk SNP		
Monophosphate Esters	10–100% (Enzymatic Assays)	Strickland and Solorzano, 1966; Kobori and Taga, 1978; Taft et al., 1977; Chrost et al., 1986
	55–77% (0–100 m; Modified UV oxidation)	Karl and Yanagi, 1997
	50% (> 100 m; Modified UV oxidation)	
Nucleotides and nucleic acids	23–45% (0–100 m; ≈ Persulfate — modified UV)	Karl and Yanagi, 1997
	50% (> 100 m; ≈ Persulfate — modified UV)	
	10–100% (Enzymatic Assays)	Strickland and Solorzano, 1966; Kobori and Taga, 1978; Taft et al., 1977; Chrost et al., 1986
	ATP: < 1% (Firefly bioluminescence)	Azam and Hodson, 1977; Azam et al., 1979; Hodson et al., 1981; Nawrocki and Karl, 1989
	DNA/RNA: < 5% (Multiple methods)	DeFlaun et al., 1986; Paul et al., 1986; Karl and Bailiff, 1989
Phospholipids	3–11% (Cross Flow Filtration (CFF) and Polymyxin B treatment)	Suzumura et al., 1998
Phosphonates	5–10% (^{31}P NMR)	Clark et al., 1998
Polyphosphates	0–50% (≈ Acid Reflux — UV oxidation)	Armstrong and Tibbets, 1968; Solorzano and Strickland, 1968; Solorzano, 1978
Size fractionated SNP		
LMW (< 10 kDa)	50–80% (CFF)	Matsuda 1985; Ridal and Moore, 1990; Suzumura et al., 1998
HMW (> 10 kDa)	20–50% (CFF)	Matsuda et al., 1985; Ridal and Moore, 1990;
HMW (> 50 kDa)	15% (CFF)	Suzumura et al., 1998
Monophosphate esters	10% (Alkaline phosphatase treatment)	Suzumura et al., 1998
	75% (^{31}P NMR)	Clark et al., 1998
Nucleic acids	25% (Phosphodisterase treatment)	Suzumura et al., 1998
Phospholipids	38–46% (Polymyxin B treatment)	Suzumura et al., 1998
Phosphonates	25% (^{31}P NMR)	Clark et al., 1998

[a]All values are based on surface waters (upper 100 m) unless otherwise noted.

Enduring mysteries…

- The composition of low molecular weight DOP?
- Viral *pstS* ?

Three *Prochl*
Signature Fe
Interpretatior

Matthew B. Sullivan[1], Maureen L

1 Joint Program in Biological Oceanography, W
America, 2 Department of Civil and Environme
of Biology, Massachusetts Institute of Technol
California, United States of America

The oceanic cyanobacteria *Proch*
that their viruses (phages) med
present an analysis of genomes f
overall genome features, and ge
T4-like (P-SSM2 and P-SSM4) pl
genome sequences to establish
T7-like genes and the two myov
each genome contains a signific
genes found in cyanobacteria. S
three phage genomes contain pl
activity during infection, as wel
metabolism during infection. Tl
suggest it is capable of integrat
phages or marine cyanophages
host. Further, both myoviruses (
phage and host responses to pl
cyanophages appear to be vari
reflect adaptations for infection

Citation: Sullivan MB, Coleman ML, Weigele P, F
PLoS Biol 3(5): e144.

Table 5. Summary Table of Unique Features of *Prochlorococcus* Cyanophage Genomes That Are Uncommon among Known Phages

Functional Category	Genes	Putative Function	P-SSP7	e-Value	Marine T7-Likes	P-SSM2	e-Value	P-SSM4	e-Value	Marine T4-Likes
Phosphate	*pstS*	Phosphate uptake				322	e^{-136}	322	e^{-137}	
	phoH	Phosphate-stress-induced			+	251	e^{-24}	258	e^{-20}	+
Carbon mobilization	*talC*	MipB/TalC family transaldolase	215	e^{-43}		216	e^{-47}	218	e^{-53}	+
Lysogeny	*int*	Phage integration	291	e^{-13}						
Nucleotide metabolism	*mazG*	pyrophosphohydrolase/ pyrophosphatase				139	e^{-11}	134	e^{-27}	
	pyrE	Orotate phosphoribosyltransferase				215	e^{-44}			
	purH	Phosphoribosylformyl glycinamide synthase				108	e–7			
	purL	Phosphoribosyl formyl glycinamide cyclo-ligase				223	e^{-80}			
	purM	AICARFT/IMPCHase bienzyme				314	e^{-97}			
	purN	phosphoribosyl glycinamide formyltransferase				175	e^{-33}			
	nrd	RNR domain	469	e^{-11}	+	universal among T4-like phages				
Photosynthesis-related genes	*psbA*	D1 protein, PSII	360	e=0		361	e = 0	366	e = 0	+
	hli	Thylakoid-associated proteins	×1 *hli* gene			× 6 *hli* genes		×4 *hli* genes		+
	petE	Plastocyanin, PET				115	e^{-21}			
	petF	Ferredoxin, PET				98	e^{-29}			
	pebA	Phycoerythrobilin biosynthesis				234	e^{-12}			
	ho1	Heme biosynthesis				234	e^{-63}			
	psbD	D2 protein, PSII						359	e = 0	+
	speD	Polyamine biosynthesis						102	e^{-17}	
	pcyA	Phycocyanobilin biosynthesis						230	e^{-26}	
Other functions	*cobS*	Vitamin B12 biosynthesis				365	e^{-21}	365	e^{-23}	
	prnA	Bacterial tryptophan halogenase				486	e^{-52}			
	nol	Carbomoyltransferase				572	e^{-52}			
	hn	HN						158	e^{-33}	
	LPS	Epimerases, transferases, phospholipases				×24 genes				

Non-marine T7-like/T4-like phages completely lack these genes. The size (amino acids) and best BLASTp e-value of each predicted coding region are presented using gene names and function assignments according to their function in cellular organisms. The *hli* genes were assigned using e-value and a signature sequence as reported in Lindell et al. [14]. A plus sign indicates that the feature is present in the phage group, otherwise the feature is absent or is yet to be identified. PET, photosynthetic electron transport; PSII, photosystem II reaction center.
DOI: 10.1371/journal.pbio.0030144.t005

Enduring mysteries…

- **The composition of low molecular weight DOP?**
- **Viral *pstS* ?**
- **A P redox cycle ?**

Microbial Metabolism of Reduced Phosphorus Compounds

Andrea K. White[1] and William W. Metcalf[2]

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[2]Department of Microbiology and Institute for Genomic Biology, University of Illinois at Urbana-Champaign, Urbana, Illinois 61801; email: metcalf@life.uiuc.edu

Annu. Rev. Microbiol. 2007. 61:379–400

Metabolism of reduced P

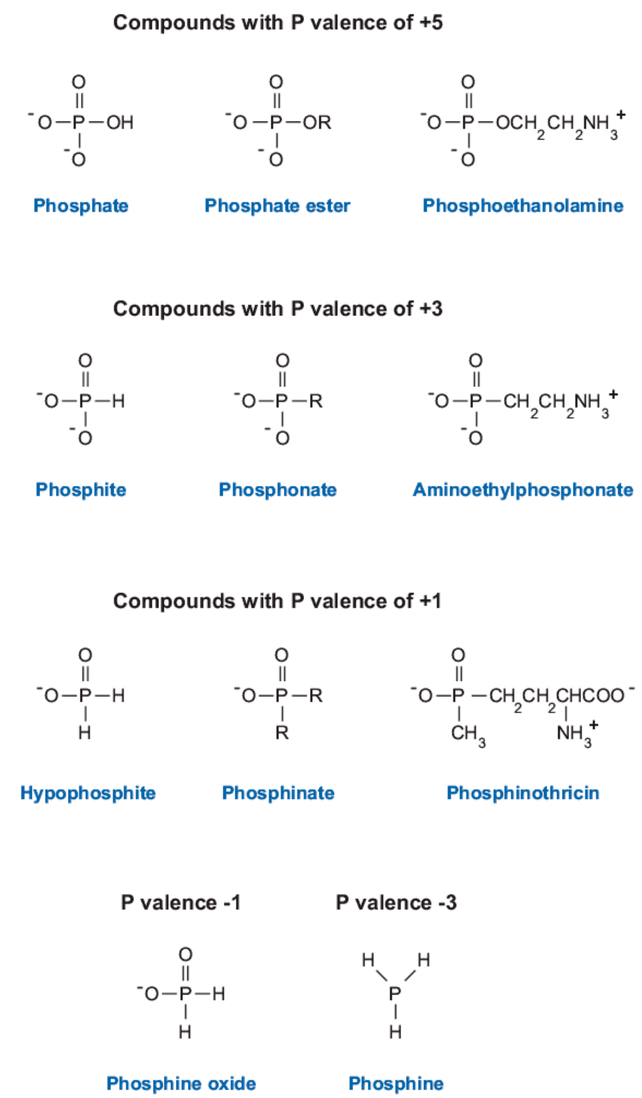


Figure 1

The chemical structures of phosphorus compounds at various redox levels. Inorganic compounds, a generalized formula, and a known biological example are shown in the left, middle, and right columns, respectively, for compounds in the +5, +3, and +1 valence states.

Growth on hypophosphite

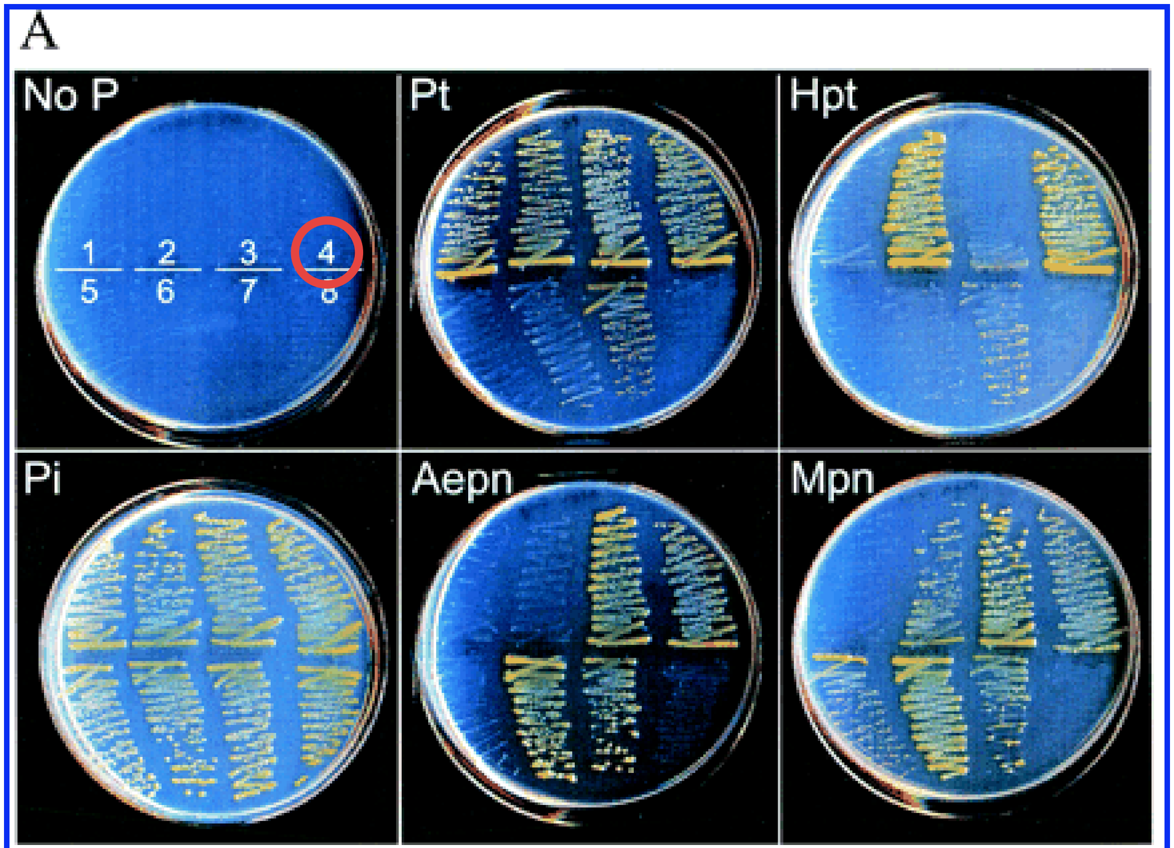
Journal of Bacteriology, July 2004, p. 4730-4739, Vol. 186, No. 14
0021-9193/04/$08.00+0 DOI: 10.1128/JB.186.14.4730-4739.2004

Two C—P Lyase Operons in *Pseudomonas stutzeri* and Their Roles in the Oxidation of Phosphonates, Phosphite, and Hypophosphite

Andrea K. White and William W. Metcalf*

Chemical and Life Sciences Laboratory, Department

Received 30 January 2004/ Accepted 5 April 2004



Growth on hypophosphite

SUMMARY POINTS

1. A wide variety of reduced P compounds are produced and consumed by microbes.
2. Bacterial synthesis of many medically important reduced P antibiotics involves the production of reduced P phosphonate and phosphinate intermediates that could provide an important source of P in the environment.
3. Four bacterial pathways for the oxidation of the inorganic reduced P compound, phosphite, have been identified: C-P lyase, BAP, NAD:phosphite oxidoreductase, and a novel but as yet uncharacterized pathway for deriving energy from phosphite oxidation in *D. phosphitoxidans*.

With the variety of pathways to oxidize phosphite to phosphate…elucidation of a biological P redox cycle may not be far off.

FUTURE ISSUES

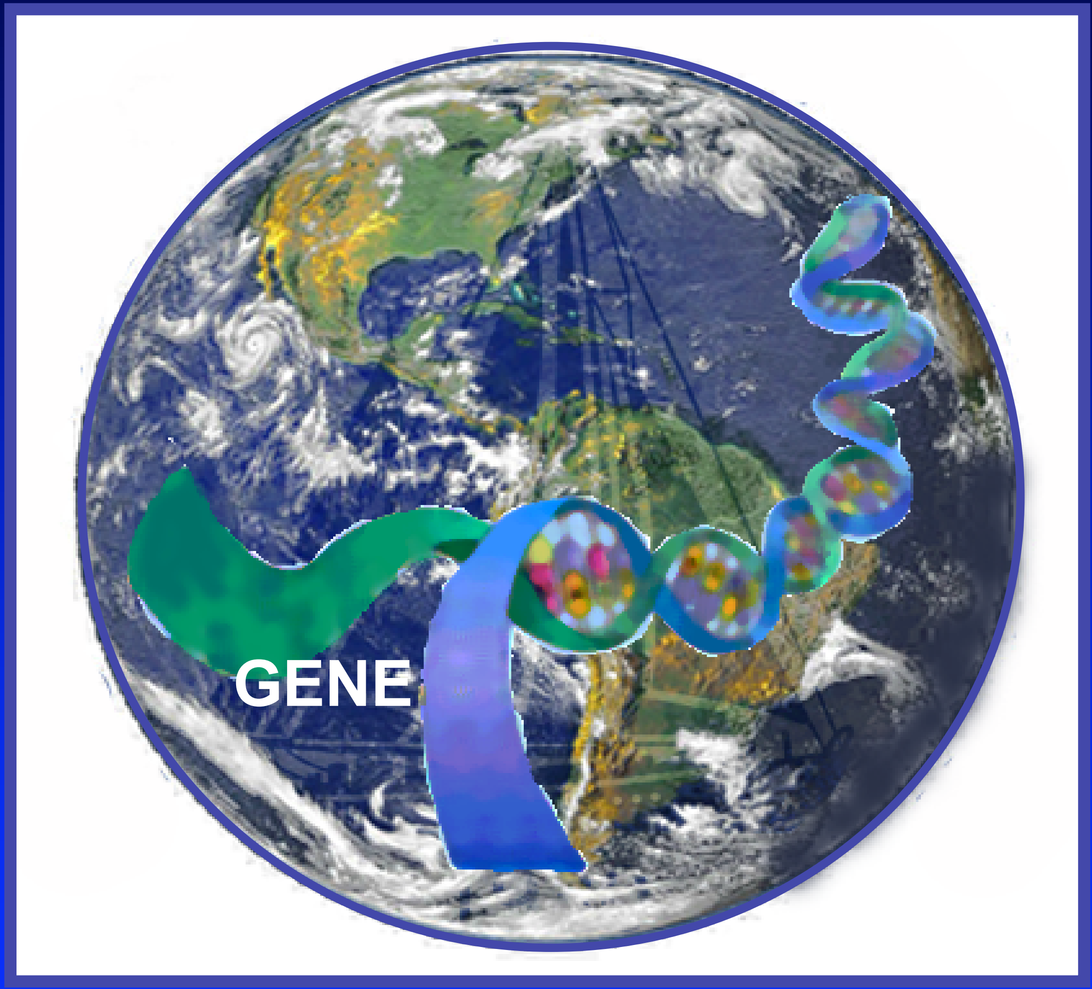
1. Attaining in vitro C-P bond cleavage activity by C-P lyase will allow the reaction sequence and mechanism to be fully described.
2. In vitro characterization of hypophosphite oxidation via *htxXY* in *X. flavus* will provide insight into this novel reaction.
3. Determining the source(s) of phosphine, hypophosphite, and phosphite in the environment would significantly add to our understanding of P availability to organisms.

Enduring mysteries…

- The composition of low molecular weight DOP?
- Viral *pstS* ?
- A P redox cycle ?
- Sources and sinks of marine phosphonates ?
    - Phosphonates have been identified in a few marine invertebrates, but but the source of phosphonates to the upper water column remains a mystery

The take home message

- The basics:
  - P is important
  - It is rapidly cycled
  - It comes in organic forms - that are poorly characterized
- Tech advances
  - Magic tells us that the inorganic form is at very low levels
  - Distribution of bond classes in high molecular weight DOP
- Adaptation to low P is common
  - Frequency and expression of *pstS*
  - The emerging importance of polyphosphate
  - Losing your phospholipids
  - Metabolism of phosphonates
- Enduring mysteries
  - Low molecular weight DOP composition
  - P machinery in the agal viruses
  - Microbial metabolism of reduced P


GENE