DISSOLVED ORGANIC MATTER (DOM) AS A DIRECT ORGANIC SUBSIDY TO AQUATIC CONSUMERS

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Acknowledgements: Hudson Roditi, Nick Fisher, Jon Cole, Cindy Lee, Dave Fischer, Benjamin Rhau, Emily Herstoff, Mary Alldred, Stoycho Velkovsky, Lucas Merlo, Ruth Stein, Matt and Mike Matthews.

Funding: Hudson River Foundation

HRF Stony Brook University

Zebra mussels: basic facts

I. Filter feeding freshwater bivalve mollusks

II. Native of region near Black and Caspian Seas

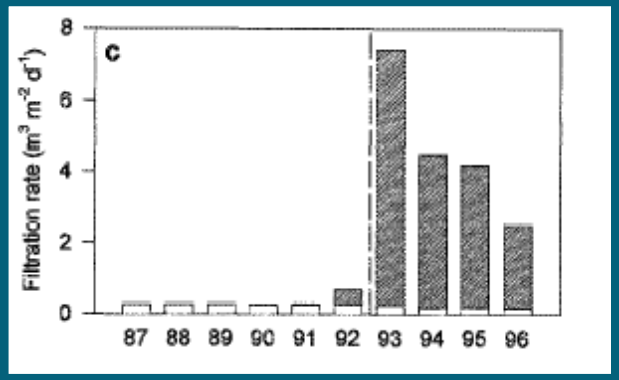
III. Evolved in the Pleistocene from marine/estuarine ancestor

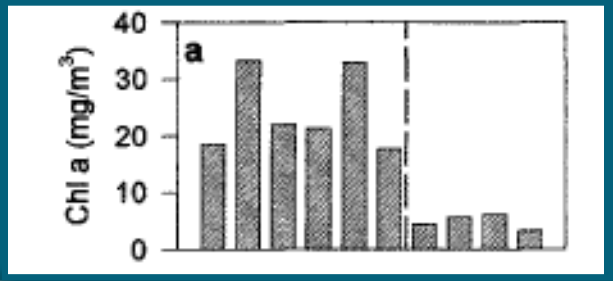
IV. Retain many marine characteristics -- including planktonic larvae

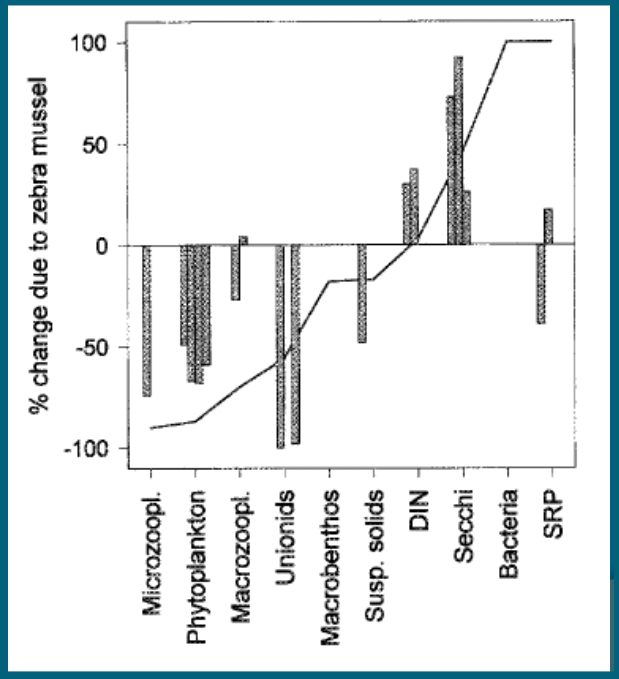
V. Invaded North America in mid 1980's via ballast water

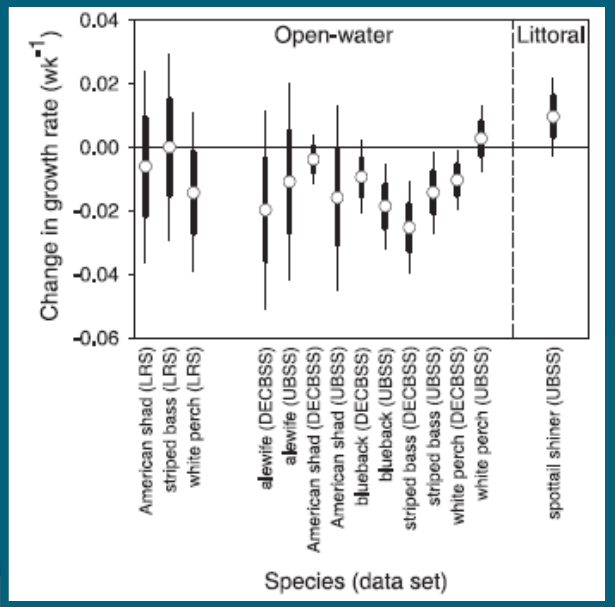
Zebra mussel effects in the Hudson

Herbivory increased > 20-fold
Algal biomass decreased by 80%
Zooplankton declined by 30-70%
Native bivalves (unionids) declined by 50-70%
Growth rates of planktivorous fish declined





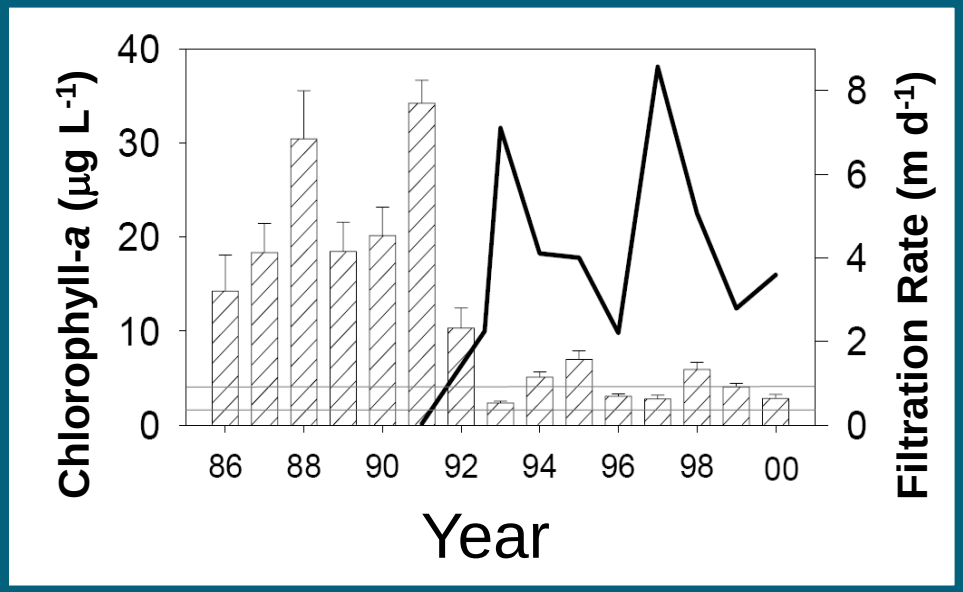


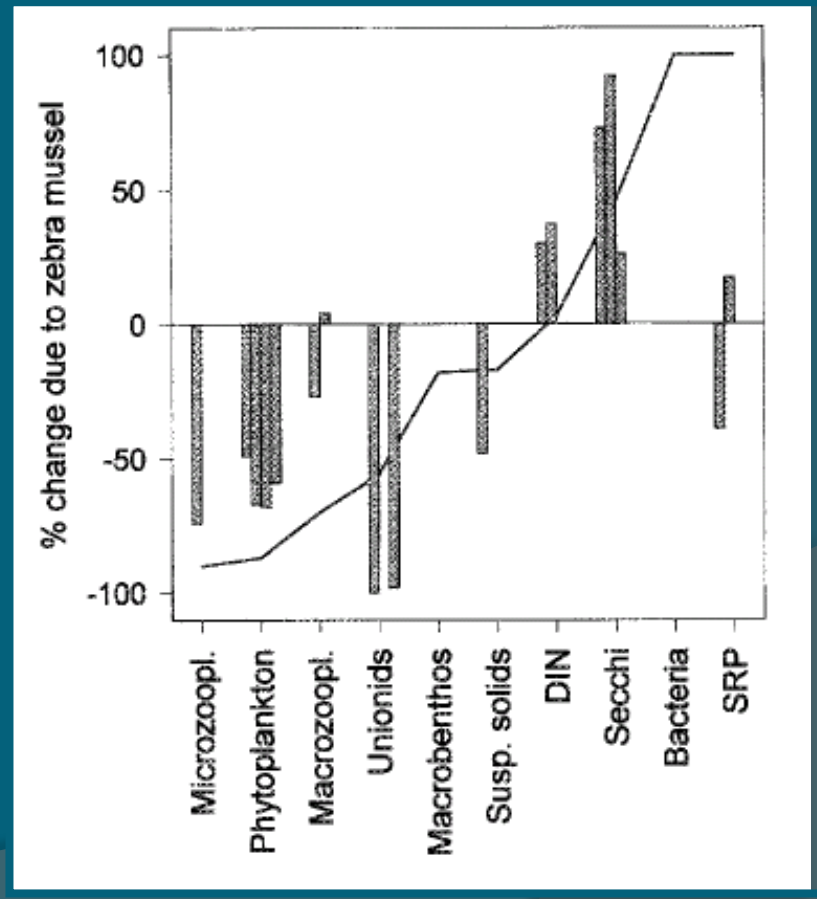


Strayer et al. 1999. Bioscience 49: 19-27

Strayer et al. 2004.
Can. J. Fish. Aquat. Sci. 61: 924-941

Persistent effects of zebra mussels

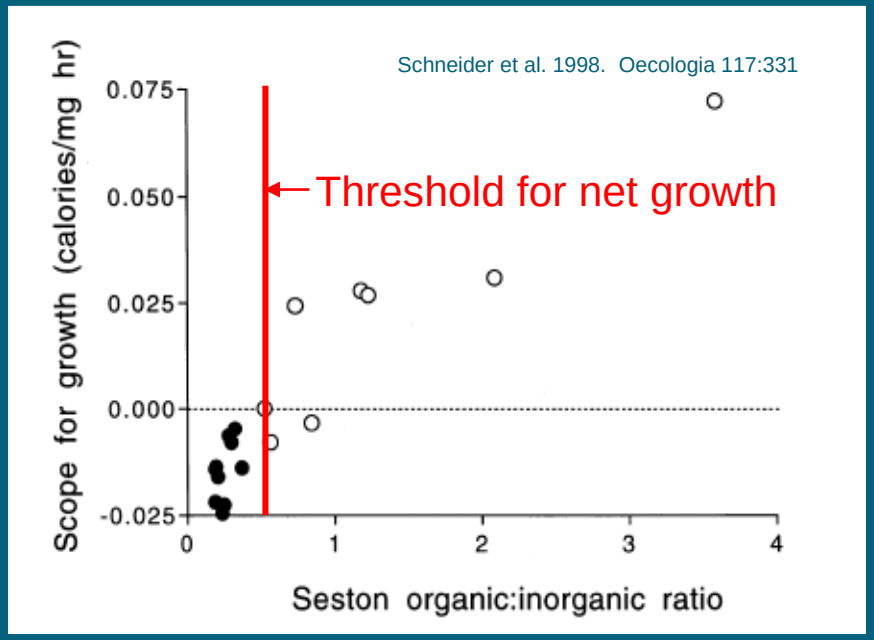




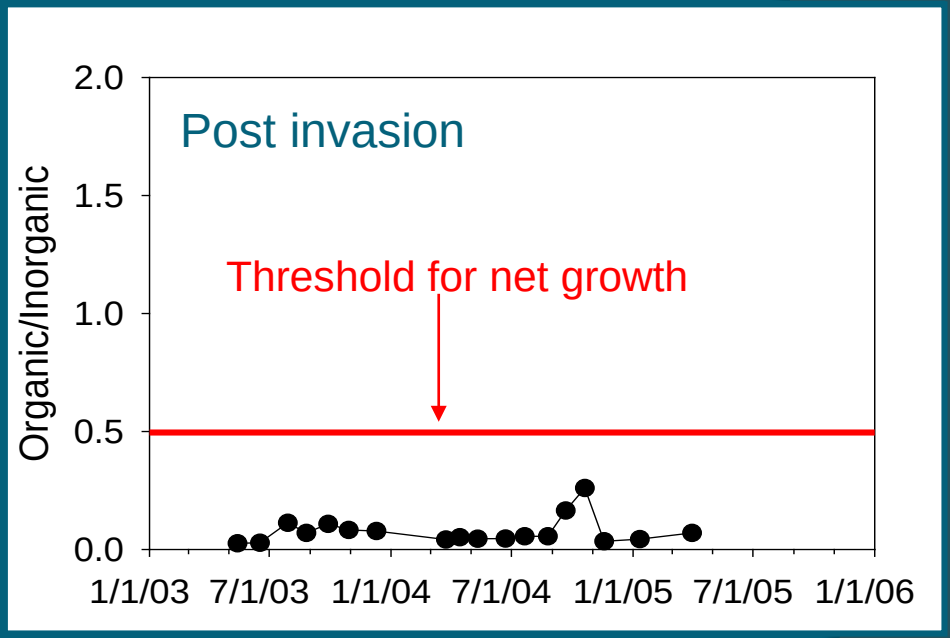
Cole et al. 2006 in Levinton

The mystery: how do they persist?

Bioenergetic constraints



Hudson River Particulate Matter



<u>Ecosystem level energetic imbalances</u>

Dreissena respiration > Phytoplankton + macrophyte CO_2 fixation

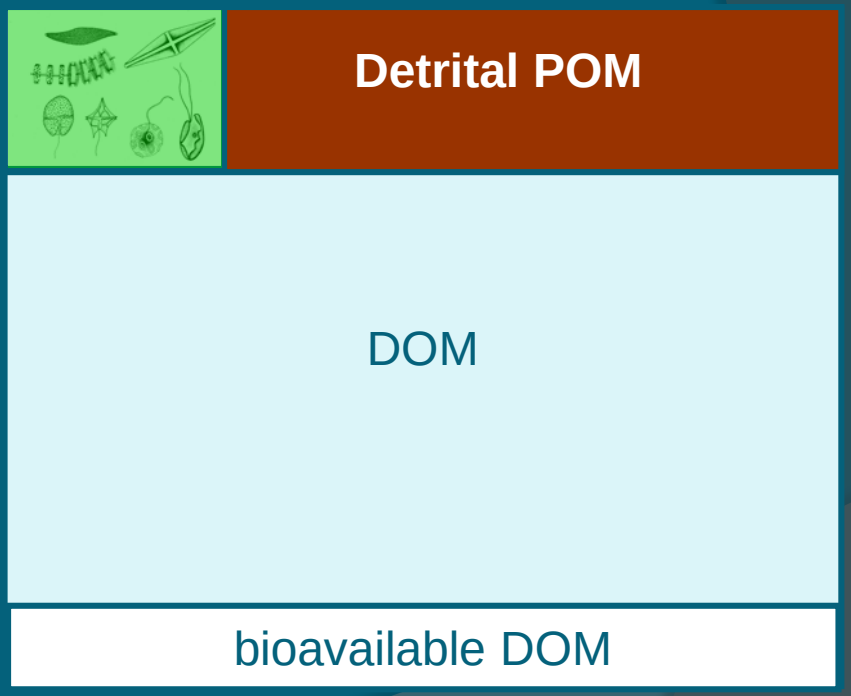
Dissolved Organic Matter (DOM): Energetic subsidy to zebra mussels?

What is DOM ?
-75-90% of organic matter
-Mostly uncharacterized chemically
-Largely terrestrial in origin

What makes it a bad subsidy
-It's dissolved
-Not considered bioavailable

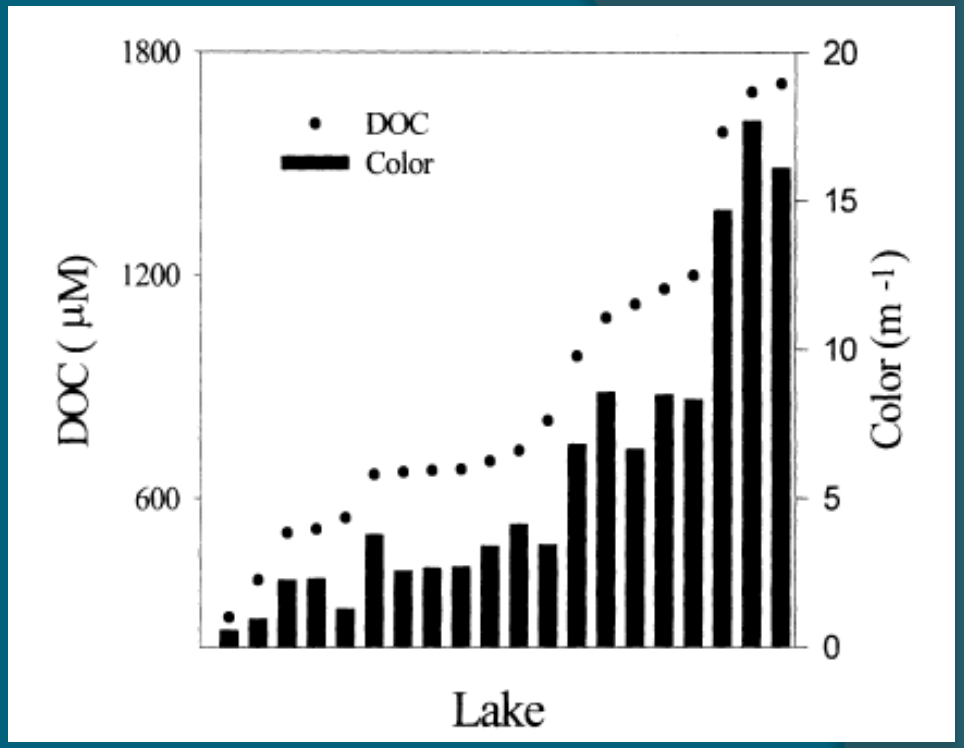
What makes a good subsidy
-Derived from outside system
-Don't need to use much

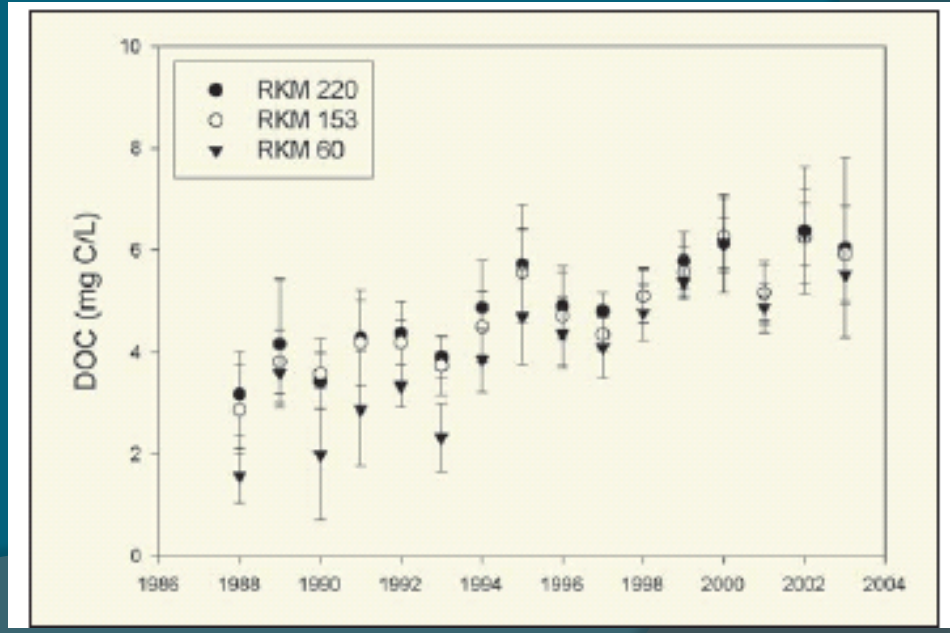
Riverine
Organic Matter Budget



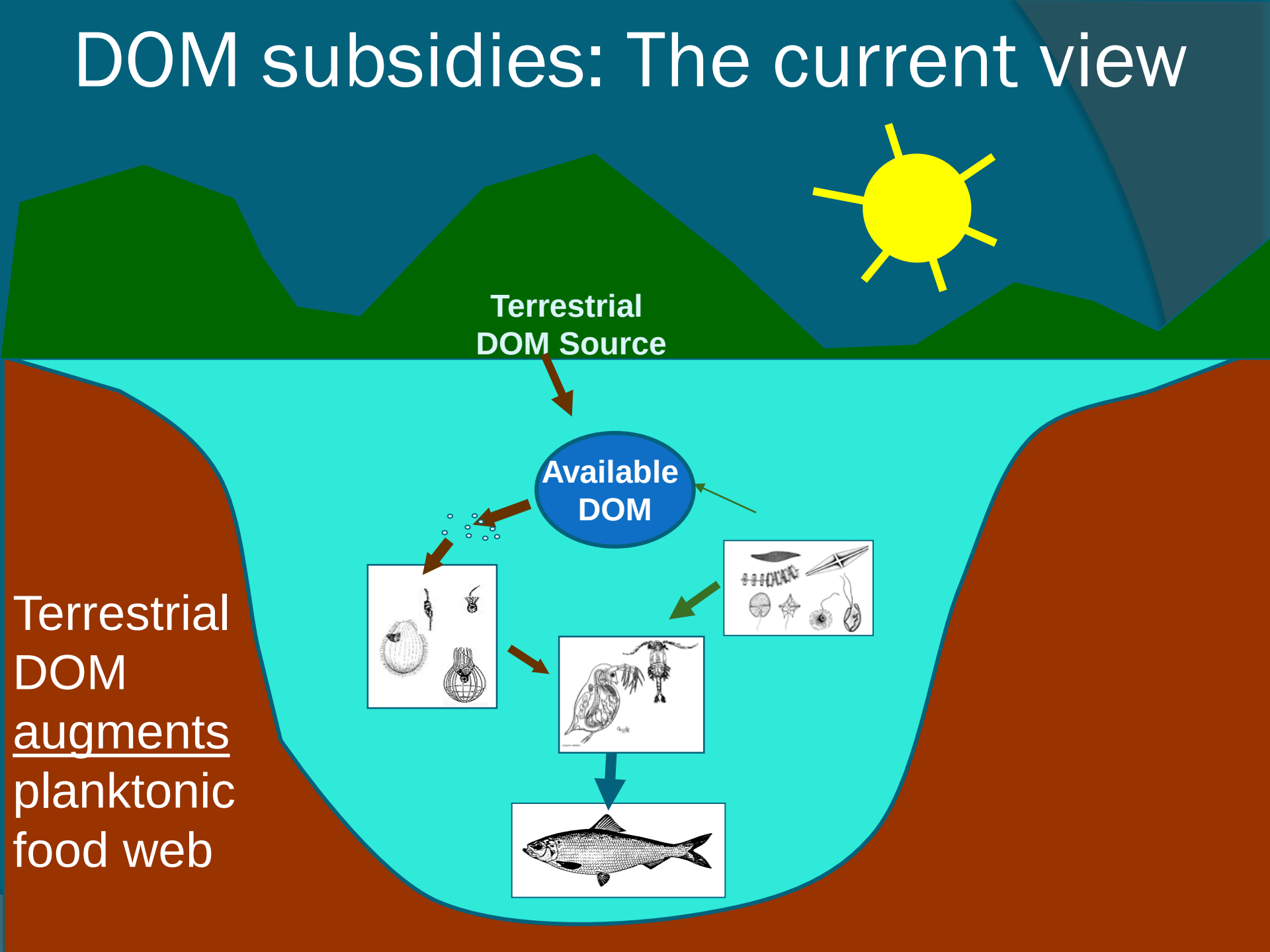
DOM as a subsidy

- Varies >10-fold among lakes
- Increasing in many north temperate systems



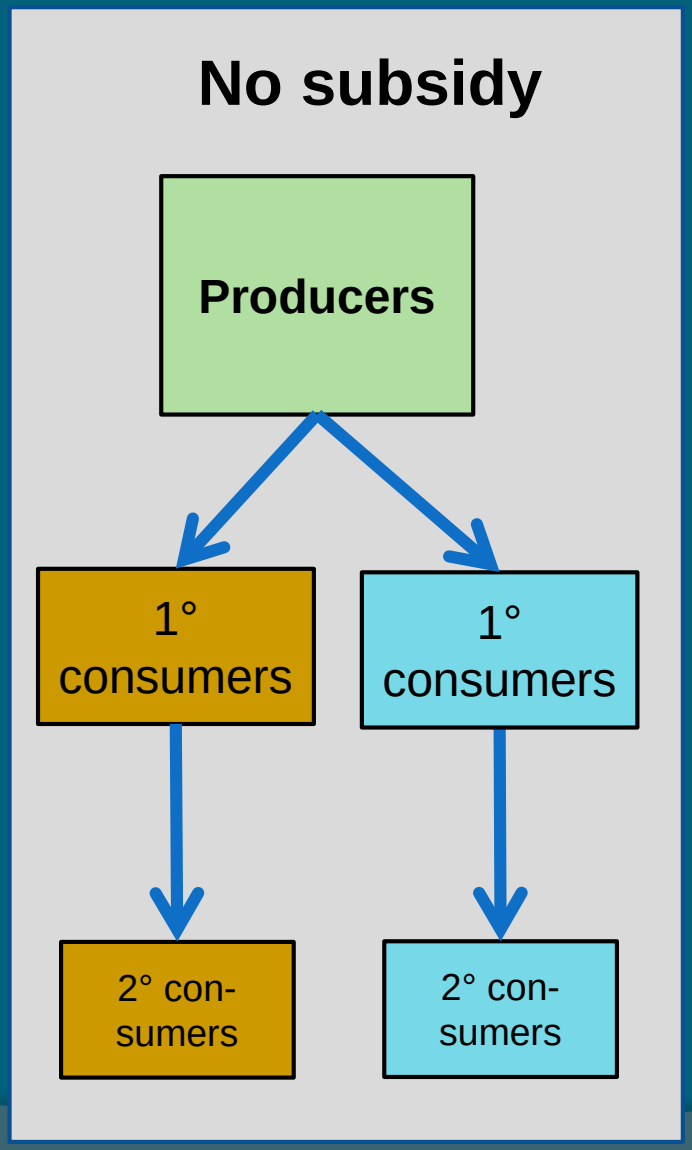


DOM subsidies: The current view



Terrestrial DOM augments planktonic food web

Subsidies, food webs and ecosystems



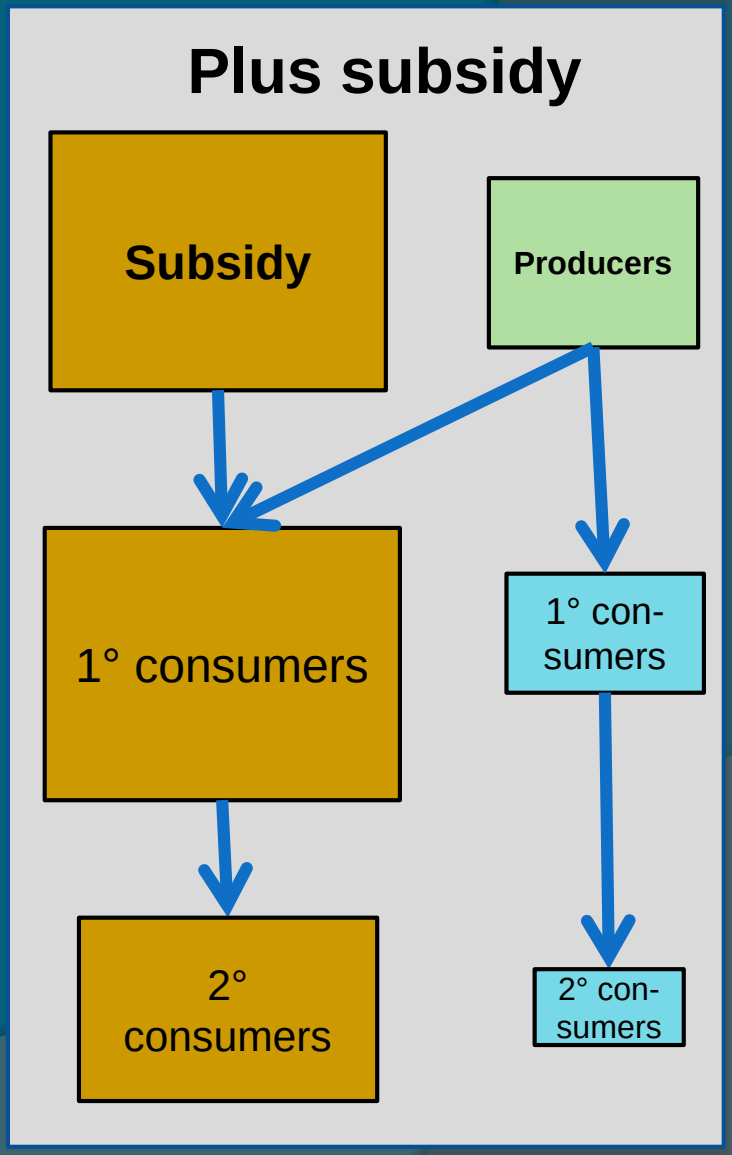
RESTRUCTURE FOOD WEBS

Relieves constraints on 1° consumers

Can alter pathways of energy and material flow

ALTERS VARIABILITY

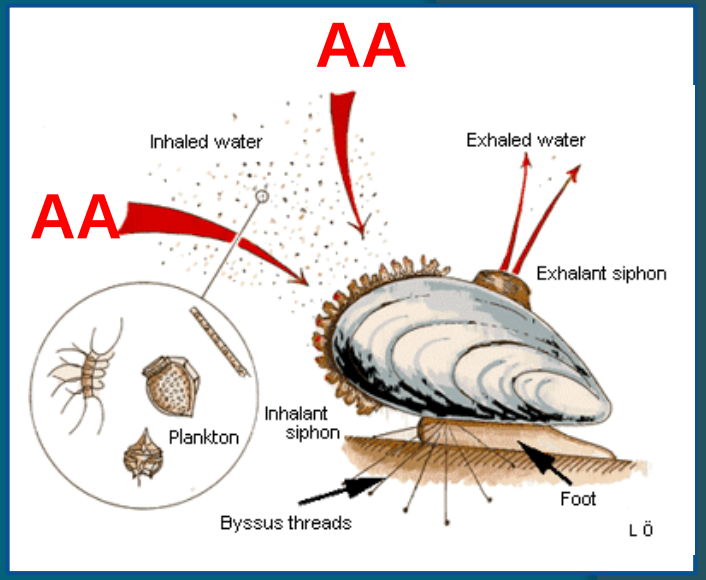
Intrinsic dynamics replaced by extrinsic signals



Direct consumer use of DOM?

Marine inverts do it, but…

- **Not metabolically important**
  - Amino acid concentrations too low
  - Rest of DOM poorly characterized
- **Not in freshwater**
  - Uptake driven by Na^+ pump
  - Gradient in freshwater not favorable



70-90% of amino acids passing gills removed by *Mytilus edulis*

Then again…

- **More DOM in freshwater**
- **Many invasive bivalves are recently evolved from marine ancestors**

Unraveling the influence of DOM on zebra mussels

Can zebra mussels take up specific dissolved organic substances ?

Is uptake of natural these substances metabolically important?

What are the ecological implications of DOM uptake?

Unraveling the influence of DOM on zebra mussels

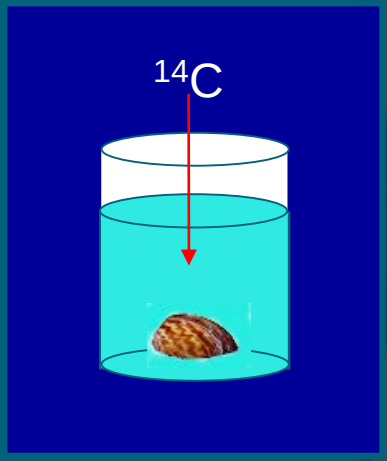
Can zebra mussels take up specific dissolved organic substances ?

Is uptake of these substance metabolically important?

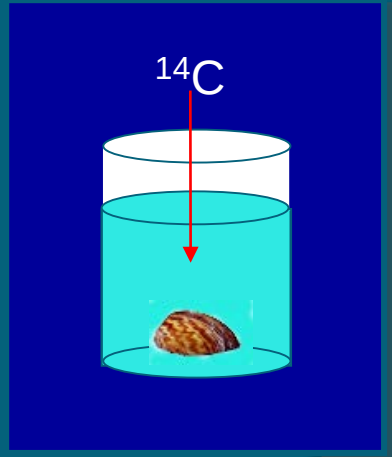
What are the ecological implications of DOM uptake?

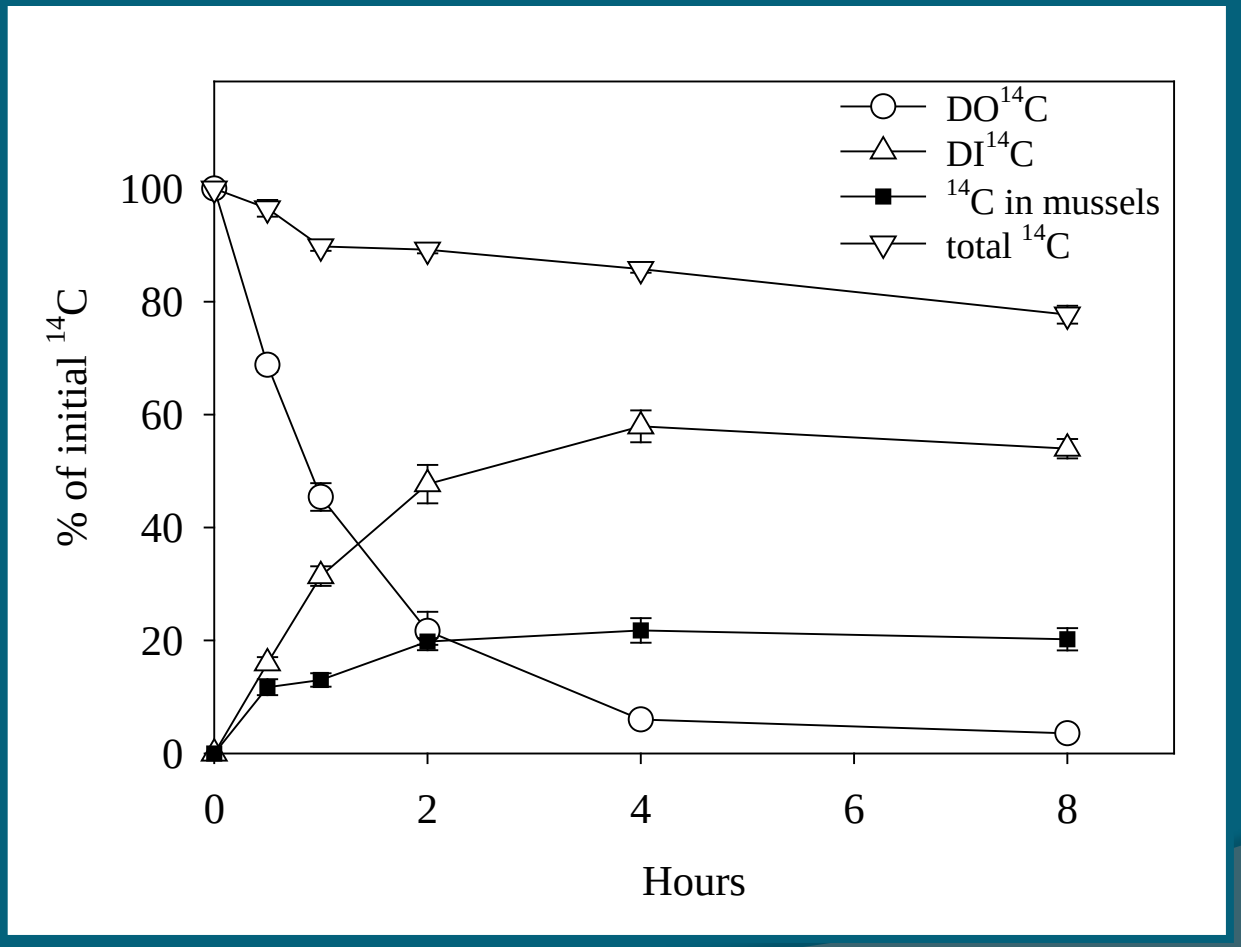
Can they do it ?

- Approach: Use radiolabeled substances
  - Realistic concentrations
  - Compare uptake of different com[o
  - Estimate uptake in field based on measured concentrations
- Experimental overview
  - Incubated mussels with radiolabel
  - Reduced microbial activity
  - Measured distribution of radiolabel over time
  - 18 substances assayed
    - Amino acids
    - Sugars
    - Fatty acids
    - Acetate



Zebra mussels take up DOM



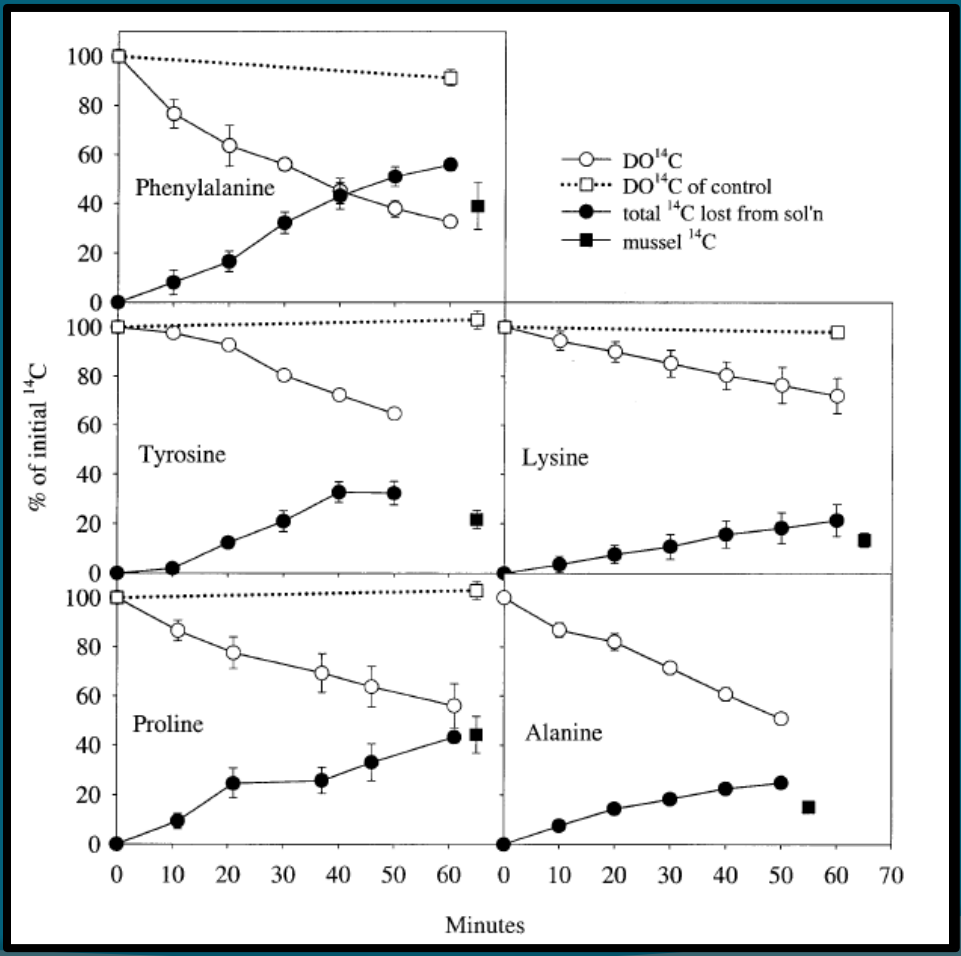


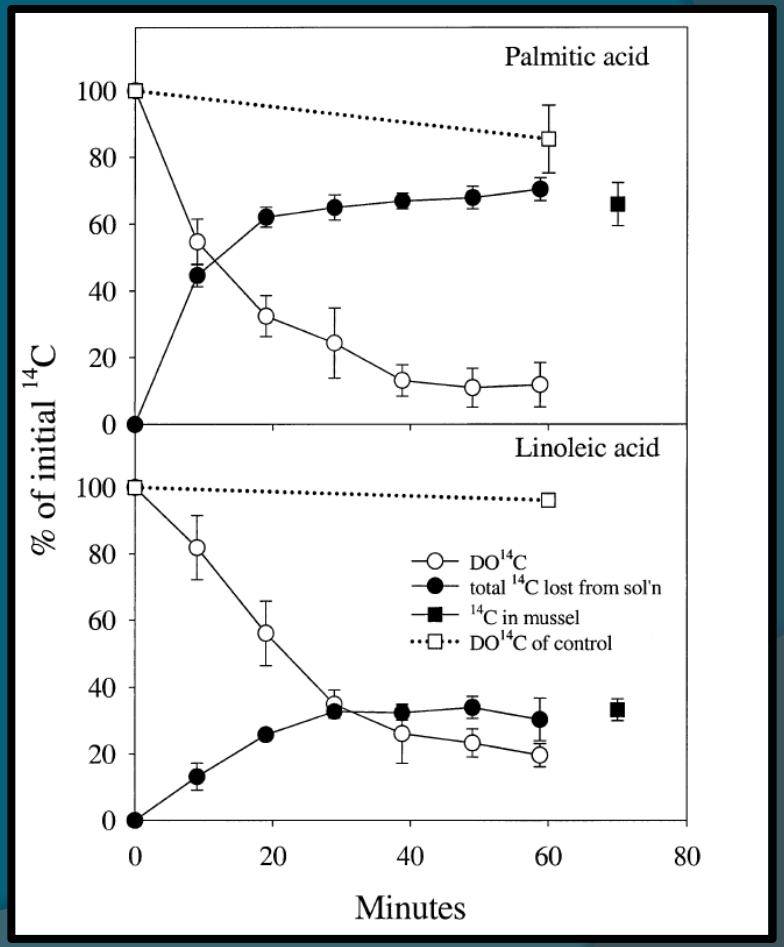
All alanine removed with 4 hours

20% of radiolabel remained in animal soft tissues

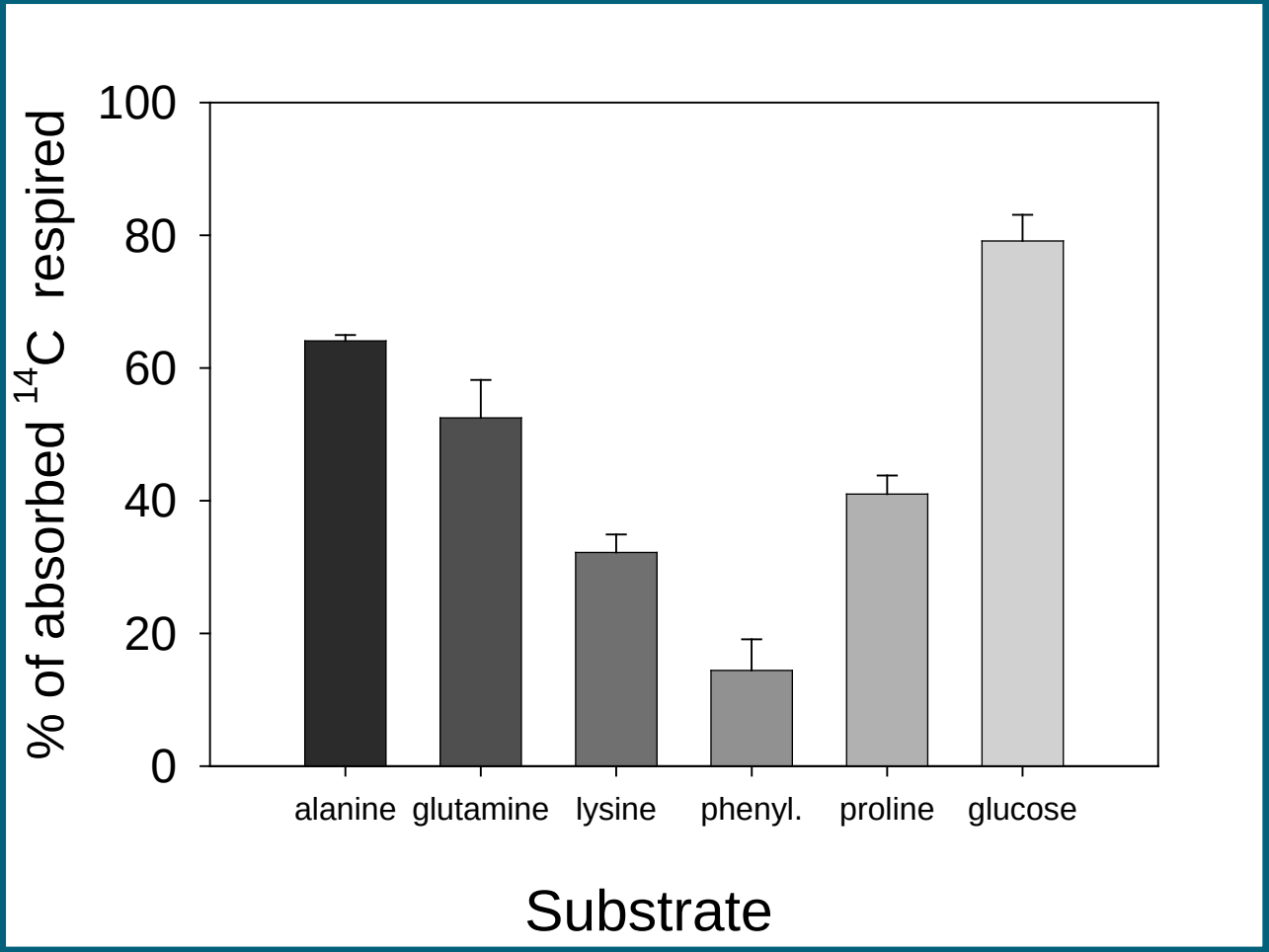
50-60% was recovered as CO_2

Uptake of other compounds





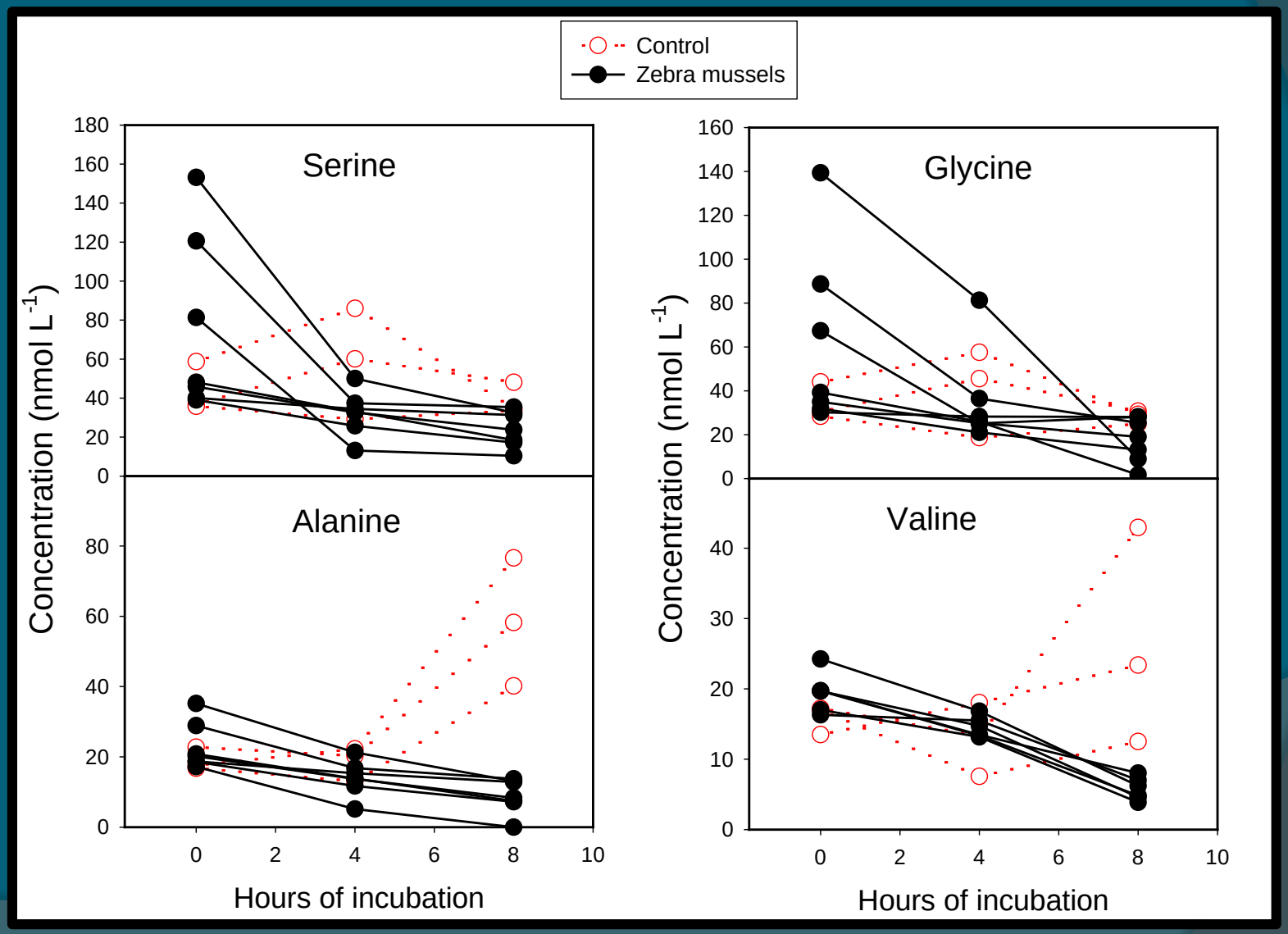
Absorbed organic C is being respired



Possible critiques

- Radioisotopes allow quick measurement
- However, they may not measure net uptake
  - Internal stores are not fully labelled
  - Therefore they do not measure losses
- Must verify against **net** depletion of amino acids

Evidence for net AA uptake



Net uptake of amino acids

- Many amino acids show net decline - similar to observed in marine species
- There may be a minimum concentration for uptake for some
- Sometimes active release of amino acids is observed in controls

Unraveling the influence of DOM on zebra mussels

Can zebra mussels take up dissolved organic substances ?

Is uptake of natural these compounds metabolically important?

What are the ecological implications of DOM uptake?

Metabolic impact estimated two ways

- From absorption efficiencies and concentrations of compounds in the Hudson River
- From weight loss in presence and absence of DOM

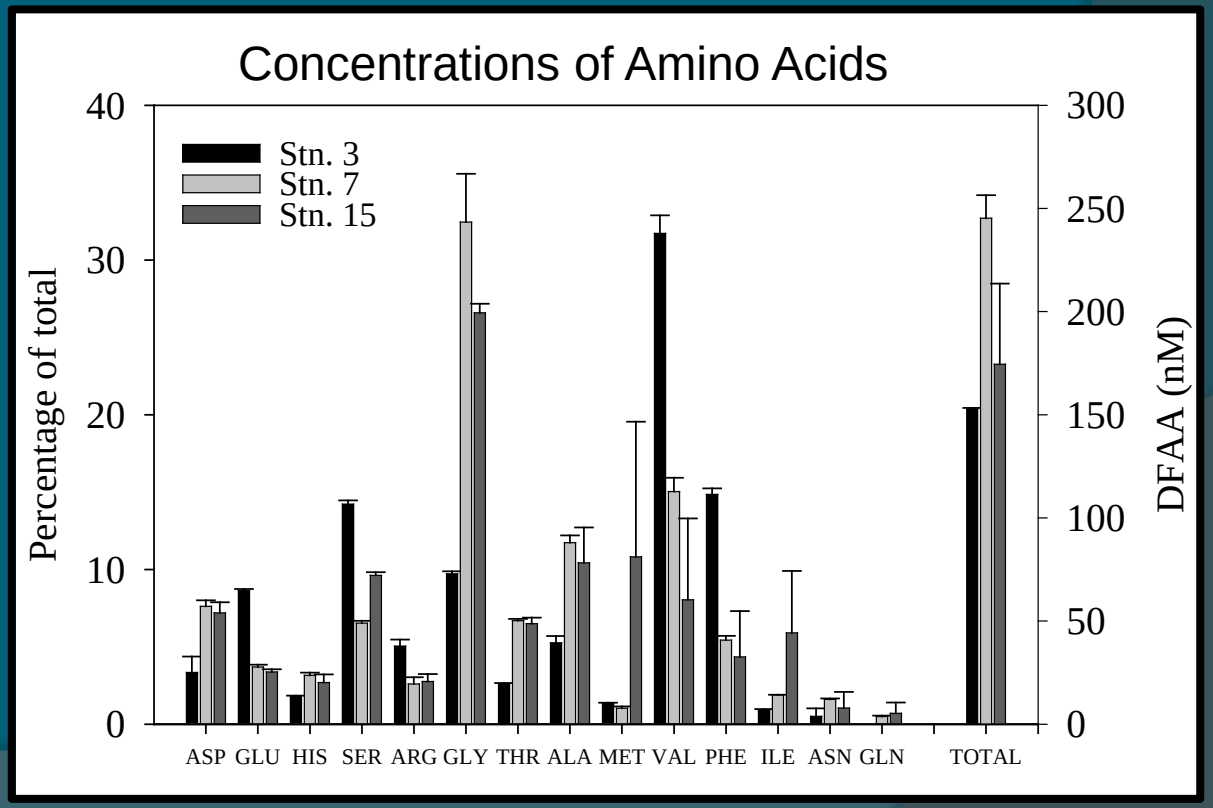
How important is uptake of these compounds to zebra mussels ?

Calculating uptake of specific substances

Filtration rate of mussels
x
Absorption efficiency for serine
x
Concentration of serine

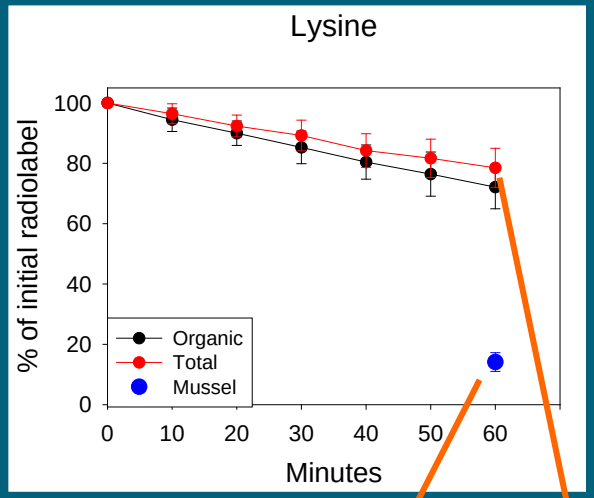
↓

Absorption of Serine



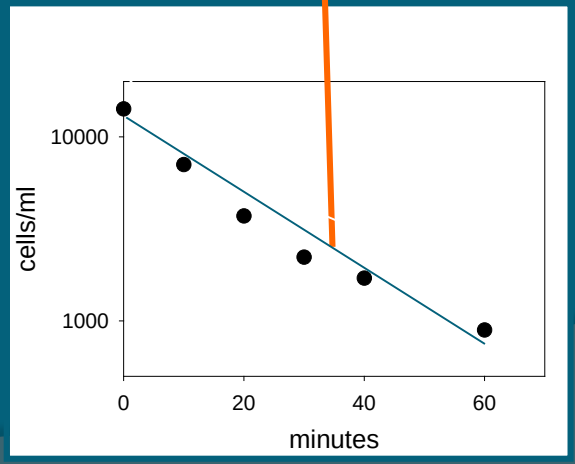
Calculations of absorption efficiency

Radiolabel uptake experiments

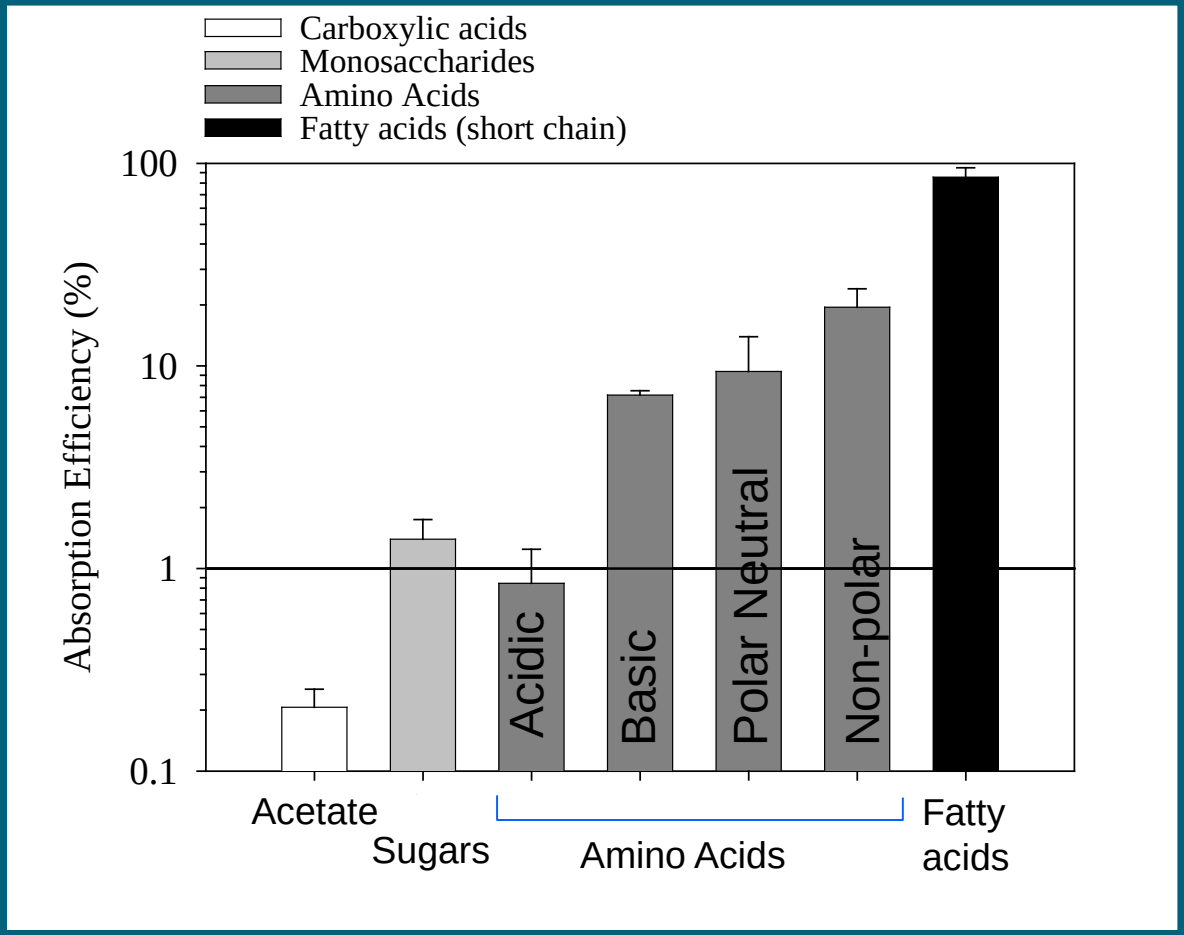


$$\frac{\text{Absorption rate}}{\text{Filtering rate}} \div \left(1 - \text{Respired Fraction}\right) = \text{Absorption Efficiency}$$

Filtration experiments (Same individual)



Absorption efficiencies



Specificity of uptake

Sugars, acetate and acidic amino acids <1%

Amino acids = 10-20%

Fatty acids > 90%

Profile resembles *M. edulis*

Contribution of simple compounds to maintenance metabolism

Substance	Carbon uptake ($\mu g\ g^{-1}\ d^{-1}$)		% of carbon demand	
	Low	High	Low	High
Acetate	3.4		4.3%	
Monosaccharides	0.8		1.1%	
Amino Acids	10.25		13.2%	
Fatty Acids	2.2	15.3	2.3%	19.7%
Total	16.6	29.8	21%	38%

Repeating old mistakes ?

A historical timeline

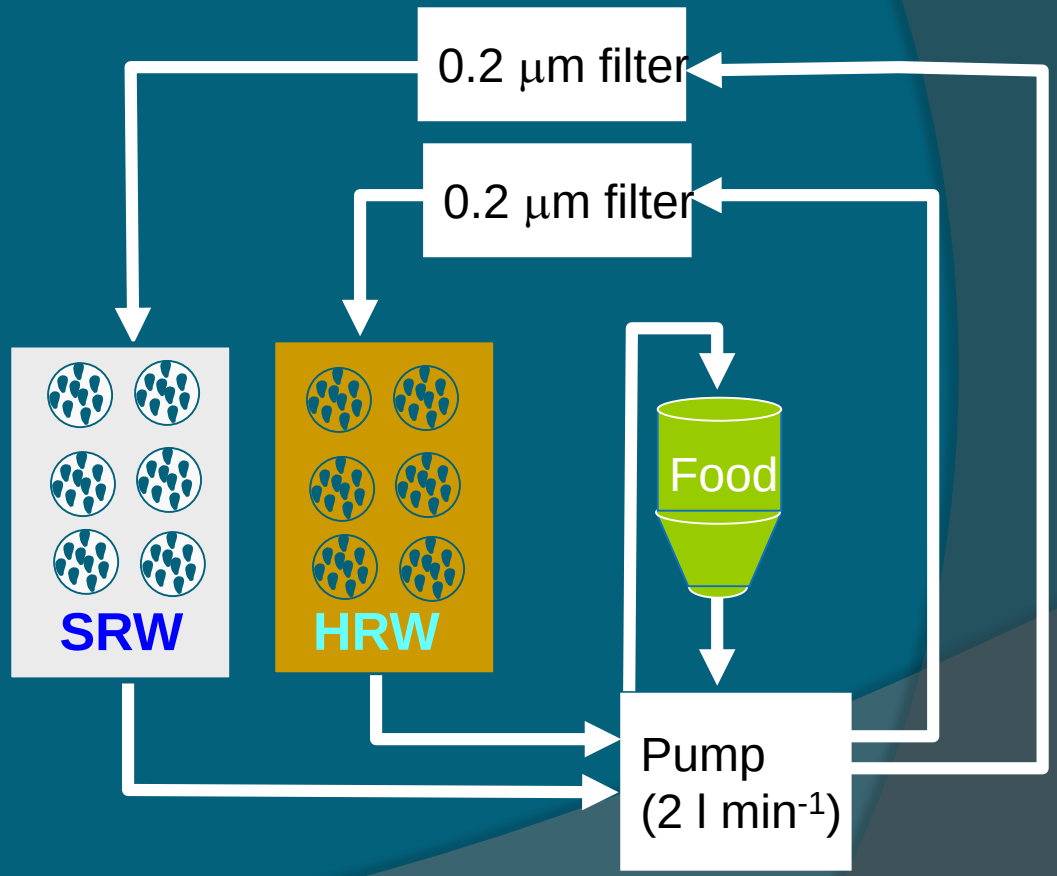
- DOM IS IMPORTANT !
  - 1900: Bivalves can remove sugars from solution.
- NO IT ISN'T !
  - 1920-1930s: Others show DOM ain't sugar.
- YES IT IS !
  - 1960s-1980s: 14C labeled model compounds taken up at low concentrations
- NO IT ISN'T !
  - 1970s-1980s: Must be microbes, guys ! Also, it's osmoregulation !
- YES IT IS !
  - 1980s-1990s: Axenic studies using HPLC show uptake.
- NO IT ISN'T !
  - 1990's to present: Proper HPLC analyses show low amino acid concentrations.
- HEY, LOOK AT ZEBRA MUSSELS !!!….

Does reliance on model compounds bias our estimates of metabolic importance?

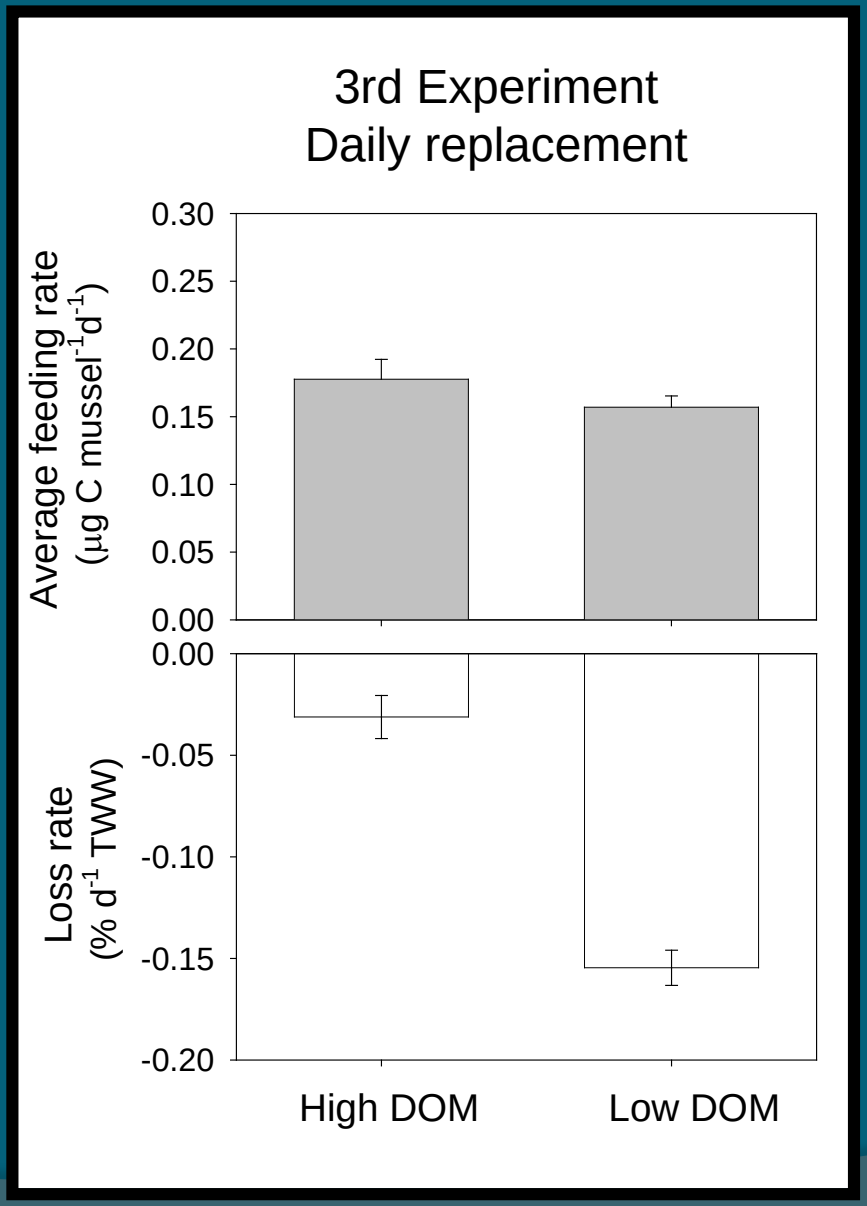
- What effect bulk DOM has on zebra mussels?
- Expose mussels to water with and without DOM
- Measure an ecologically relevant physiological end-point

Net effects of DOM exposure on weight loss

- **<u>Natural DOM treatments</u>: Filtered Hudson River water (HRW).**
- **<u>Low DOM treatments:</u> Synthetic river water (SRW) with major ions but no DOM**
- **Continuously filtered**
- **Fed starvation ration daily**
- **Followed weight loss over 1-2 months**



DOM reduces weight loss in starving mussels



Weight loss 5-fold > in absence of DOM

Not due to differences in ingestion of algal food or bacteria

Contribution of DOM to metabolism

Carbon:Soft Tissue Wet Weight (STWW)
does not vary with time or among treatments

THEREFORE

Specific rate of STWW loss ($g\ g^{-1}\ d^{-1}$)	=	Specific rate of carbon loss ($g\ g^{-1}\ d^{-1}$)

Specific rate of DOC uptake = Δ in STWW loss rates between treatments

Carbon demand of mussels = Specific carbon loss rate in low DOM treatment + carbon assimilation rate

Contribution of DOM to metabolism

DOM	STWW Loss % d^{-1}	U_{DOM} % C d^{-1}	Algae Assim. % C d^{-1}	Carbon Demand % C d^{-1}	U_{DOM}/R
Low	0.36		0.14	0.50	**60%**
High	0.06	0.3			

DOM contribution to adult metabolism much larger than past estimates (based on uptake of specific compounds)

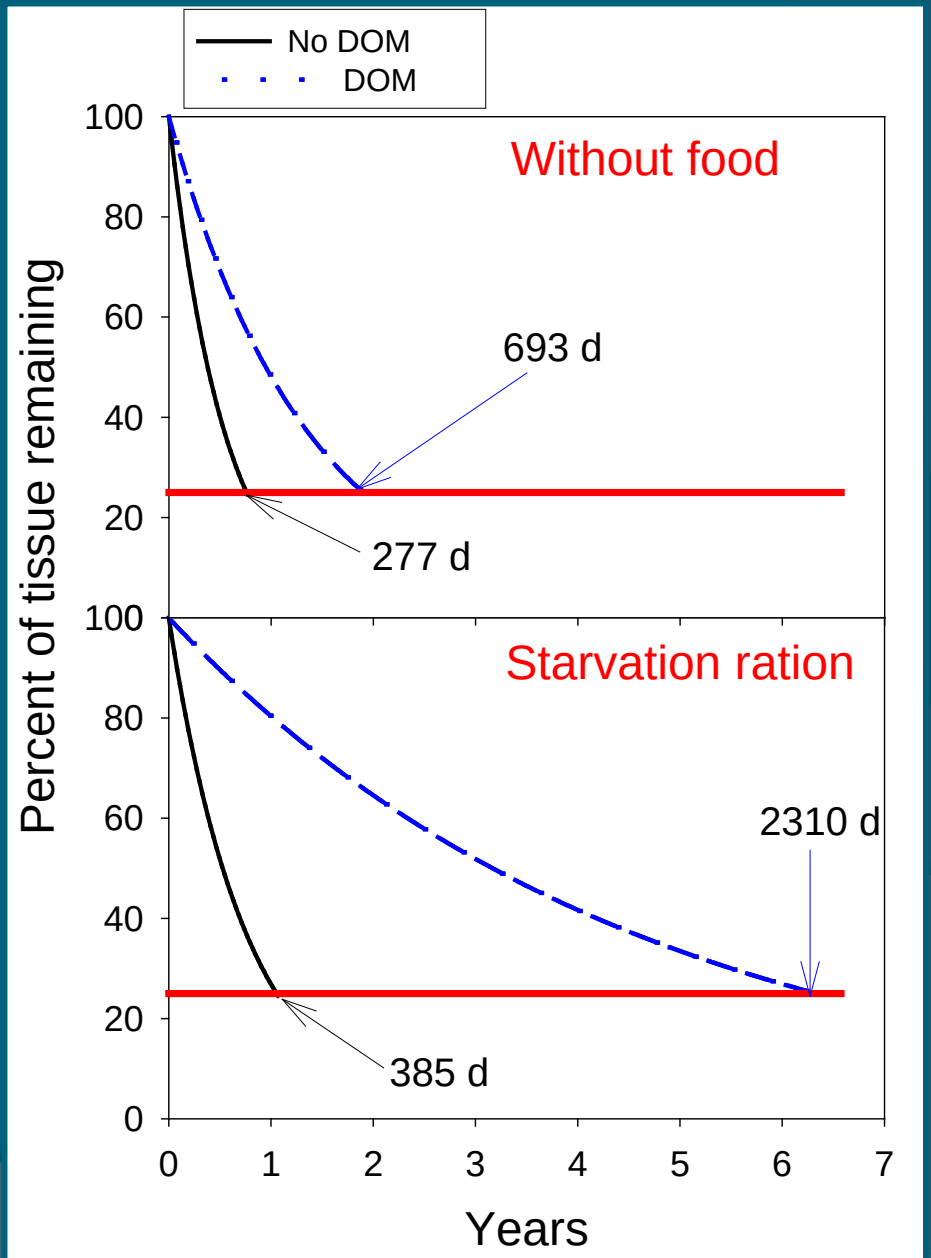
Also 2x larger than can be supported by amino and fatty acids

Estimated time to death by starvation

50 % of individuals die of starvation after losing 75% of initial weight (Chase McMahon 1996)

In presence of DOM can survive very long periods of starvation

Buffers adults against variability in phytoplankton biomass



But what is the source of DOM?

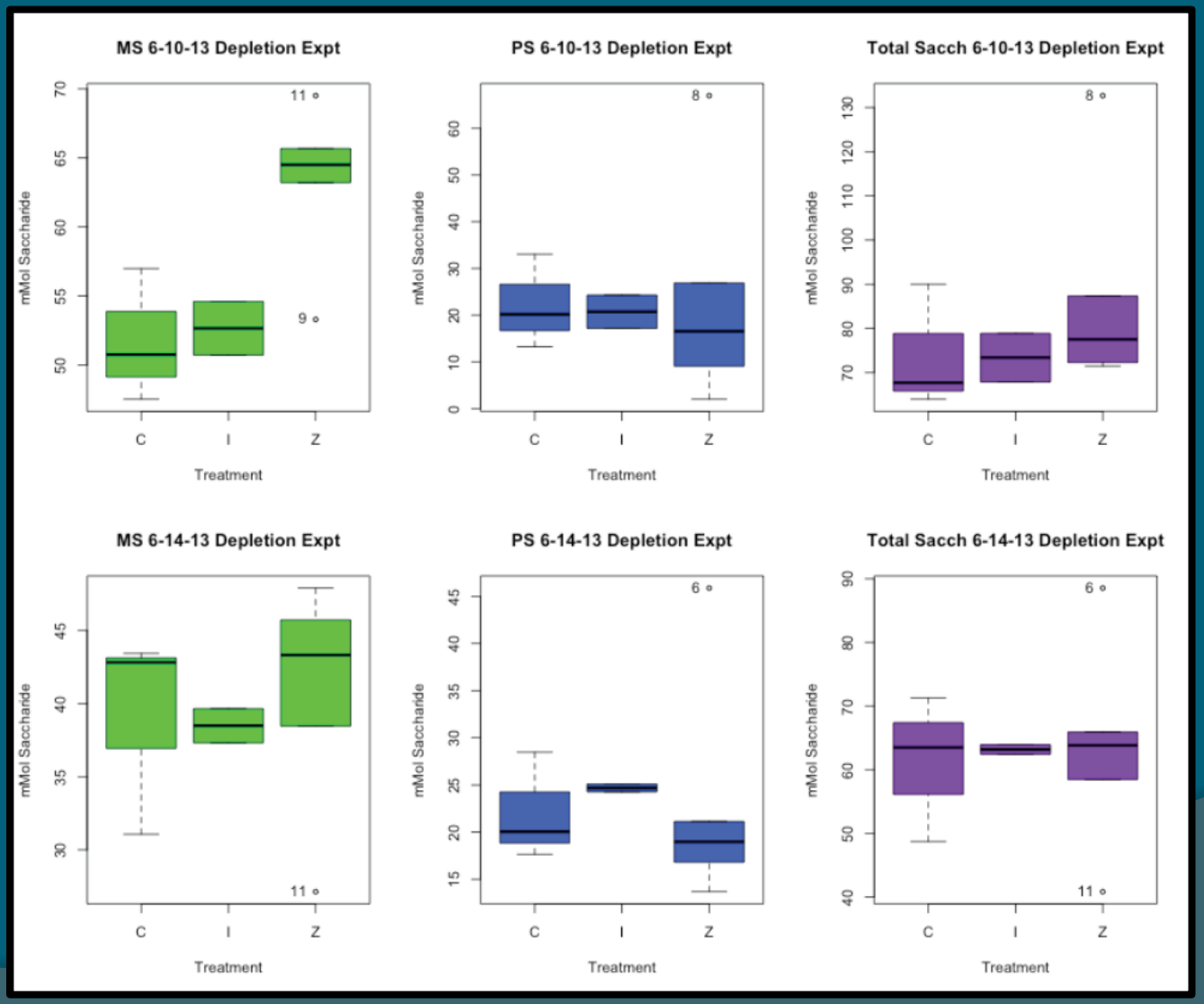
- Contribution of free amino acids is half of the observed effect of bulk DOM

- Hypotheses
  - Uptake of other compounds accounts for difference
  - We underestimate the concentrations of amino acids

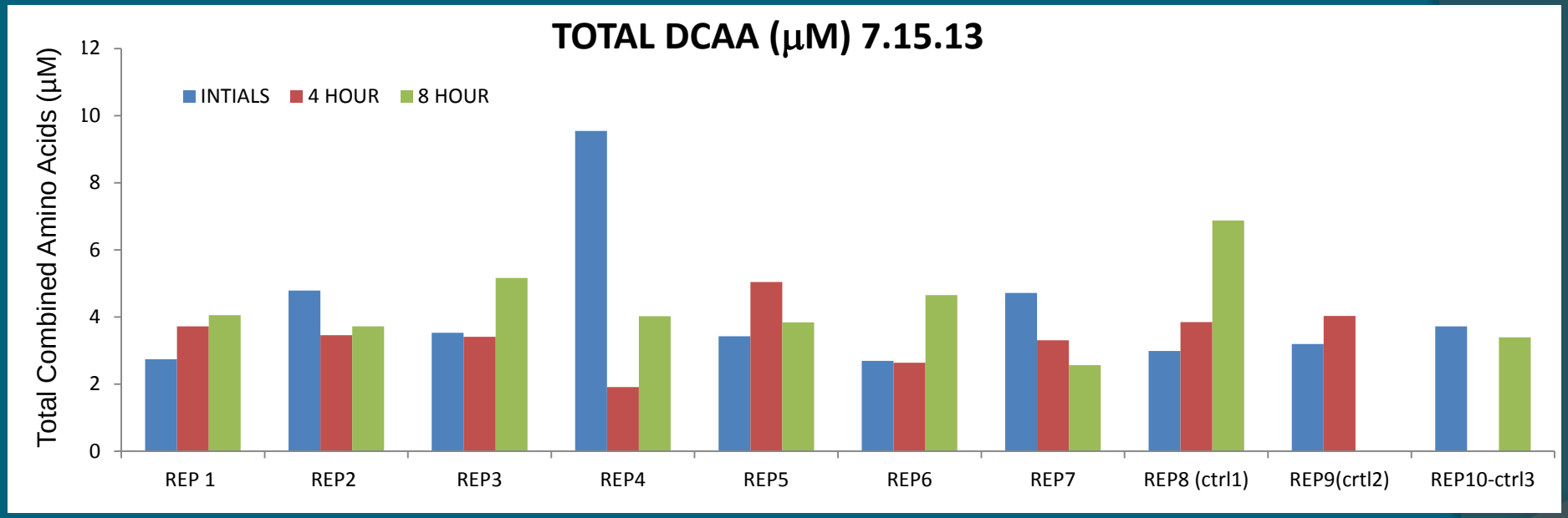
Other possible compounds

- Polysaccharides
- Polyamines

Polysaccharides ? No.



Combined amino acids? Also no.



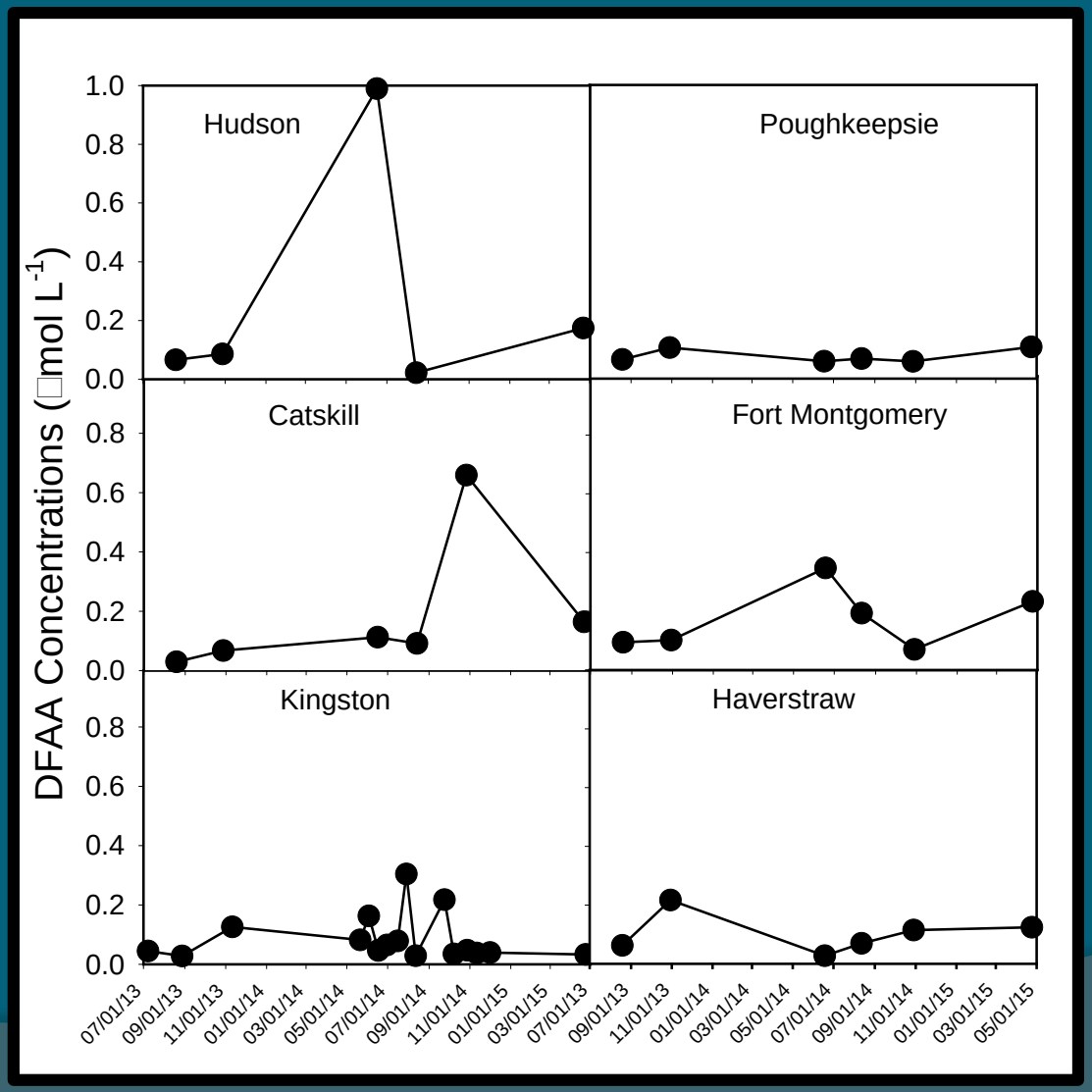
Other possibilities under study

- Fatty acids –
  - Complex fatty acids
  - Complexed to other substances
- Colloidal material
  - Electrostatic uptake on to gills
  - Possibly followed by ingestion
- Mystery substances
  - Characterize DOM with broad spectrum mass spec
  - Study how zebra mussels affect makeup

What about free amino acids ?

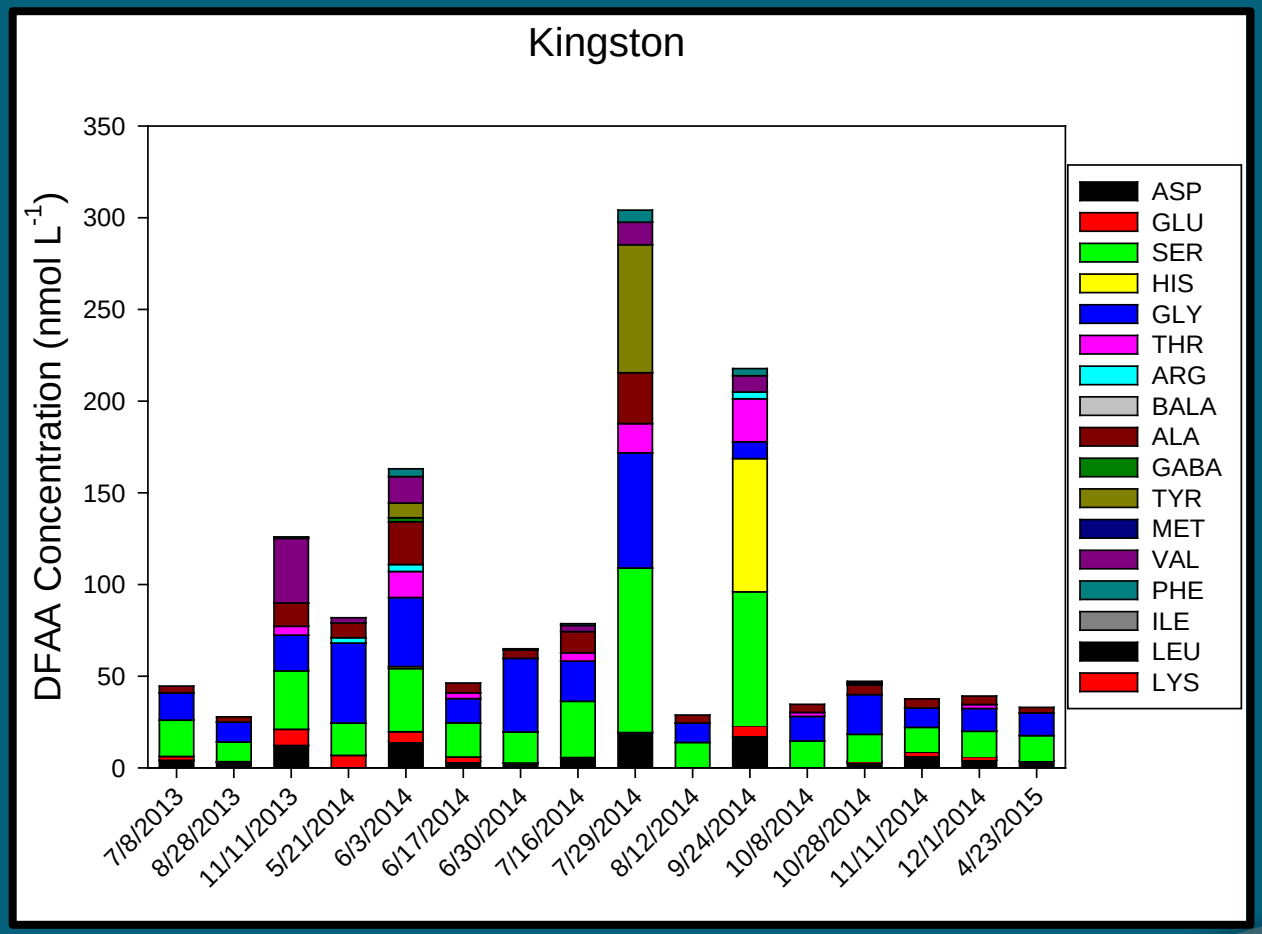
- We had only a snap shot of three stations at one date
- What does temporal and spatial variation if DFAA really look like?
- Are there generalities?

Temporal and spatial variation in total DFAA



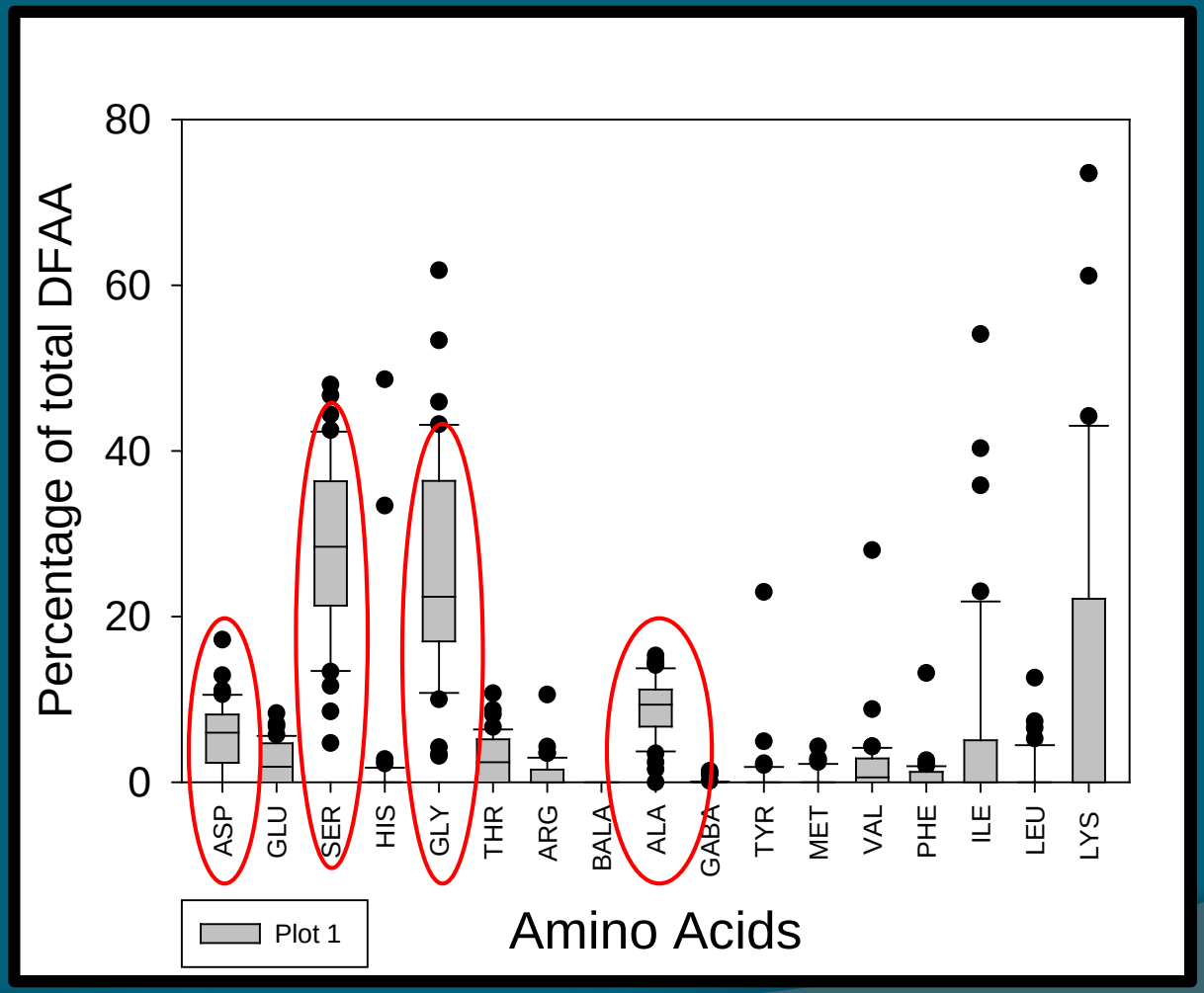
- DFAA are much more variable than DOC, especially in upper river
- There is no longitudinal or seasonal pattern in average values
- Suggests it will be hard to assume a constant proportion of DOC is DFAAs

Variation in composition



- No systematic differences between sites or seasons
- There are a few DFAAs that regularly dominate
- Several others dominate only rarely (Histidine, Tyrosine, Lysine)

Dominant DFAAs in all samples



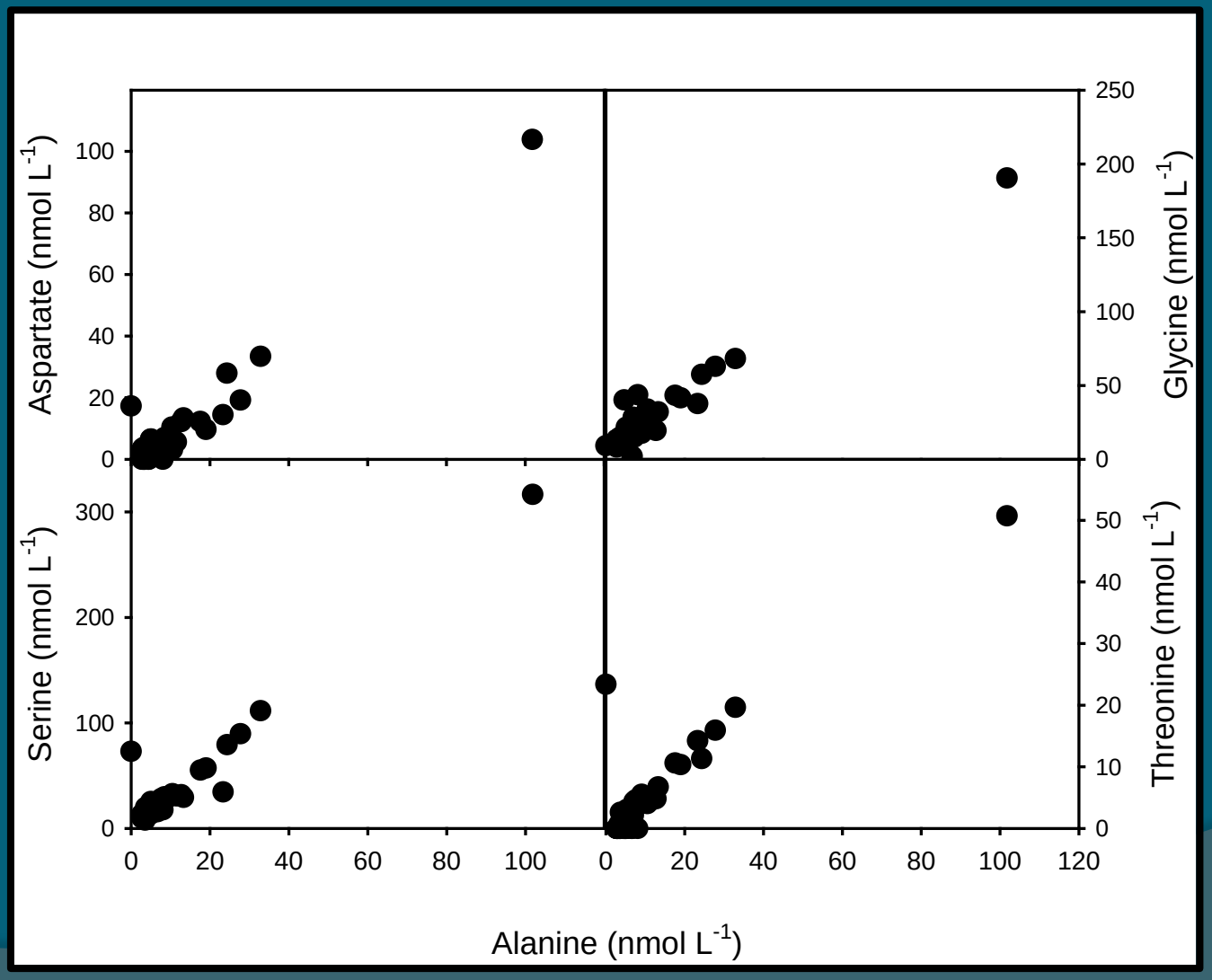
MAJOR DFAAs

Serine
Glycine
Alanine
Aspartate

Also…

Glutamate
Threonine

Correlations among dominant DFAAs



Indicates constant proportionality

Suggests bioavailability of DFAA pool may be fairly constant

This simplifies modeling IF a correlate to DFAA concentration can be found

Possible effect on Algal biomass

- Assumption: Zebra mussels depress algal biomass to point where Scope for Growth (SFG) = 0
- Calculate this value with and without DOM subsidy
- Compare to average chlorophyll values in Hudson

Limiting concentration of algal biomass

C_m	12.6 mg	This study
AE	50 %	Walz 1977; Schneider et al 1998
PF	67 %	Walz 1977; Schneider et al 1998
CR	3.6 L d^{-1}	Roditi et al 1996
C:Chl	26	Cloern et al. 1995
CD	0.5 % d^{-1}	This study
CD_{DOM}	0.2 % d^{-1}	This Study

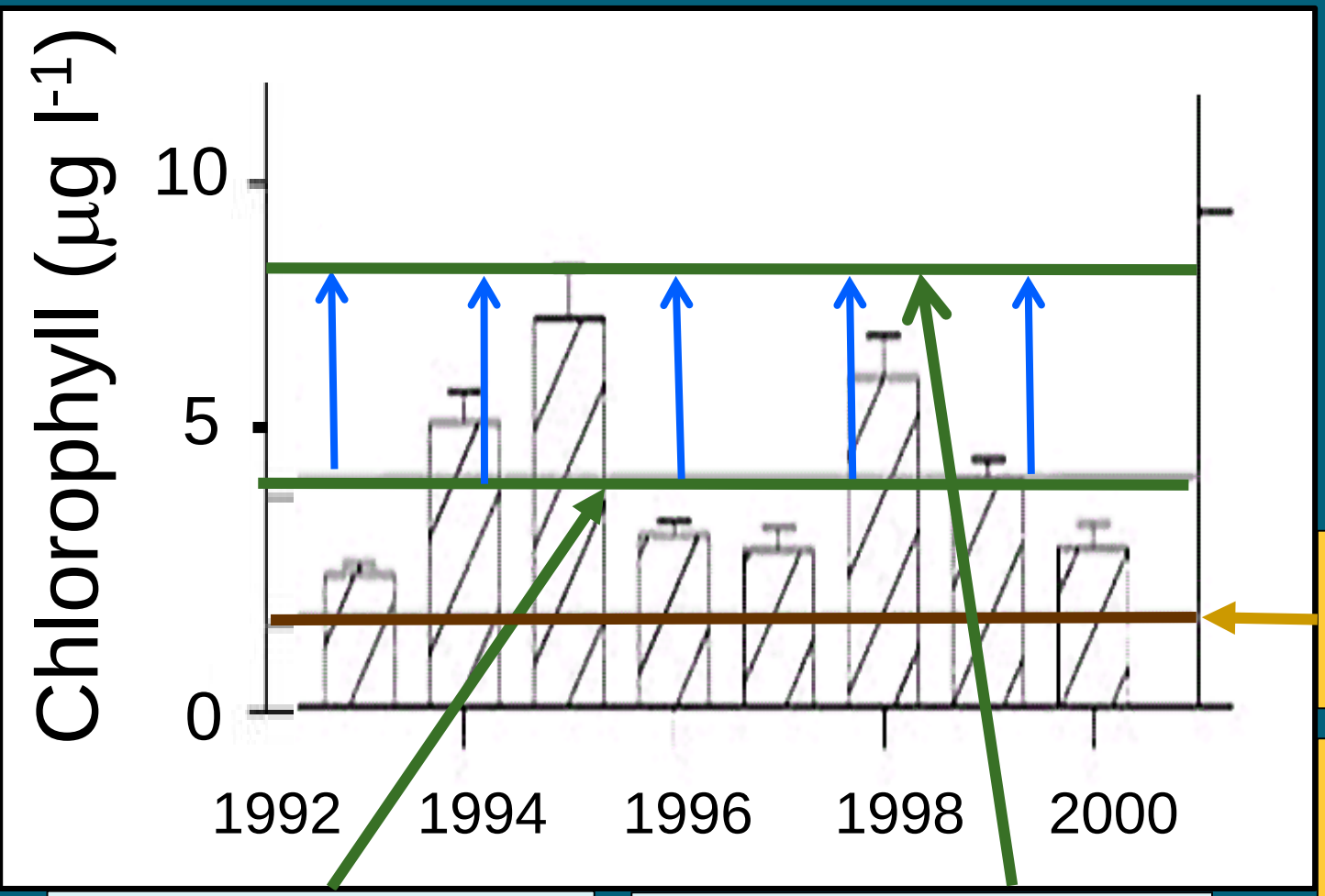
At zero net growth
Carbon demand = Assimilation

Without DOM

$C_m \bullet CD = Chl^* \bullet C{:}Chl \bullet CR \bullet (1\text{-}PF) \bullet AE$

With DOM

$C_m \bullet CD = Chl^* \bullet C{:}Chl \bullet CR \bullet (1\text{-}PF) \bullet AE + DOM$



With DOM there is ALWAYS sufficient Chl post invasion

Avg Chl since the invasion is double the maintenance level

Costs of mortality or hydrologic variability may prevent further reductions of Chl

Without DOM subsidies
Chl after invasion would often be below maintenance level

"Equilibrium " Chl would be higher than maintenance level (mortality, hydrologic variability, increased predator prey dynamics).

Lessons

- The calculated benefit is consistent with observed depression of chlorophyll in Hudson River, given physiological constraints
- Without this DOM subsidy, mussels would still have an impact, but it would not be nearly as large.
- Also in inverts our understanding of the effect of DOM on aquatic food webs

Effects of DOM subsidy to mussels