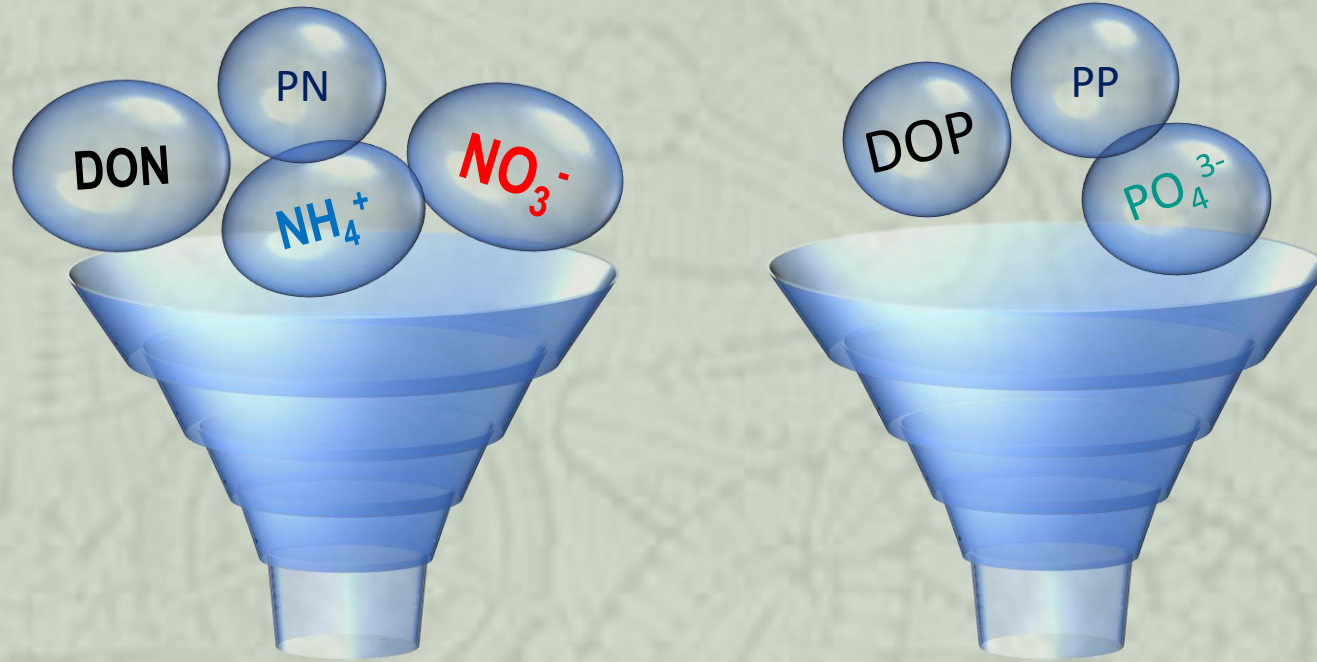


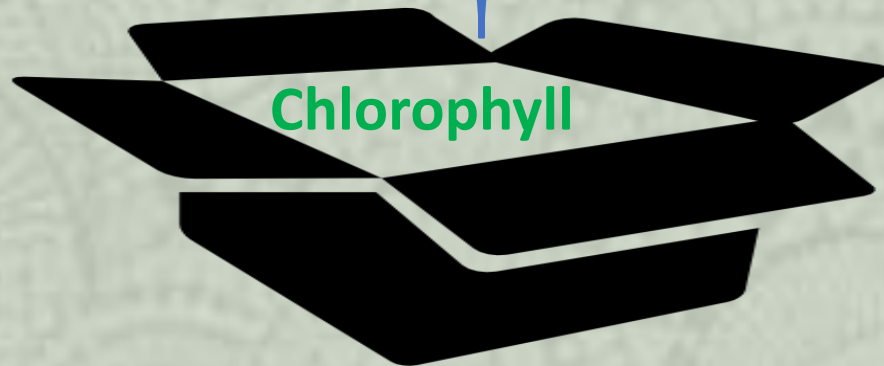
# Biological responses to nutrient forms and proportions

Pat Glibert

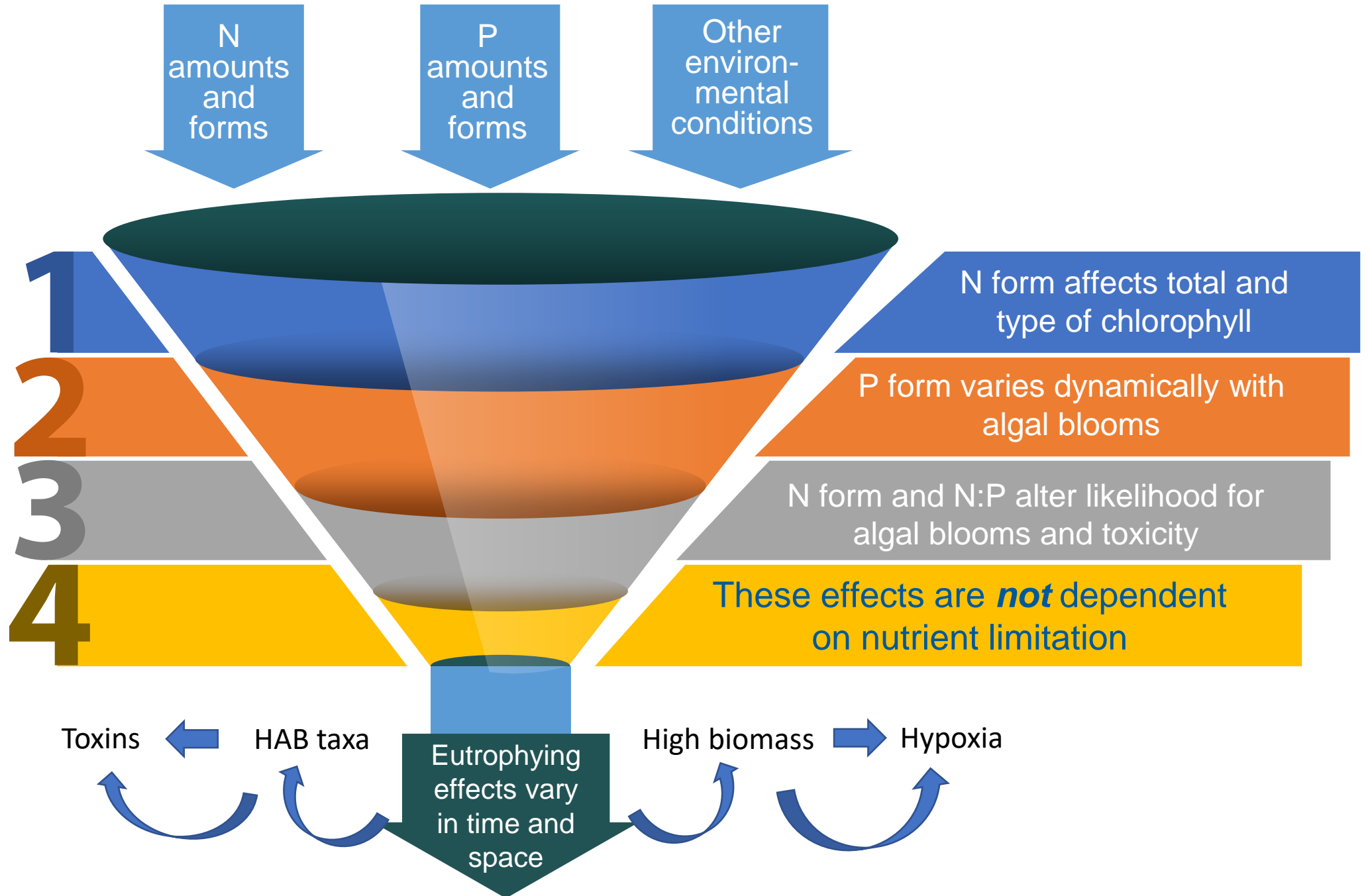


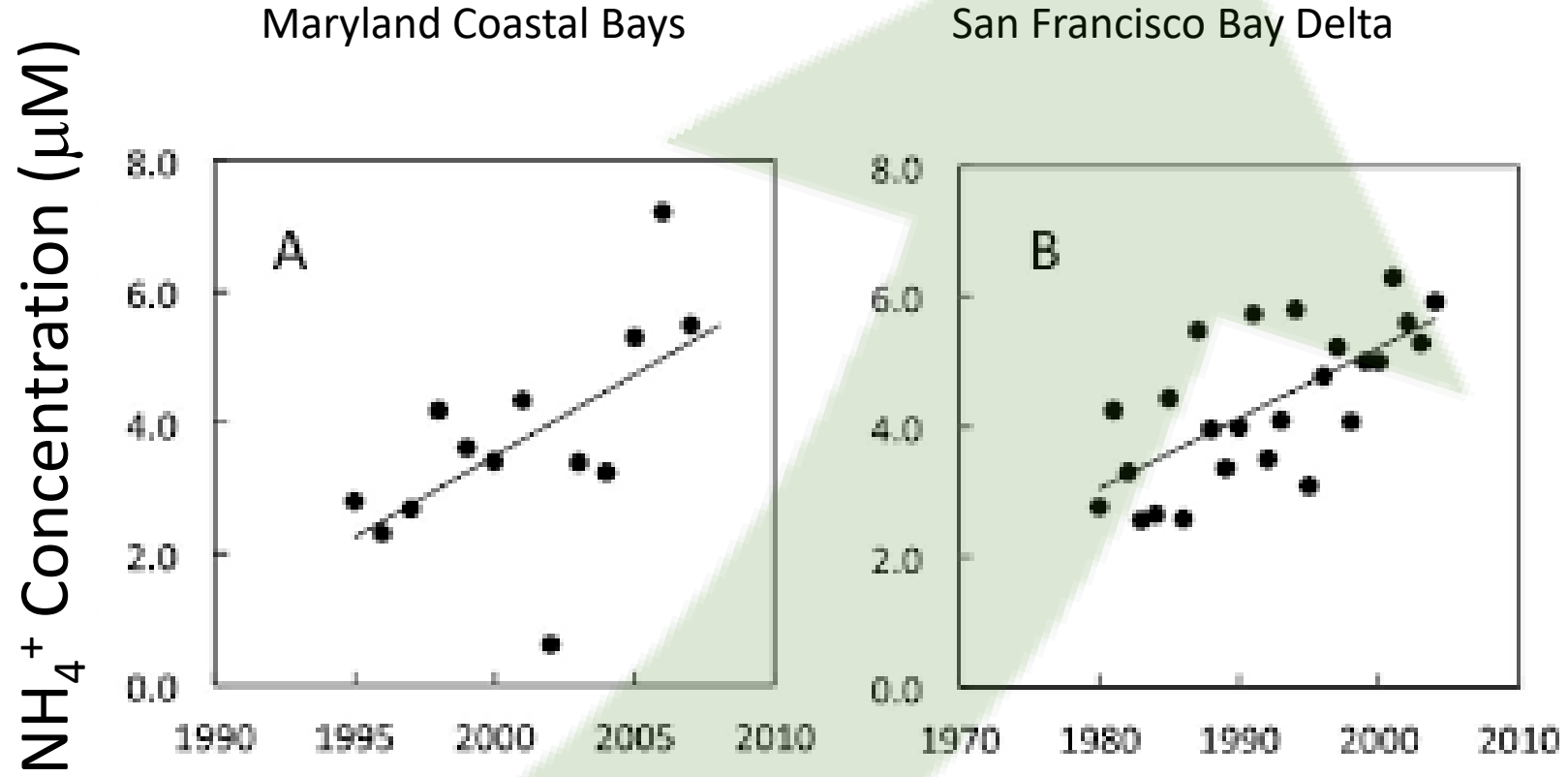


**TN** : **TP**



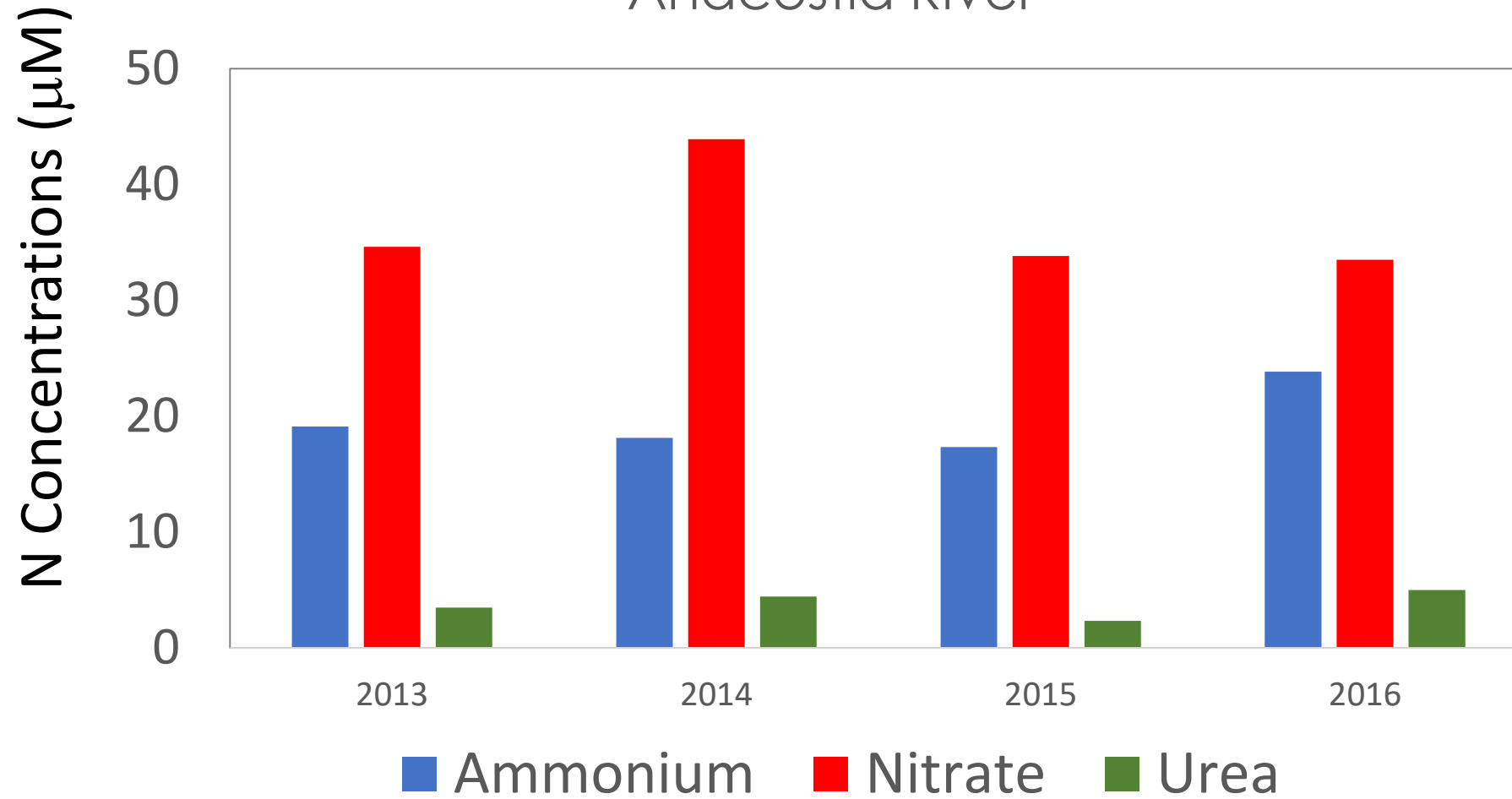
How do N and P speciation affect **total** chlorophyll– as well as the **type** of chlorophyll?



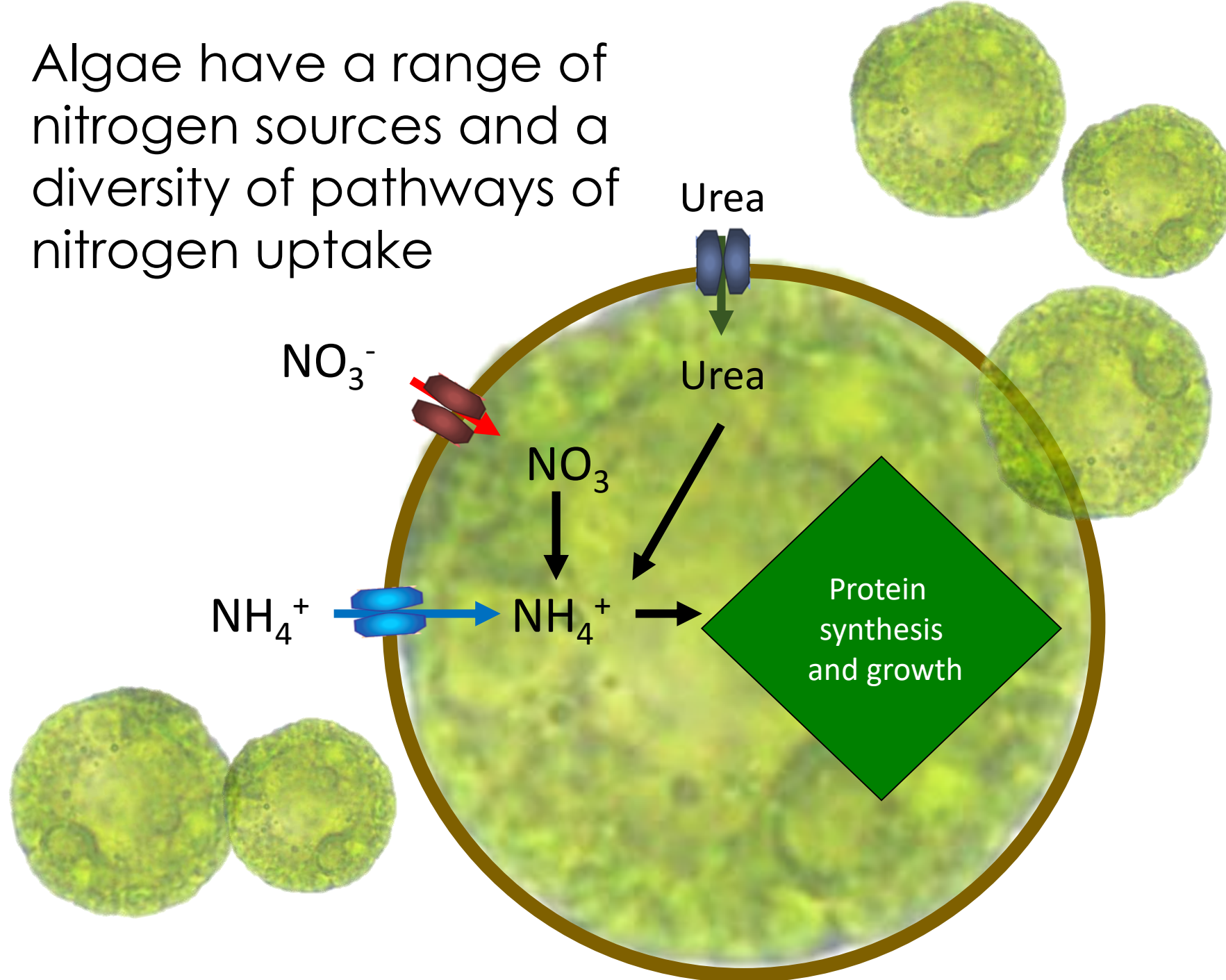


$\text{NH}_4^+$

# Annual average N concentrations in Anacostia River



Algae have a range of nitrogen sources and a diversity of pathways of nitrogen uptake



## Dogma:

“There should be no selective effect ... that might distinguish between the potential performance of any pair of planktonic algae, so long as the resource concentrations are able to saturate the growth demand...”

Reynolds 1999

*i.e., at saturation, nutrients are not “regulating”  
(other than ecosystem effects of too much biomass)*

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## Dogma:

If the use of the resource needing more manipulation [e.g.,  $\text{NO}_3^-$ ]..., in order to achieve the same product formation [moles product per second], then the cell doubling time will be significantly increased since more [moles] of the product of the resource manipulation will be required to double cell mass...

Raven et al. (1992)

*i.e., growth rate on  $\text{NH}_4$  should be faster than on  $\text{NO}_3$*

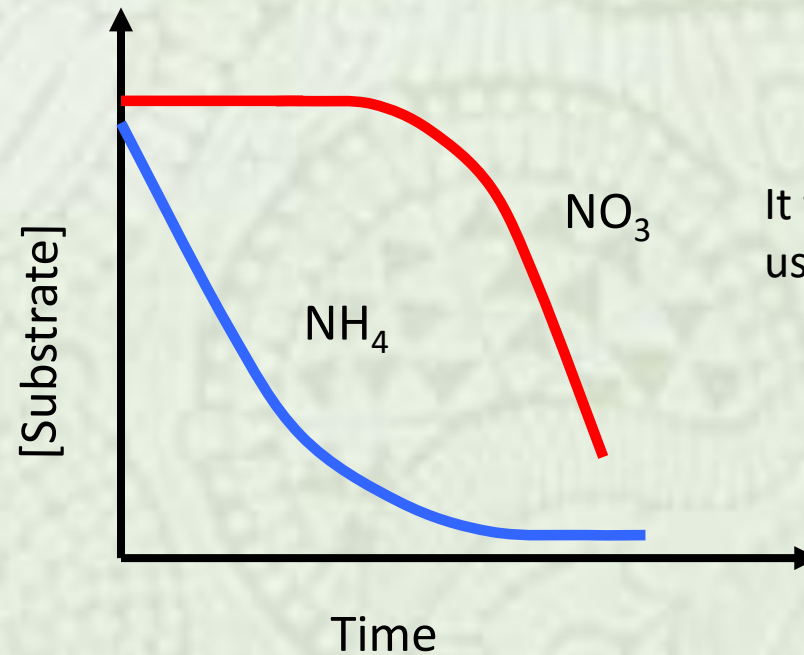
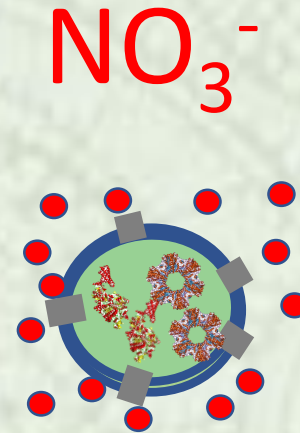
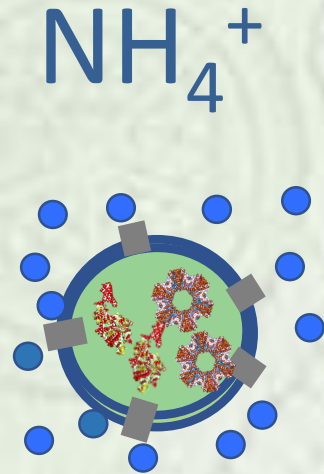
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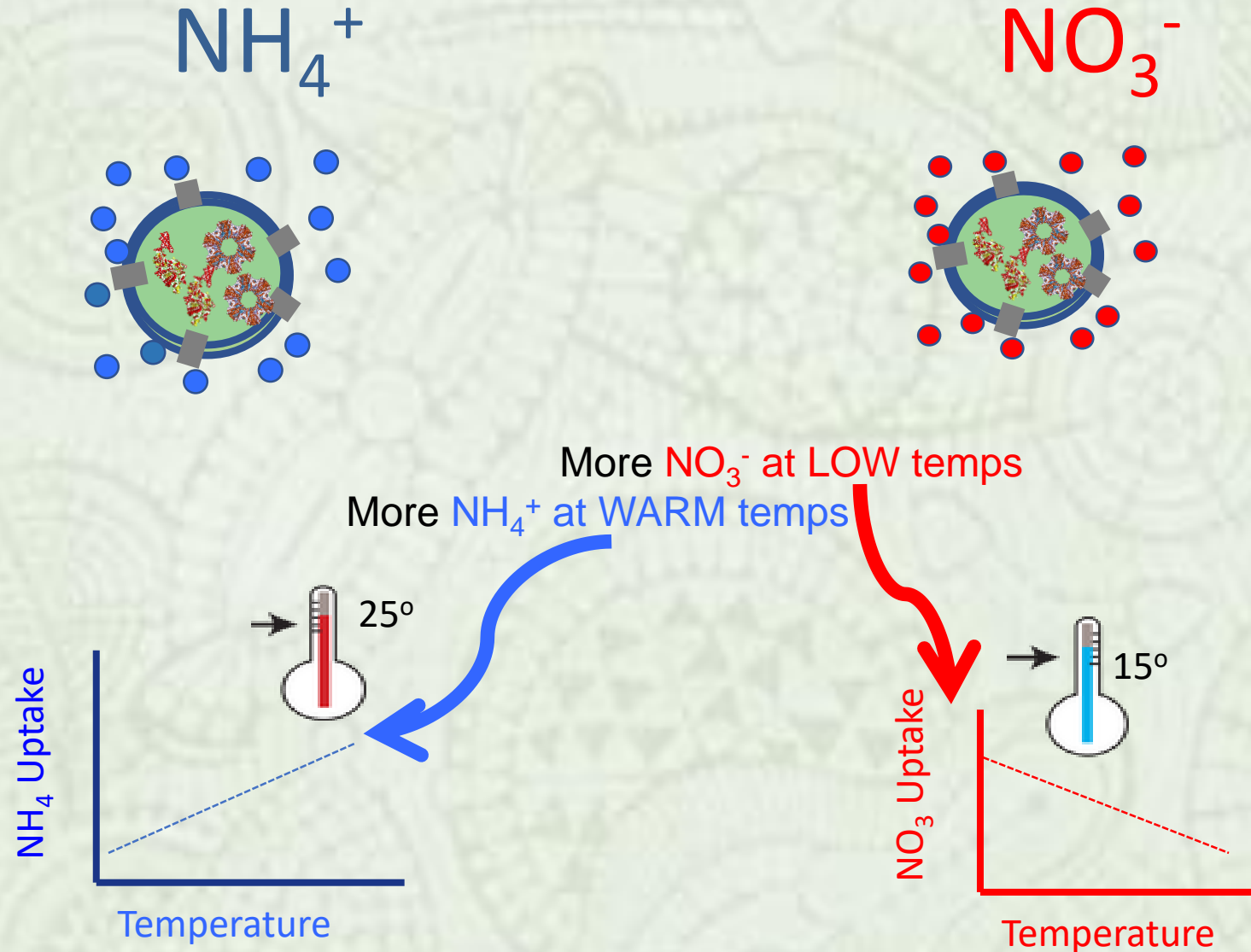
*i.e., growth rate on  $\text{NH}_4$  should be faster than on  $\text{NO}_3$*

$\text{NH}_4$  is classically considered the “preferred” form of N

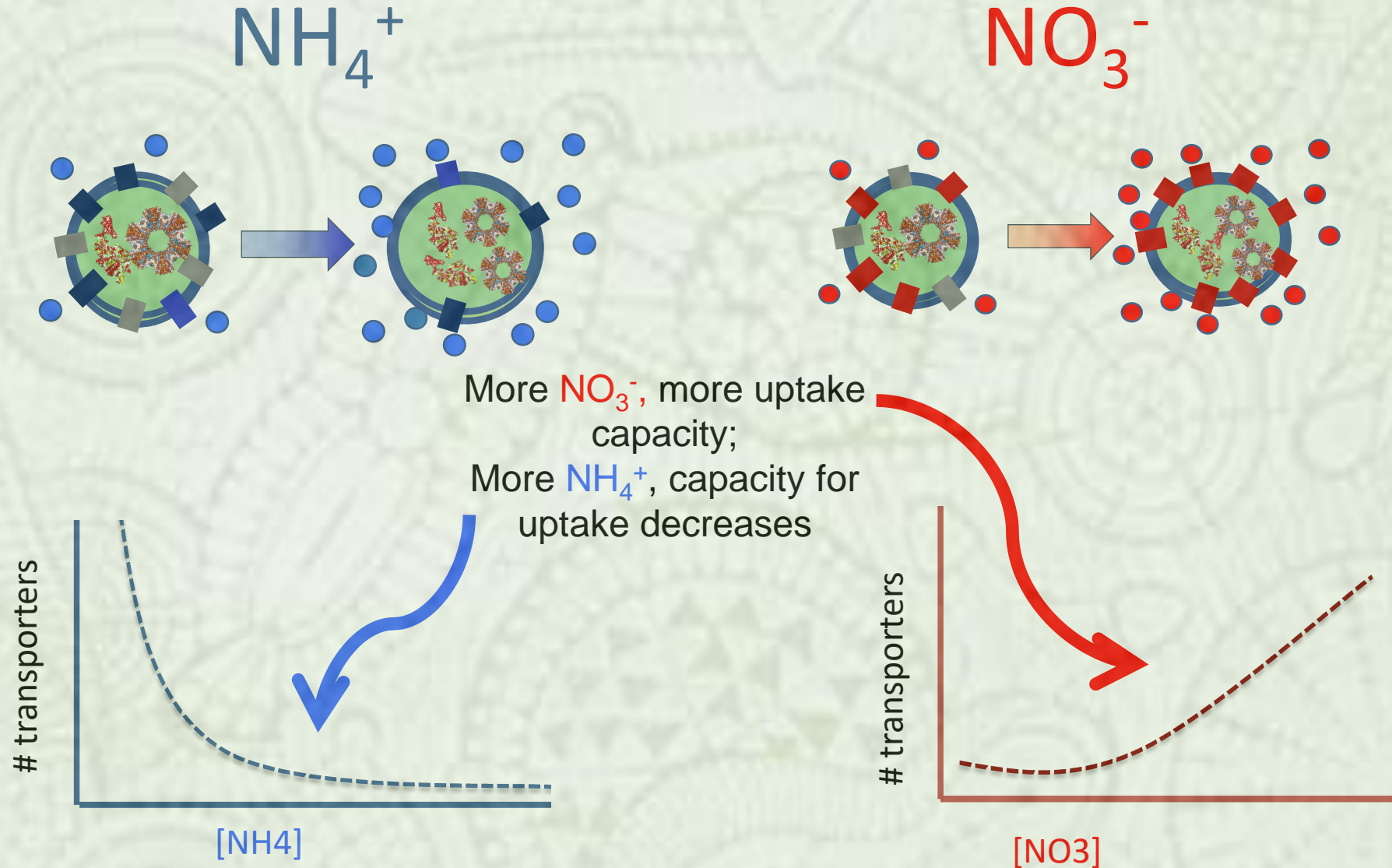


It takes more energy to use  $\text{NO}_3$

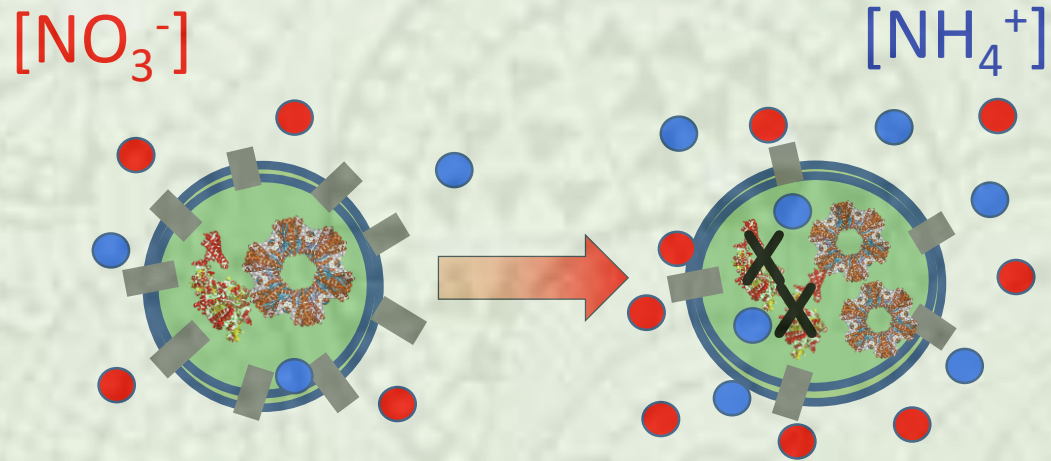
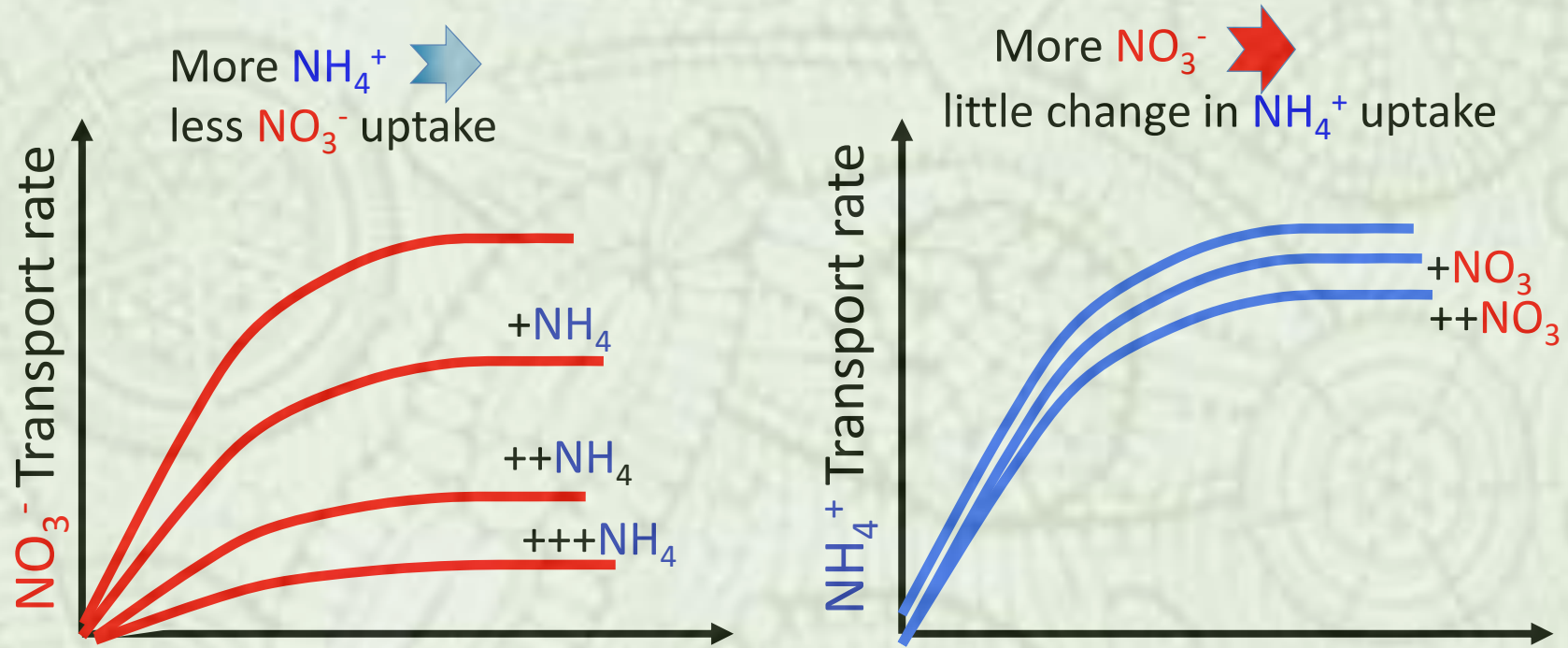
The regulation of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  assimilation is very different



The regulation of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  assimilation is very different

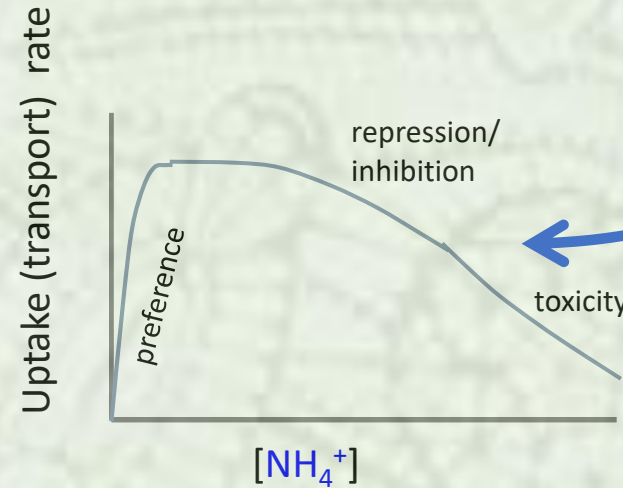


The regulation of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  assimilation is very different

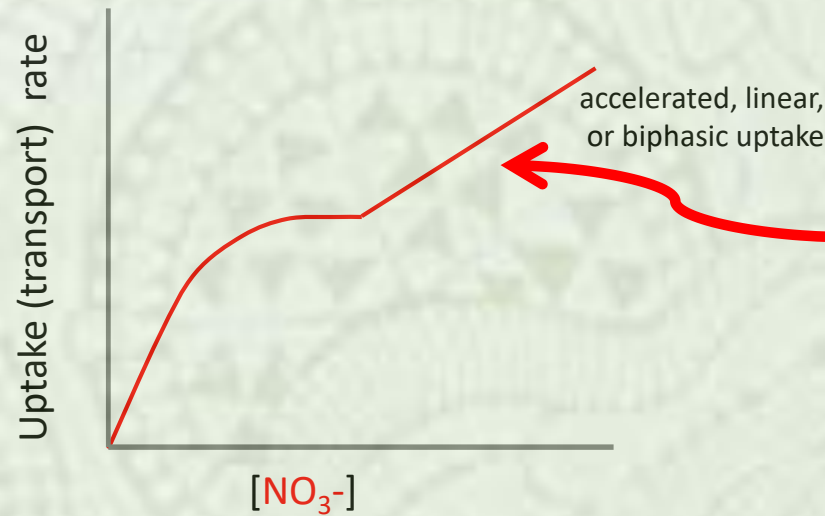


# The regulation of $\text{NH}_4^+$ and $\text{NO}_3^-$ uptake is very different

This can result in very different types of kinetics of uptake

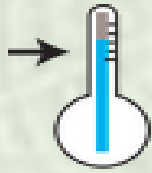


Inhibition kinetics are often observed for  $\text{NH}_4^+$  uptake



Nonsaturable (linear)  $\text{NO}_3^-$  uptake is commonly observed

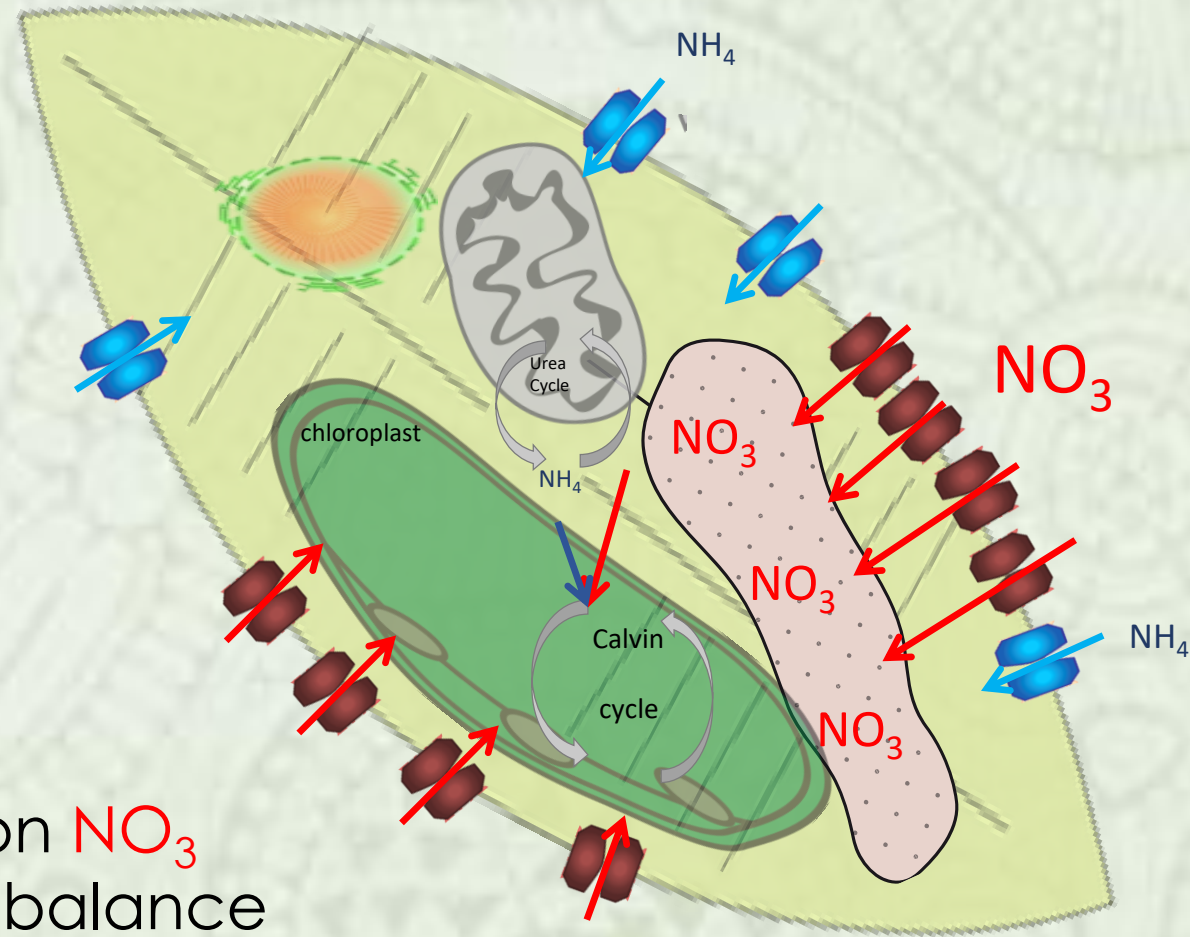
# Diatoms



Diatoms have a large capacity to take up and assimilate  $\text{NO}_3^-$

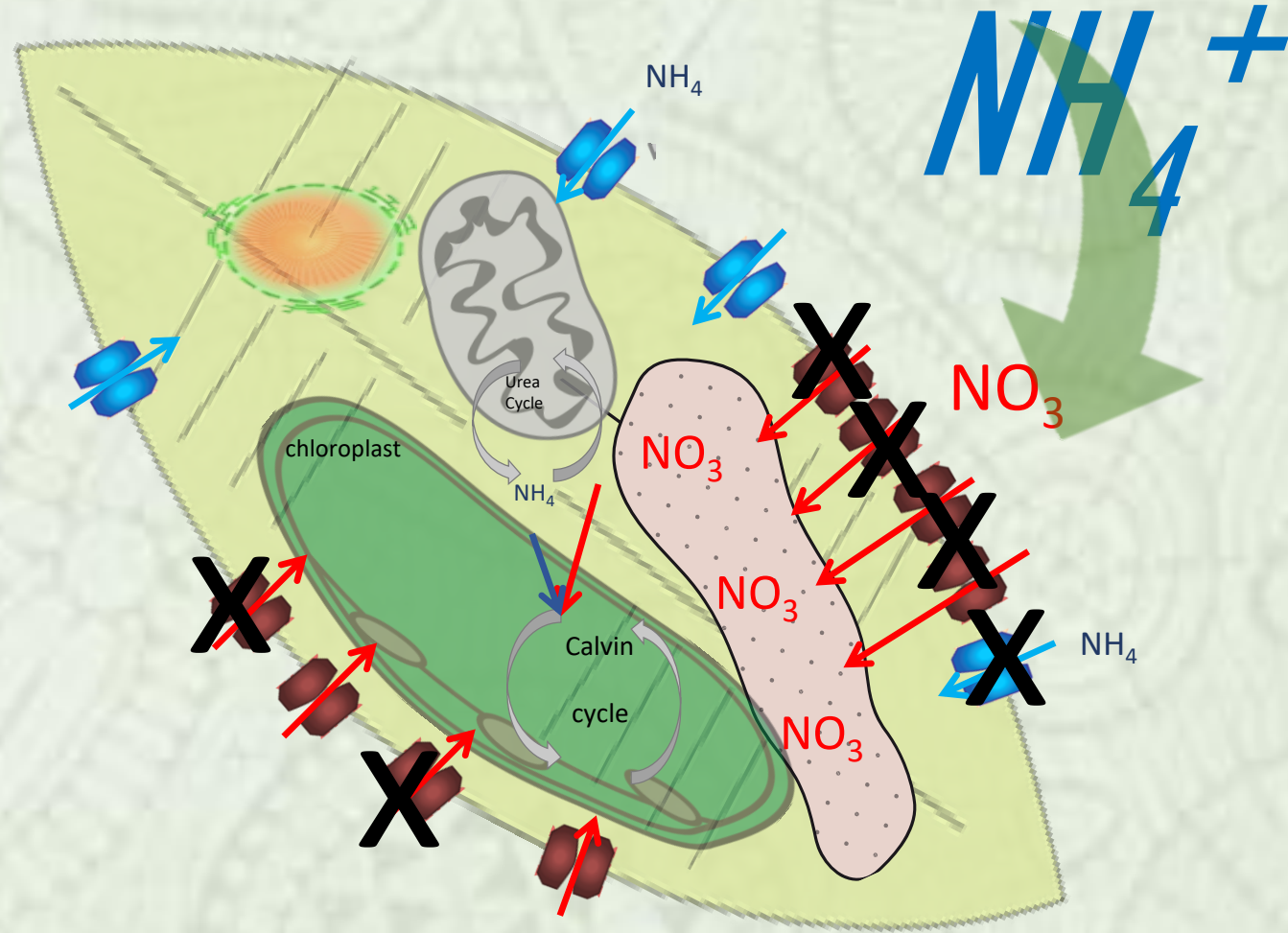
*Why?*

They depend on  $\text{NO}_3^-$  for cell energy balance



# Diatoms

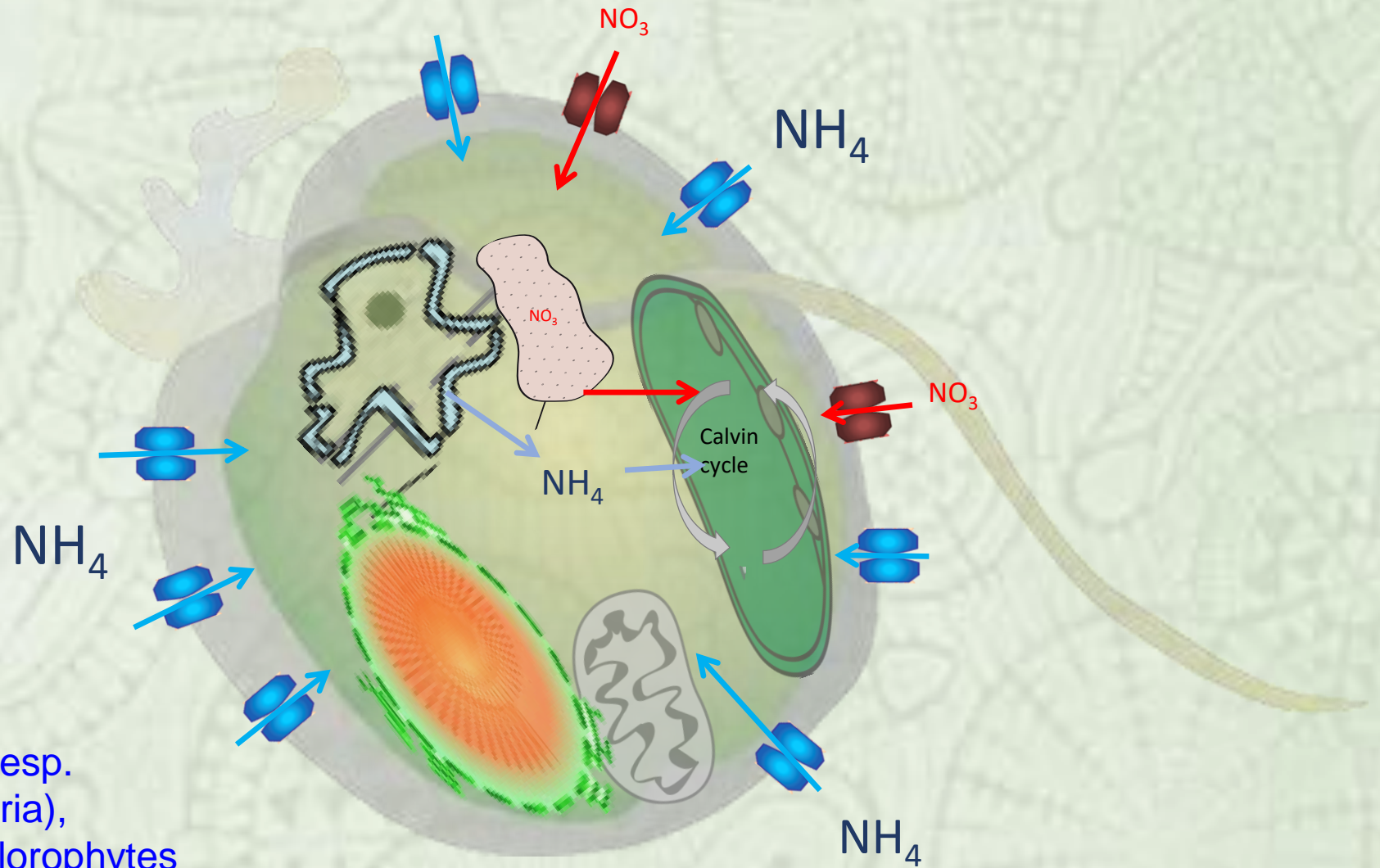
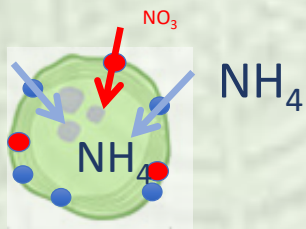
Diatoms have a large capacity to take up and assimilate  $\text{NO}_3^-$



This mechanism can be repressed by  $\text{NH}_4$  especially in cool waters (winter/spring)

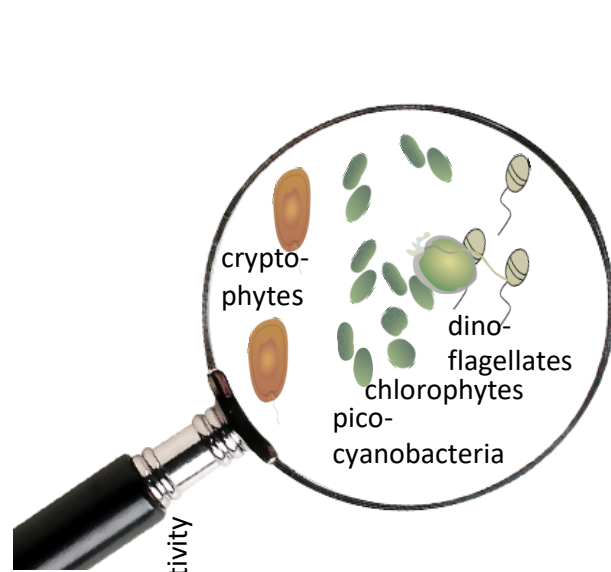
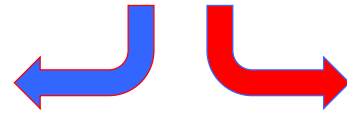
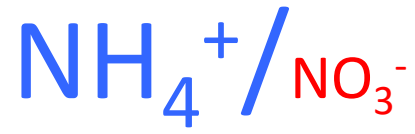
# Dinoflagellates

Picocyanobacteria

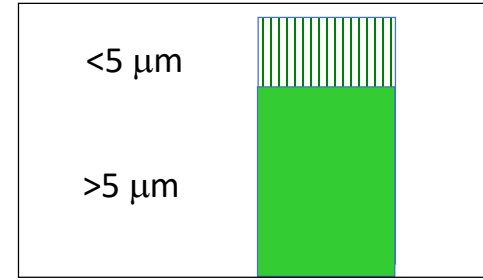
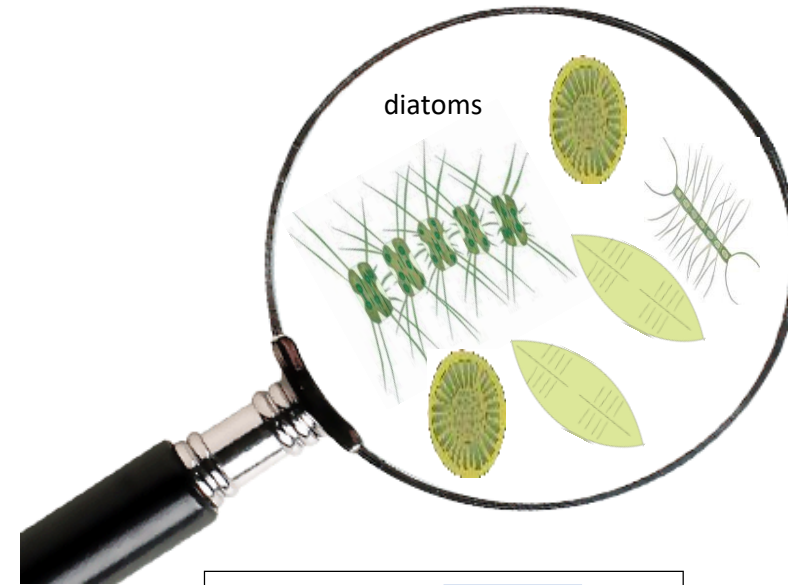
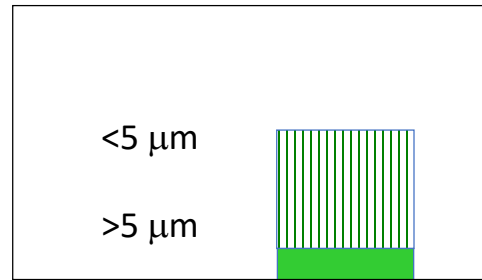


Cyanobacteria (esp. picocyanobacteria), dinoflagellates and chlorophytes have a large capacity to take up and assimilate  $\text{NH}_4$

N Inputs



Rate of productivity

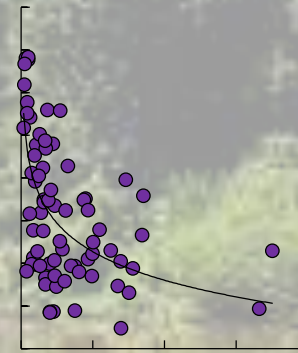
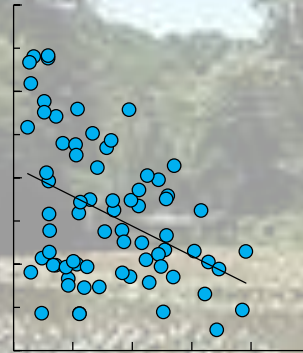
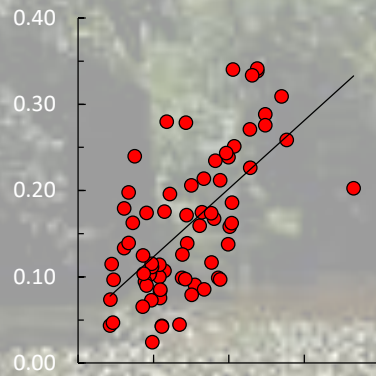


# Results from the Anacostia River



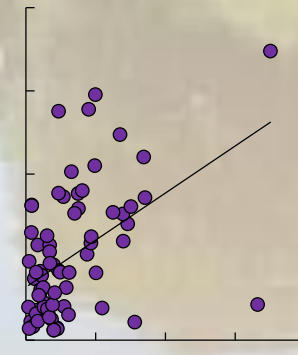
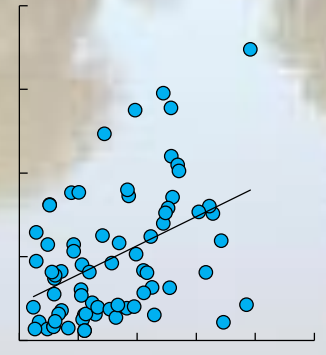
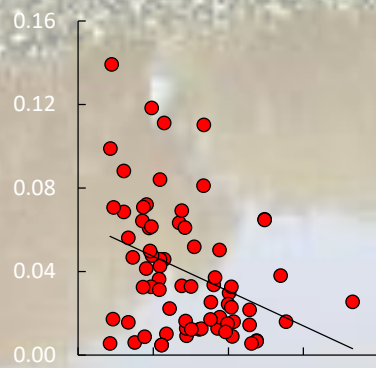
Fucoxanthin:

chlorophyll *a*



Zeaxanthin:

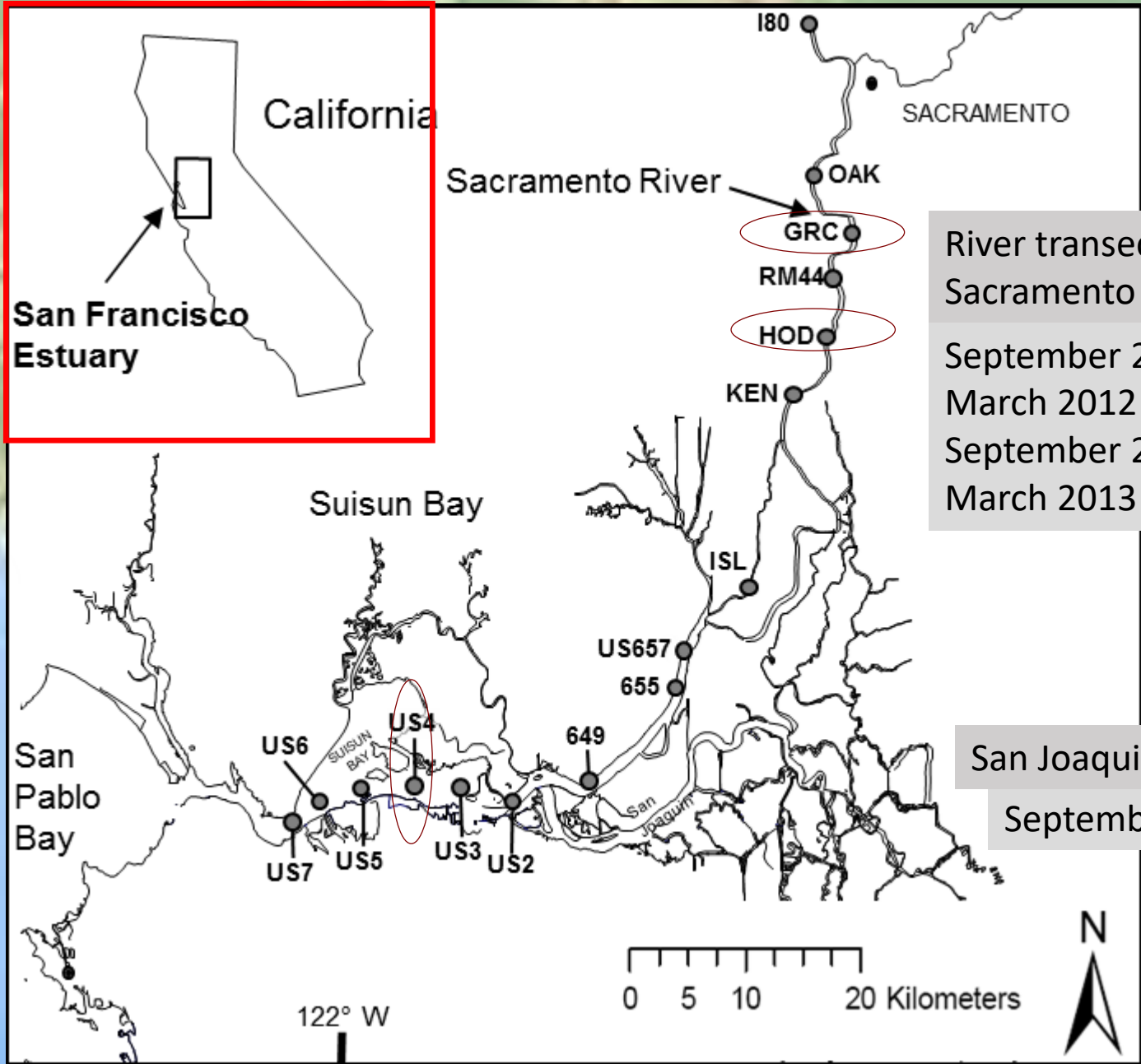
chlorophyll *a*



$\text{NO}_3^-$  ( $\mu\text{M}$ )

$\text{NH}_4^+$  ( $\mu\text{M}$ )

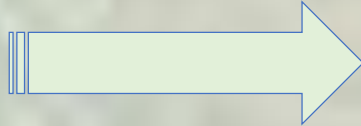
$\text{NH}_4^+:\text{NO}_3^-$  (molar)



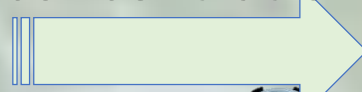
River transects:  
Sacramento to Suisun  
September 2011  
March 2012  
September 2012  
March 2013

San Joaquin sampling  
September 2013

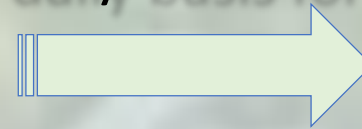
Sample collection



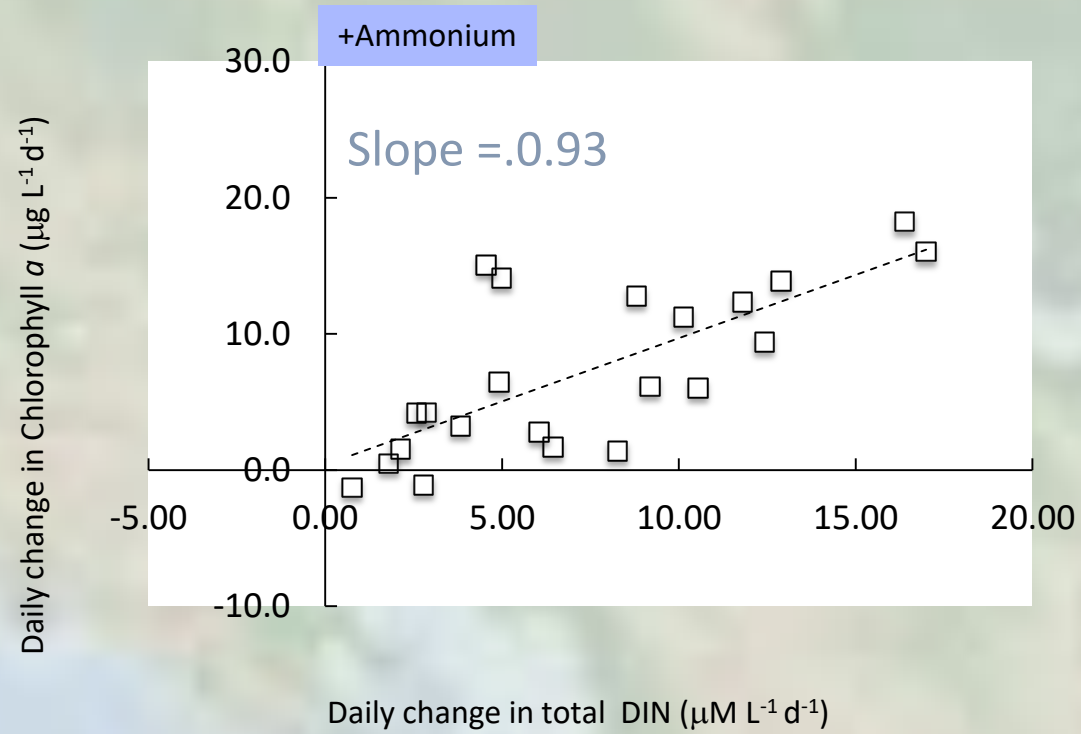
Enrich with different forms of N (same concentration)



Measure processes and biomass changes on daily basis for ~5 days



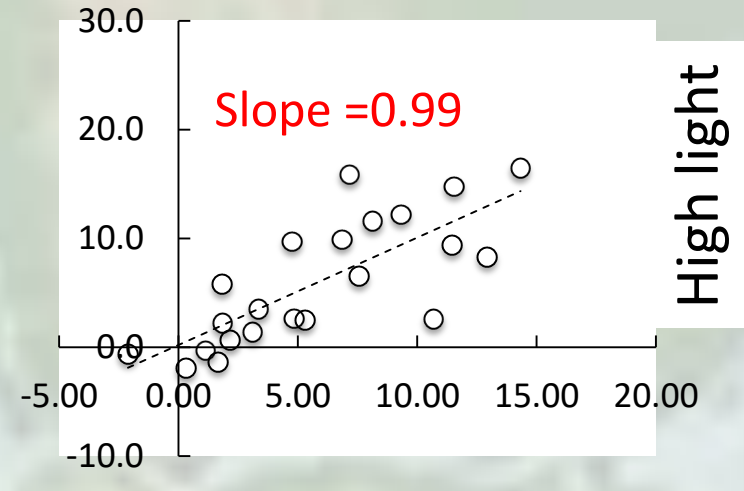
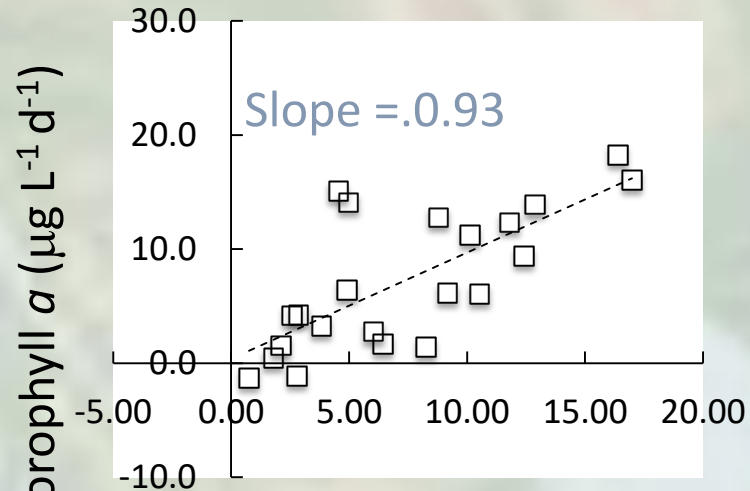
# Data from all sites, seasons compared by treatment



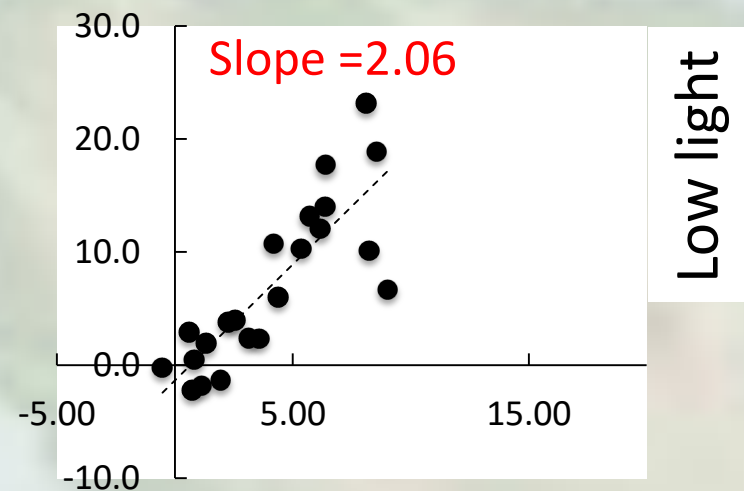
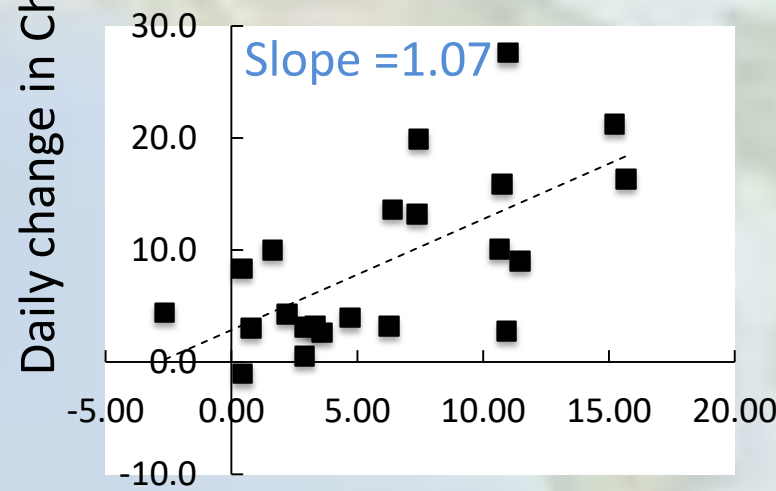
Note- nutrient changes are shown with inverse sign

+Ammonium

+Nitrate



High light



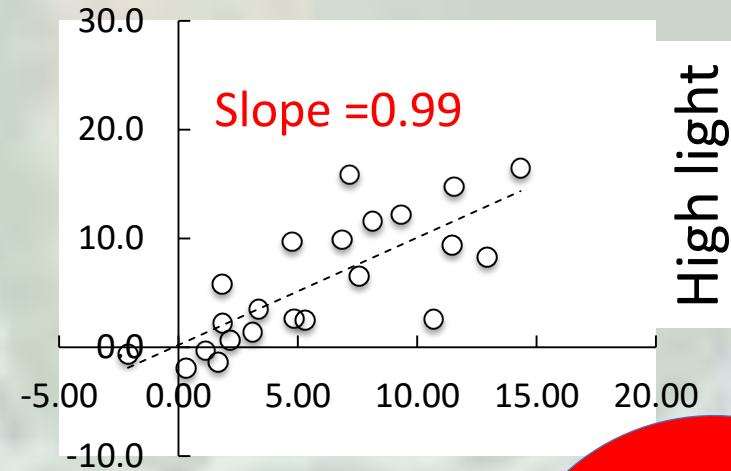
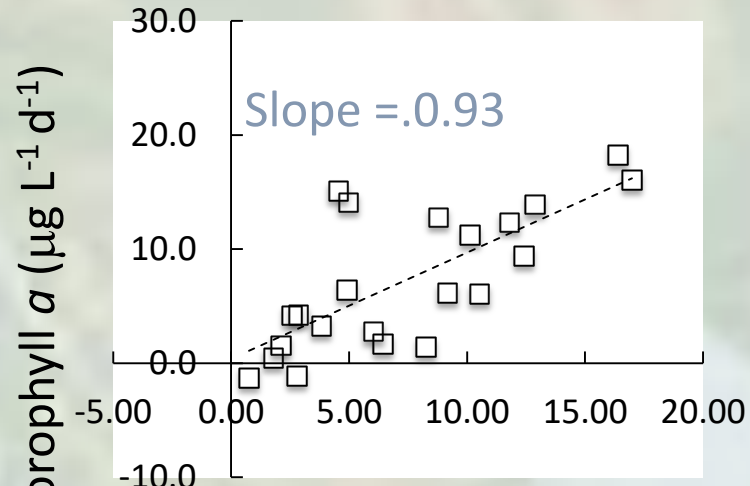
Low light

Daily change in total DIN ( $\mu\text{M L}^{-1} \text{d}^{-1}$ )

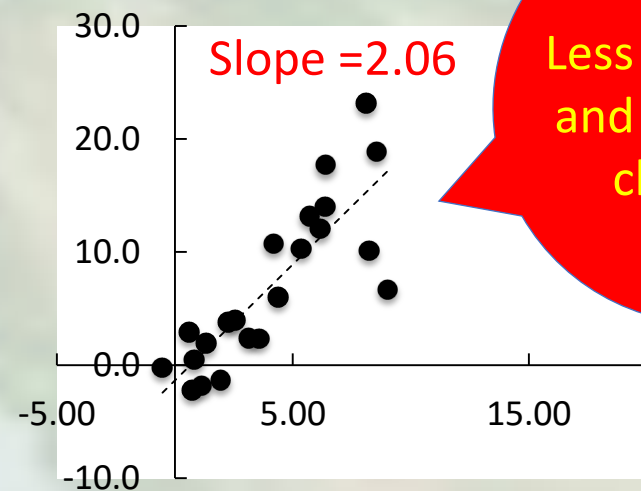
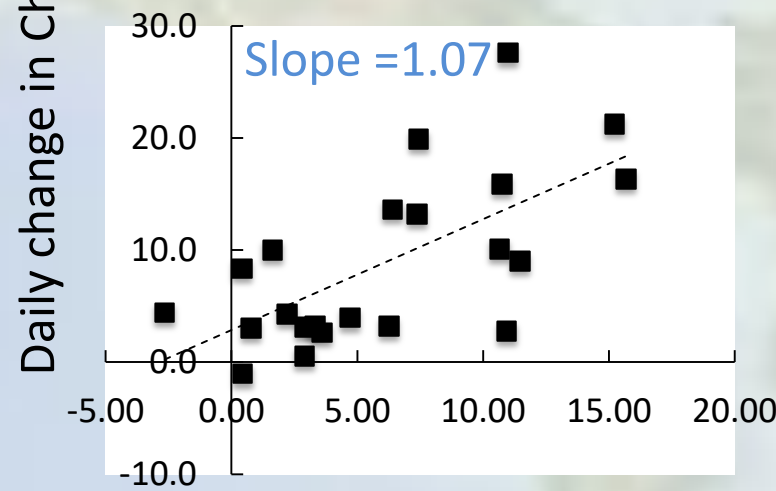
Note- nutrient changes are shown with inverse sign

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High light

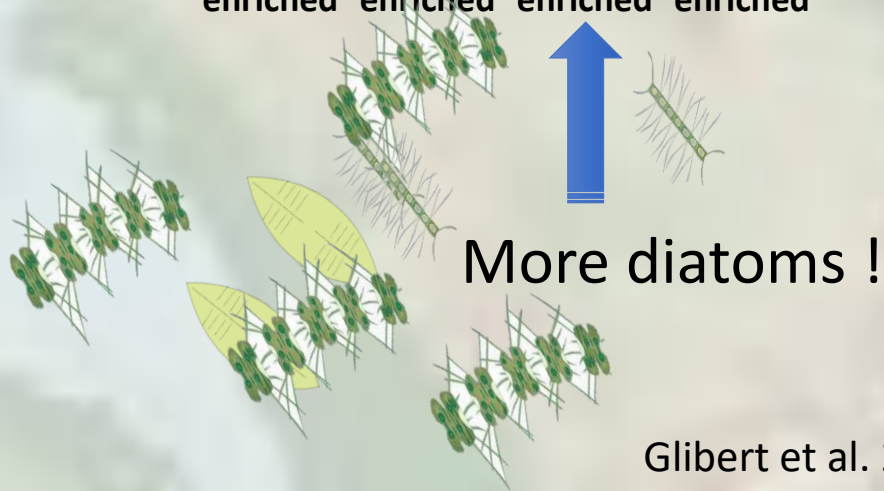
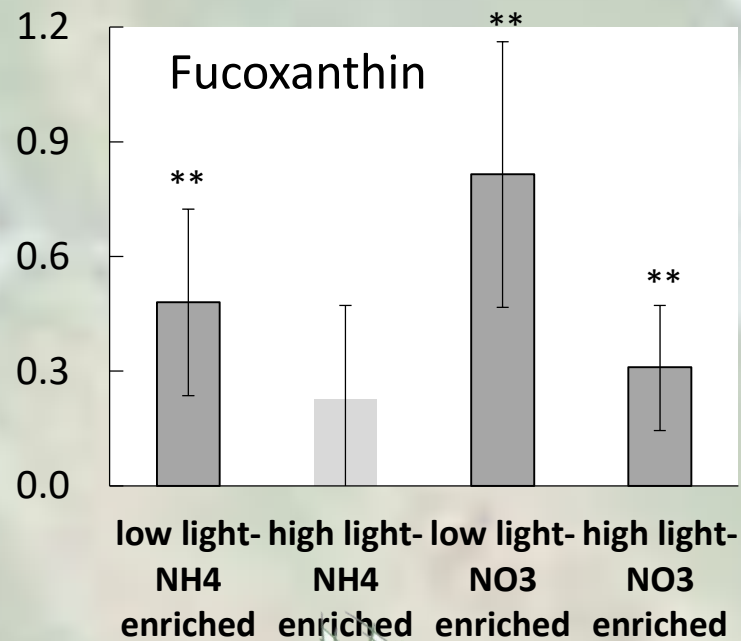
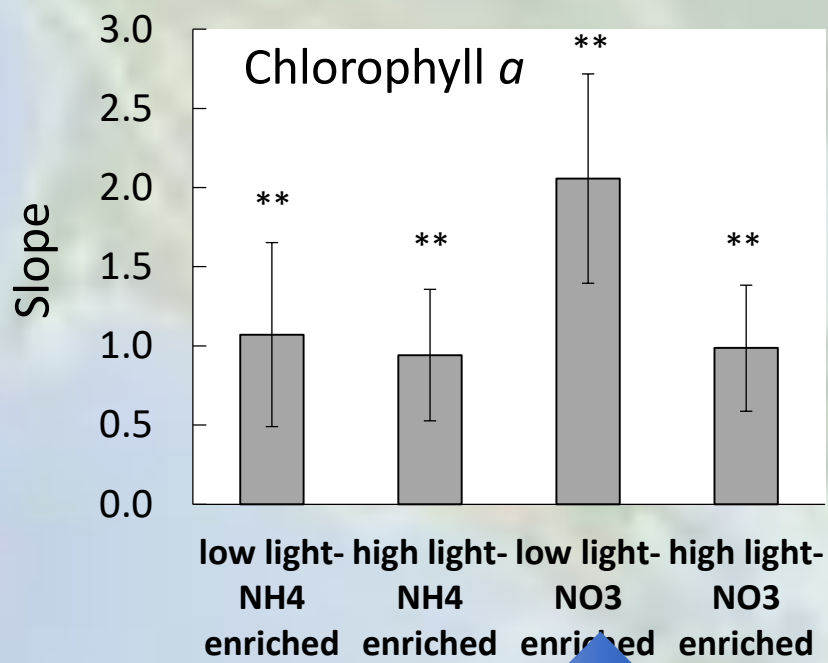


Less variability and twice the chl yield

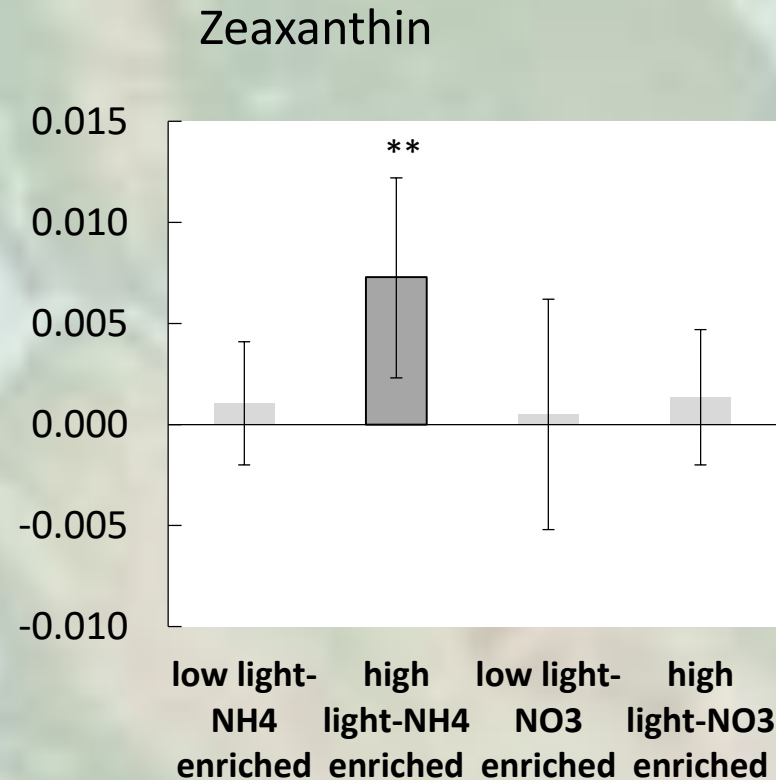
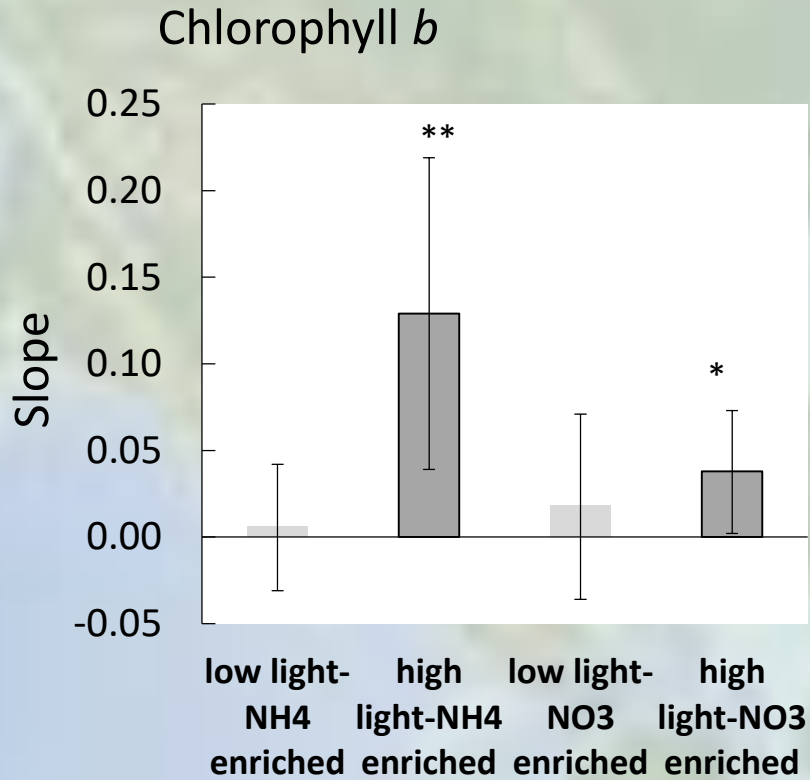
Daily change in total DIN ( $\mu\text{M L}^{-1} \text{d}^{-1}$ )

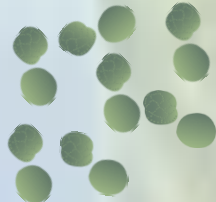
Note- nutrient changes are shown with inverse sign

More diatoms produced under  $\text{NO}_3^-$  enrichment (and low light)

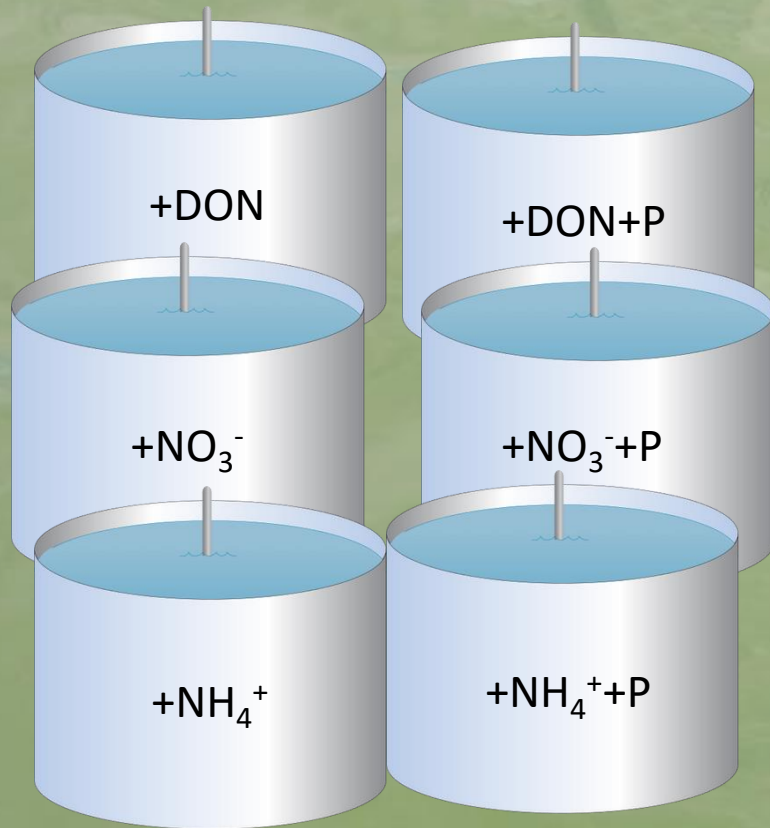


# More cyanobacteria produced under $\text{NH}_4^+$ enrichment (and high light)



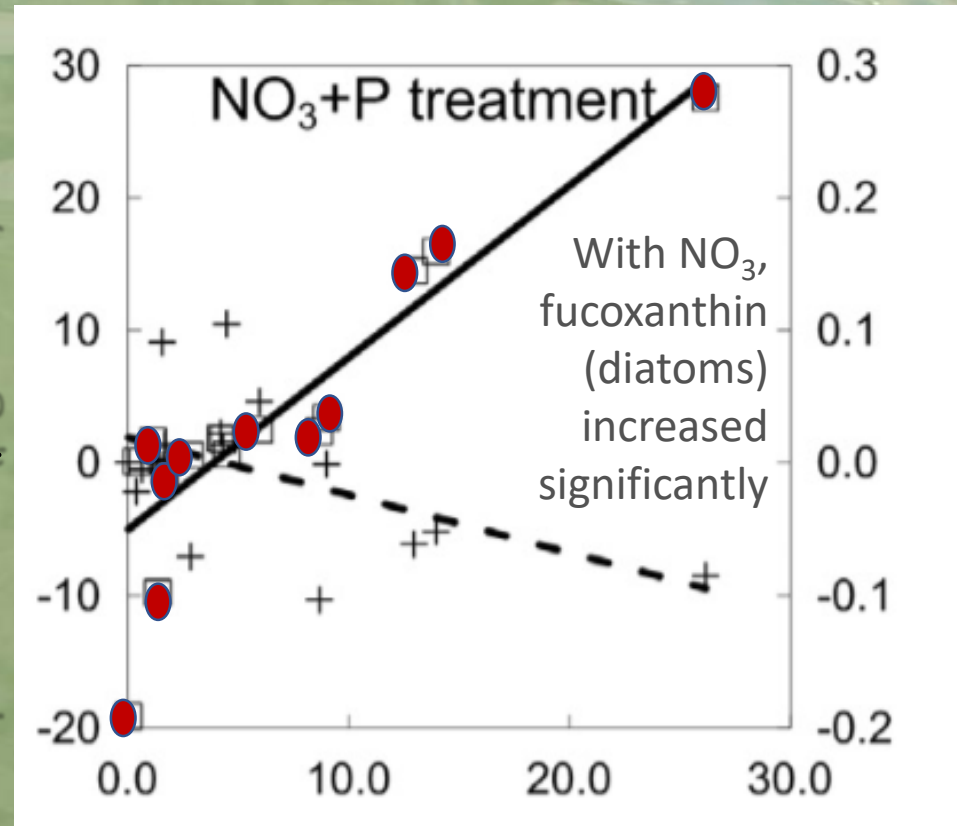
↑  
  
More cyanobacteria!





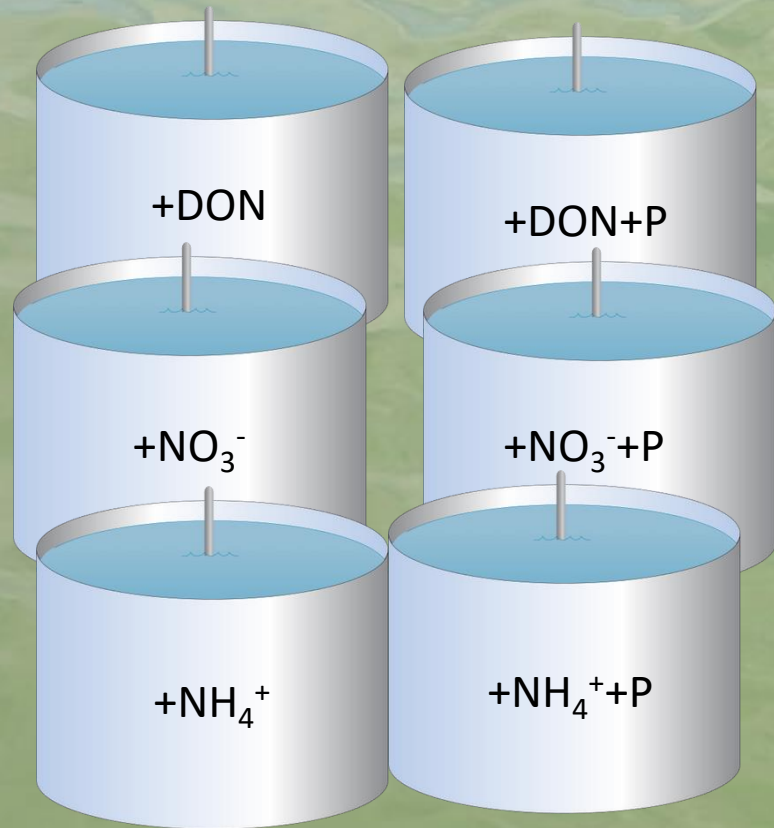
1000 Liter mesocosms- 5 day experiments  
 Experiments run over multiple seasons and years

Daily change in fucoxanthin and peridinin ( $\mu\text{g L}^{-1} \text{d}^{-1}$ )



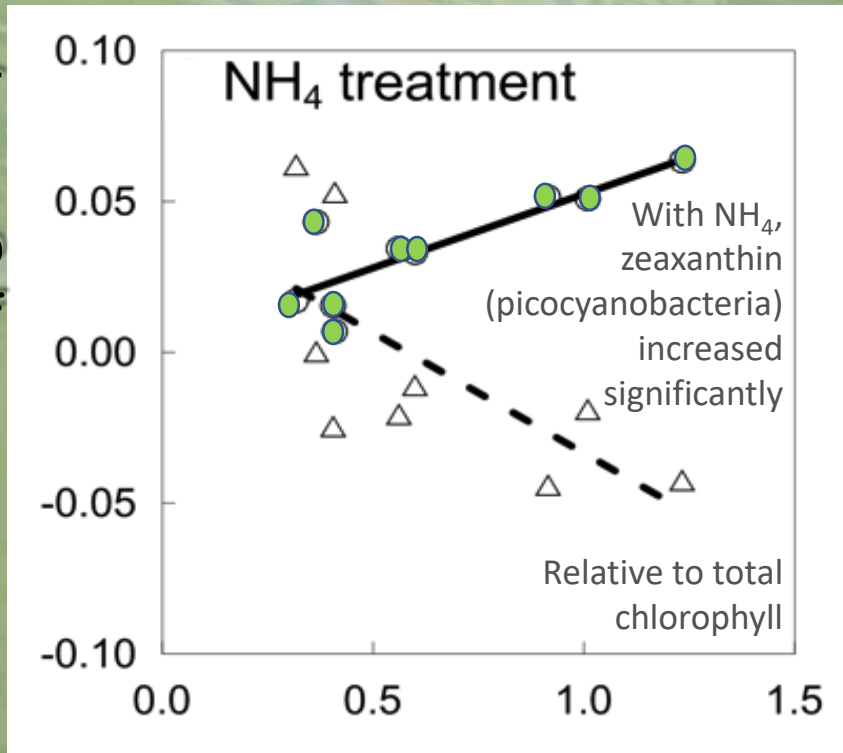
Daily change in chlorophyll *a* ( $\mu\text{g L}^{-1} \text{d}^{-1}$ )

Comparable results from Florida Bay



1000 Liter mesocosms  
 Experiments run over  
 multiple seasons and  
 years

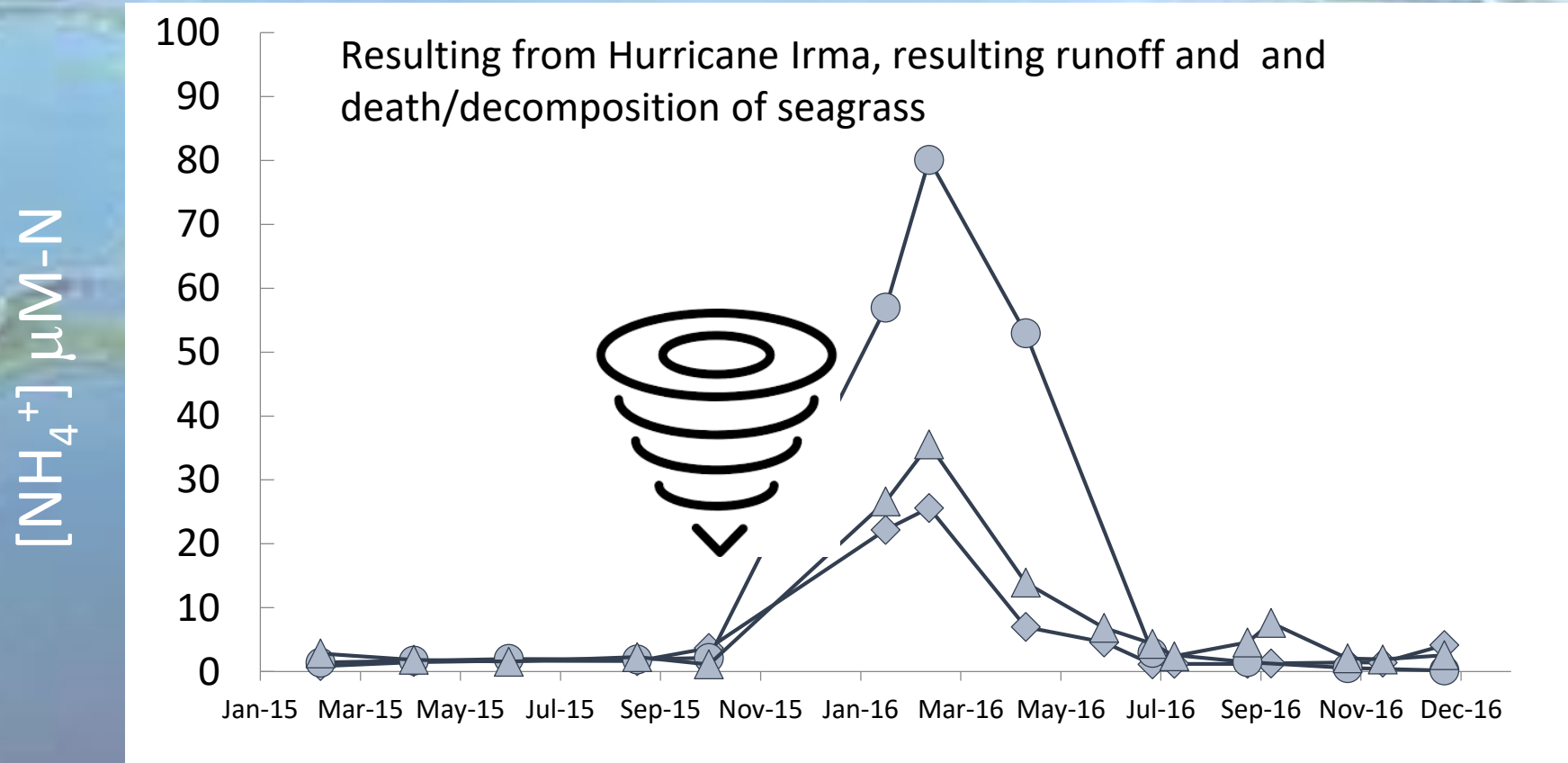
Daily change in zeaxanthin  
 and alloxanthin ( $\mu\text{g L}^{-1} \text{d}^{-1}$ )



Daily change in chlorophyll  $a$  ( $\mu\text{g L}^{-1} \text{d}^{-1}$ )

Comparable results from Florida Bay

A natural enrichment experiment in Florida Bay:  
Extremely high concentrations of  $\text{NH}_4^+$



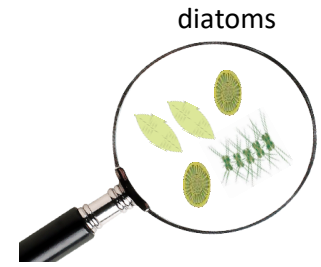
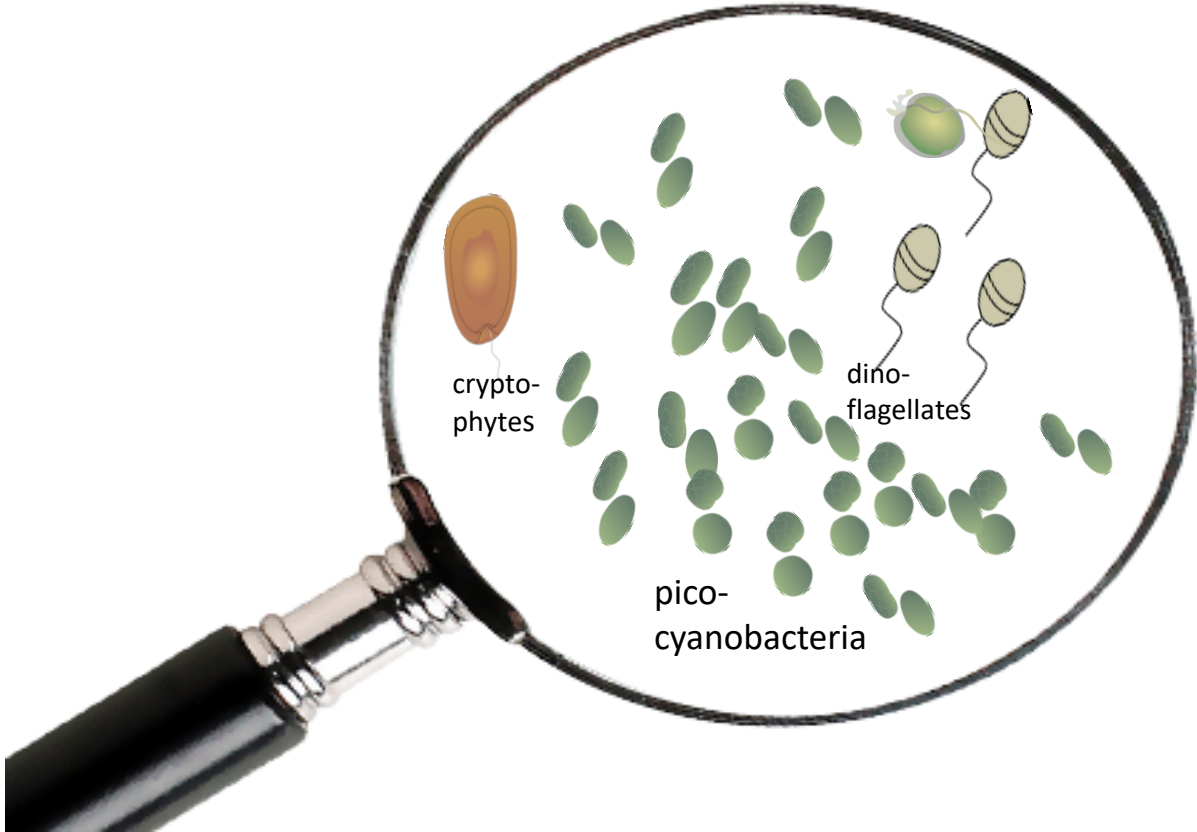
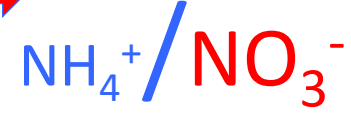
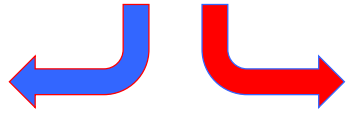
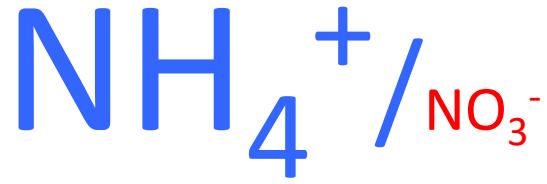
Florida Bay

2015-2016

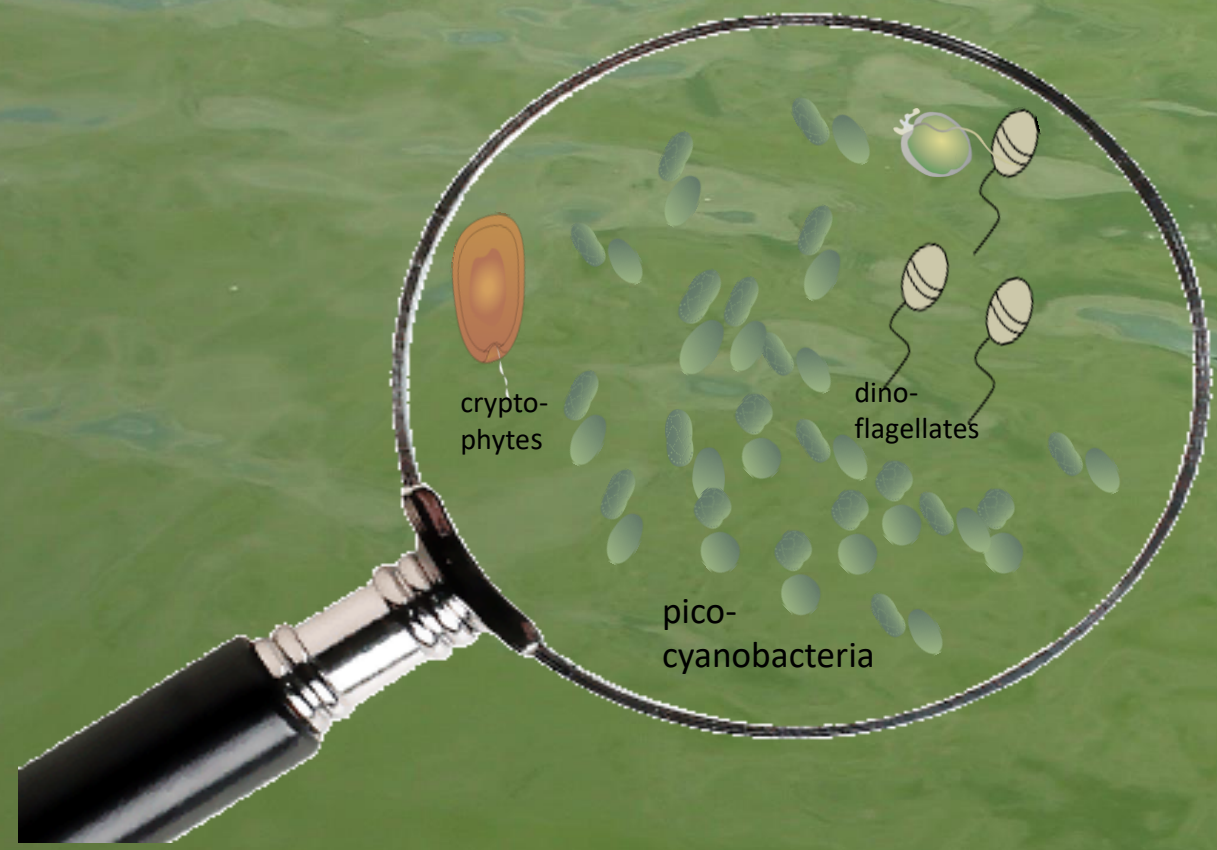


blooms developed,  
dominated by the picoplankton  
*Synechococcus*

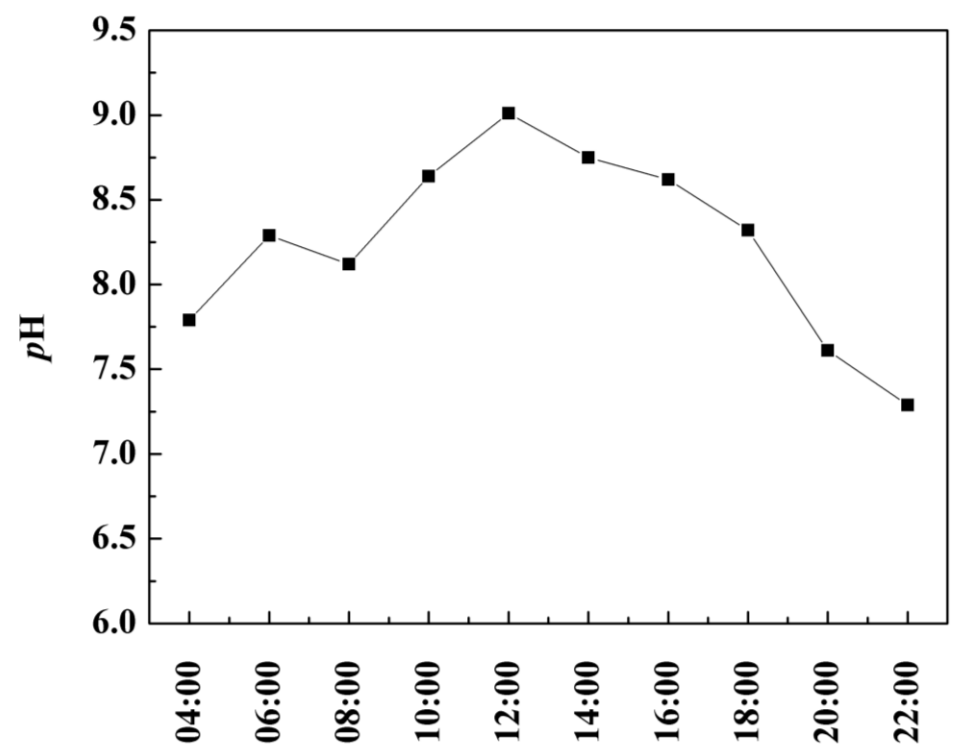
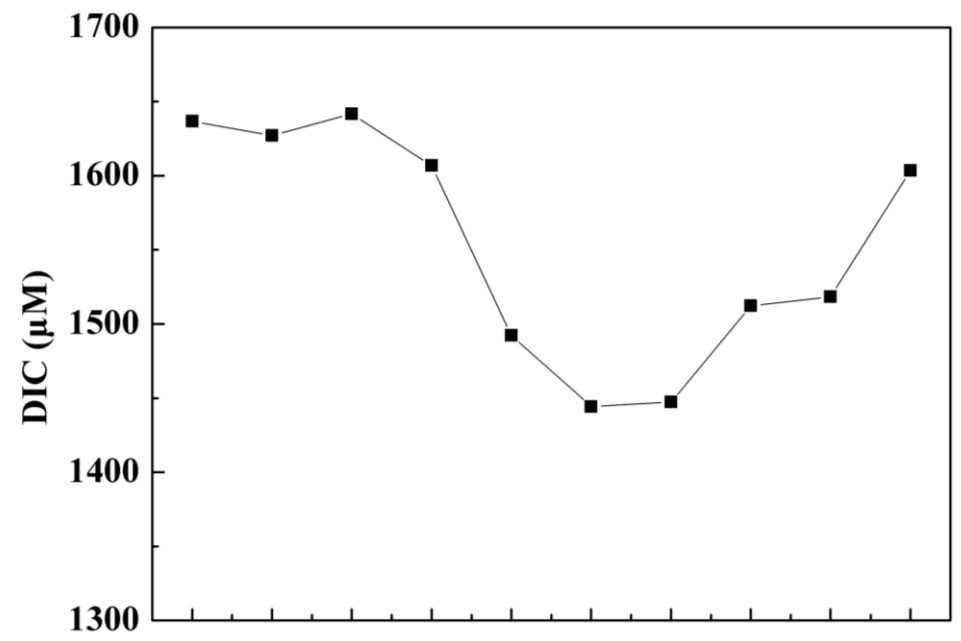
N Inputs



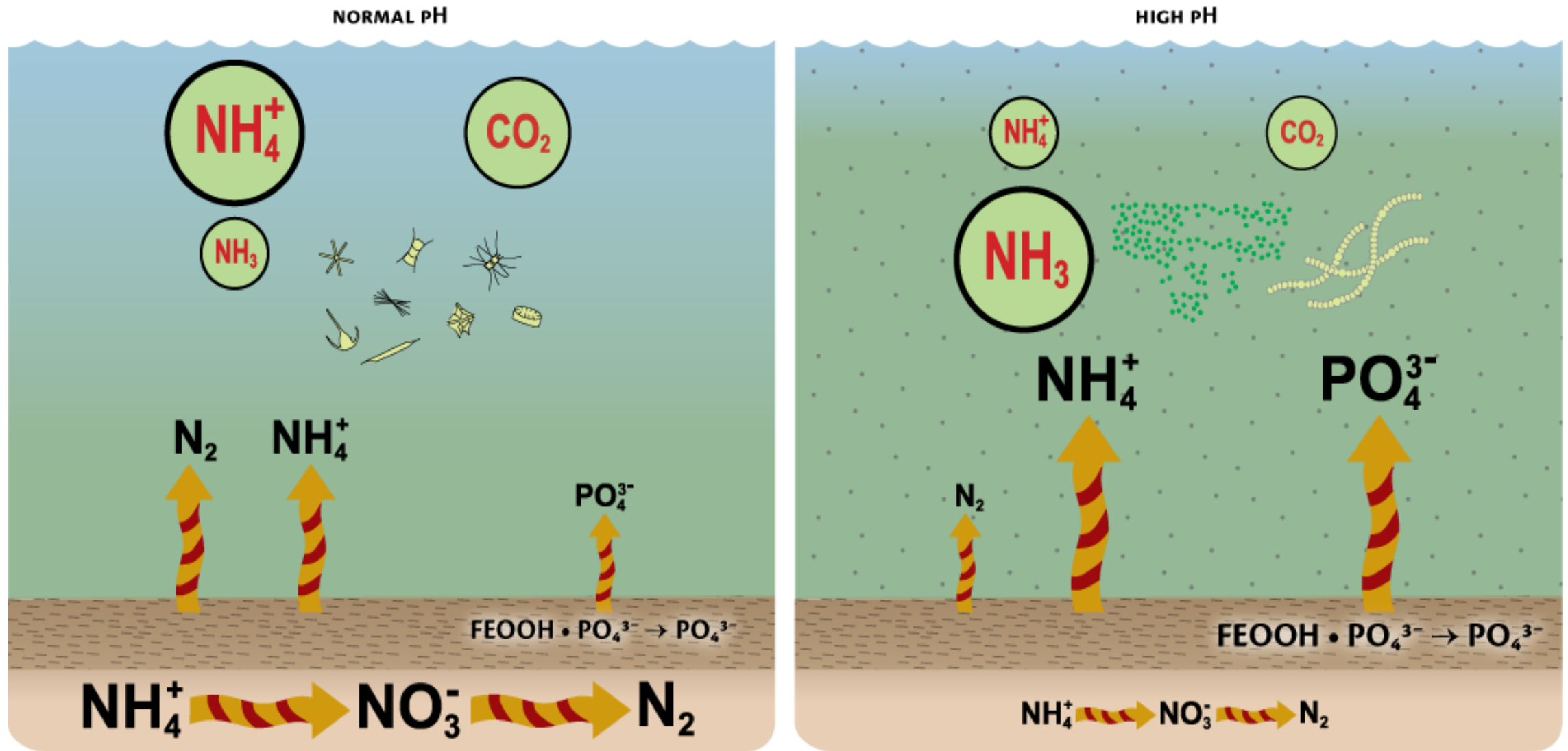
# Algal blooms alter pH through daily DIC drawdown



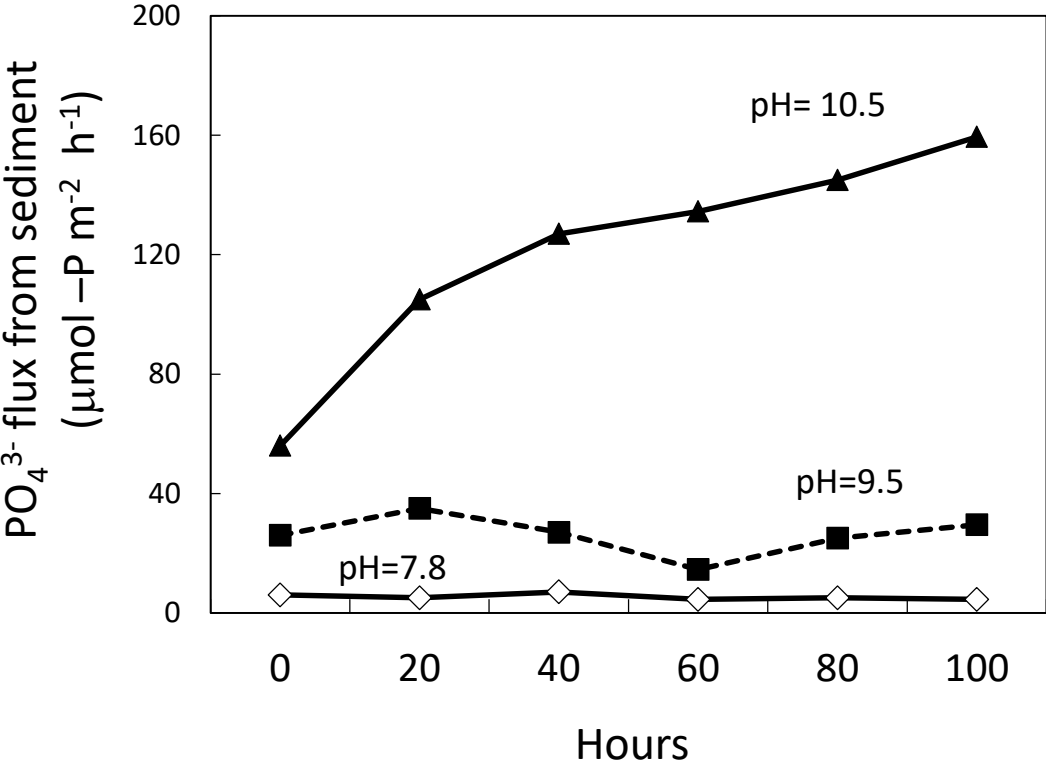
Yang et al. 2017



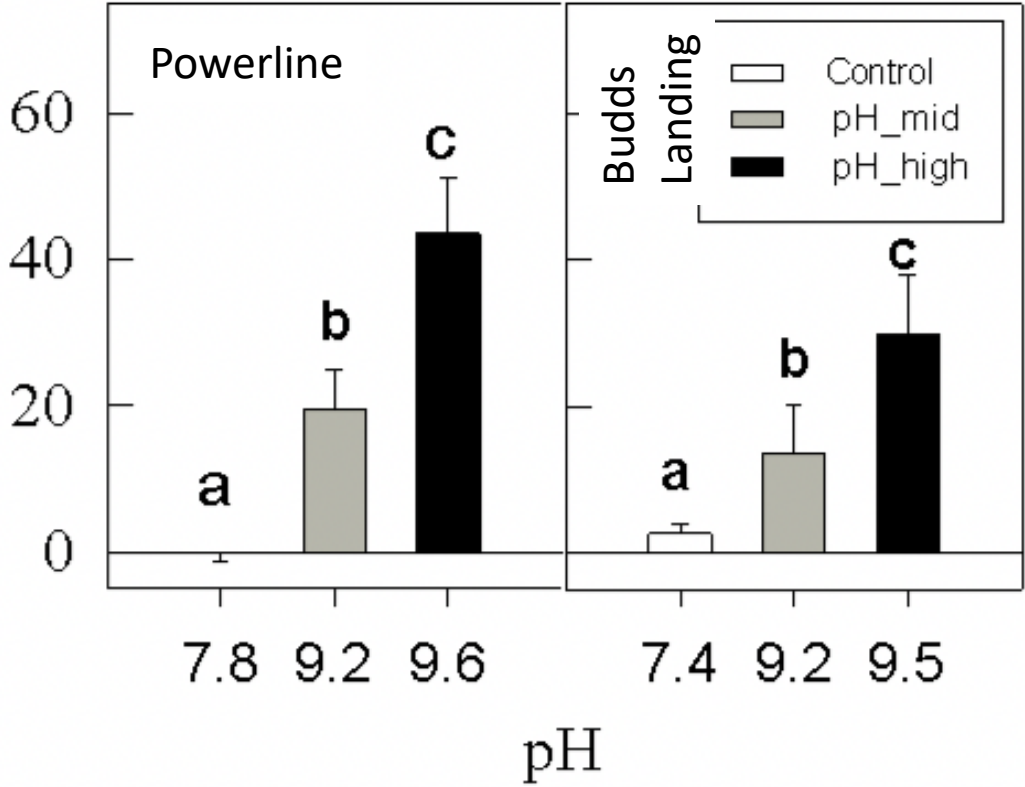
# pH alters nutrient efflux



Exchanges between bound P and soluble reactive P can be **fast**



Bailey et al. 2006



Gao et al. 2012

As we target P for nutrient reduction,  
the result is large increases in N:P

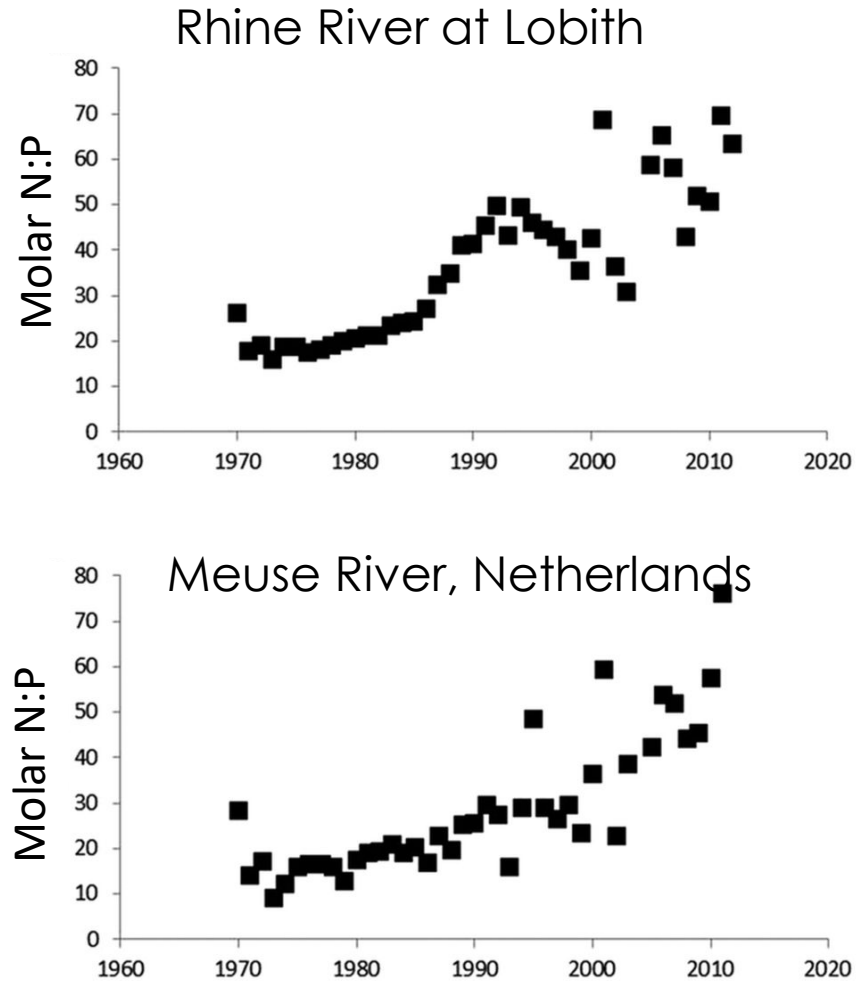
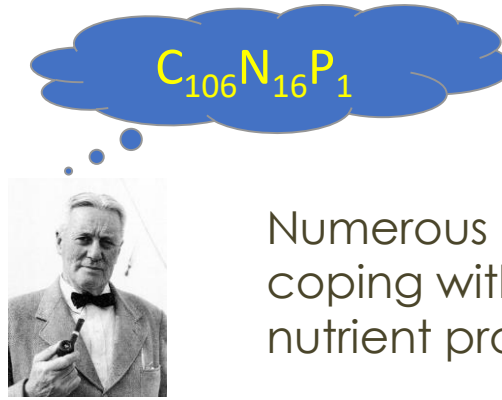
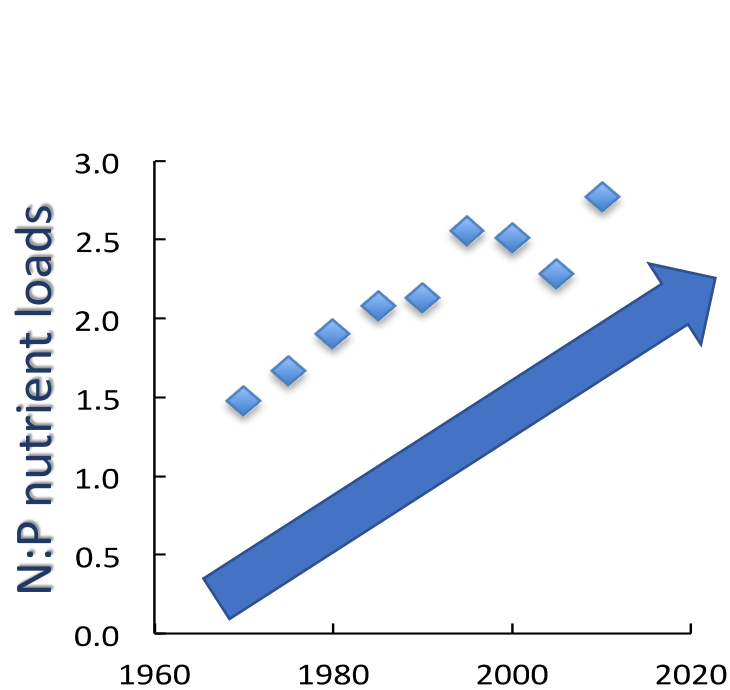


Figure from Bouwman et al. 2017

Map from Marcus et al. 2013

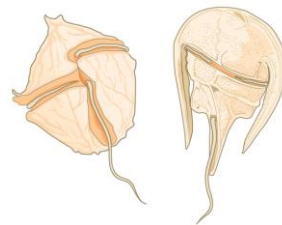


Numerous “strategies” for coping with imbalanced nutrient proportions:

Cells may substitute P-rich lipids

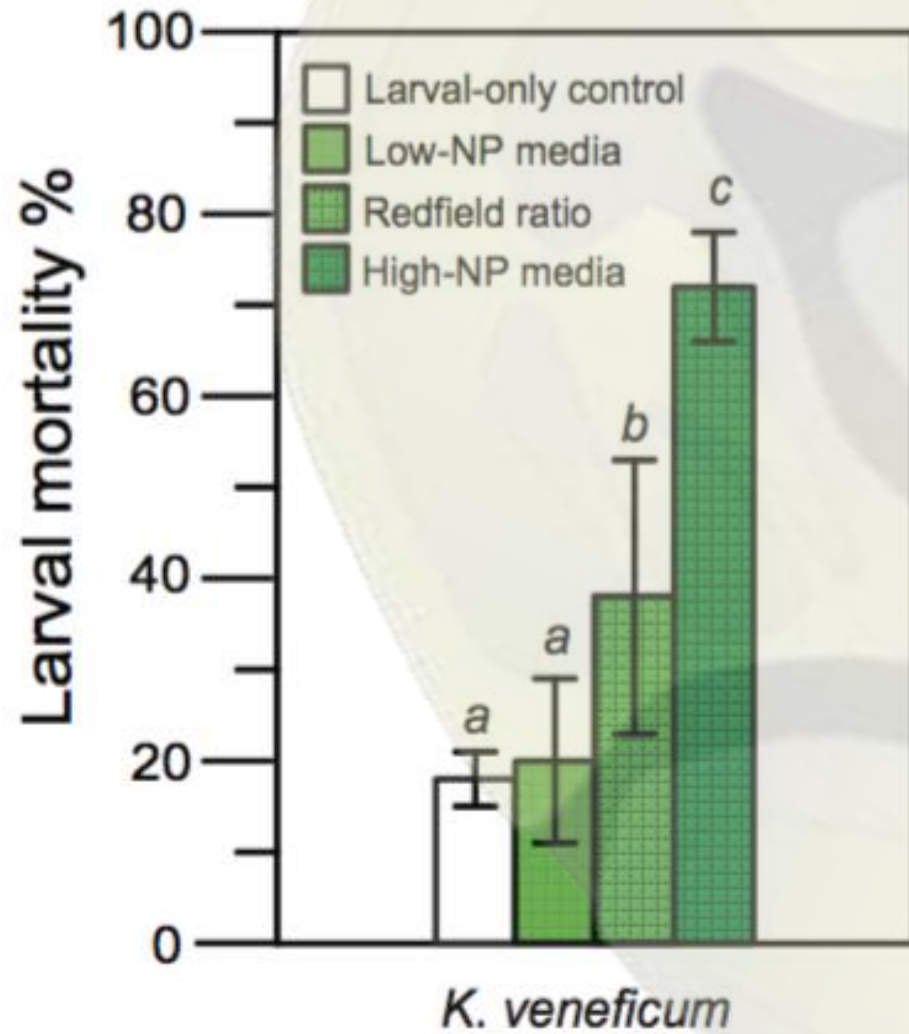
Cells may access alternate substrates- such as organic nutrients **or particulates**

Cells may dissipate the excess nutrient- some of these compounds are C, or N-rich toxins



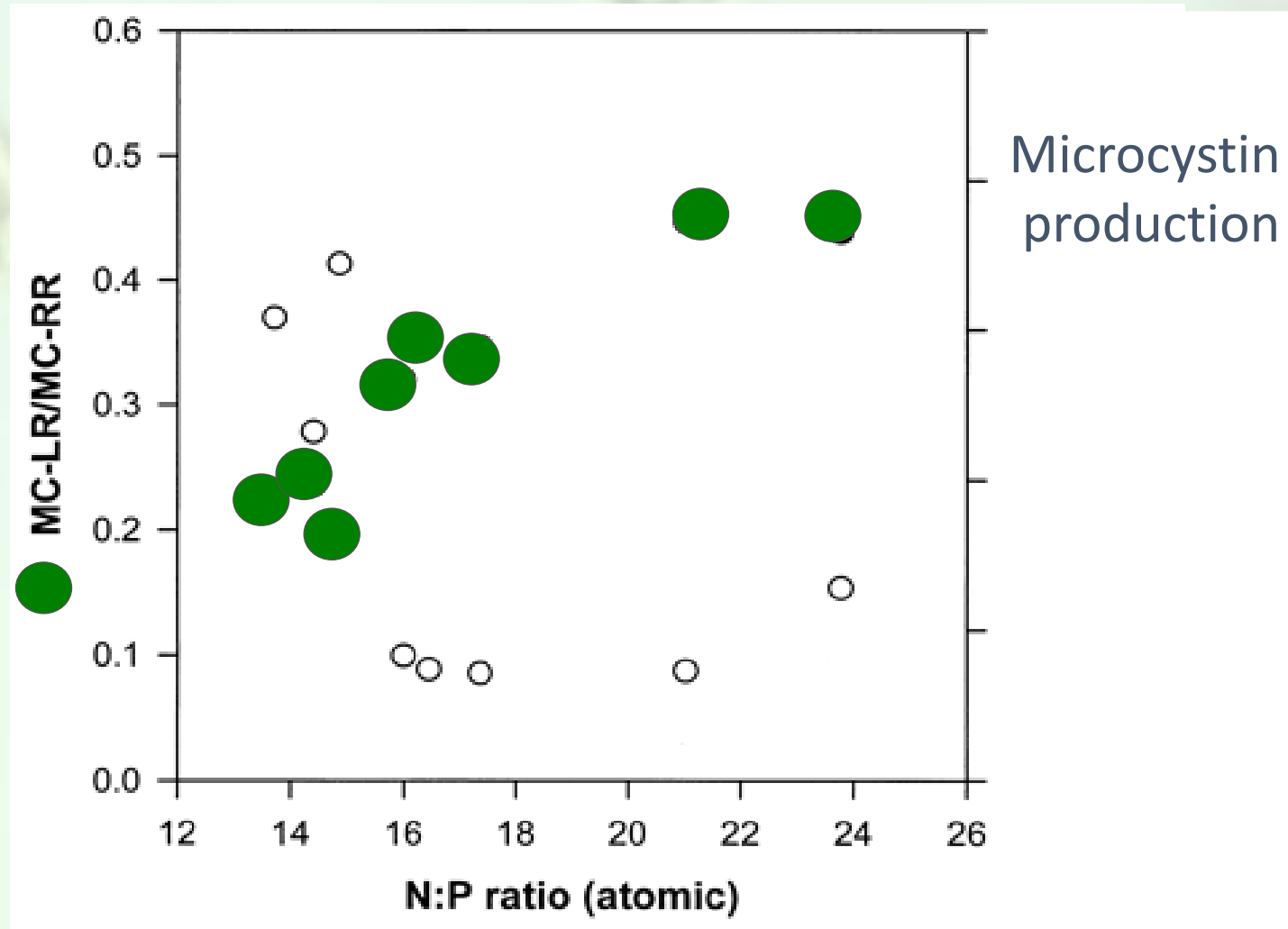
Glibert and Burkholder 2011.

*Rise of the mixotrophs  
(and HABs!)*

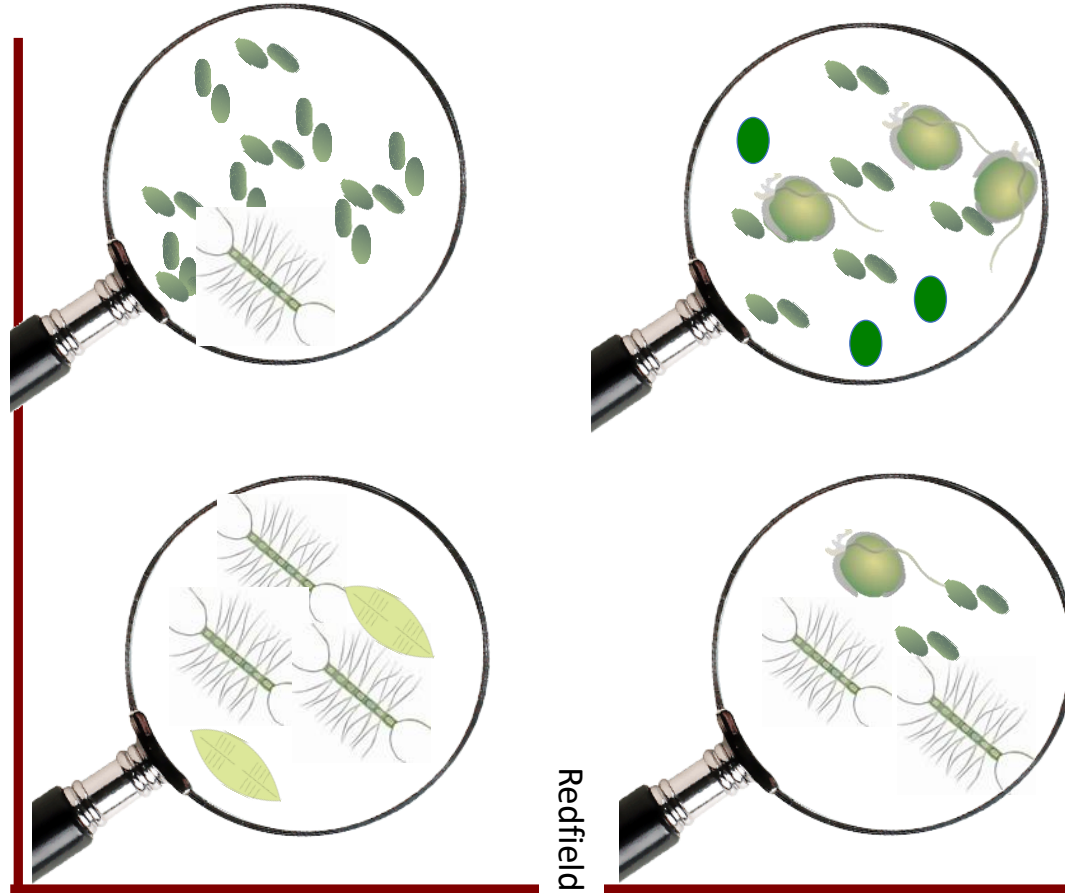
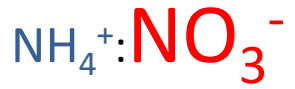
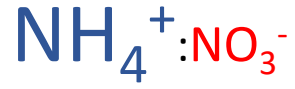


The mixotroph *Karlodinium veneficum* is more toxic at high N:P (oyster larvae bioassay)

# *Microcystis* produces more toxin at high N:P




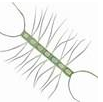


*Nutrient forms and ratios  
set the biodiversity trajectory*

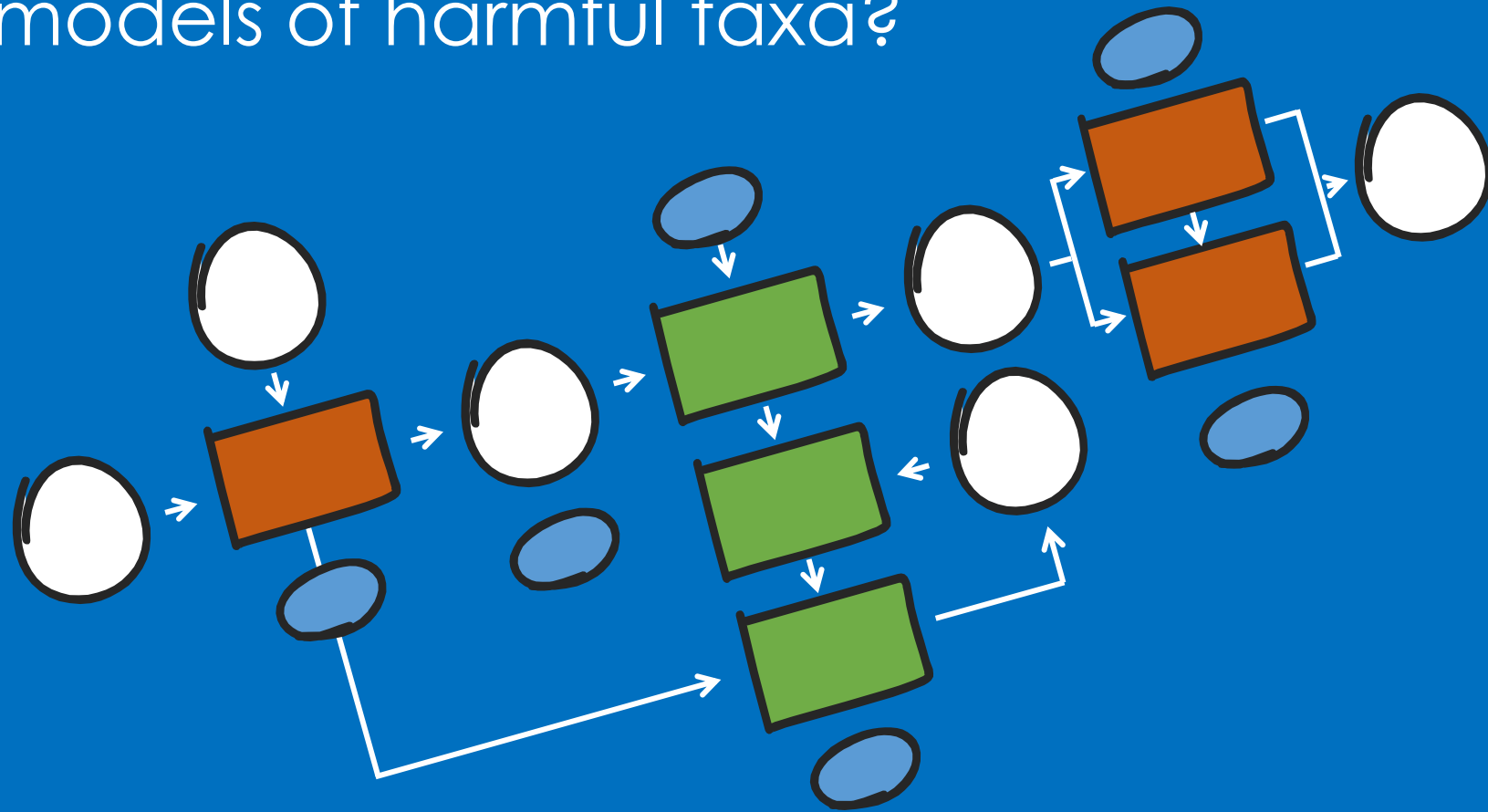


N:P

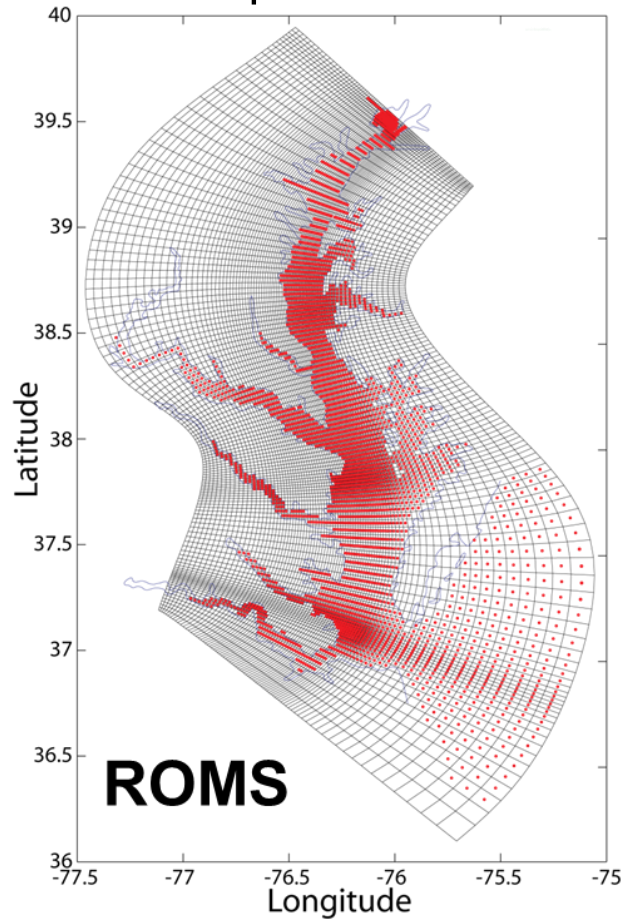
N:P

	Picocyanobacteria		Chlorophytes
	Dinos		Diatoms

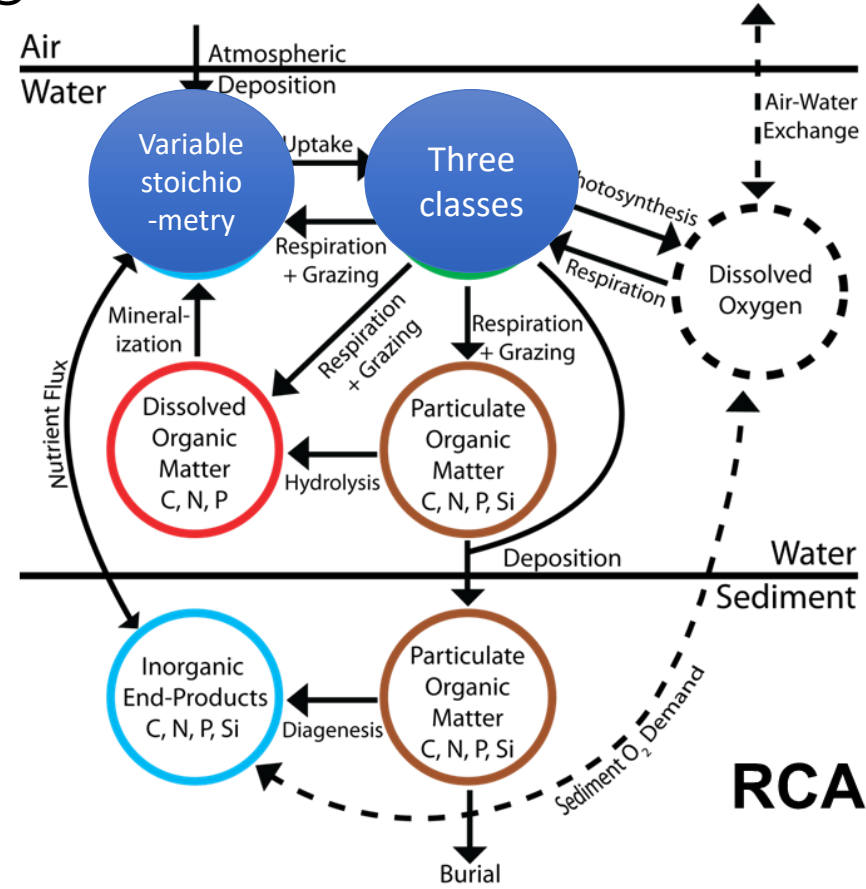
How can we incorporate nutrient proportions and forms in models of harmful taxa?



# Building spatially explicit HAB models, developed on a biogeochemical framework



- Forced by freshwater from 8 major tributaries
- Resolution = 80 cells east-west, 120 cells north-south  
20 vertical layers, 68,000 Cells



- 23 state variables
- Coupled sediment biogeochemical model
- External loads from 8 tributaries, point sources, atmospheric deposition
- Calibrated to water-column concentrations, sediment and water-column metabolic rates

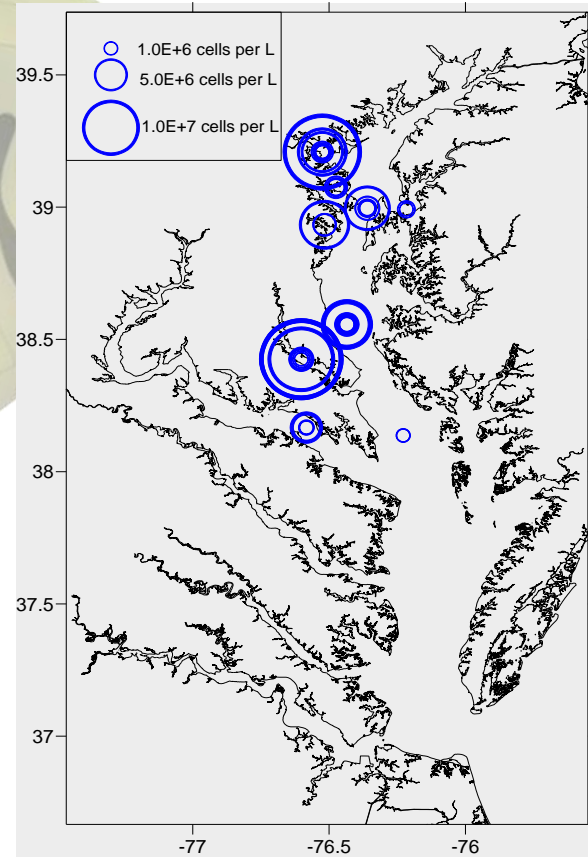
*Building on years of application of this model for predicting hypoxia*

*Karlodinium* and *Prorocentrum* are common in the mid-upper reaches of Chesapeake Bay forming visible blooms and contributing to fish kills and other ecological problems

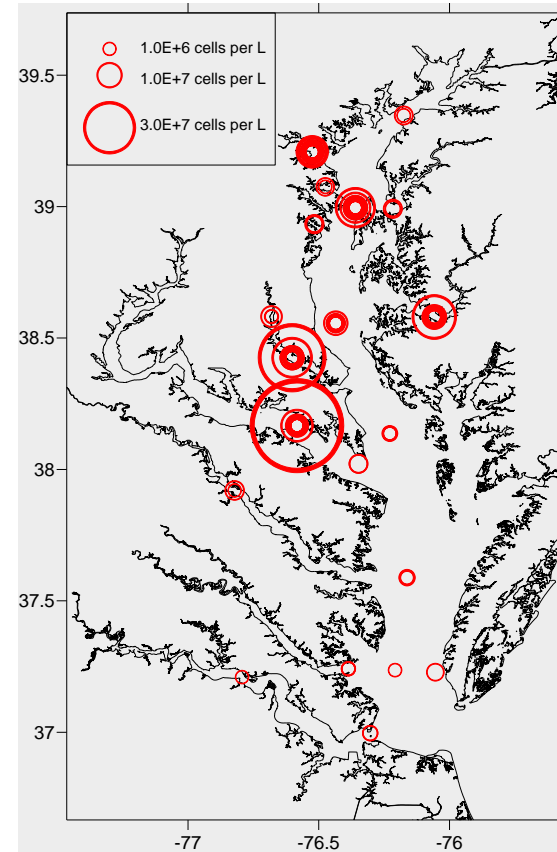


These species are found in the mid to upper Bay regions

*Karlodinium*



*Prorocentrum*



Li et al. 2014

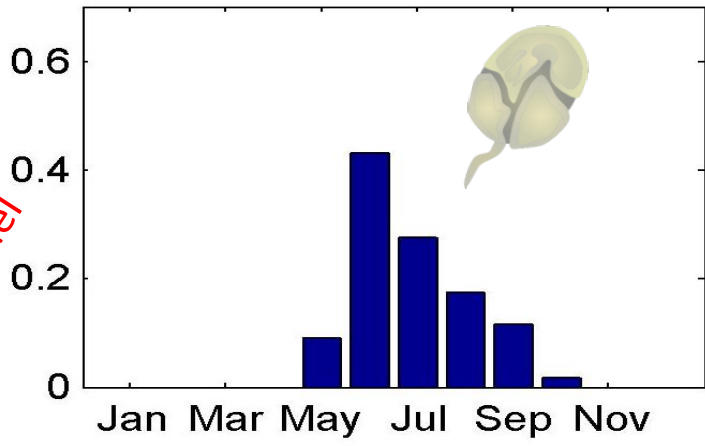
Compare model output with available data for past 2 decades

Physical conditions and nutrient ratios alone yield good correspondence seasonally with analyses based on long term records (overestimate of fall *P. minimum*)

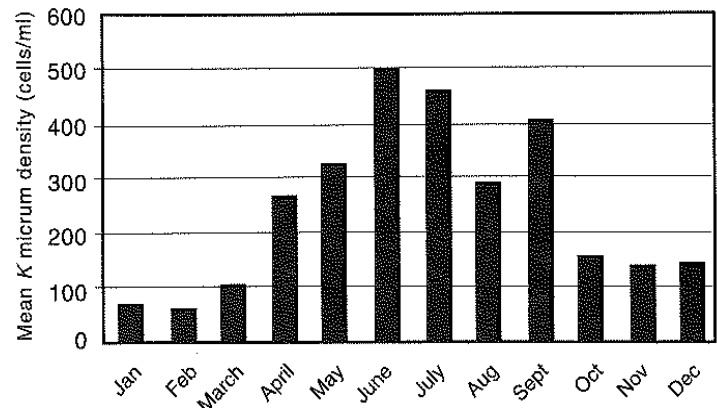
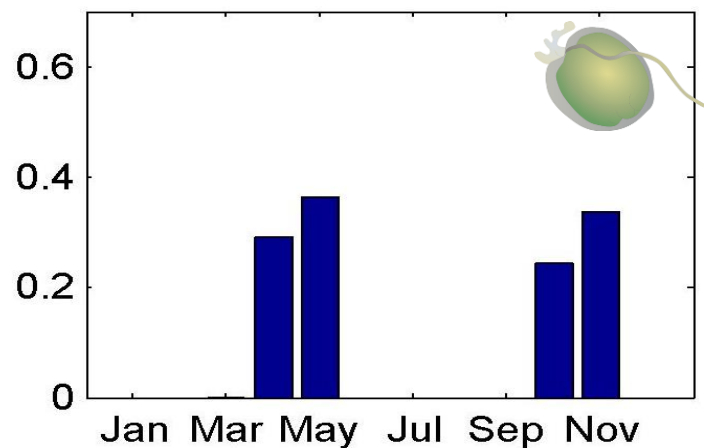
Long term data

Habitat model

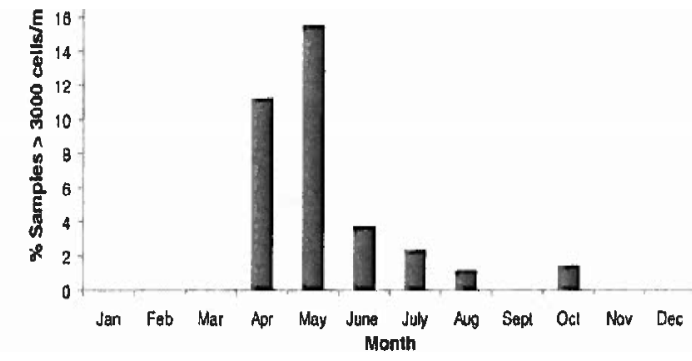
Karlodinium



Prorocentrum



Goshorn 2004



Tango 2005

# Summary

1

$\text{NH}_4^+$  can be repressive at high concentrations while being a preferred N substrate under low concentrations

2

$\text{NH}_4^+$  and  $\text{NO}_3^-$  are assimilated differently—leading to different algal assemblages and total chlorophyll. [similar conclusions with other N substrates]

3

Algal accumulations affect pH, in turn affecting  $\text{PP-PO}_4^{3-}$  dynamics

4

Nutrient speciation affects phytoplankton dynamics—from limitation to excess, with implications for HABs

Total nutrient load sets the total amount of productivity of a system

**BUT**

The relative proportions of nutrients sets the **QUALITY** (who is there and how they are doing)... a finely tuned interplay of organisms driven by their organismal needs, their efficiency at acquiring what they need, how they balance what they don't, and the effects on growth and nutrient recycling

“Changed balances and ratios of nutrients at huge scales may have major impact on the distributions of plants, animals, and microbes at smaller scales”

Sterner and Elser 2002



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Michelle Lin





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If we  nitrogen then  biomass

If we  phosphorus then  biomass

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If we  phosphorus then  biomass