Disproportionate nutrient loads and resulting stoichiometry impacts food webs, from toxic algae to higher trophic levels

ratios matter

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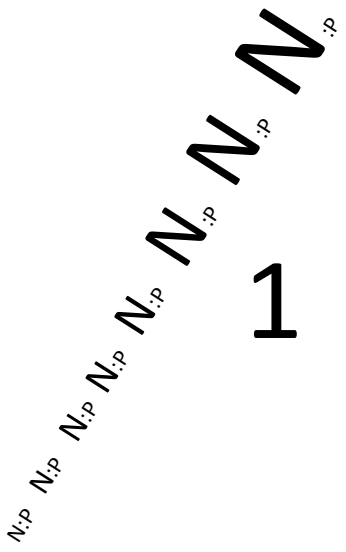


Two Key questions

Do changes in N:P loads and concentrations have consequences for the ***food web*** -- even when ambient nutrients are at levels above those normally taken to be sufficient for growth?

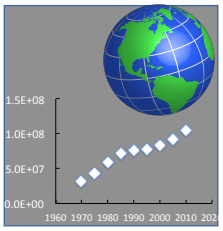
N:P N:P N:P N:P N:P N:P N:P

2

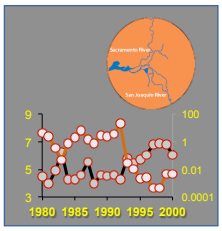
Two Key questions

How are changes in microbial N:P affecting ***C cycles***?

ratios matter

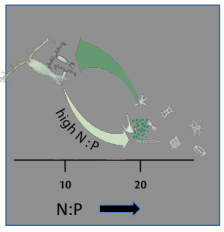


01 Motivation: global trends

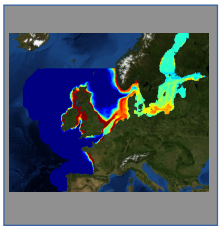


02 Motivation: regional trends

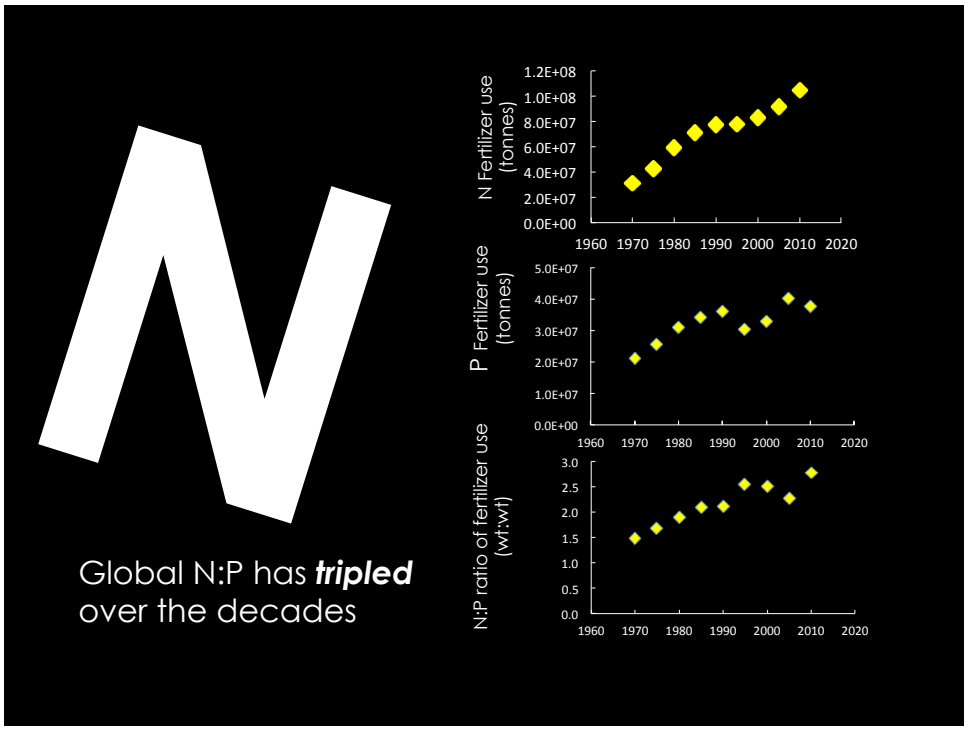
03 Drilling down: - the physiological perspective

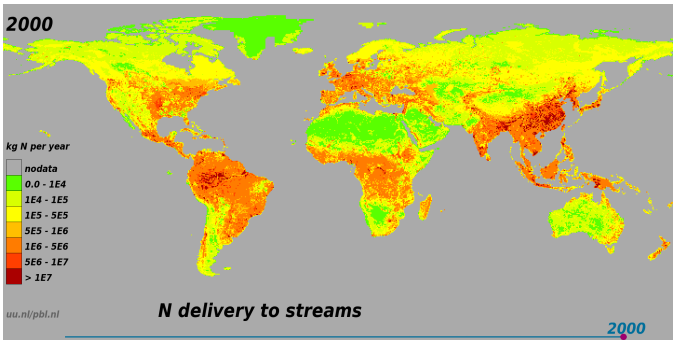


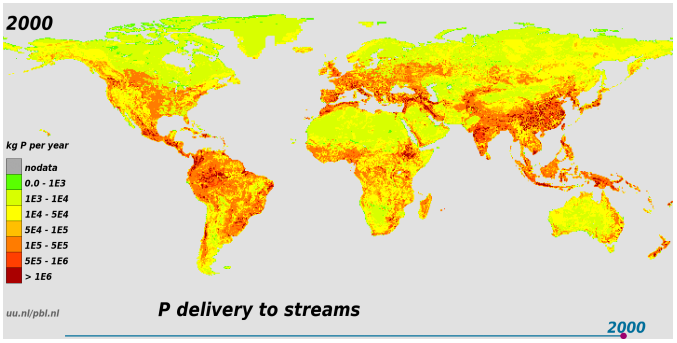
04 Returning to the BIG picture




N
We have a HUGE global N footprint


N
Global N:P has tripled over the decades
N Fertilizer use (tonnes)
1.2E+08
1.0E+08
8.0E+07
6.0E+07
4.0E+07
2.0E+07
0.0E+00
1960 1970 1980 1990 2000 2010 2020
P Fertilizer use (tonnes)
5.0E+07
4.0E+07
3.0E+07
2.0E+07
1.0E+07
0.0E+00
1960 1970 1980 1990 2000 2010 2020
N:P ratio of fertilizer use (wt:wt)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1960 1970 1980 1990 2000 2010 2020

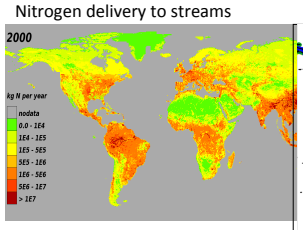




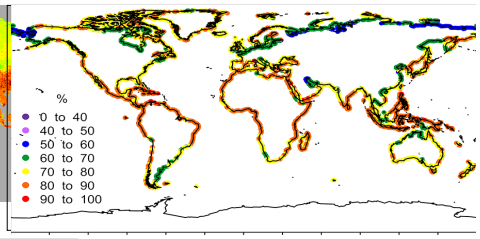
Data and figures from Beusen et al. 2016

This is not just a coastal oceanographers problem anymore!

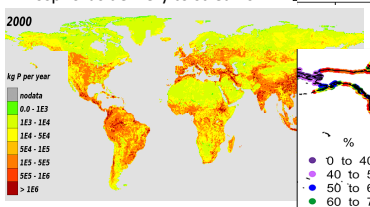
Nitrogen delivery to streams



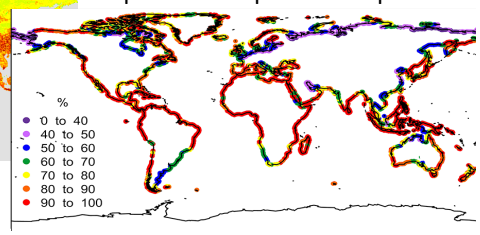
Proportion N exported to open ocean



Phosphorus delivery to streams



Proportion P exported to open ocean



Figures from Beusen et al. 2016

Figures from Sharples et al. 2017

Many-fold increases in N:P are seen around the world

N:P N:P N:P N:P N:P N:P N:P

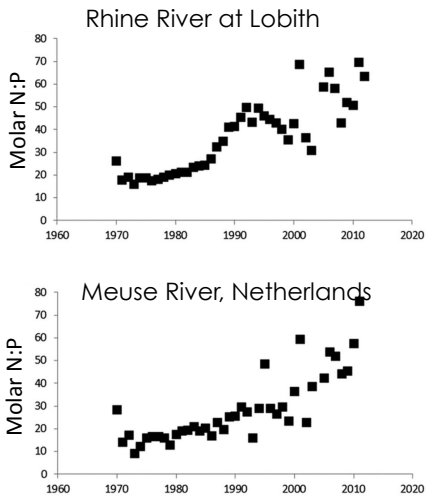


Figure from Bouwman et al. 2017

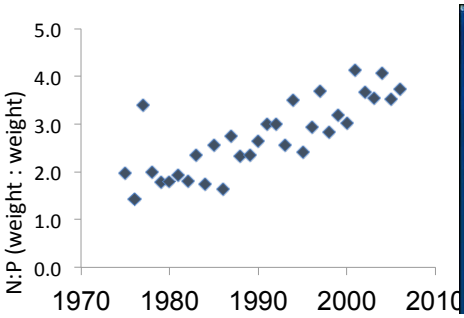
Map from Marcus et al. 2013

Many-fold increases in N:P are seen around the world

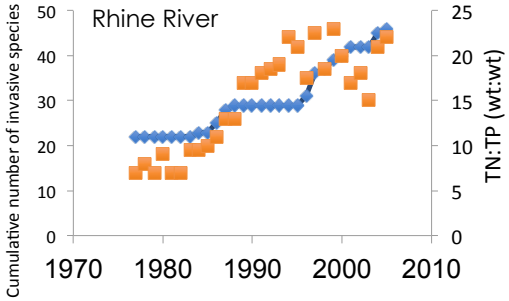
N:P N:P N:P N:P N:P N:P N:P

San Francisco Bay Delta

(more of an urban issue)- but same trend

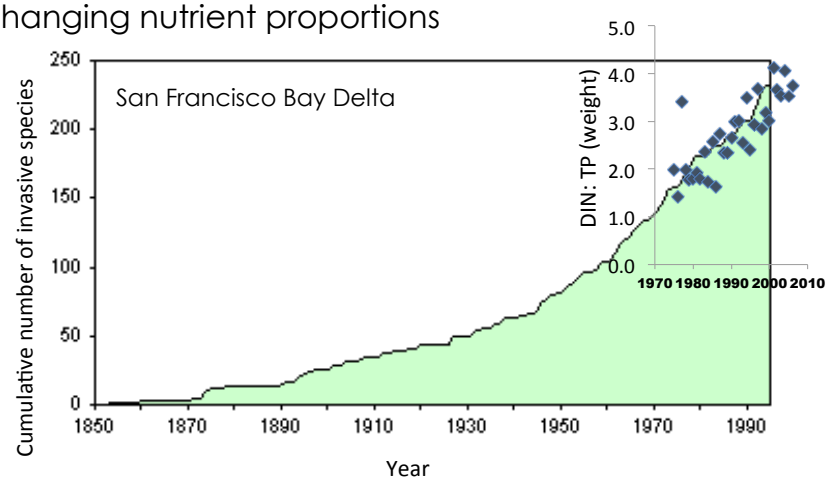


Changing species assemblages track changing nutrient proportions



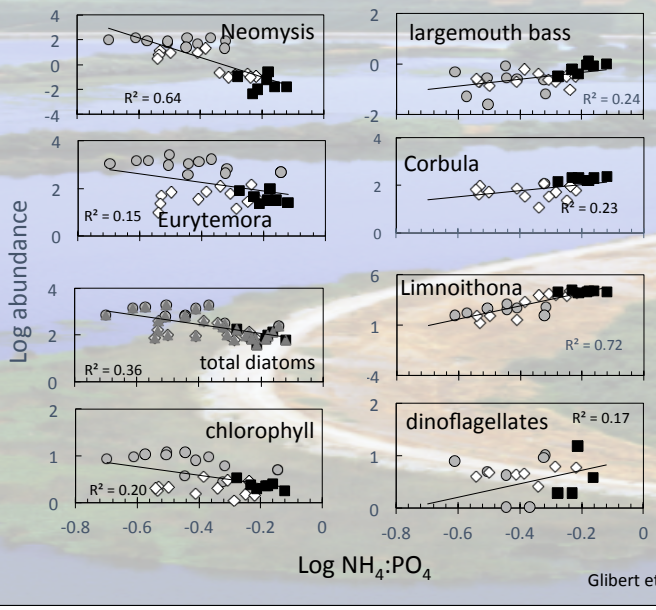
Glibert et al. 2013 (Curr Opin);
Source data: Van Niewenhuyse 2007; Leuvin et al. 2009

Changing species assemblages track changing nutrient proportions



Invasive figure from Cohen and Carlton

Changing species assemblages track changing nutrient proportions



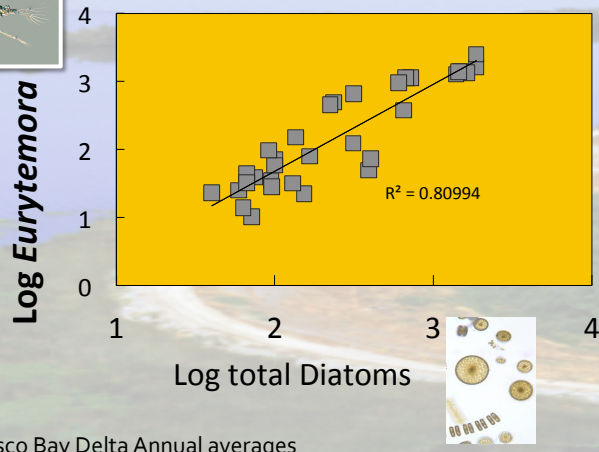
"invasives" range from phytoplankton to fish- at the cost of previously dominant species

Loss of total chlorophyll (mostly diatoms); Increase in dinoflagellates

Glibert et al. 2011 Rev Fish Sci

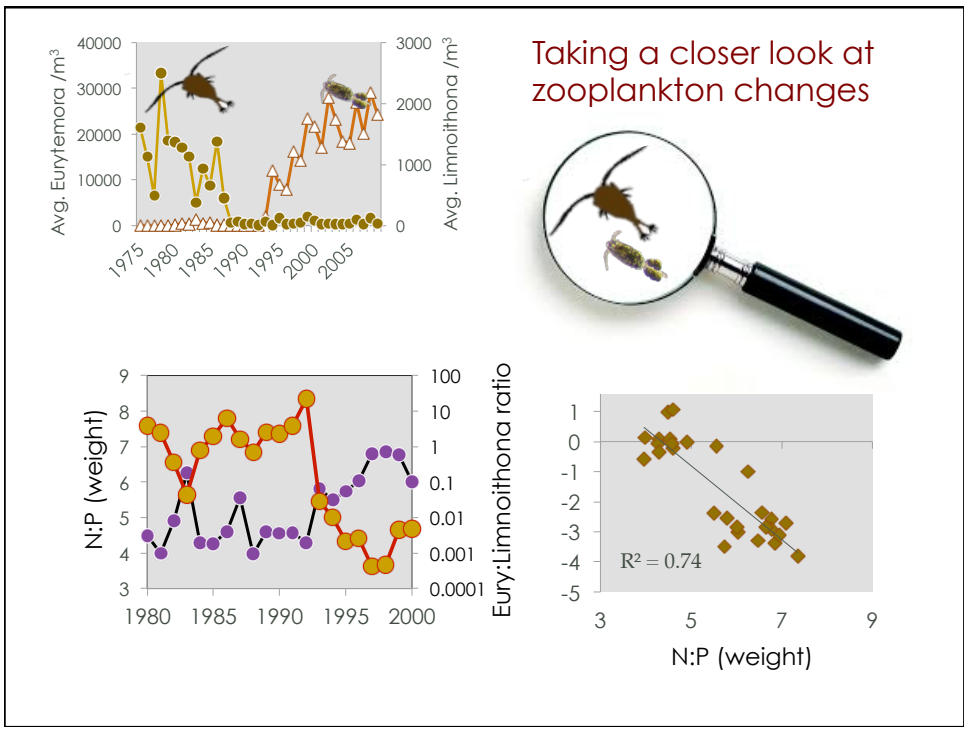
Changes at the bottom of the food web alter the community at the top:

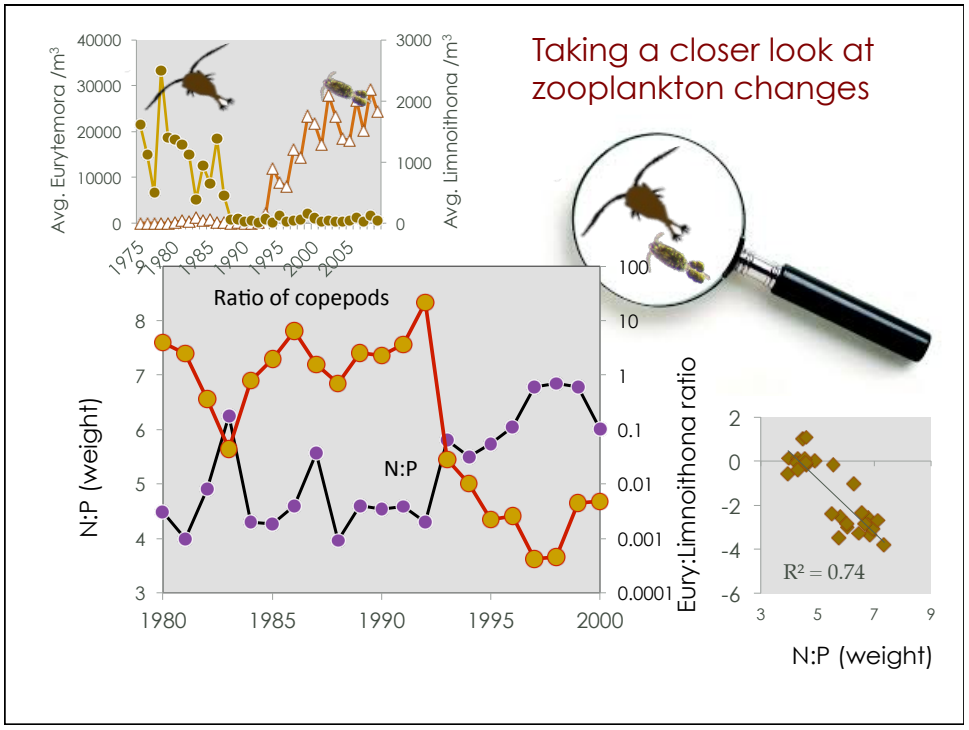
Is this only a food ***quantity*** problem –
or is there an effect of food ***quality***?



San Francisco Bay Delta Annual averages

Glibert et al. 2011


Taking a closer look at zooplankton changes
Avg. Eurytemora /m³
Avg. Limnoithona /m³
N:P (weight)
Eury:Limnoithona ratio
R² = 0.74
N:P (weight)

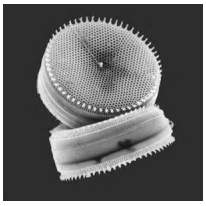

Taking a closer look at zooplankton changes
Avg. Eurytemora /m³
Avg. Limnoithona /m³
Ratio of copepods
N:P
N:P (weight)
Eury:Limnoithona ratio
R² = 0.74
N:P (weight)

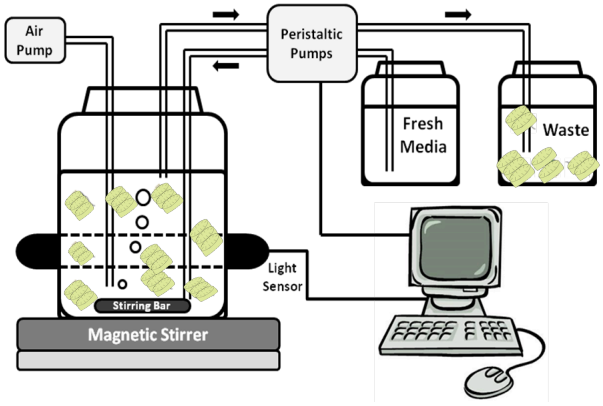
Do zooplankton **C:N:P composition**, N and P excretion, C:N:P egg content, egg production, **and egg viability** change when N:P of their food changes?

To avoid blurring of attribution with effects of food quantity, we held:
1) Algae in healthy physiological state (not N or P limited)
2) Copepods in healthy physiological state (non-limiting food provided in same amount in terms of C)

Step 1: Grow algae (the diatom *Thalassiosira weissflogii*) to different N:P ratios

T. w is a small, common centric diatom



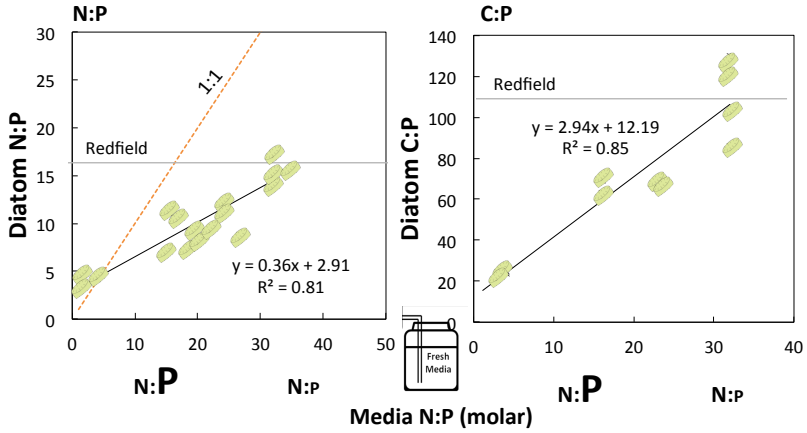


Turbidostat algal culture growth

Keeps cell growing at constant maximal growth rate

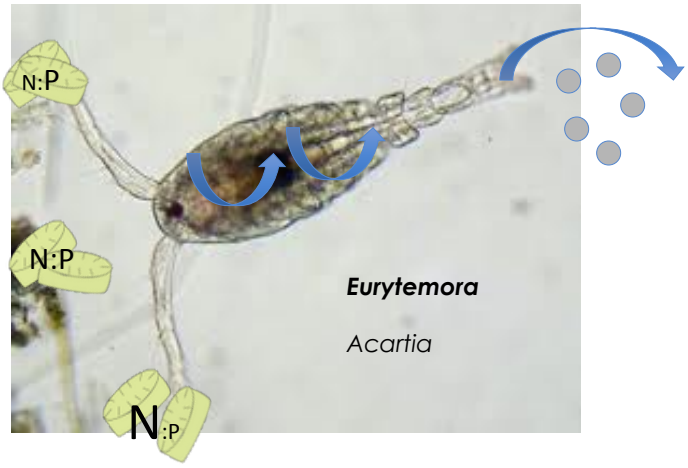
Media nutrient ratios can be altered without driving cells into nutrient limitation (N was held constant, P was varied)

Variable diatom stoichiometry: *success!*

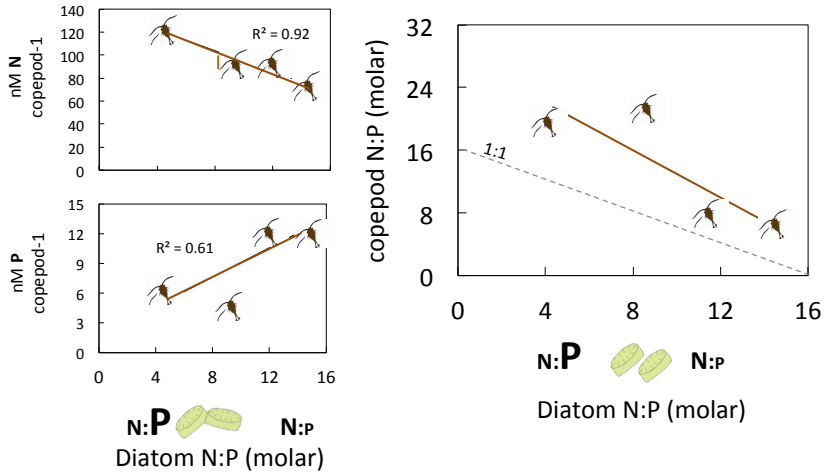


Diatoms composition varied with media N:P-
all were growing at the same rate and not nutrient limited

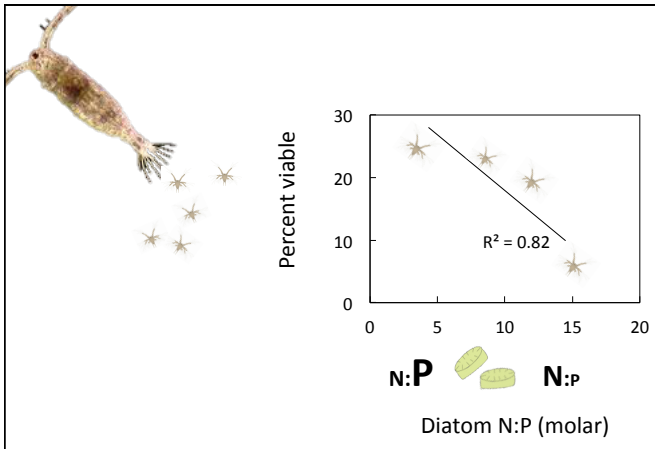
Step 2: Feed these different N:P algae to the copepods-
keeping the food quantity (as C) constant



Copepod N and P changed as N:P of the diatom food changed
(after 7 days of grazing)



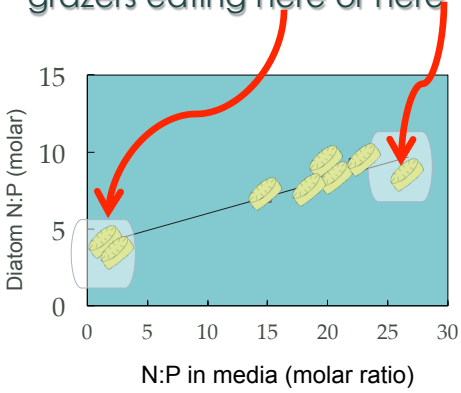
Bentley et al. in review



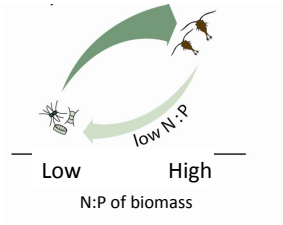
Viability of all eggs/hatching success was lower with increasing N:P of the prey-

…even though food (as C) was the same

There are many consequences for grazers eating here or here



...even when there is no nutrient or food limitation

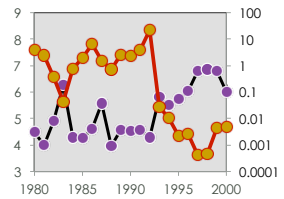


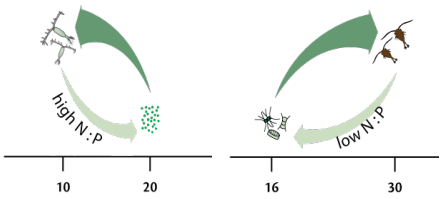
Effects on biomass composition

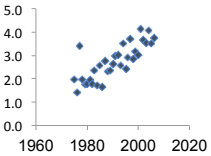
Nutrient regeneration

Egg composition and viability

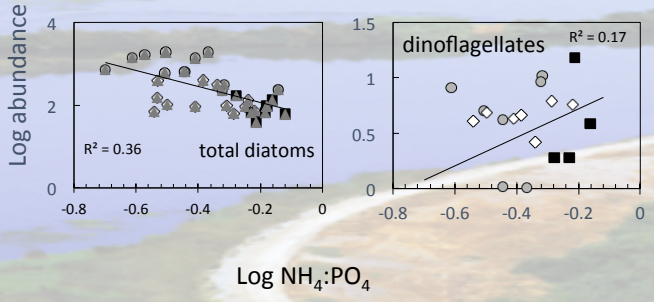
Changes in N:P (due to anthropogenic activities) can change food quality, in turn changing the physiology of higher trophic levels – and consequently their ecological success







Changing species assemblages track changing nutrient proportions



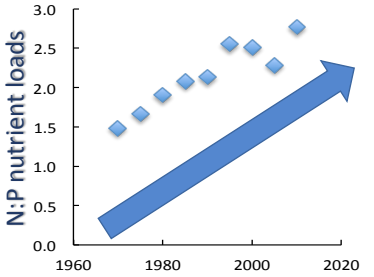
Log NH_4:PO_4

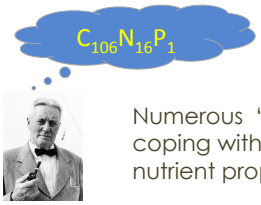
"invasives" range from phytoplankton to fish- at the cost of previously dominant species

Loss of total chlorophyll (mostly diatoms); Increase in dinoflagellates

Glibert et al. 2011 Rev Fish Sci

Does N:P matter when both N and P are available in concentrations normally taken to be sufficient for growth?





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***

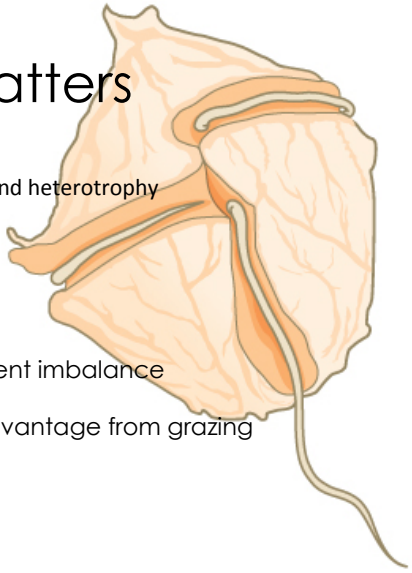
Cells may dissipate the excess nutrient- some of these compounds are C, or N-rich toxins

Glibert and Burkholder 2011. Chinese J Ocean Limnol

Rise of the mixotrophs (and HABs!)

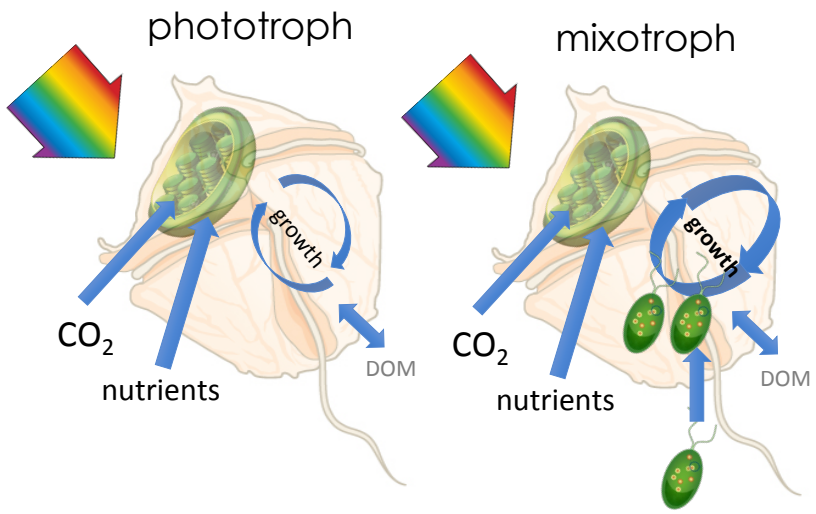
Mixotrophy matters

Mixotrophy combines phototrophy and heterotrophy
…it is far more than a curiousity



Mixotrophs can thrive under nutrient imbalance

Mixotrophs can gain a growth advantage from grazing



Mixotrophs may graze for a limiting nutrient

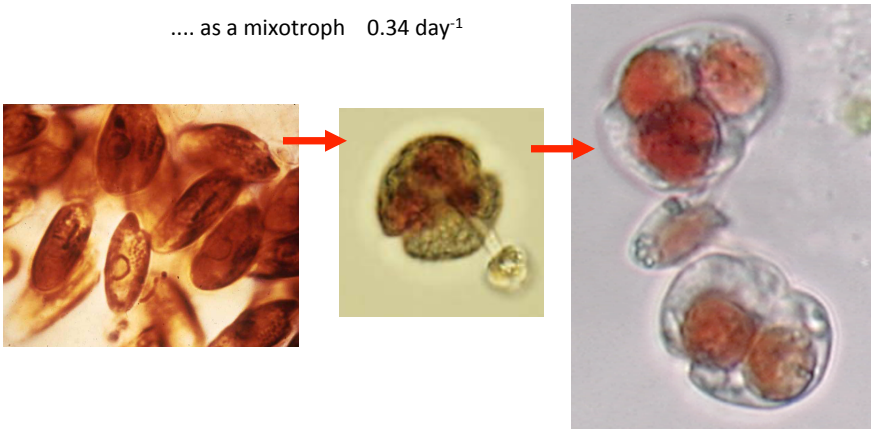
but they get extra **C** and a growth boost

Mixotrophs do change growth rate when feeding—

Is this quantity or food quality– or both???

Cochlodinium….as a phototroph 0.17 day^{-1}

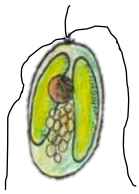
…. as a mixotroph 0.34 day^{-1}



?

If mixotrophy is a strategy for the cells to access nutrients not otherwise available in dissolved form, how does mixotrophy vary when the predator and prey nutritional status varies? Do mixotrophs respond to changes in *food quality?*

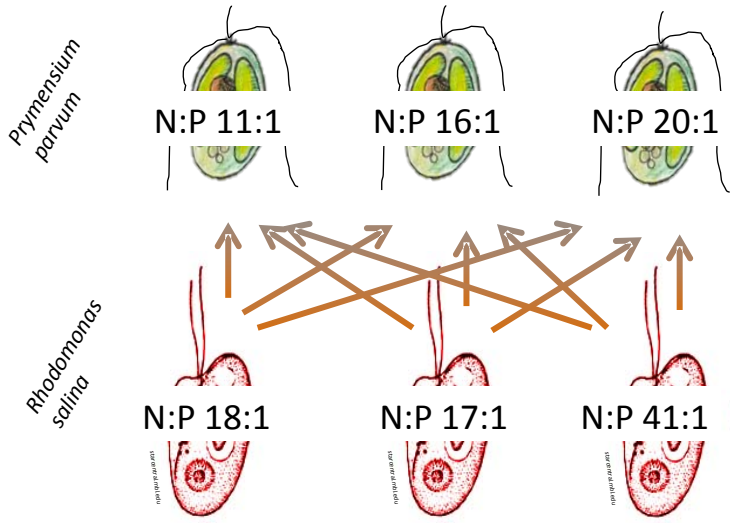
How does the tendency for toxicity vary when the predator and prey nutritional status change?



Prymnesium parvum

Karlodinium veneficum

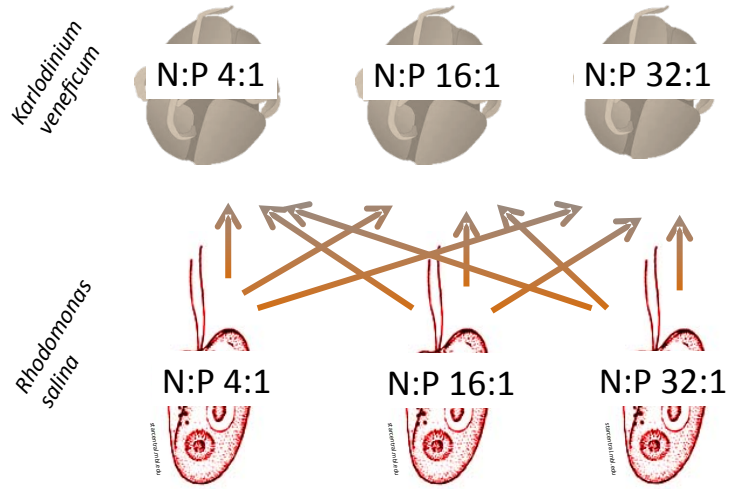
Experiment 1: Cells of predator (*Prymensium parvum*) and prey (*Rhodomonas salina*) were grown at 3 nutrient levels: 3X 3 factorial (in triplicate)



Changes were measured over a time course of 3 days

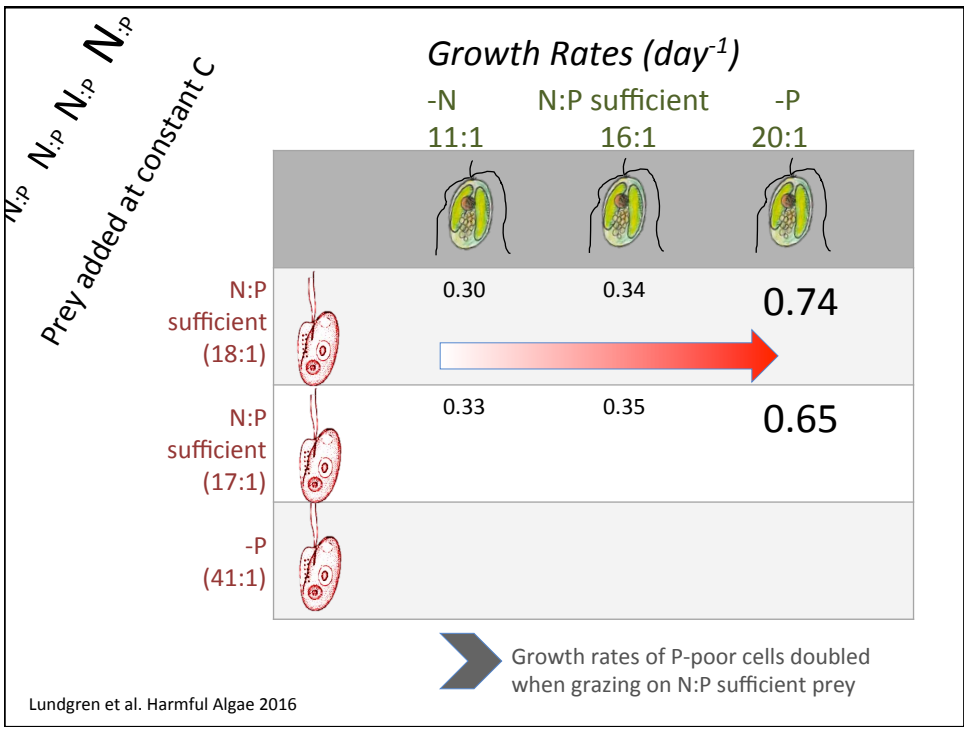
Lundgren et al. Harmful Algae 2016

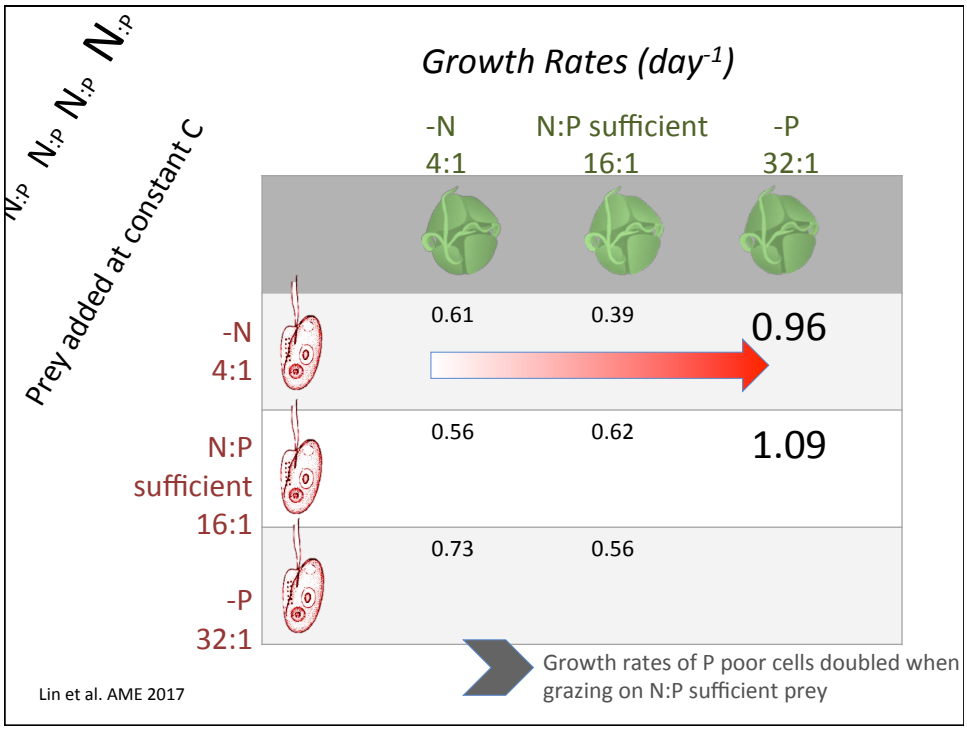
Experiment 2: Similar experimental design but with *Karlodinium veneficum* (predator) and *Rhodomonas* (prey)

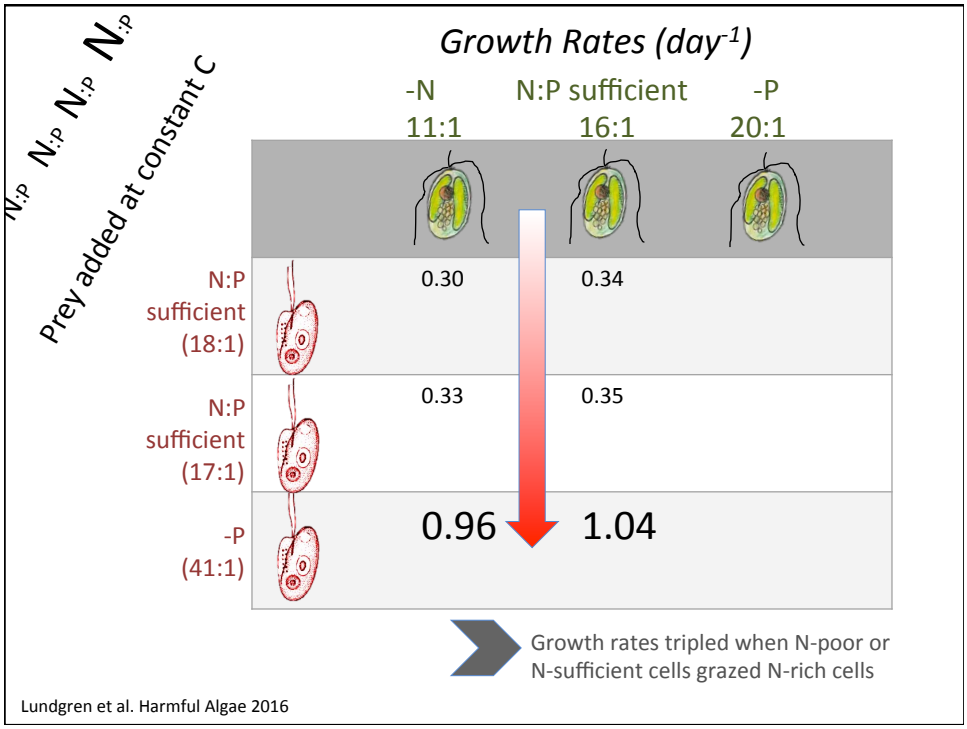


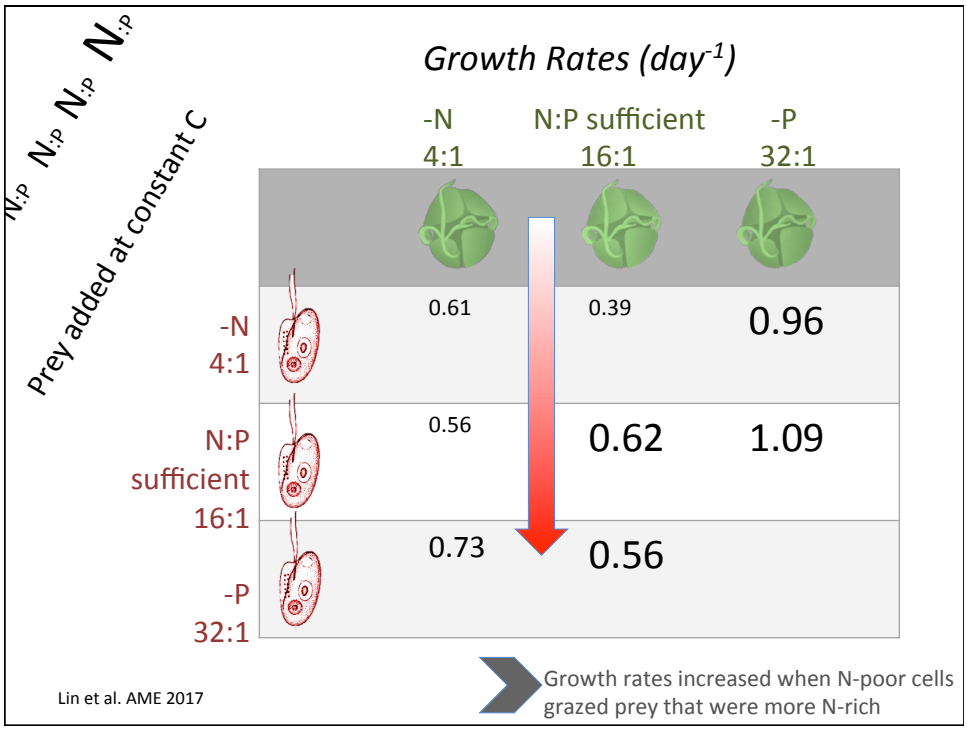
Changes were measured over a time course of 3 days

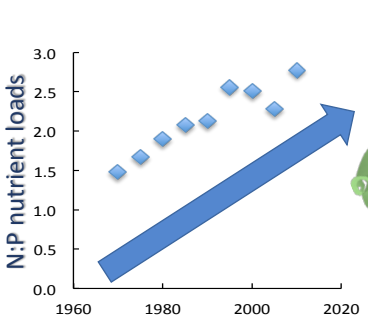
Lin et al. AME 2017


N:P N:P N:P N:P
Prey added at constant C
Growth Rates (day-1)
-N 11:1
N:P sufficient 16:1
-P 20:1
N:P sufficient (18:1)
0.30
0.34
0.74
N:P sufficient (17:1)
0.33
0.35
0.65
-P (41:1)
Growth rates of P-poor cells doubled when grazing on N:P sufficient prey
Lundgren et al. Harmful Algae 2016


N:P N:P N:P N:P
Prey added at constant C
Growth Rates (day-1)
-N 4:1
N:P sufficient 16:1
-P 32:1
-N 4:1
0.61
0.39
0.96
N:P sufficient 16:1
0.56
0.62
1.09
-P 32:1
0.73
0.56
Growth rates of P poor cells doubled when grazing on N:P sufficient prey
Lin et al. AME 2017


Growth Rates (day-1)
N:P N:P N:P N:P
Prey added at constant C
-N
11:1
N:P sufficient
16:1
-P
20:1
N:P sufficient (18:1)
0.30
0.34
N:P sufficient (17:1)
0.33
0.35
-P (41:1)
0.96
1.04
Growth rates tripled when N-poor or N-sufficient cells grazed N-rich cells
Lundgren et al. Harmful Algae 2016

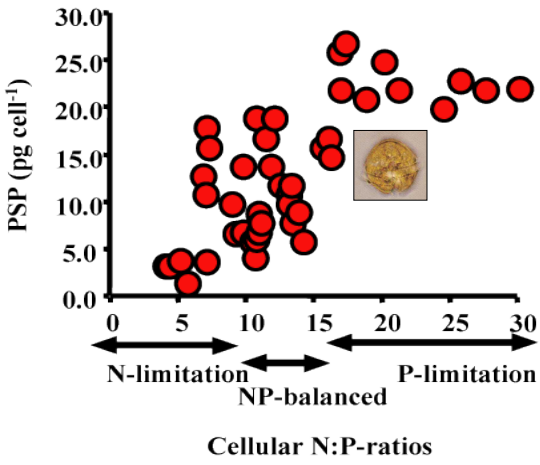

Growth Rates (day-1)
N:P N:P N:P N:P
Prey added at constant C
-N
4:1
N:P sufficient
16:1
-P
32:1
-N 4:1
0.61
0.39
0.96
N:P sufficient 16:1
0.56
0.62
1.09
-P 32:1
0.73
0.56
Growth rates increased when N-poor cells grazed prey that were more N-rich
Lin et al. AME 2017



Mixotrophy and toxicity may be synergistic;

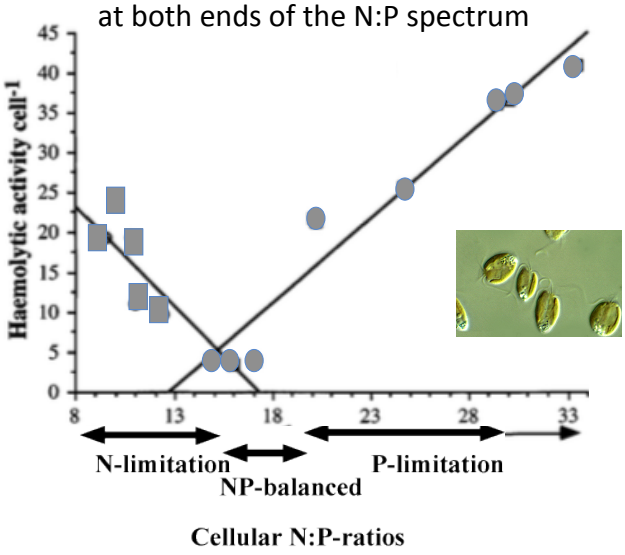
Release of toxins harms prey, releasing dissolved nutrients or making the prey easier to capture

More PSP is produced at high N:P ratios



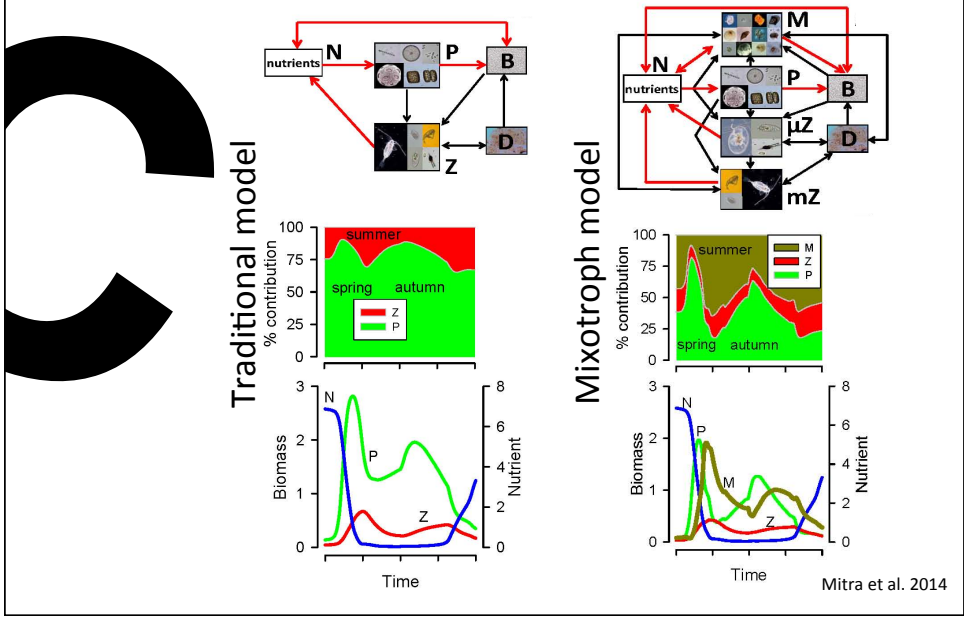
From Graneli 2005 based on Boyer et al., 1987

Prymensium parvum produces more toxin at both ends of the N:P spectrum

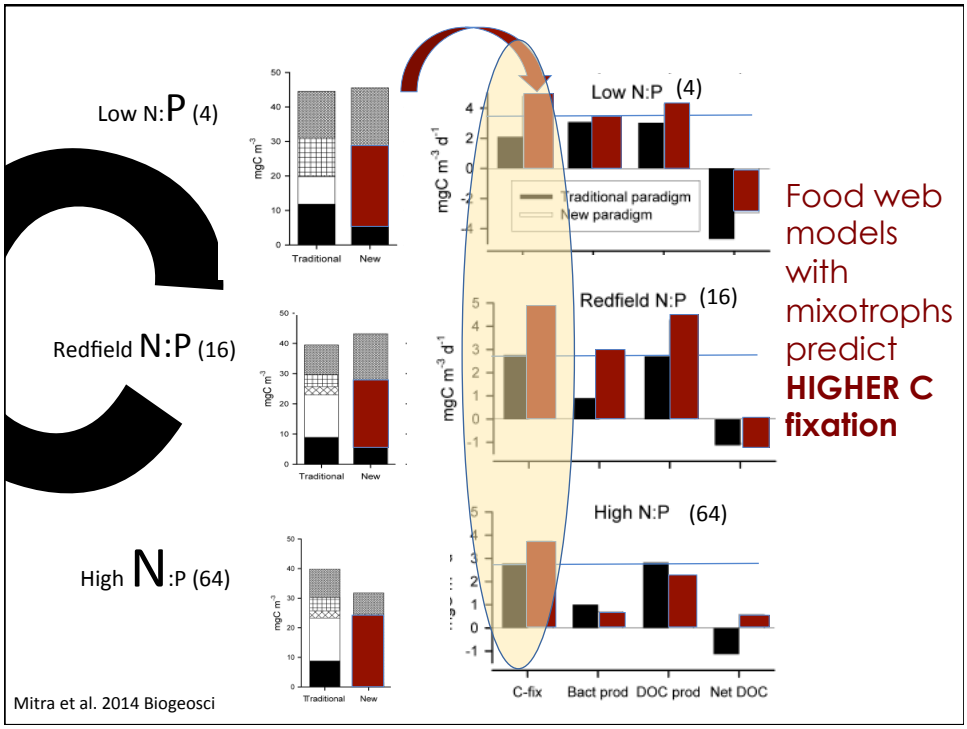


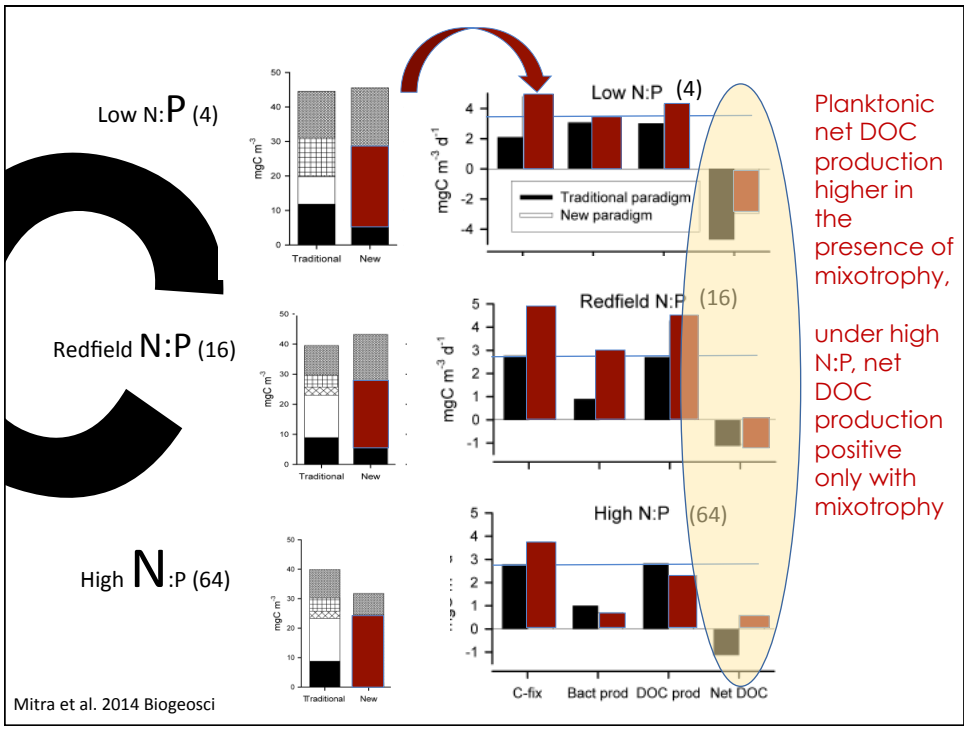
From Johansson and Graneli 1999 AME

Incorporating our increasing appreciation of mixotrophs in models: Important consequences for food webs and C cycling

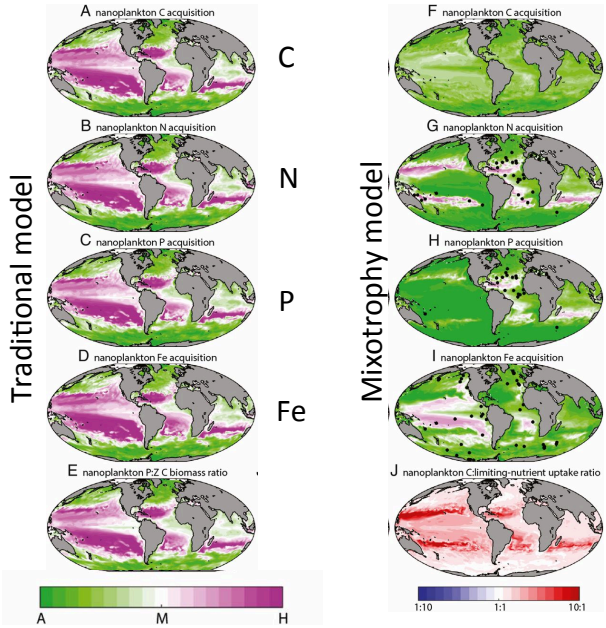


Mitra et al. 2014


Low N:P (4)
Redfield N:P (16)
High N:P (64)
Traditional
New
mgC m-3
Low N:P (4)
Redfield N:P (16)
High N:P (64)
mgC m-3 d-1
Traditional paradigm
New paradigm
C-fix
Bact prod
DOC prod
Net DOC
Food web models with mixotrophs predict HIGHER C fixation
Mitra et al. 2014 Biogeosci


Low N:P (4)
Redfield N:P (16)
High N:P (64)
Traditional
New
mgC m-3
Low N:P (4)
Redfield N:P (16)
High N:P (64)
mgC m-3 d-1
Traditional paradigm
New paradigm
C-fix
Bact prod
DOC prod
Net DOC
Planktonic net DOC production higher in the presence of mixotrophy,
under high N:P, net DOC production positive only with mixotrophy
Mitra et al. 2014 Biogeosci

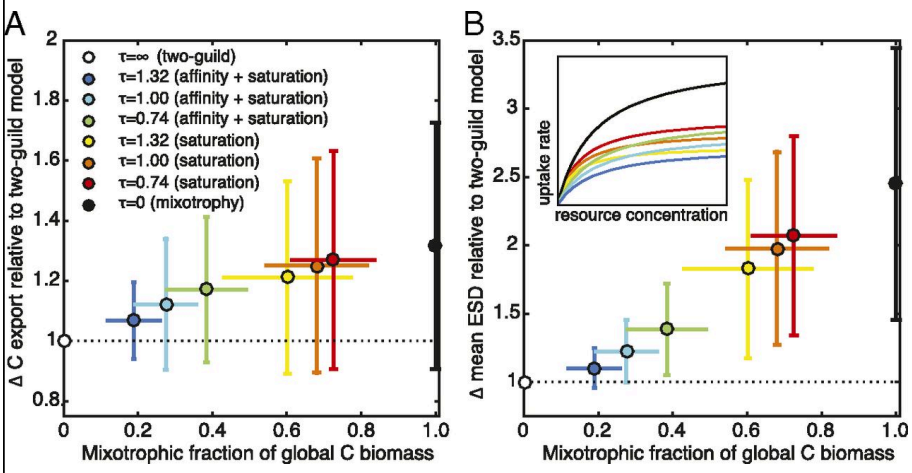
Global role of mixotrophy



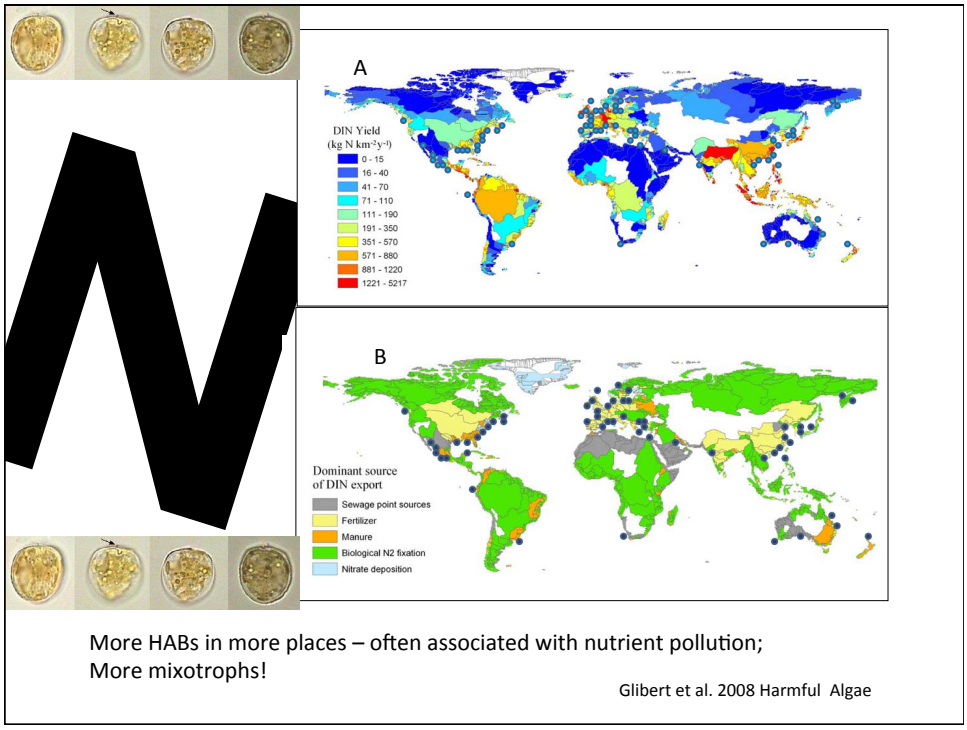
Ben A. Ward, and Michael J. Follows PNAS 2016;113:2958-2963

Relative change in photosynthetic C acquisition to the limiting nutrient in the two models…

Production of larger cells, which may sink faster



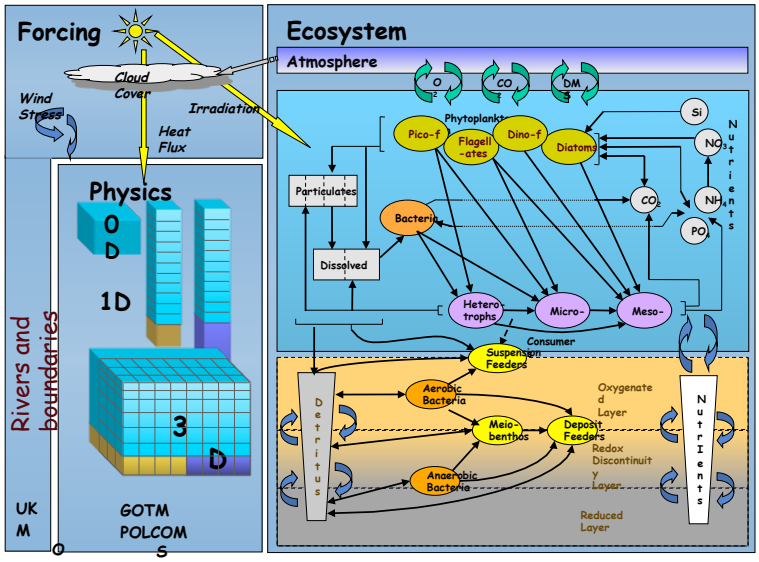
Ben A. Ward, and Michael J. Follows PNAS 2016;113:2958-2963



More HABs in more places – often associated with nutrient pollution;
More mixotrophs!

Glibert et al. 2008 Harmful Algae

Using models that couple land-based nutrient loads with climate change, physics and ecosystem change to assess future conditions



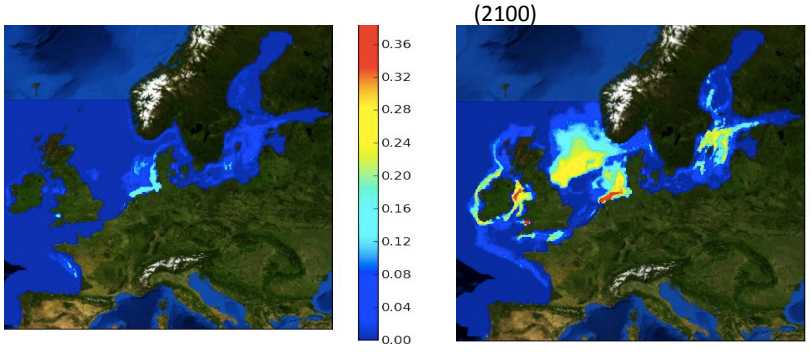
Allen et al- Plymouth Mar Lab

Comparing present condition with future projection: N European coast

Prorocentrum spp

Present Day

Future Projection (2100)



Scale indicates percent of pixels in model with suitable habitat conditions

Large expansion in potential habitat

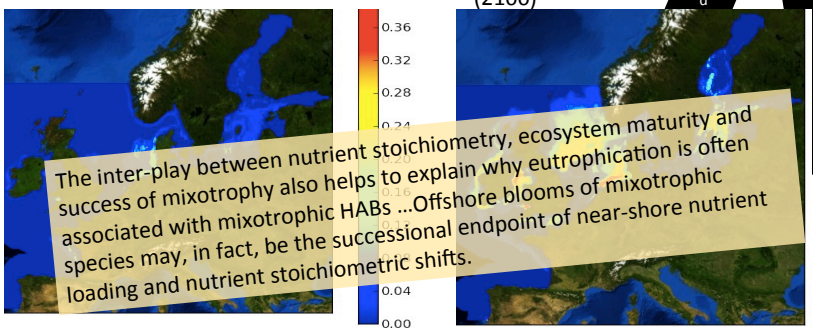
Glibert et al. 2014 Glob Change Biol

Comparing present condition with future projection: N European coast

Prorocentrum spp

Present Day

Future Projection (2100)



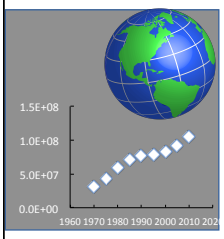
The inter-play between nutrient stoichiometry, ecosystem maturity and success of mixotrophy also helps to explain why eutrophication is often associated with mixotrophic HABs …Offshore blooms of mixotrophic species may, in fact, be the successional endpoint of near-shore nutrient loading and nutrient stoichiometric shifts.

Scale indicates percent of pixels in model with suitable habitat conditions

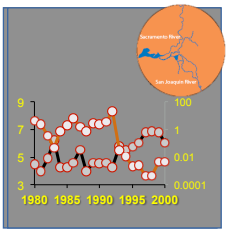
Large expansion in potential habitat

Glibert et al. 2014 Glob Change Biol

ratios matter

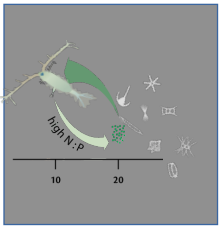


01
N is increasing globally, faster than P and a high proportion is exported beyond the coastal ocean

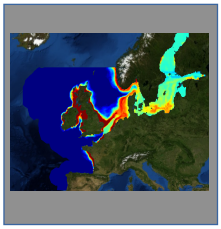


02
From the Rhine to San Francisco, N:P loads are changing, and food webs have responded accordingly

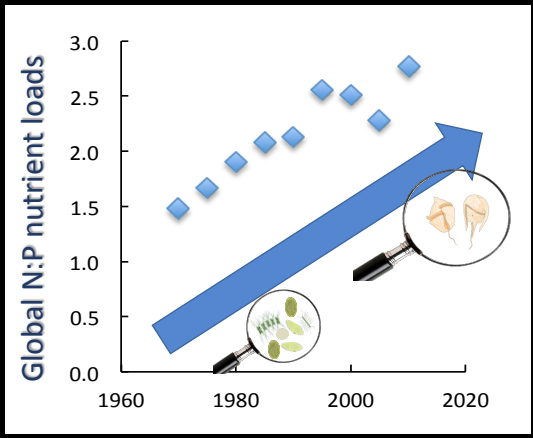
03
Stoichiometry affects physiology of algae, zooplankton mixotrophs, and alters algal toxicity



04
Altered N:P stoichiometry is contributing to the increasing success of mixotrophs and HABs



ratios matter



Imbalances in N:P (even in non-nutrient limiting conditions) have important implications for mixotrophy, growth rates, abundance and toxicity of many HABs

Changes in nutrient loads (in quantity, ratio and form) alter the stoichiometry and food quality for all grazers

A mixotroph-centric world alters C fixation, C export, trophic dynamics and biogeochemistry

mixotrophy matters!

Thanks

For collaborations, inspiration, experiments

Lex Bouwman, Arthur Beusen- global perspectives

Icarus Allen, Yuri Artioli- global modeling

Kevin Flynn, Aditee Mitra- mixotrophy modeling

Veronica Lundgren, Michelle Lin, Katie Bentley- experiments

Dick Dugdale, Frances Wilkerson- San Francisco Bay Delta collaboration

For support