

An aerial photograph of a coastal wetland area. In the foreground, there is a large, irregularly shaped body of water with a light blue hue. To the right of the water, a wide, light-colored dirt road or path curves through a marshy area. The background shows a vast expanse of green marshland and a distant urban or suburban landscape under a clear sky.

Nutrients and the food web

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“Ammonium is a paradoxical nutrient”

Ammonium is a preferred form of nitrogen for phytoplankton under some conditions



Ammonium can be inhibitory or even toxic under some conditions and to some species

“Sensitivity to NH_4^+ may be a universal biological phenomenon”

There is no controversy or uncertainty regarding the effects of ammonium on plants (including algae) and animals (including humans)

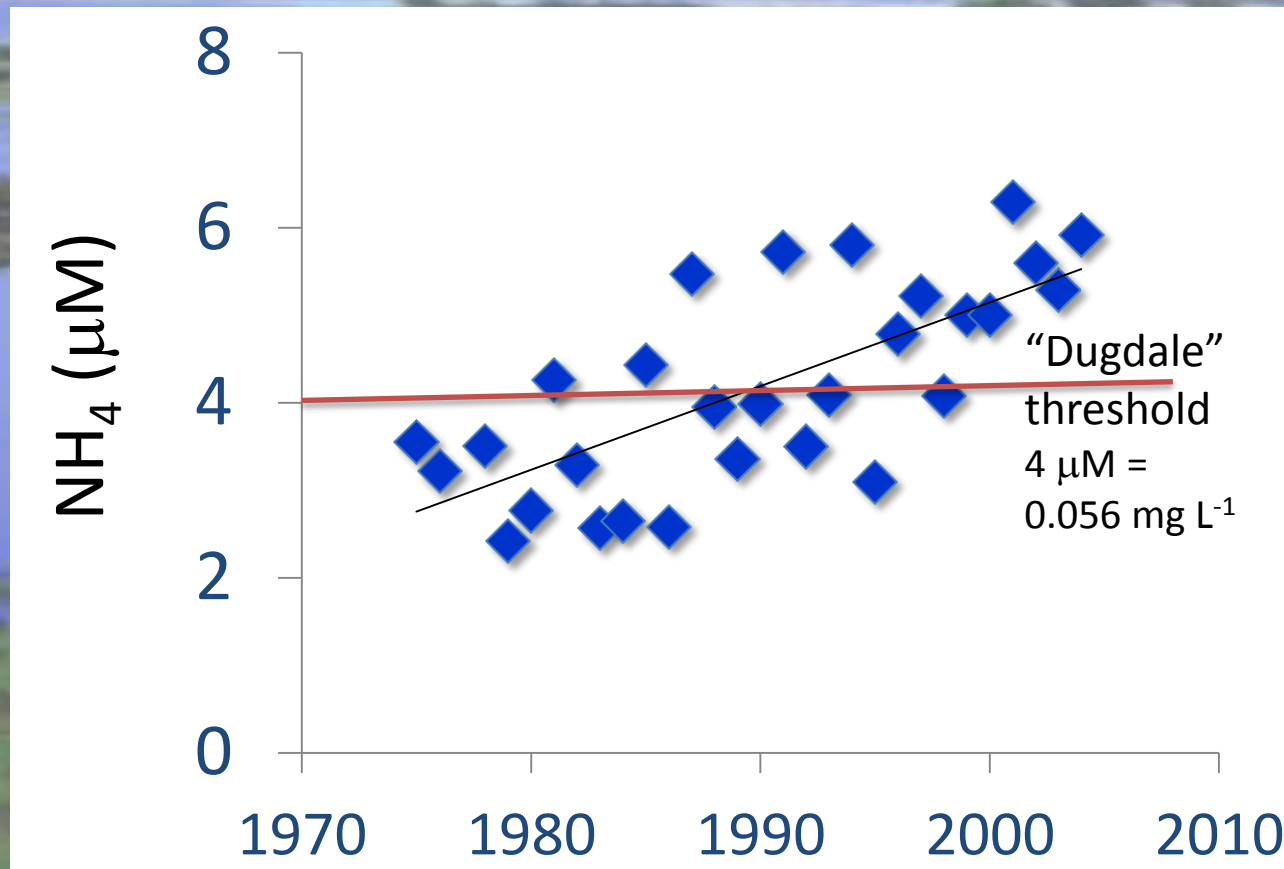
“... but the threshold at which symptoms of toxicity become manifested differs...”

Concentrations at which ammonium has been shown to inhibit the uptake of nitrate by phytoplankton range from 1 μM or less to $>20 \mu\text{m}$

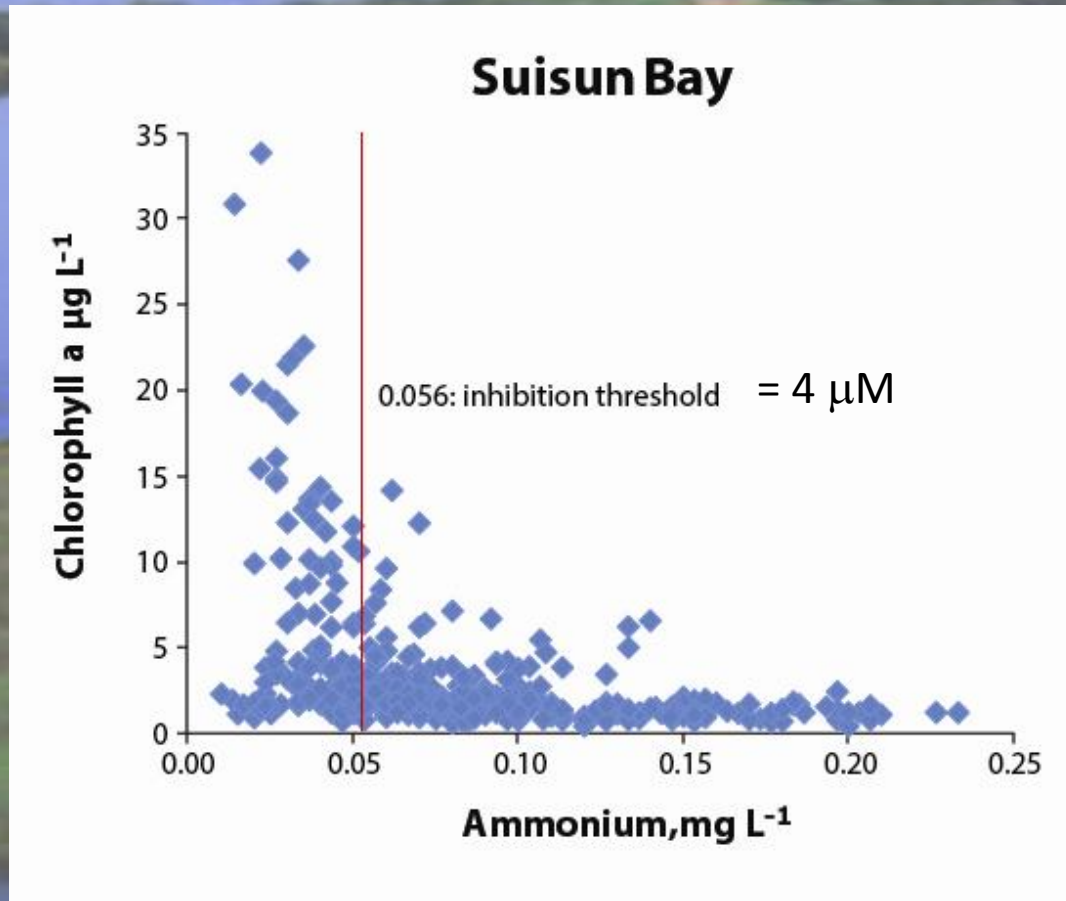
“the extent and threshold concentrations involved depend on the species under study, its physiological status, and the environmental conditions to which this particular species or the natural assemblage has been exposed”

(Varela and Harrison 1999)

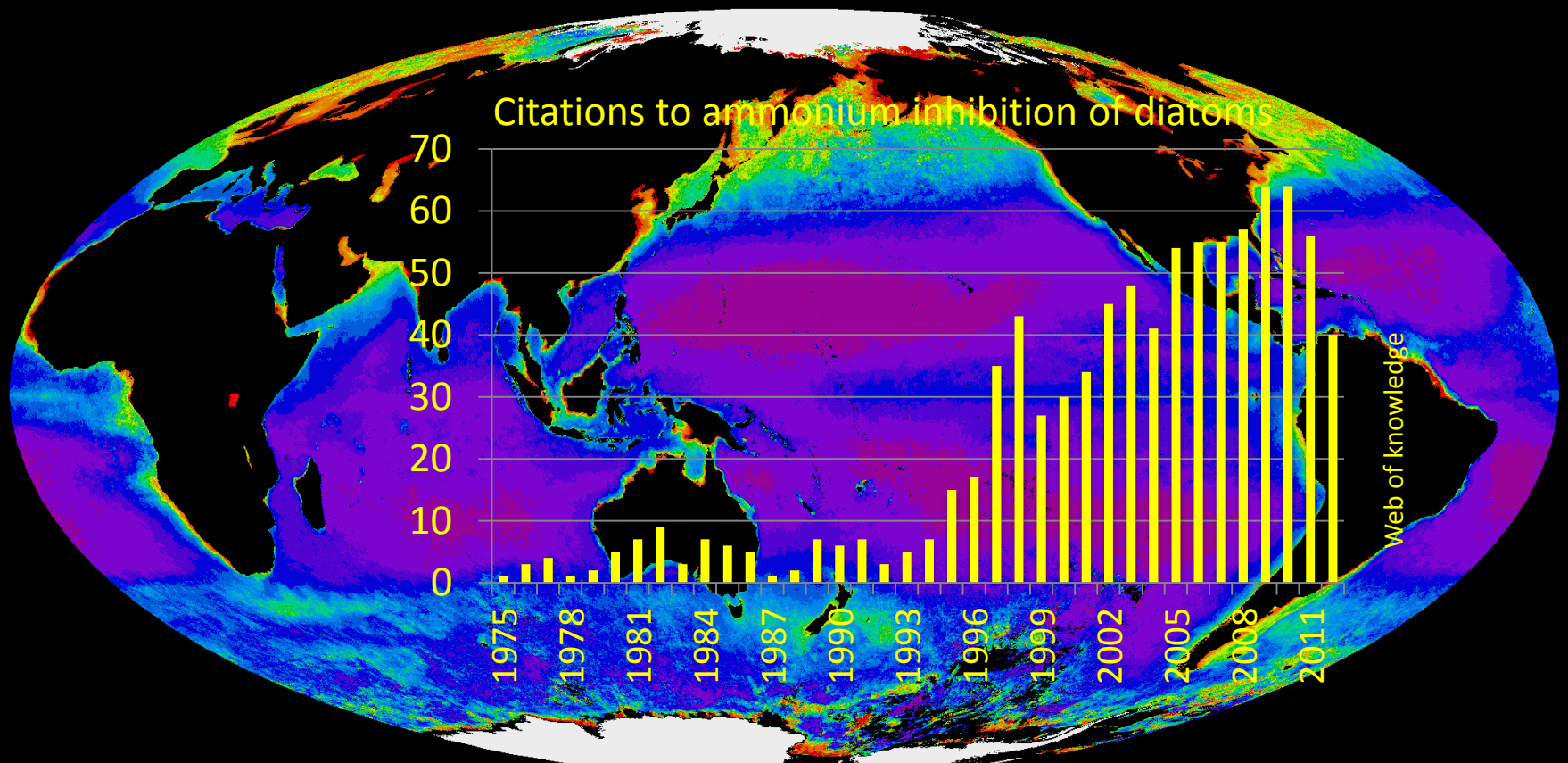
Ammonium in San Francisco Bay Delta: increasing over time



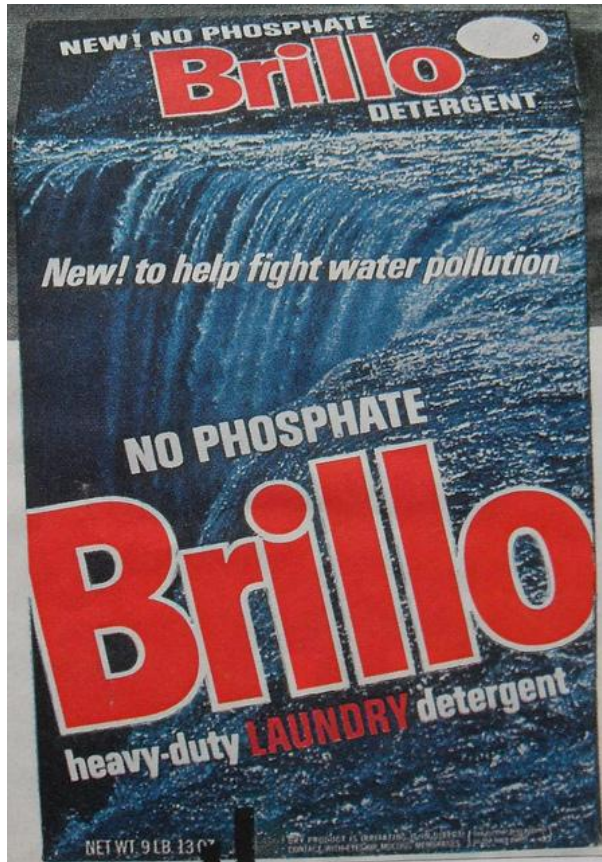
Overall, long-term ammonium data show strong negative relationship with chlorophyll in the water column



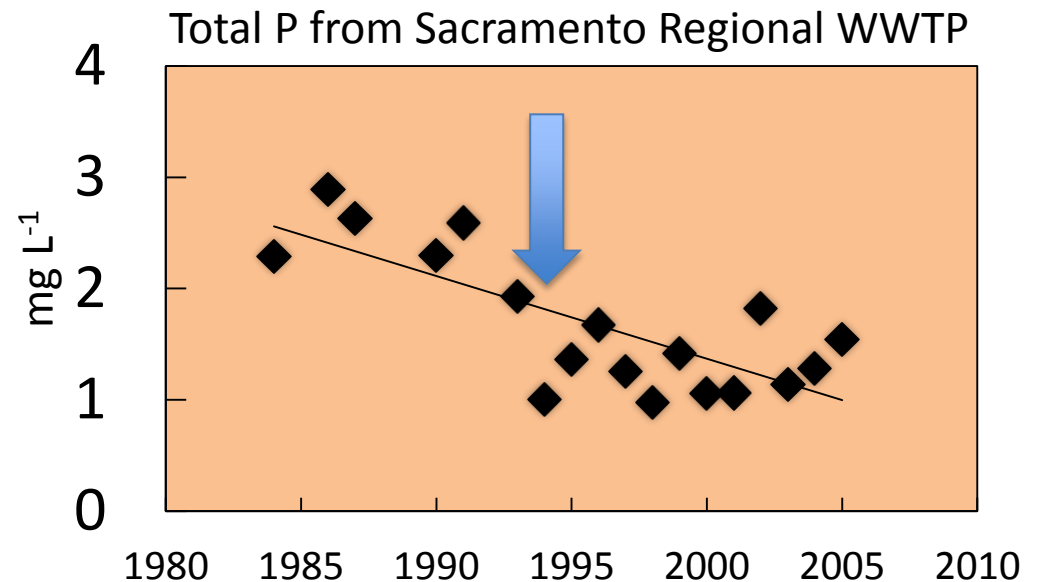
Inhibition of diatoms by ammonium is being increasingly recognized – and included in ecosystem models of ocean productivity



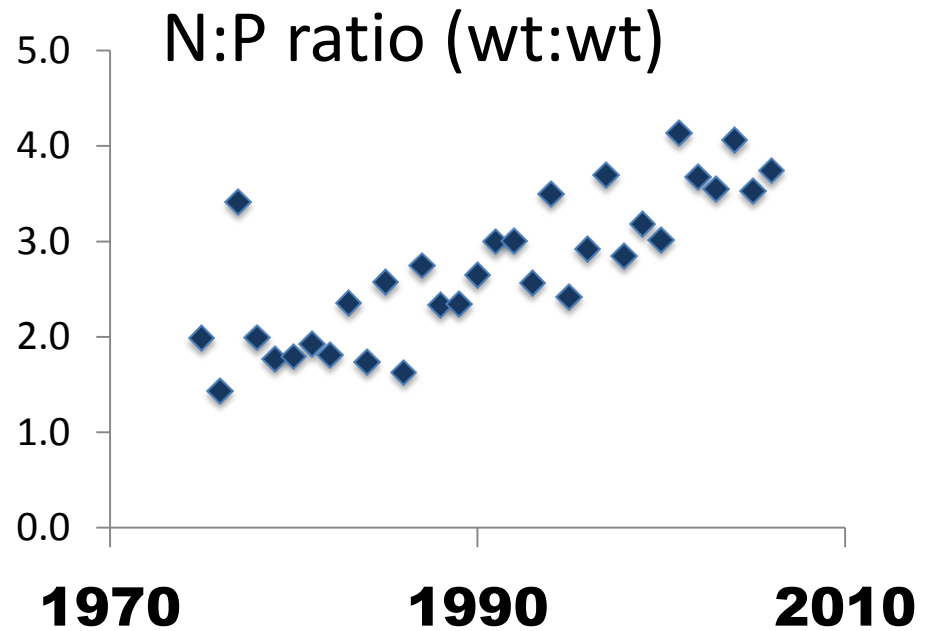
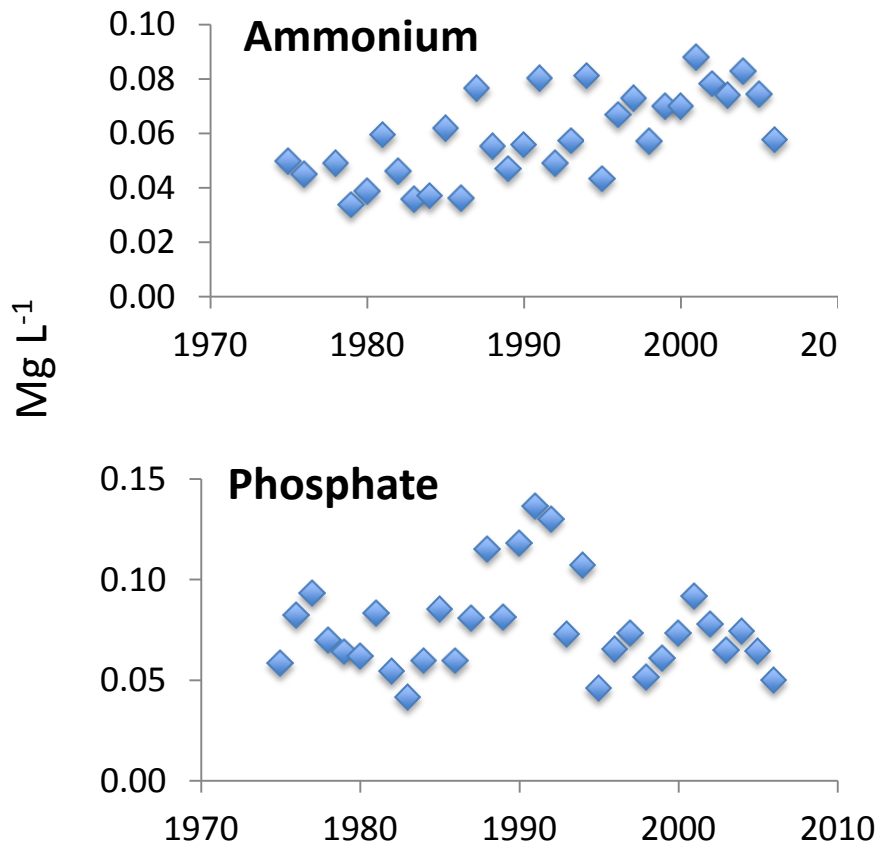
Ammonium is not the only nutrient that has changed



By the mid 1990s the switch to non-P detergents had occurred throughout the US and Europe. The manufacturers made the switch regardless of state (or country) laws to avoid region-by-region formulations



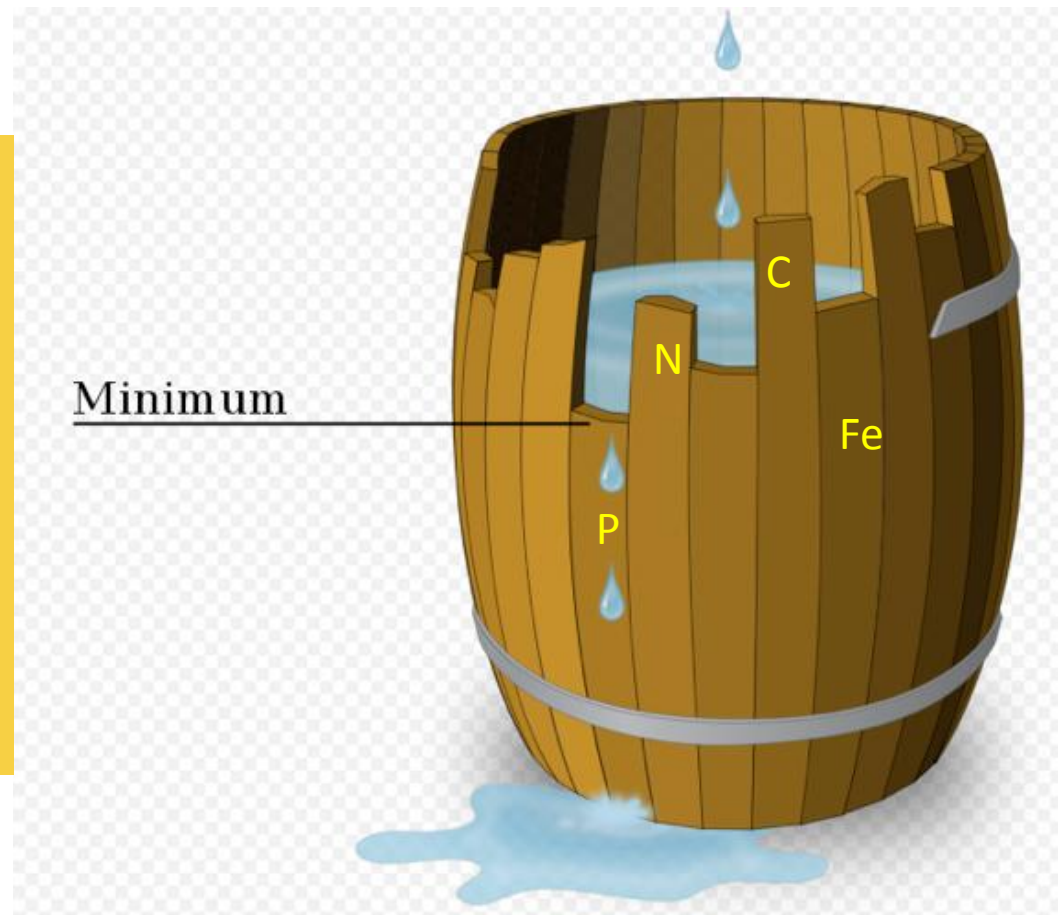
Nitrogen: Phosphorus ratios have increased



Liebig' Law of the minimum

Growth is limited by the nutrient that is in shortest supply relative to the needs of the organism.

But- in this system the nutrients, including P, rarely are low enough to be considered “limiting” using simple, classic metrics (half-saturations constants)



Classic 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., if nutrients are 'sufficient' they should not regulate the species composition of the algae

Contemporary Perspective:

While total nutrient load sets the total amount of productivity/biomass of an ecosystem,

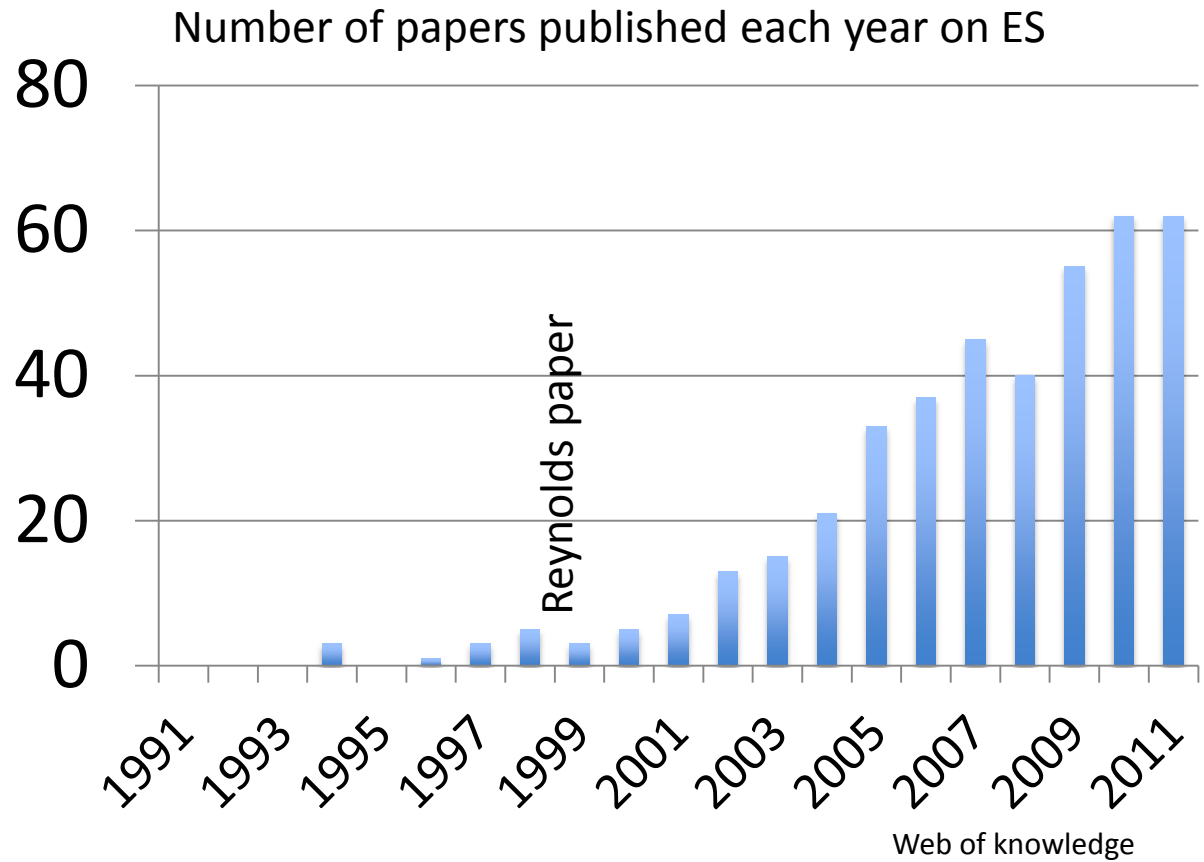
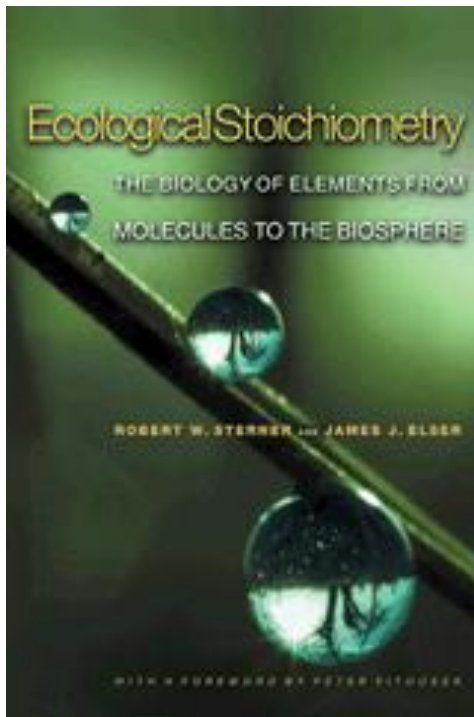
The relative proportions of nutrients sets the QUALITY

(who is there and how they are doing)

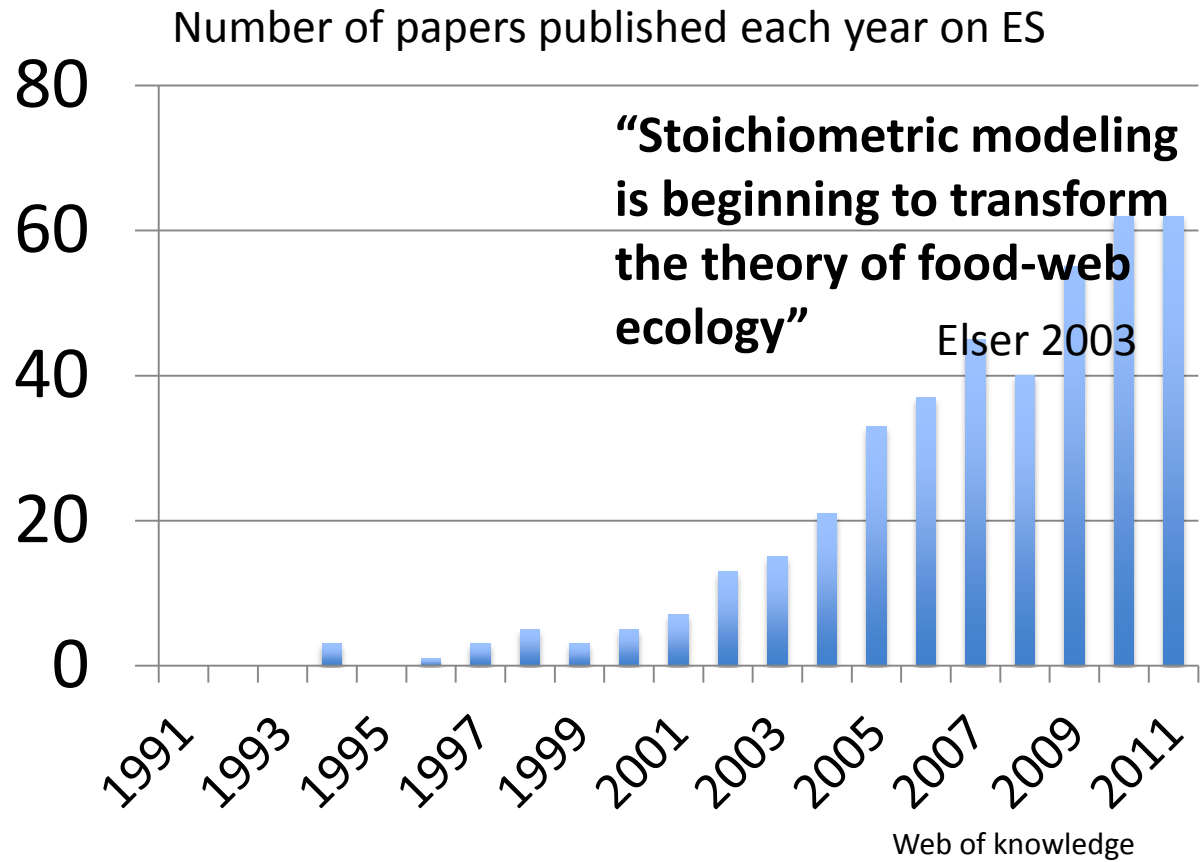
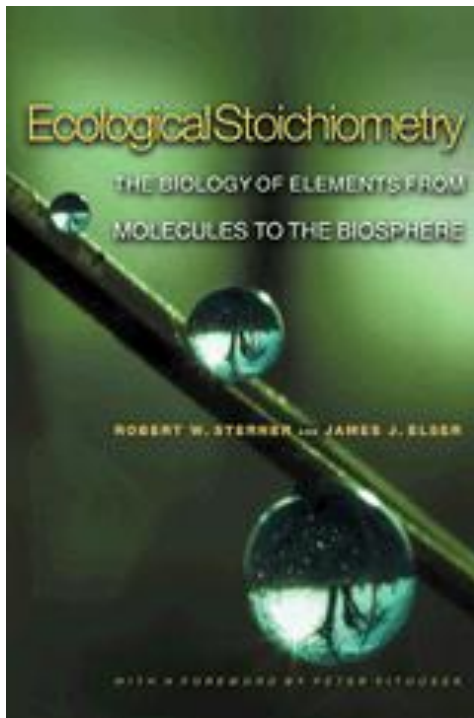
- The balance of chemical resources and their interactions;
- Match/mis-match between organismal requirement for nutrients and their availability



This concept formalized as Ecological Stoichiometry



This concept formalized as Ecological Stoichiometry



Nutrient composition regulates organism metabolism at concentrations well above those that are limiting

- *It's a balancing act.*
- Organisms sequester what they need and dissipate the rest.
- Too much presents metabolic costs as does too little
- Organisms have different needs for, and different strategies to regulate their nutrients



Cellular
metabolism
changes

GROWTH RATE
Changes

Algal
community
shifts

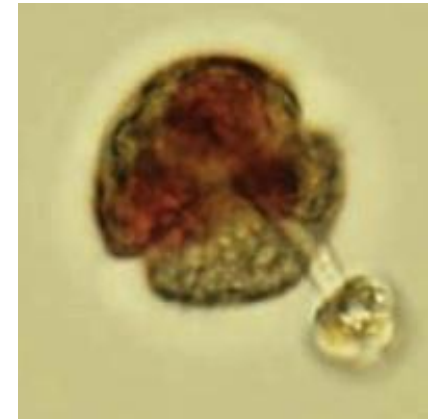
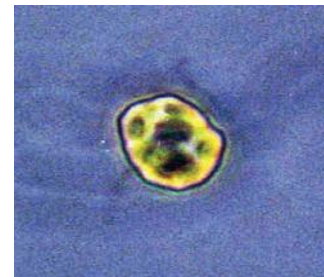
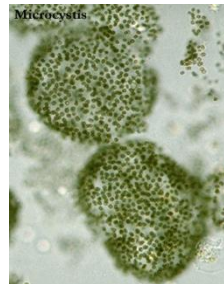
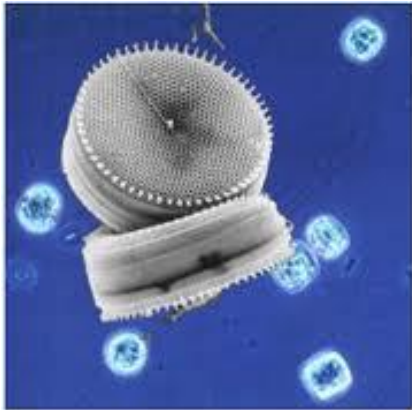
Food web
shifts

Nutrient loads, forms and ratio changes

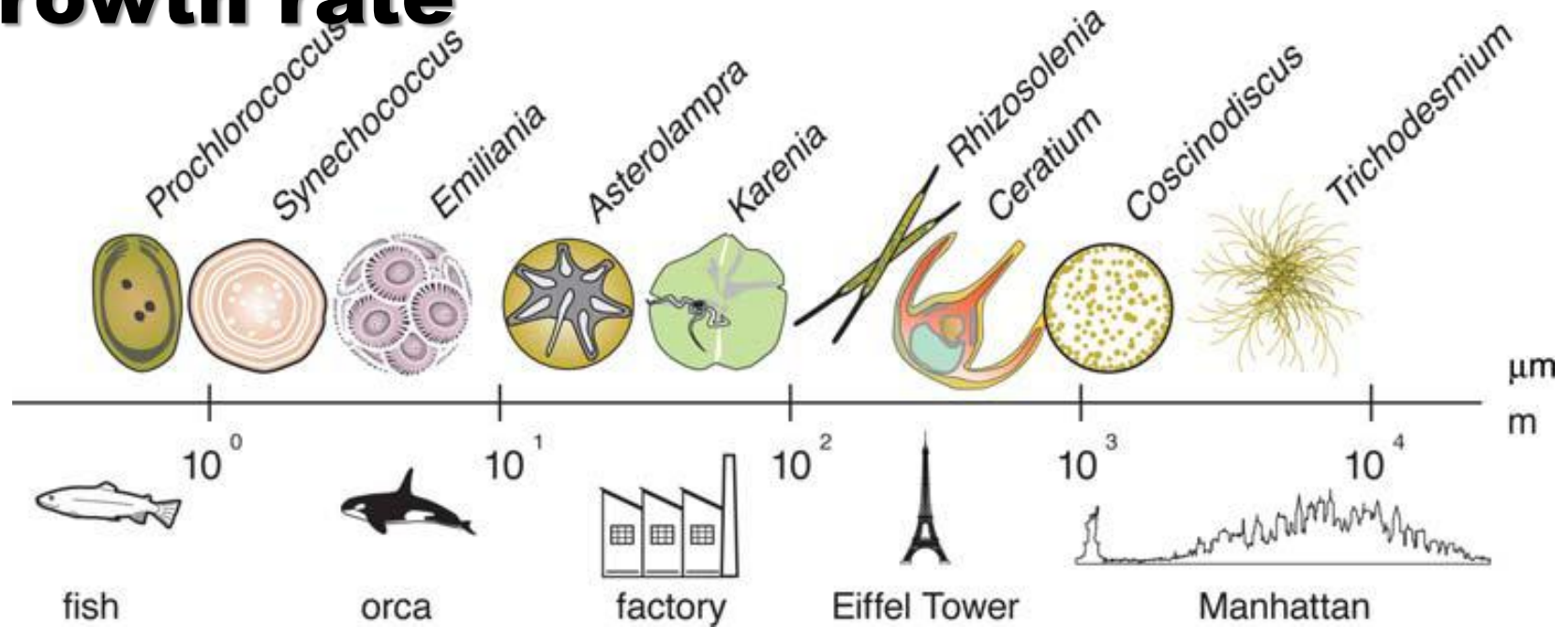
Fundamental responses are
predictable based on biology

Ecological stoichiometry at the base of the Food Web

- Algae generally follow a “*you are what you eat*” strategy
- They have limited capability to regulate their nutrient content



Across species there is a great diversity in size, composition and growth rate



| Organism | Cell Size | C:P |
|----------------------|-----------------------------|------------|
| <i>Synechococcus</i> | $10^0 \mu\text{m}^3$ | ~ 100 |
| Diatoms | $10^2 - 10^3 \mu\text{m}^3$ | ~ 50 |
| Cryptophytes | $10^1 - 10^4 \mu\text{m}^3$ | ~ 60 |

Data and figure from Finkel et al. 2010

Cellular
metabolism
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Algal
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Nutrient loads, forms and ratio changes

**Cellular
physiology
changes across
the entire
spectrum of
substrate
availability**

Cell size

Cellular pigmentation

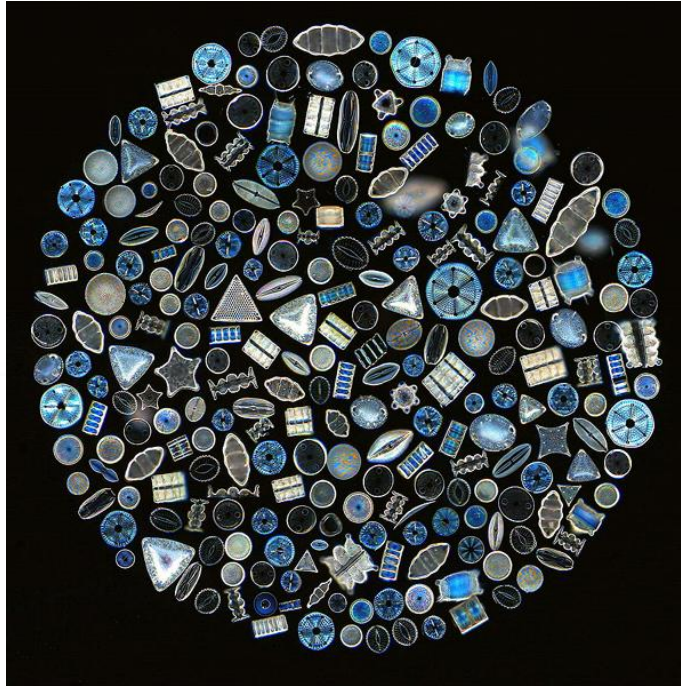
N:C, C:P, N:P

Enzyme activities

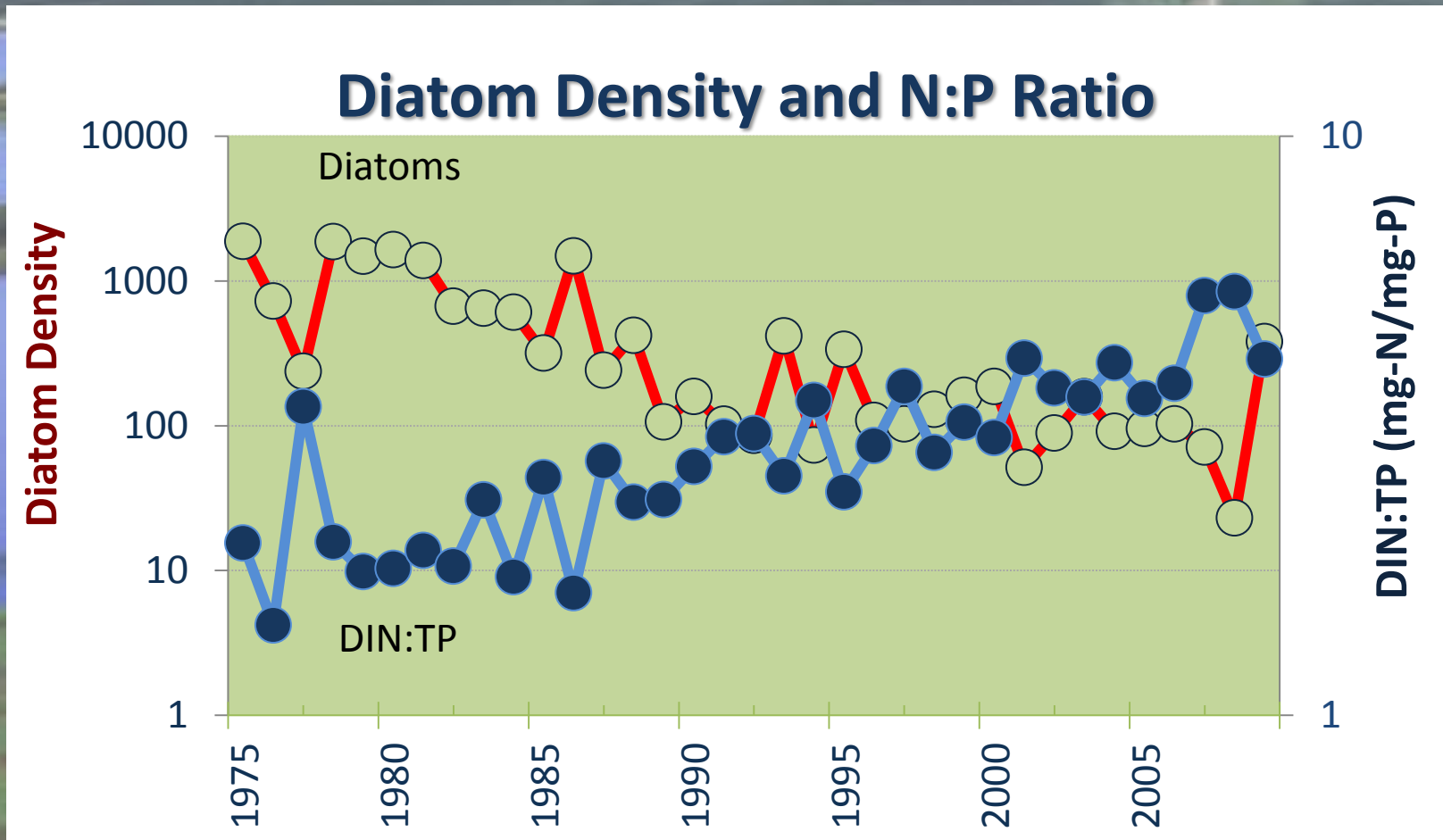
Growth rate

Toxin production

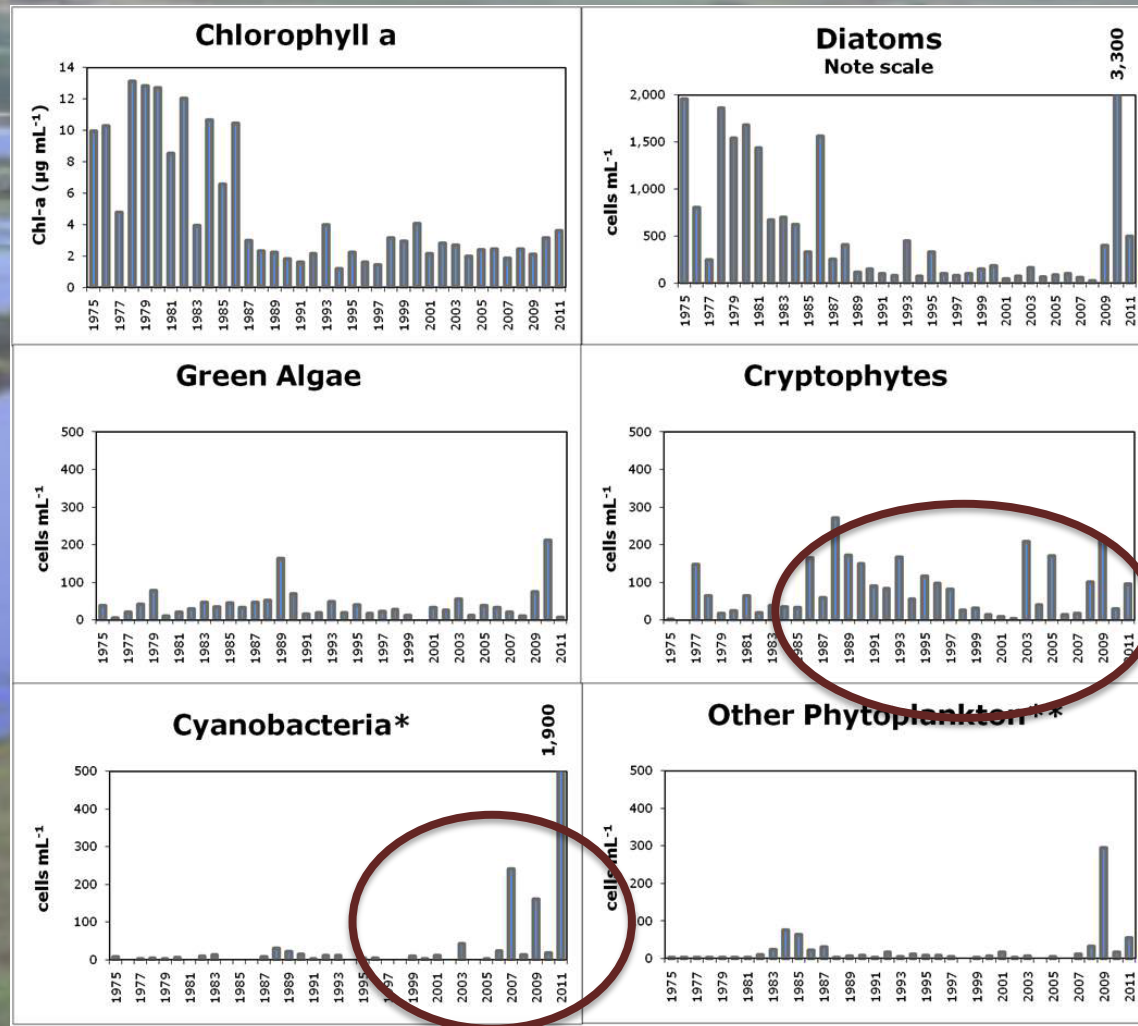
Even good food can go bad



Algal community composition changes



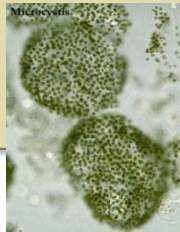
Algal community composition changes



The QUALITY of algae has changed,
not just the QUANTITY

Ecological stoichiometry at higher trophic levels

Changes in
the QUALITY
and quantity
of the algae



Grazers
change in
GROWTH,
community
shifts

Food web
shifts

Nutrient loads, forms and ratio changes

Ecological stoichiometry at higher trophic levels



Changes begin at the metabolic scale

Changes in diet can affect reproduction, egg viability,
and ultimately population success, **GROWTH**

Ecological stoichiometry at higher trophic levels

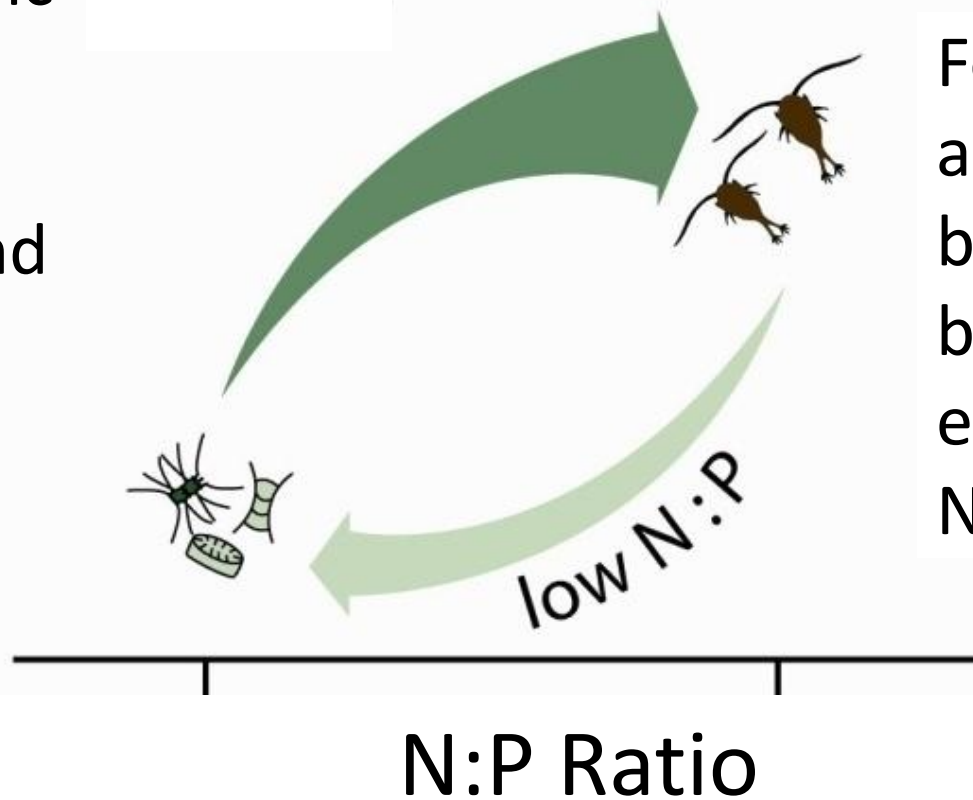
“An animal’s elemental composition is linked to its evolved structure and life history...

It takes a different proportion of nutrients to make skeleton and bones than it does to make muscle;
Different types of organisms thrive as nutrition changes



Ecological stoichiometry at higher trophic levels

Stoichiometric needs of the secondary consumer and the prey are “fine tuned”

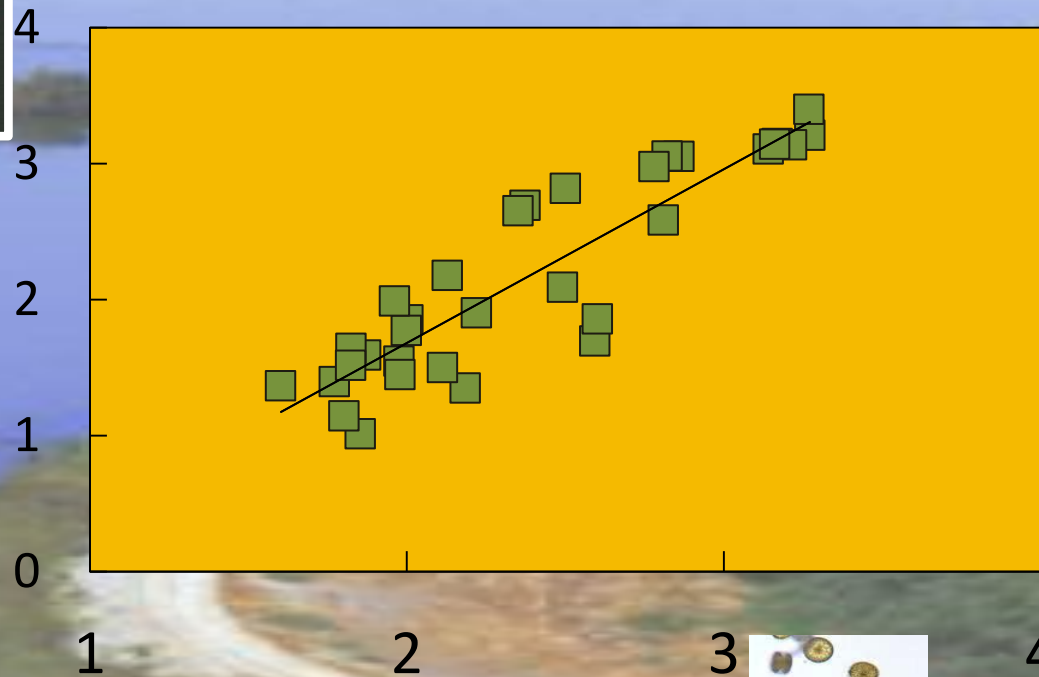


Food biomass and grazer biomass may be at opposite ends of the N:P spectrum

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



Log *Eurytemora*



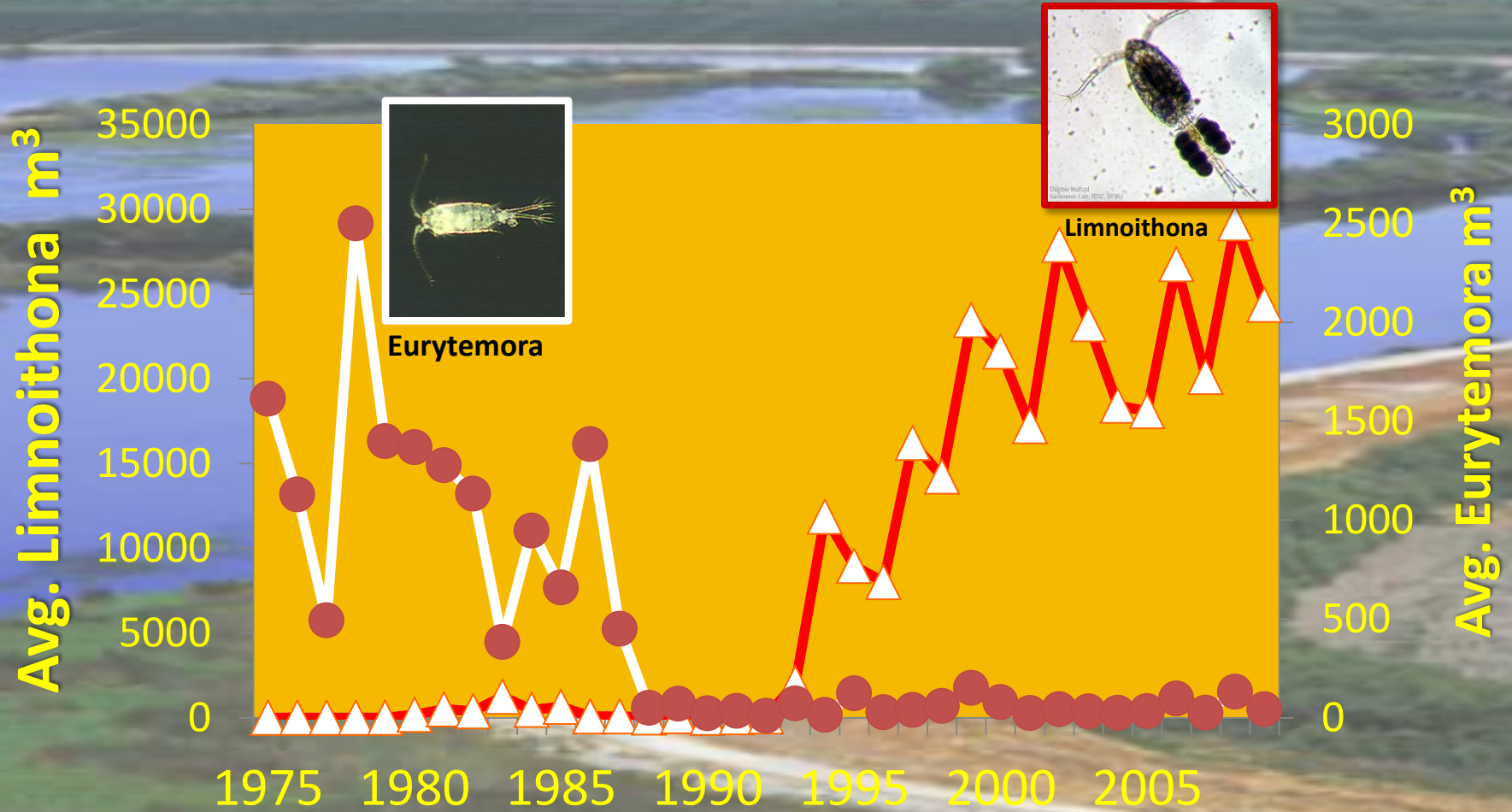
Log total Diatoms



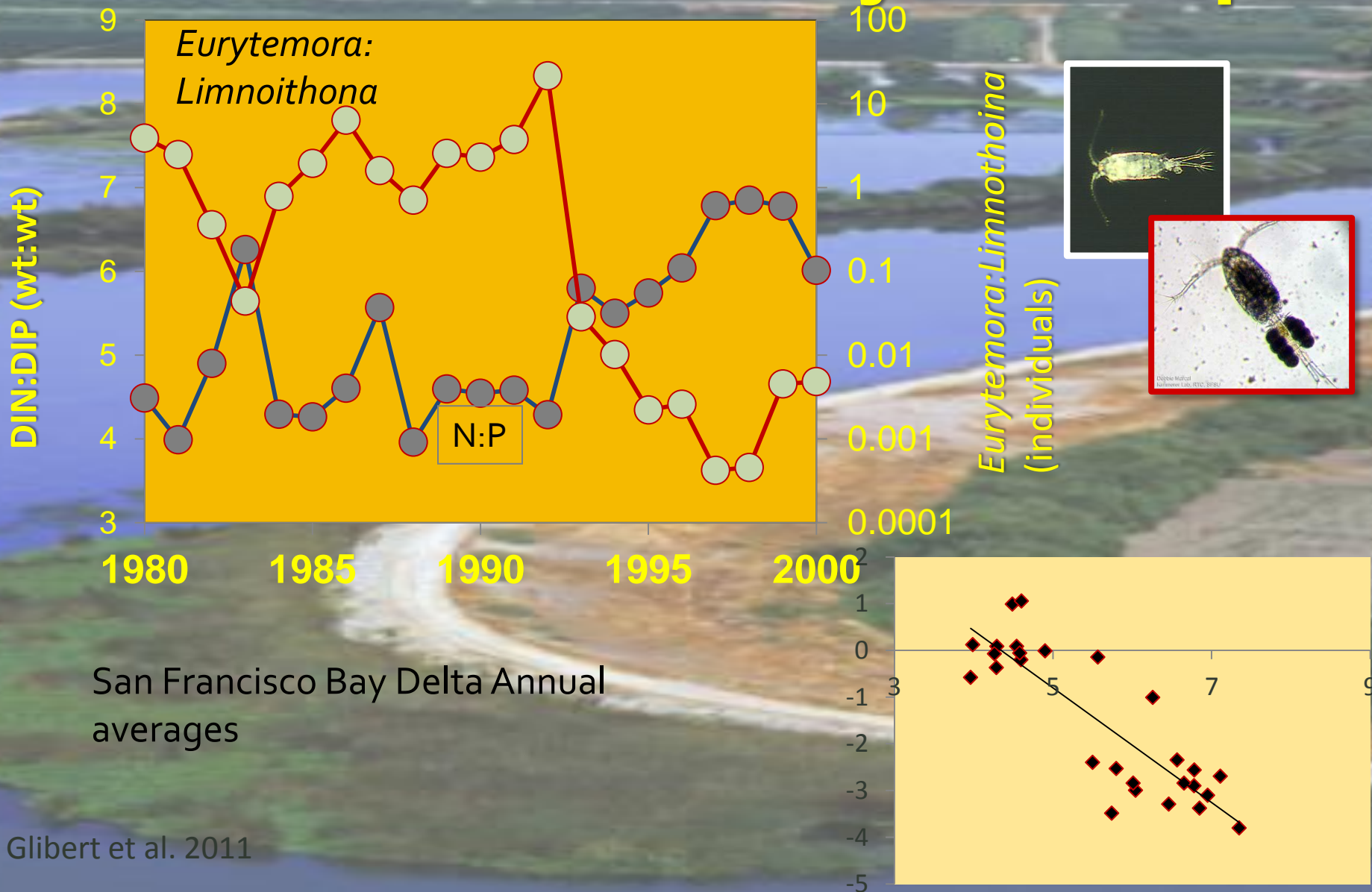
San Francisco Bay Delta Annual averages

Glibert et al. 2011

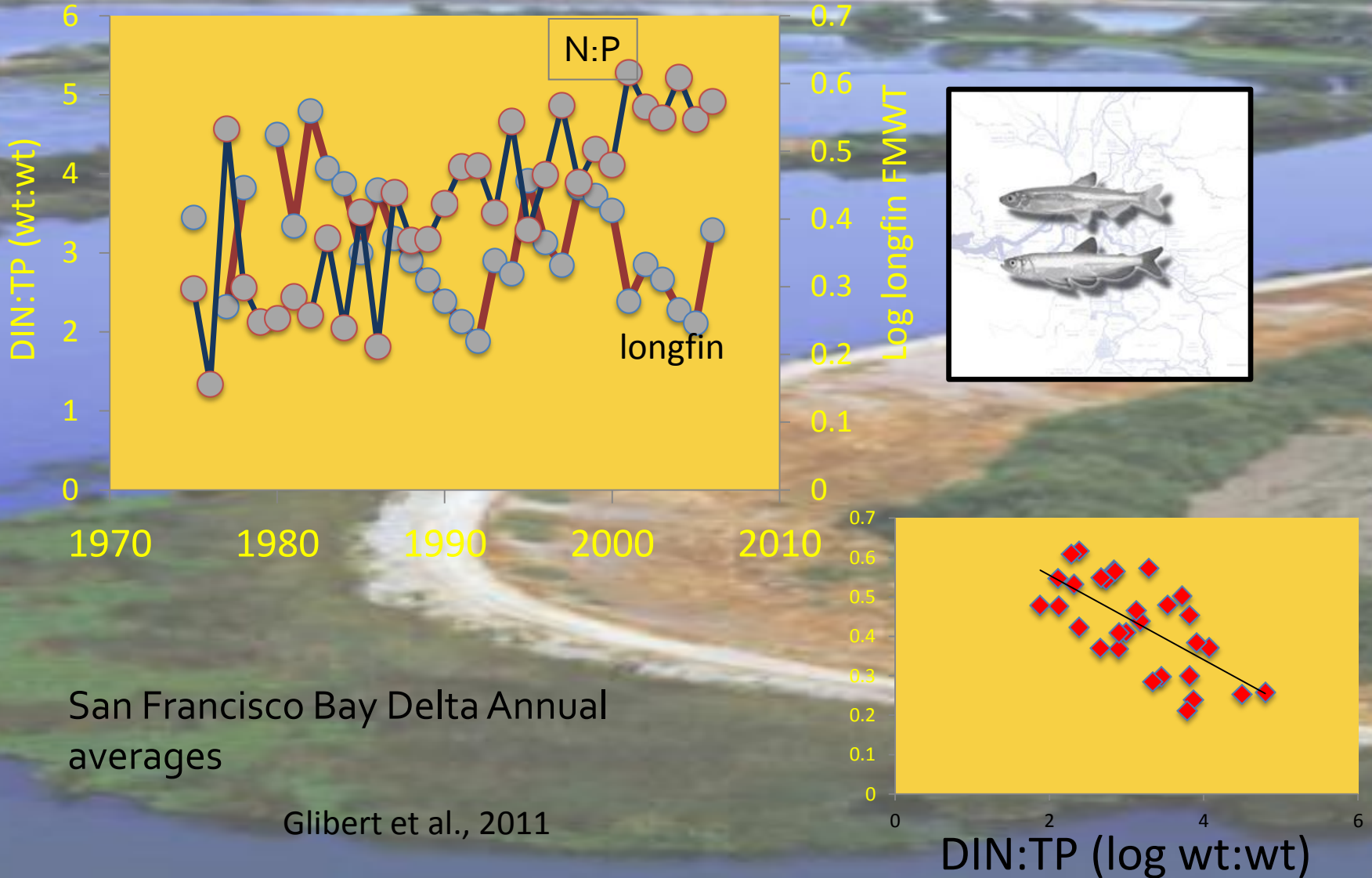
Changes at the bottom of the food web alter the community at the top



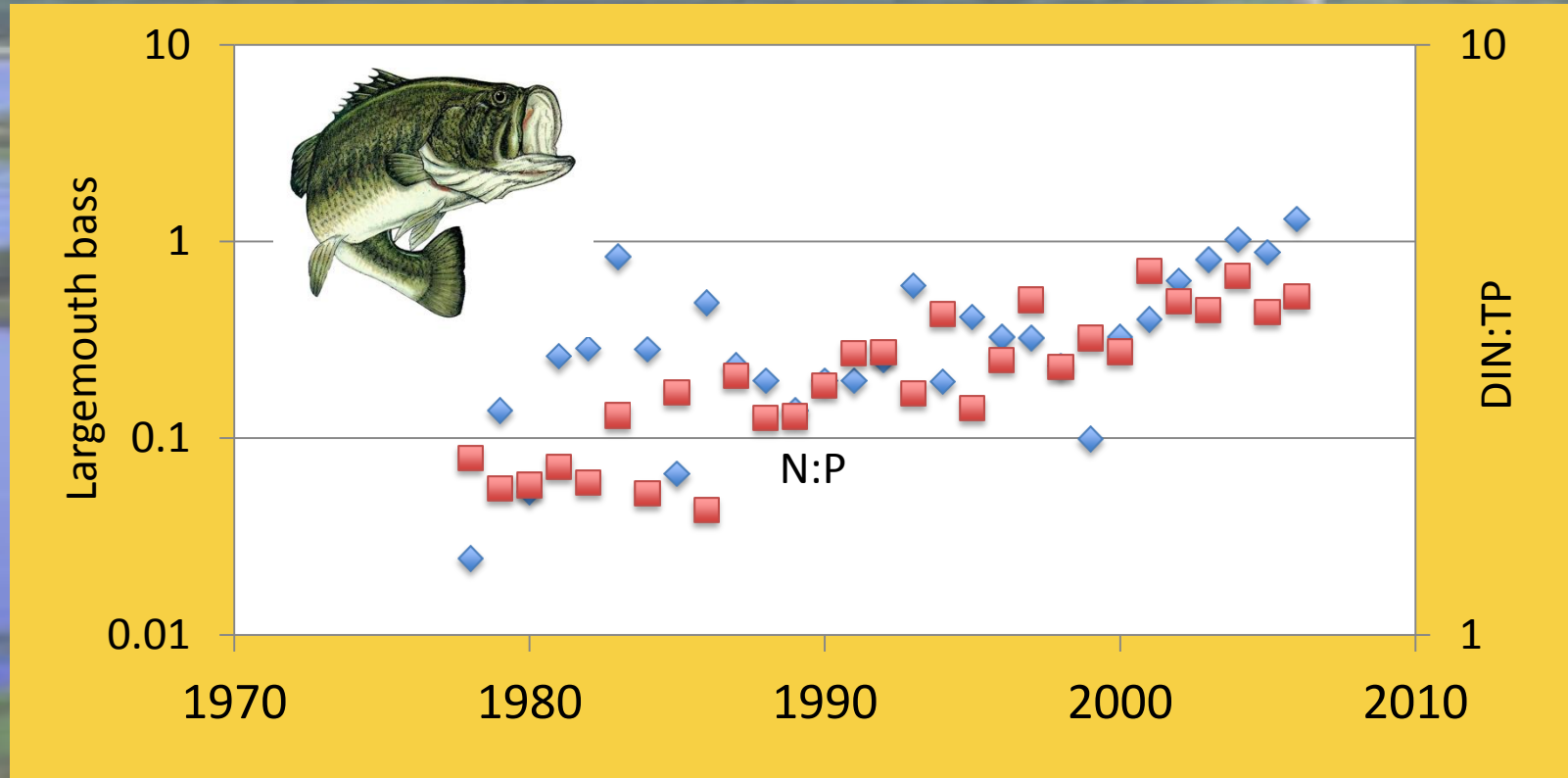
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Changes at the bottom of the food web alter the community at the top

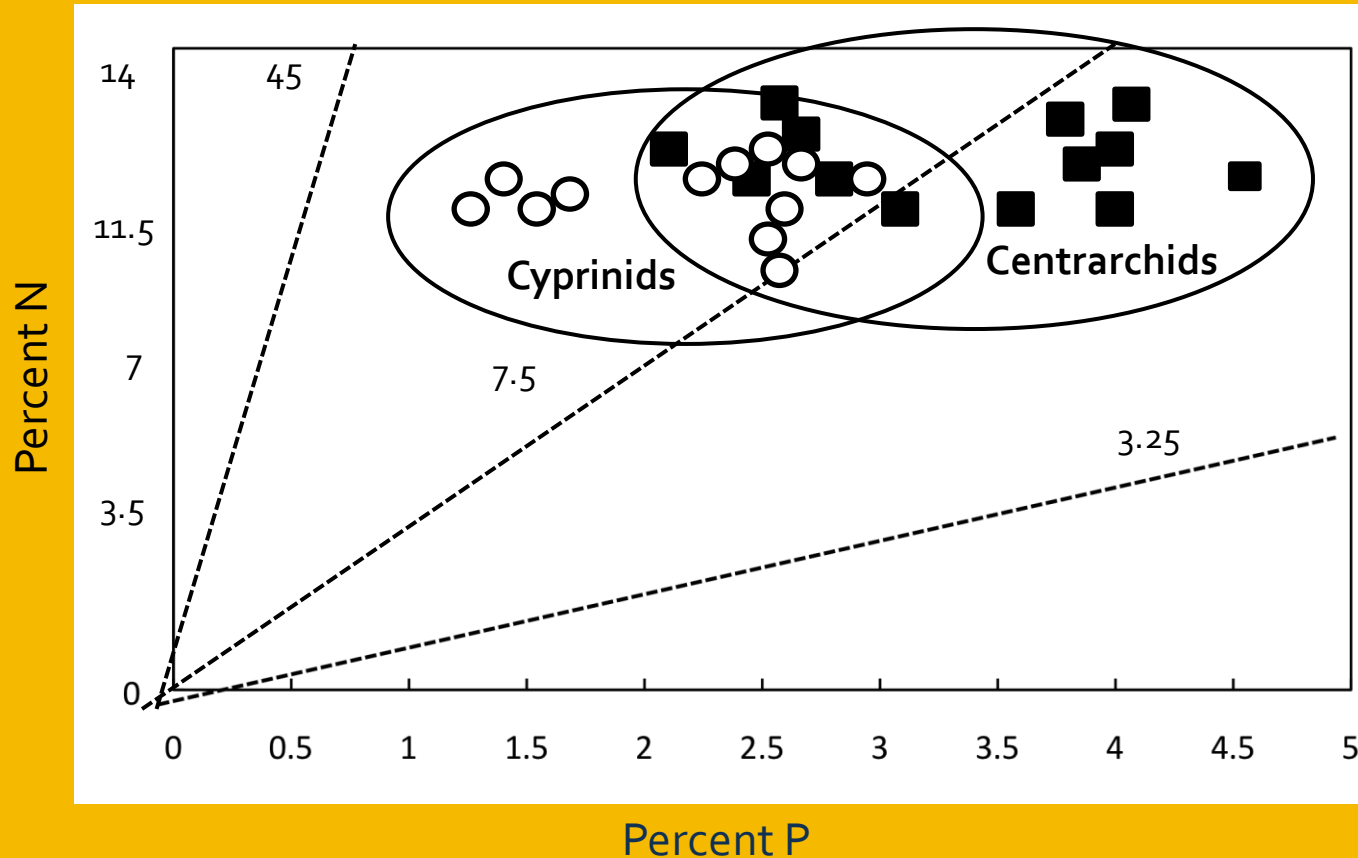


Changes at the bottom of the food web alter the community at the top



“As one ascends the pelagic food web...trophic groups grow increasingly nutrient and especially P rich...”

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

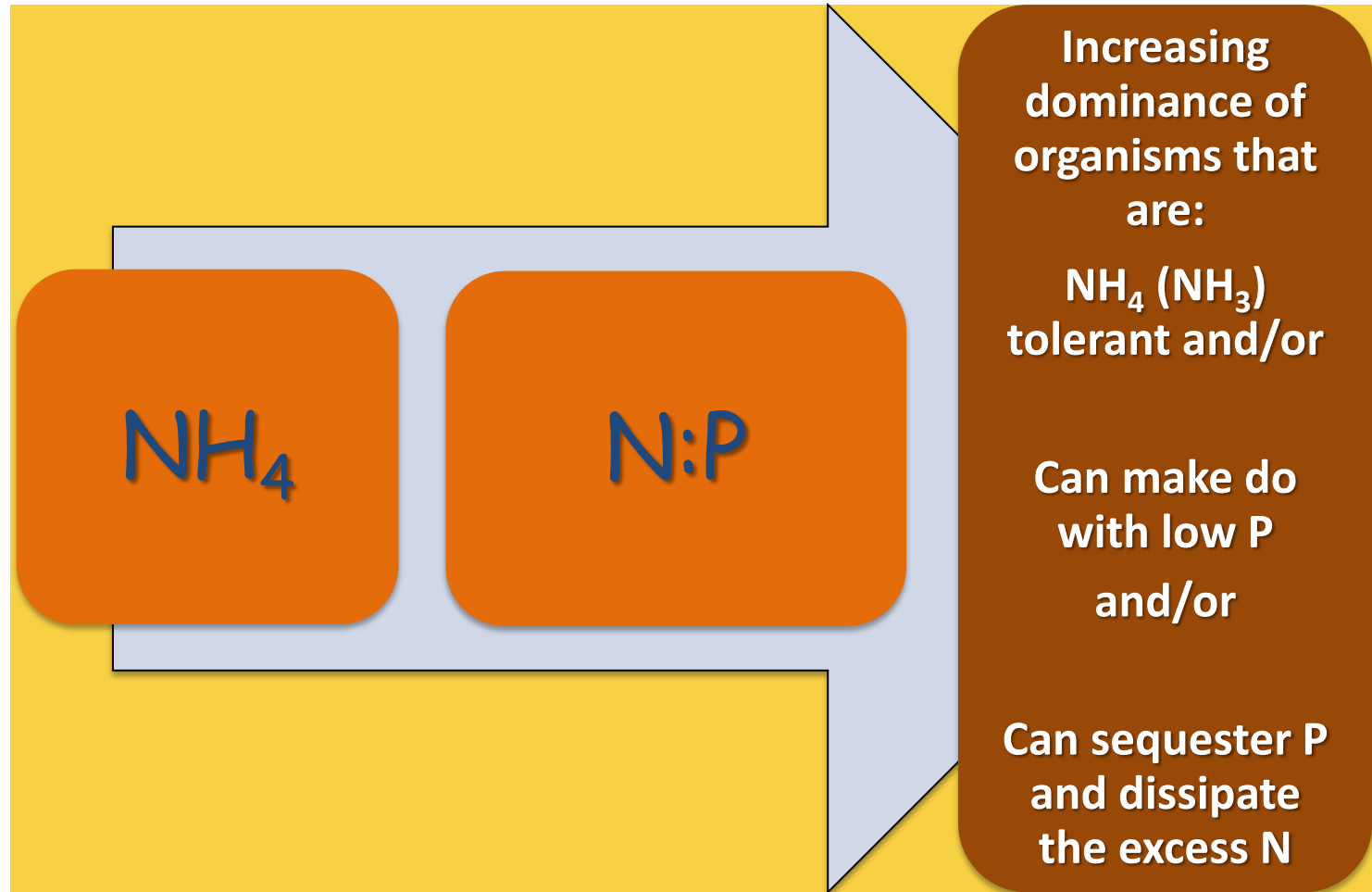


Highly evolved excretion mechanisms to help balance nutrient stoichiometry

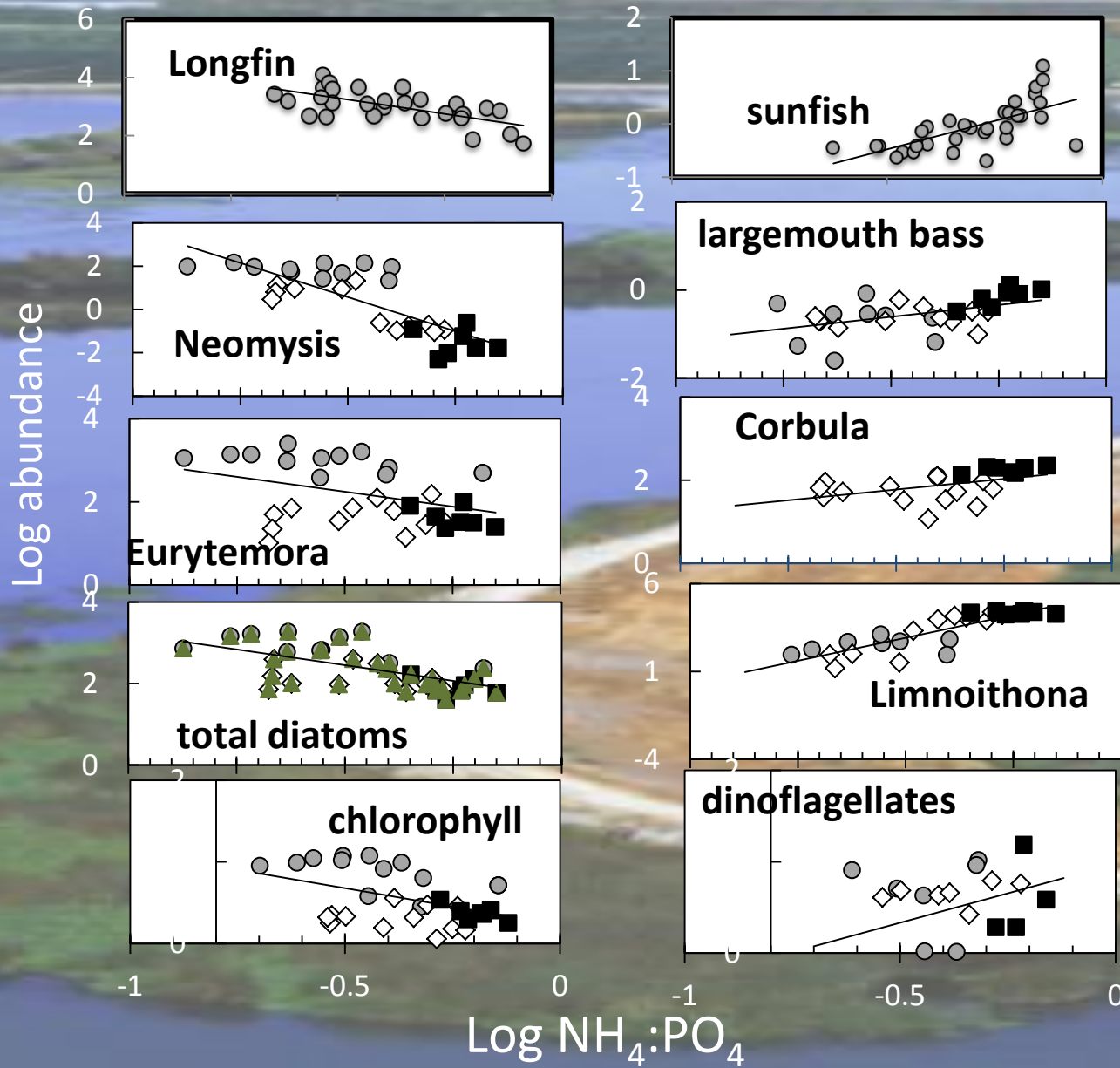
Modified from Sterner and George 2000



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



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



As nutrients change there are winners and losers at all levels of the food web

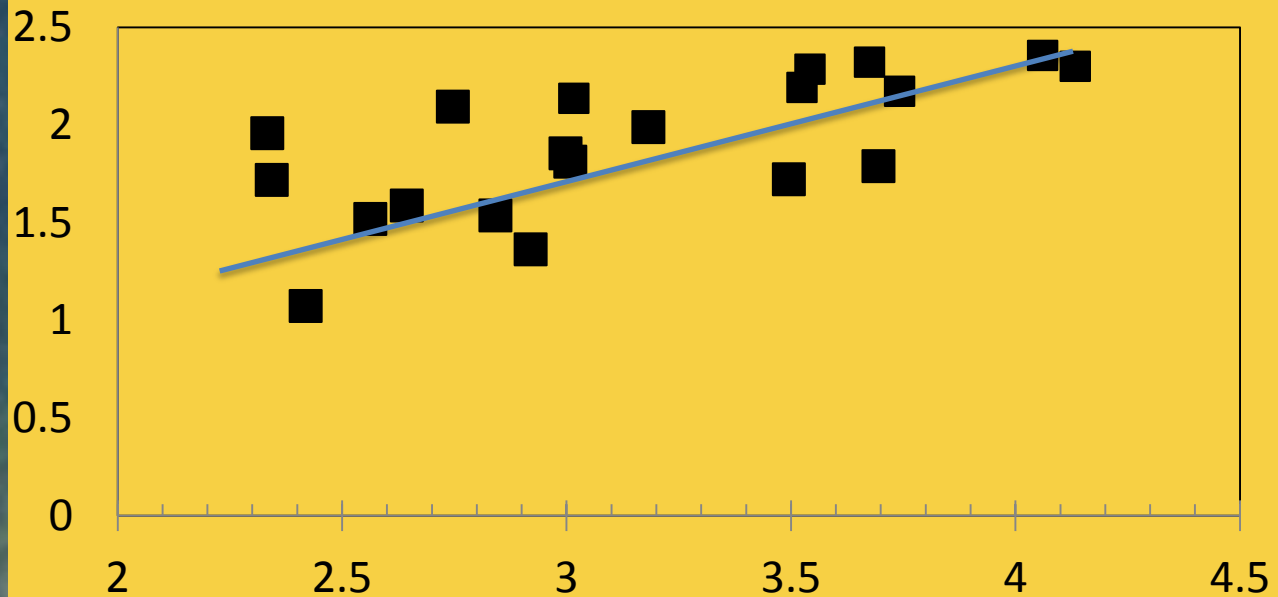
The winners and losers are predictable based on fundamental biological principles

Some of the winners are invasives



Potamocorbula

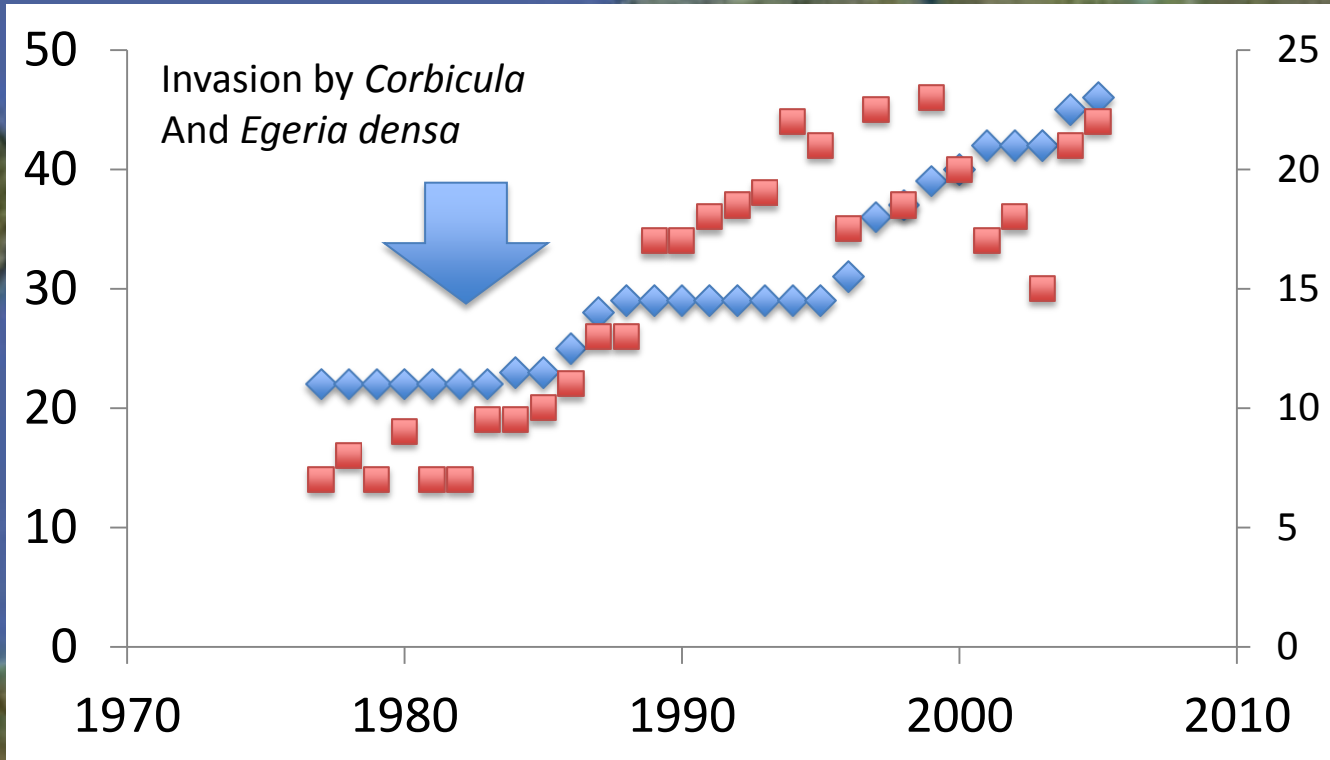
Log abundance (indiv m⁻²)



Invasive species may be as much a RESPONSE to nutrient and ecosystem change as they are a CAUSE of ecosystem change

Rhine River

cumulative number of invasive species

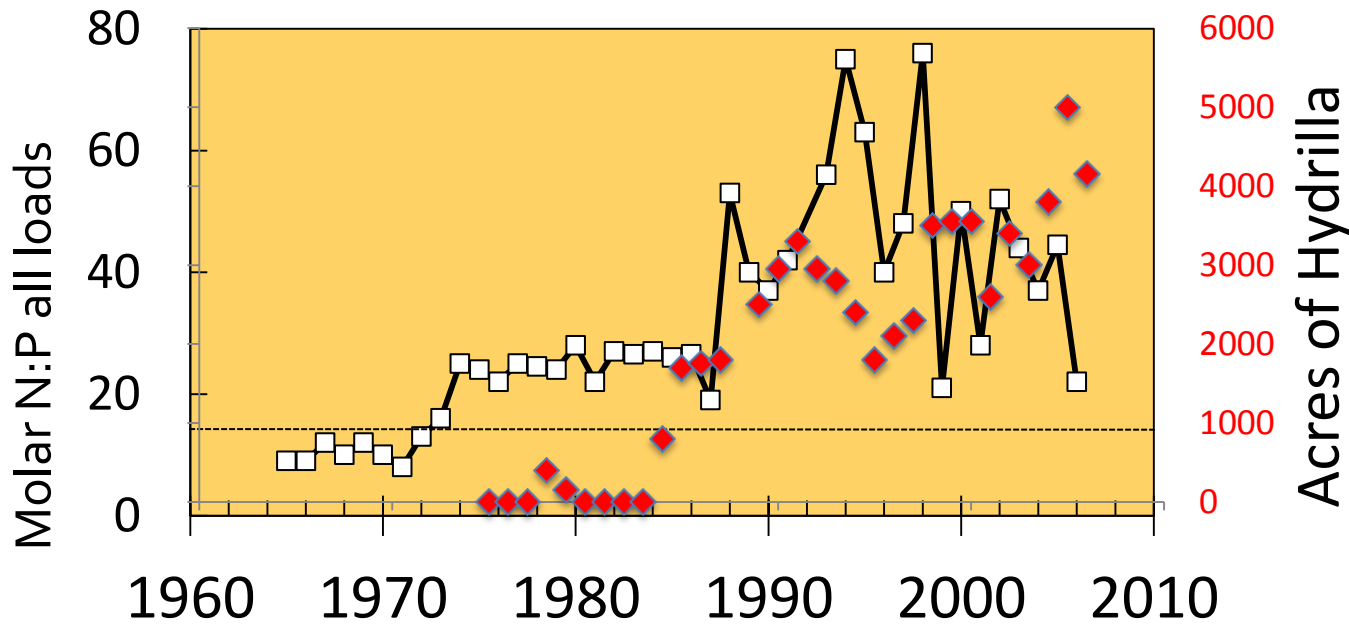


TN:TP (wt:wt)

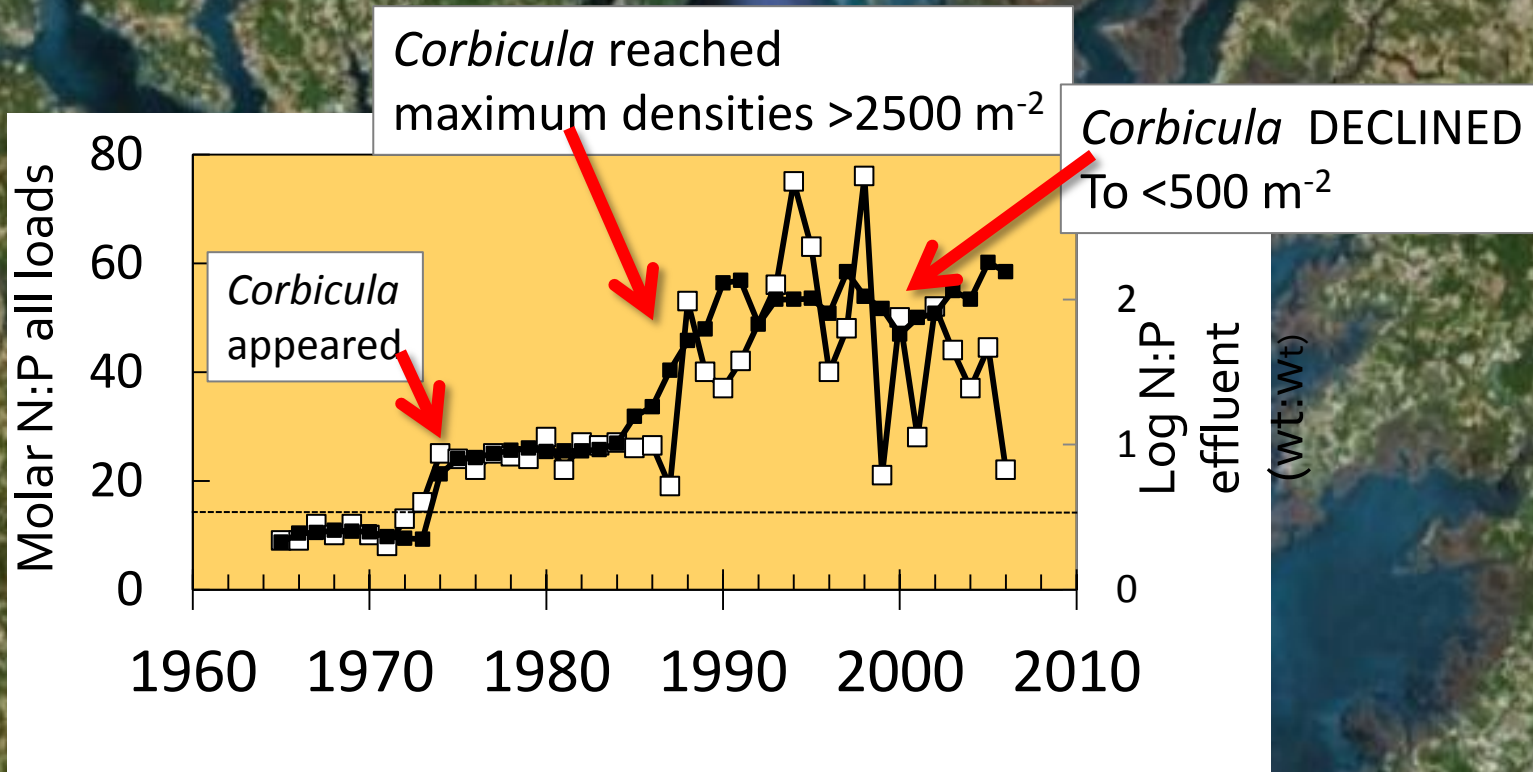
Source data: Van Niewenhuyse 2007; Leuvin et al. 2009

Rhine

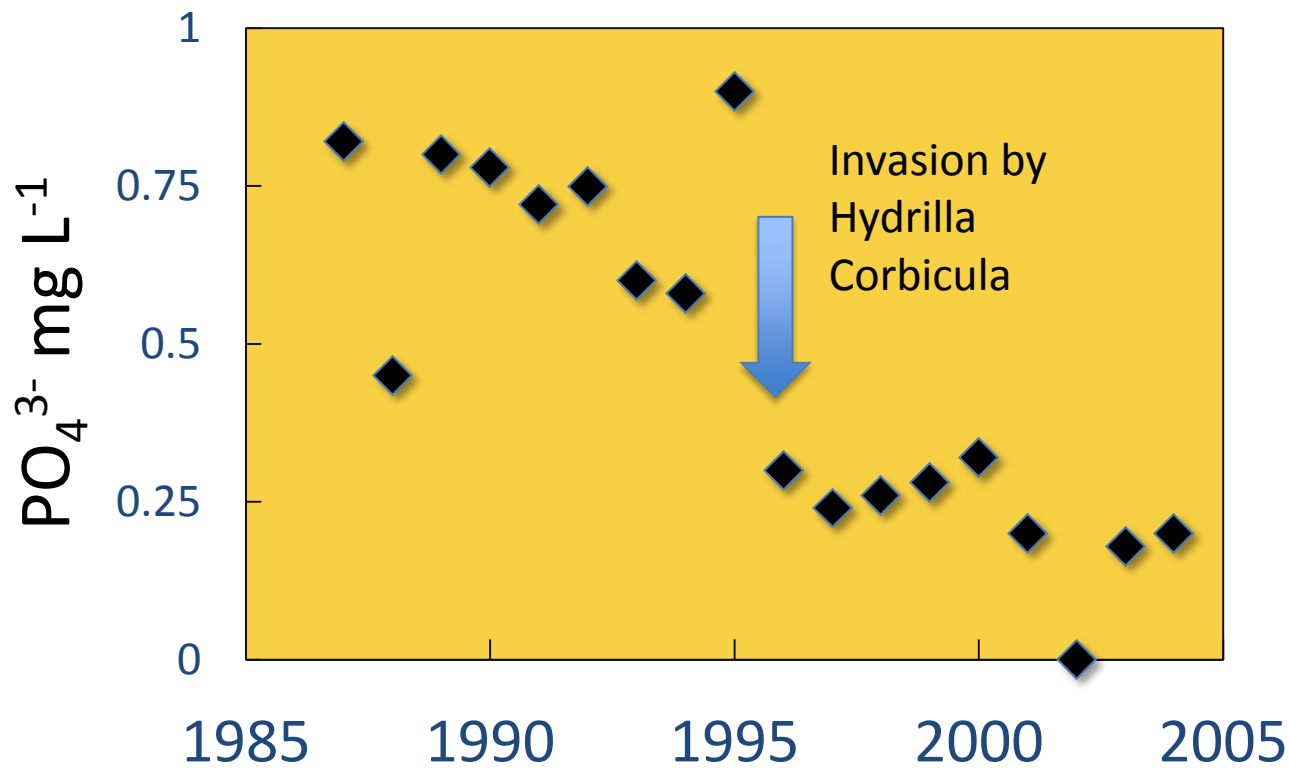
Potomac River, Chesapeake Bay



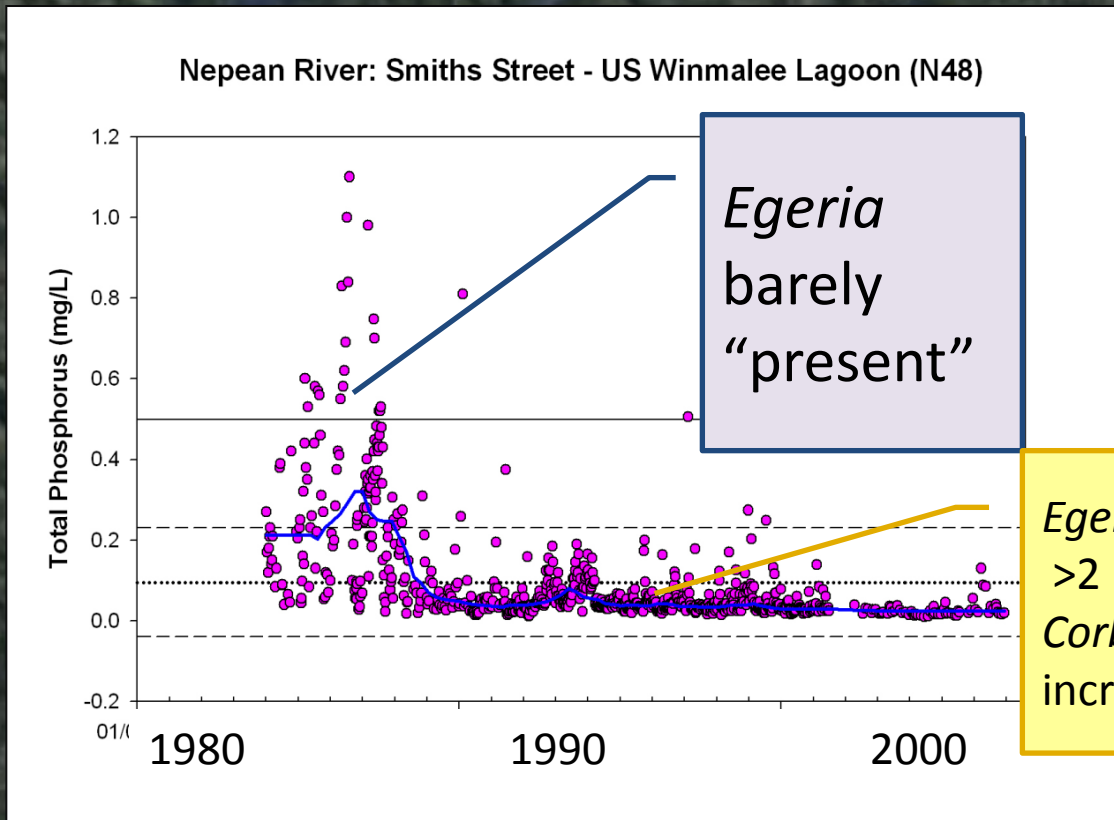
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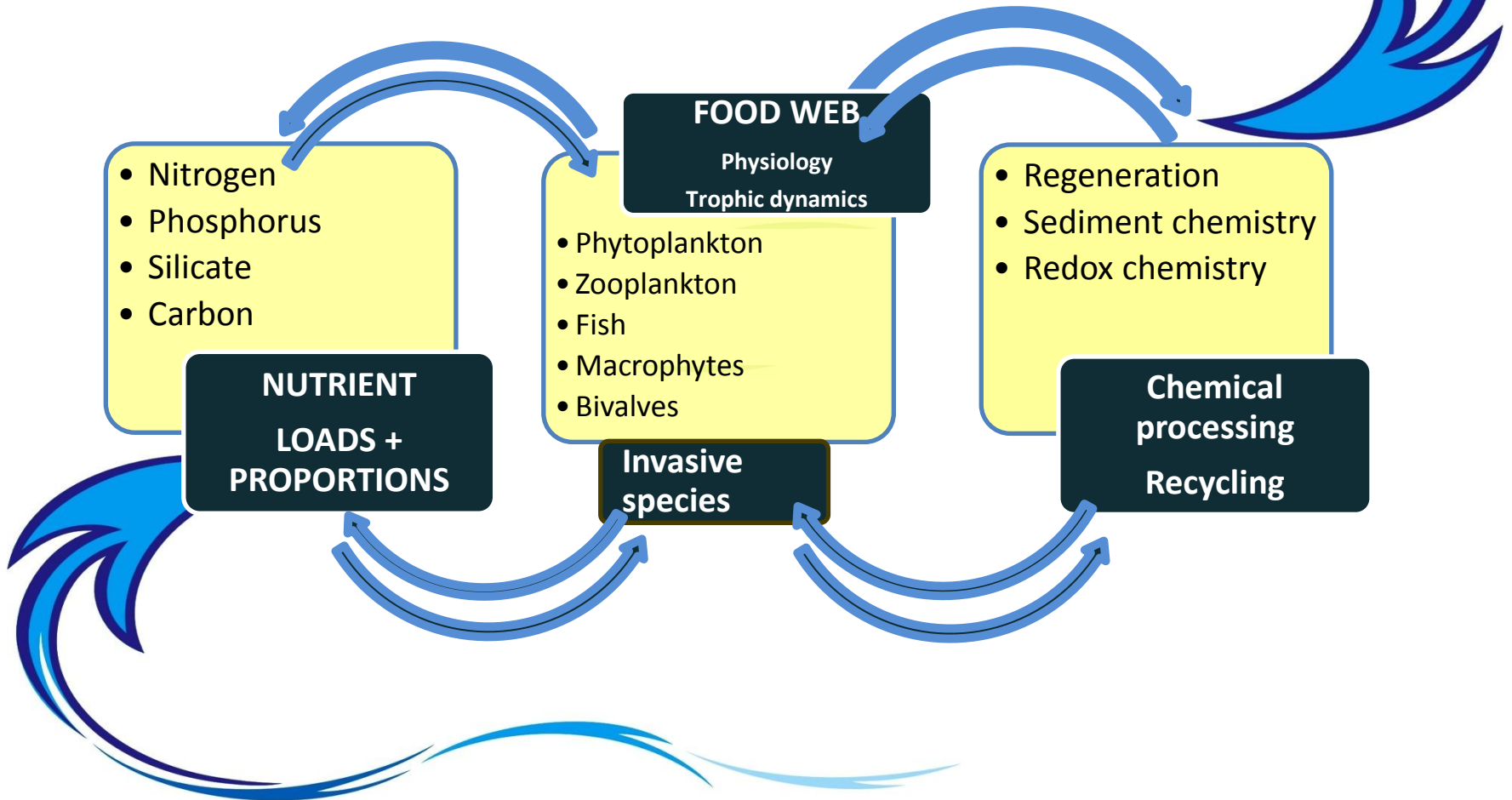
Lower Ebro River, Spain



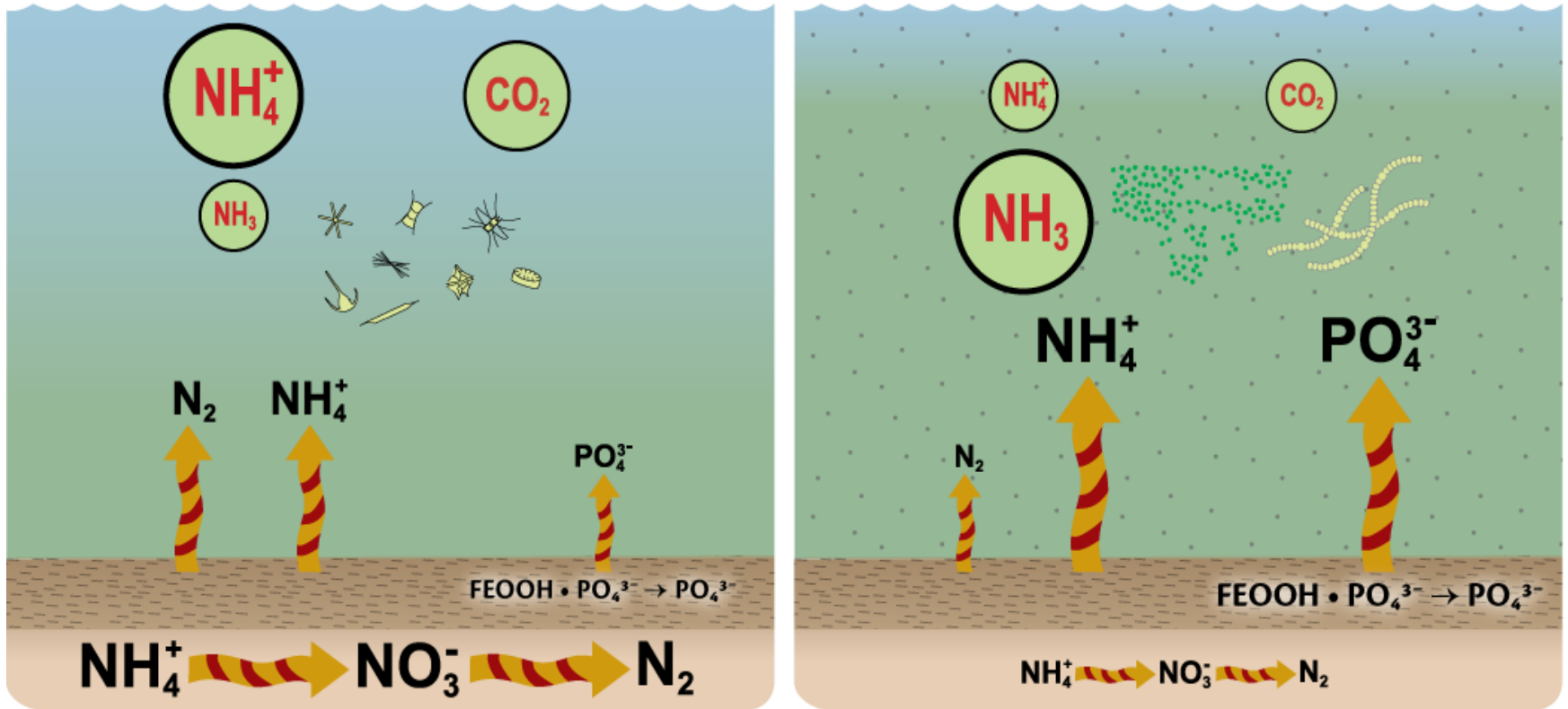
Lower Hawkesbury-Nepean River, Australia



Ultimately it's all connected ...and a grand mass balance



Nutrients and flow



Sediments are reservoirs of nutrients
 Fluxes change with salinity, pH, temperature

Nutrients and flow

Salt



Fresh

Residence time (exposure time) to
beneficial nutrients or inhibitory/toxic compounds

Flow

- Imports new nutrients
- Dilutes point source inputs
- Alters reactions at the sediment surface
- Exports nutrients downstream where they can form blooms displaced in time and space from the source.

Ecosystem is in Dynamic Balance

Nutrients are part of that balance



Preference/inhibition+toxicity
Too little/too much
Ammonium/nitrate
Nitrogen/phosphorus
'top-down'/'bottom up' control



“Simple rules can yield intricately complex outcomes...stoichiometry is one of those simple rules underlying ecological and biological complexity”

Sterner and Elser 2002

Food webs are shaped by the balance between nutrient resources and the elemental demands of the organisms

RECAP

- ❑ Ammonium is a *paradoxical* nutrient
- ❑ Nutrient ratios DO matter, altering the QUALITY of food at all levels
- ❑ Too much nutrient can be a stress, as is too little
- ❑ The Bay Delta is not unique in the trajectory of many food web changes with changes in nutrient loads and ratios
- ❑ Nutrient changes can alter the ecosystem providing opportunities for invasive species to thrive
- ❑ Ecological stoichiometry may help to provide a mechanism for relationships between fish and flow

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“Consumers can be ‘destined for extinction’ when faced with poor food quality”

