Getting it together: Quantifying the trophic connections between micro- and mesozooplankton in marine food webs

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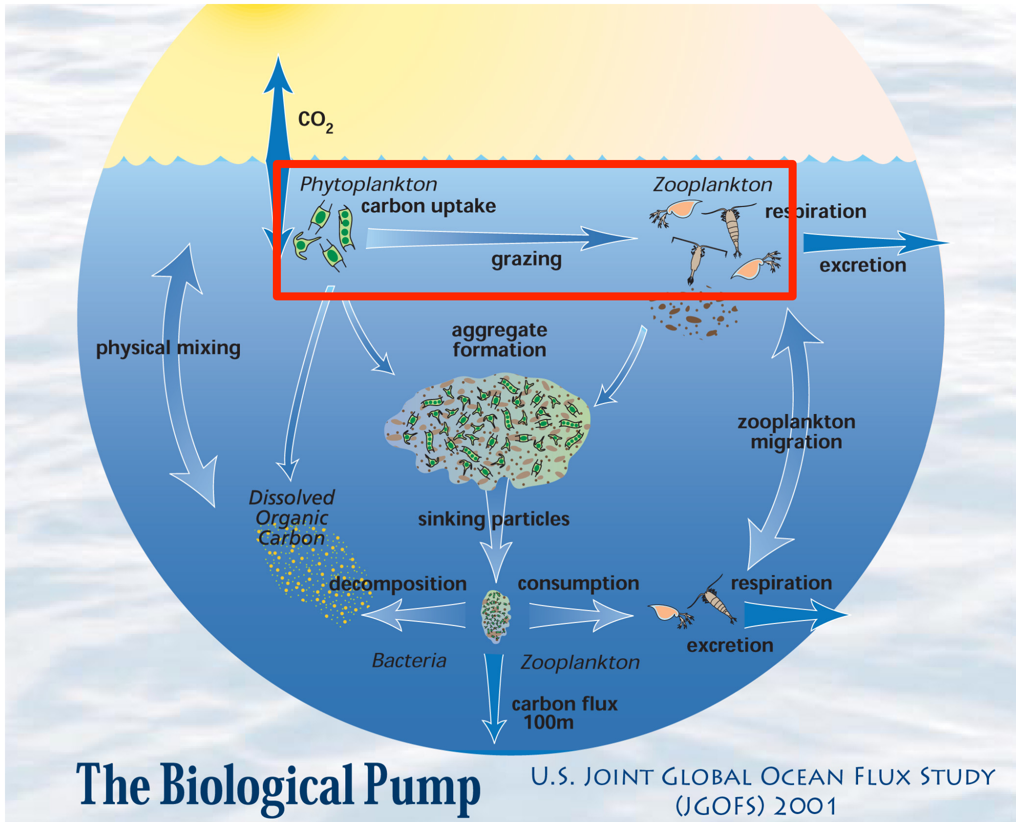
OCE

Microzooplankton and the Biological Pump



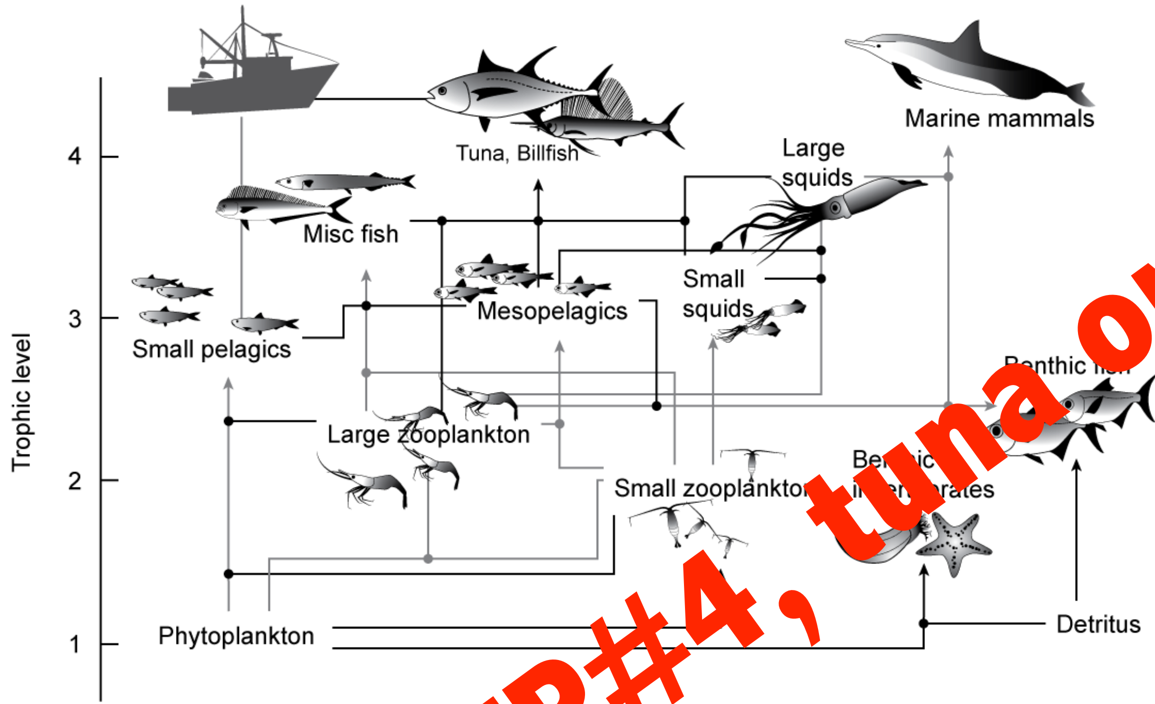
<u>Strict interpretation</u>

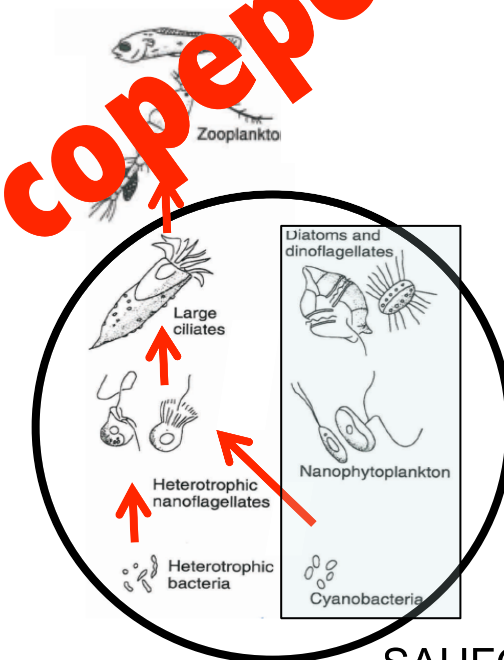
Classic food web: mesoZoo are major herbivores

No alternate consumers, food resources

Export Ratios always high, >30%

Microzooplankton in Fishery Models





SAHFOS

Who's in TP#4, tuna or copepods?

Compressed trophic structure, based on direct dietary evidence (identifiable stomach contents)

"… while some fish reach trophic levels in excess of 4.0, the overwhelming bulk of them have trophic levels between 2 (in herbivorous species such as anchovies …) and 4 (cod, snappers, tuna …)." D. Pauly, ***Fishing Down the Food Web***

If most ocean PrimProd flows through MicroZoo (dominant herbivores), the linkage between MicroZoo and MesoZoo is critical for understanding:

- Trophic transfer efficiency to higher consumers
- Food web transfer efficiency to export
- How MesoZoo make a living in the open ocean
- Food web sensitivities to climate change

Problem Statement: How to account for the magnitude and variability for an important trophic linkage that is difficult to measure directly?

Overview

Magnitude of the Micro-Meso linkage

- Literature – local experimental results
- Constrained global carbon budget
- Regional example – Equatorial Pacific

Progress toward an isotopic approach

Compound-Specific Isotopic Analysis of Amino Acids

- CSIA-AA potential
- Issues with CSIA-AA
- Validating an alternate approach
- Recent experimental findings

MicroZoo % Contribution to Mesozoo diet

Examples: Methods and results vary widely

16-100%	Oregon coast	Fressenden & Cowles (1994)
17-73%	South Africa	Fronemann et al. (1996)
67-86%	Equatorial Pacific	Roman & Gauzens (1997)
7-15%	Galacia coast	Batten et al. (2001)
11-85%	West Greenland	Turner et al. (2001)
62%	Subtropical front	Zeldis et al. (2002)
30-70%	Subarctic Pacific	Liu et al. (2005)

Calbet & Saiz (2011) Synthesis: ciliate-copepod link

Global estimate = 2.4 Gt C/y (~5% PrimProd)

Highly conservative, 2-3 fold underestimate?

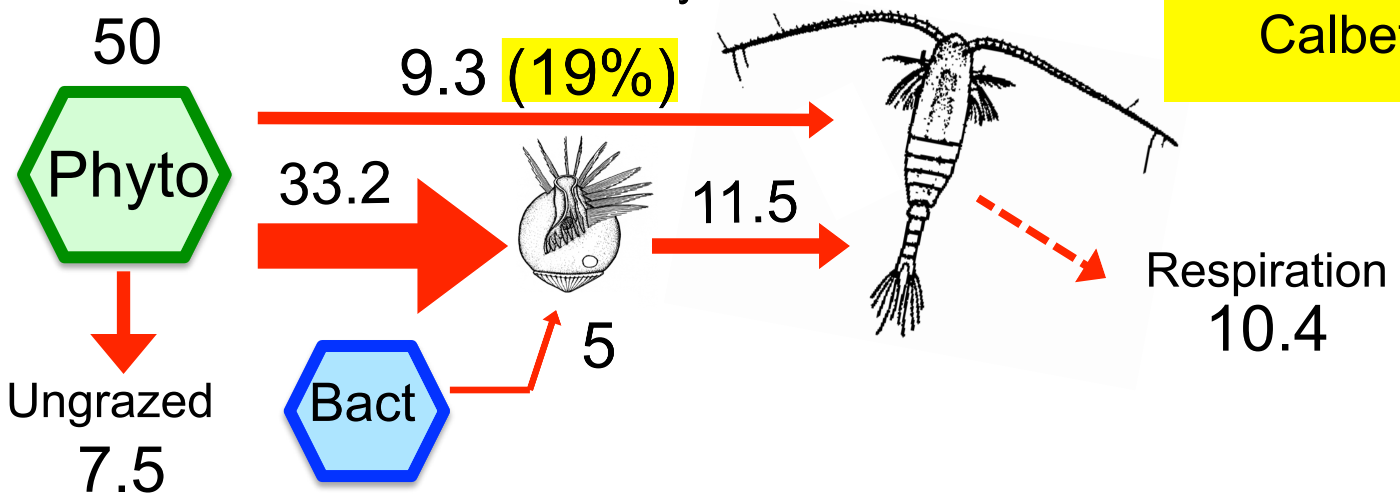
To extend to all MicroZoo consumed by all MesoZoo

Global Carbon Balance

All estimates are Gt C y^{-1}

Relative to PrimProd 50 Gt C y^{-1}

<u>MesoZoo Herbivory</u>:
Mean = 23% PrimProd
Calbet (2001)

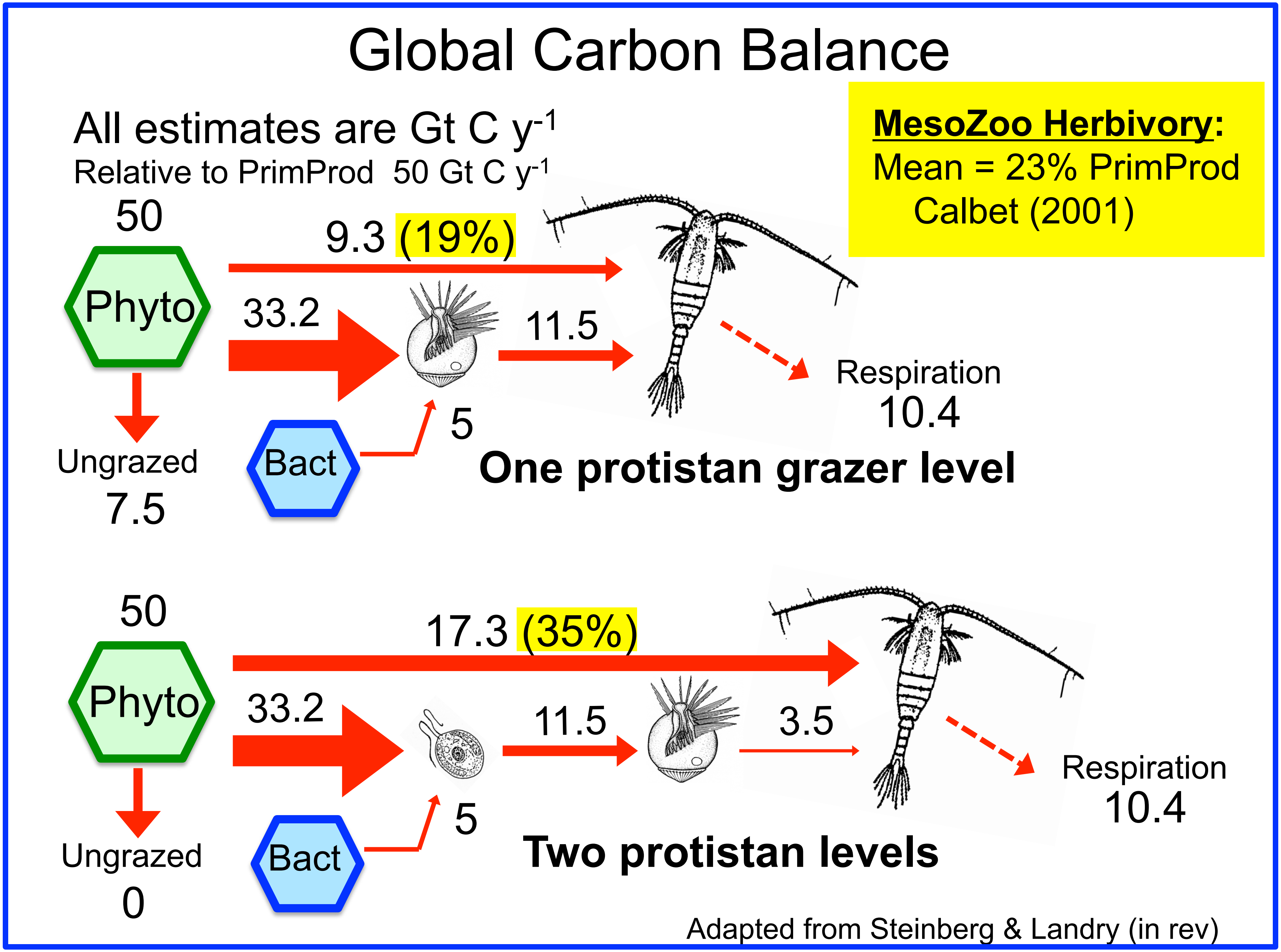


<u>Constraints</u>:

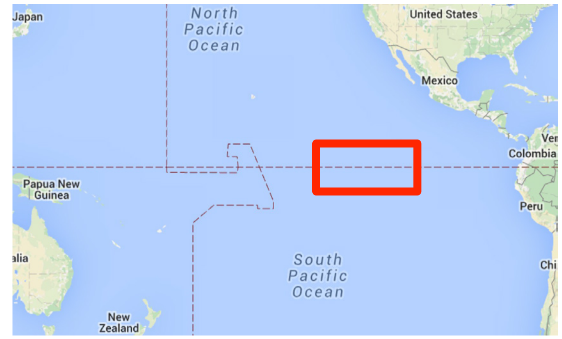
MicroZoo herbivory: Schmoker et al. (2013) dilution data synthesis:
Arctan mean = 66.4% PrimProd

MesoZoo respiration: Hernández-León & Ikeda (2005)
0-200 m global MesoZoo respiration = 10.4 Gt C y^{-1}

Adapted from Steinberg & Landry (in rev)


Global Carbon Balance
All estimates are Gt C y-1
Relative to PrimProd 50 Gt C y-1
MesoZoo Herbivory:
Mean = 23% PrimProd
Calbet (2001)
50
Phyto
9.3 (19%)
33.2
11.5
Respiration
10.4
Ungrazed
7.5
Bact
5
One protistan grazer level
50
Phyto
17.3 (35%)
33.2
11.5
3.5
Respiration
10.4
Ungrazed
0
Bact
5
Two protistan levels
Adapted from Steinberg & Landry (in rev)

A Regional Example



Eastern Equatorial Pacific
Cruises - Dec 2004, Sept 2005
4°N-4°S, 110°W-140°W

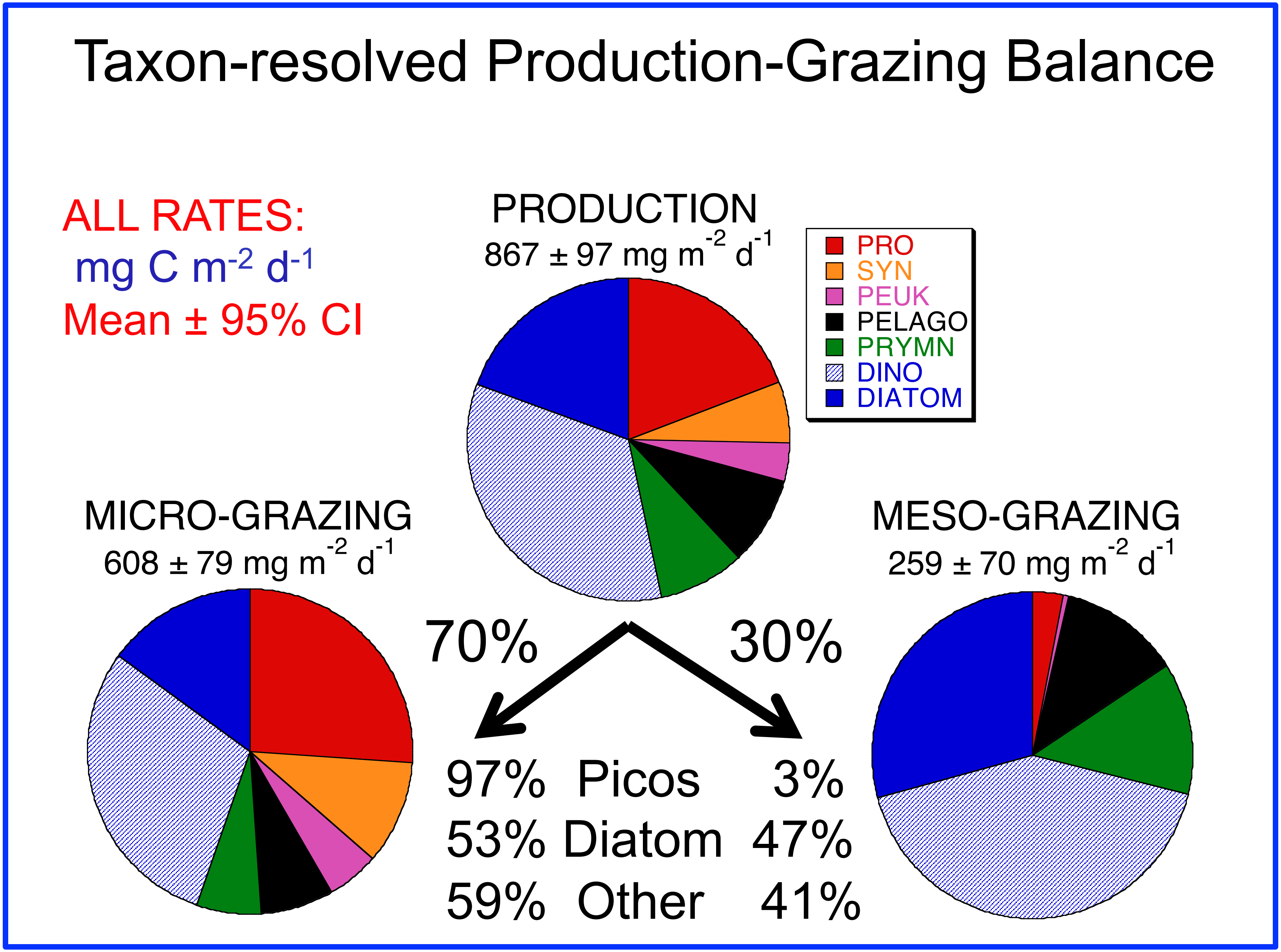
<u>31 station profiles</u>, <u>stocks & rates</u>

Taxon-resolved phytoplankton growth (μ) – dilution (8 depths/stn)
Taxon-resolved microzooplankton grazing (m) – dilution (8 depths/stn)
Phytoplankton primary production – 8 depths/stn
Phytoplankton & microzooplankton abundance & biomass
Mesozooplankton size-fractioned biomass (D & N tows)
Mesozooplankton herbivory (M) – gut fluorescence (D & N)

Phyto μ and biomass consistent with measured PrimProd

Steady-State: $\mu - m - M = 0$ (net residual = - 0.01 ± 0.02 d^{-1})

Landry et al. 2011


Taxon-resolved Production-Grazing Balance
ALL RATES:
mg C m-2 d-1
Mean ± 95% CI
PRODUCTION
867 ± 97 mg m-2 d-1
PRO
SYN
PEUK
PELAGO
PRYMN
DINO
DIATOM
MICRO-GRAZING
608 ± 79 mg m-2 d-1
MESO-GRAZING
259 ± 70 mg m-2 d-1
70%
30%
97% Picos 3%
53% Diatom 47%
59% Other 41%

Inverse Model

Self-organizes flows within broad constraints

Inputs: taxon-spec production & grazing with station variability
biomass structure - bacteria, phyto- & zooplankton

Other: BP = 10-22% ^{14}C-PP (Ducklow et al. 1995)
GPP = 1.9-2.2 X ^{14}C-PP (Bender et al. 1999)
carnivore = 16% mesozoo biomass (LeBorgne et al. 2003)

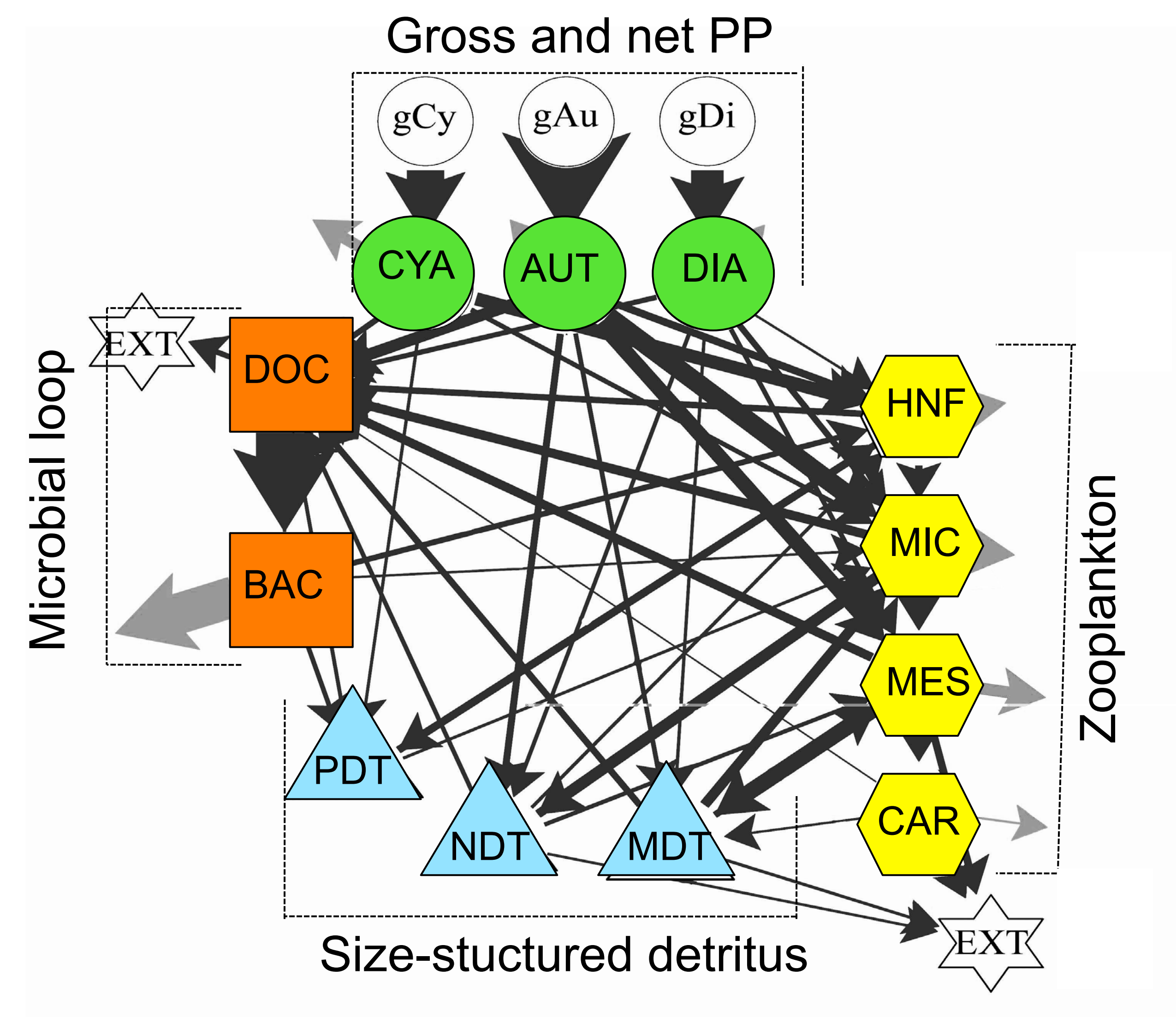
Solution scheme:

Markov Chain Monte Carlo (MCMC) approach

Input parameters sampled randomly from statistical distributions of actual rate measurements (data means and variances).

Solutions for 100,000 runs, satisfy mass balance & inequalities.

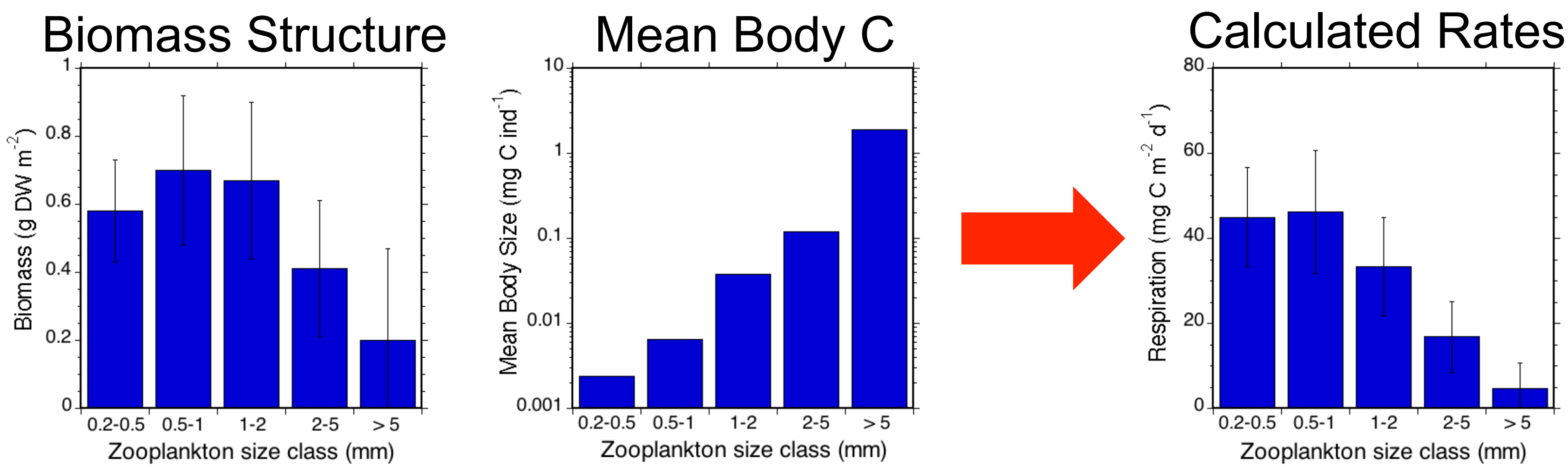
Produces means and std dev of rate solutions. Not typical "L_2 minimum norm (L_2MN)" approach, which yields one solution.



Gross and net PP
gCy
gAu
gDi
CYA
AUT
DIA
EXT
DOC
BAC
Microbial loop
HNF
MIC
MES
CAR
Zooplankton
PDT
NDT
MDT
EXT
Size-stuctured detritus

RESPIRATION (Ikeda, 1985)
PRODUCTION (Hirst & Shreader, 1997)

Rate = f (body size, T = 25°C, RQ = 0.8)

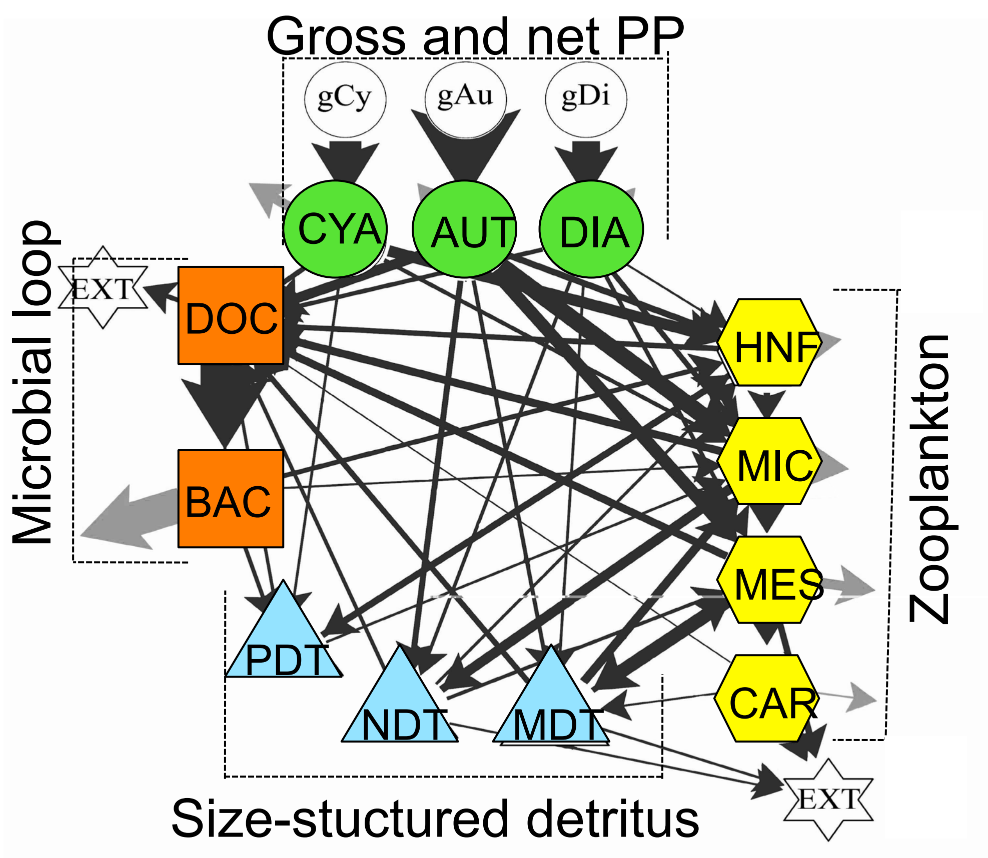


<u>Computed/Predicted</u>

RESP 146 mg C m^{-2} d^{-1}
PROD 145 mg C m^{-2} d^{-1}

Inverse Model: MesoZoo Results

Steady-state, open-ocean food web
Measured rates: balanced production-grazing
Meets MesoZoo requirements for RESP & PROD



MicroZoo = major food
231 mg C m^{-2} d^{-1}
204 - herbivory
60 - carnivory

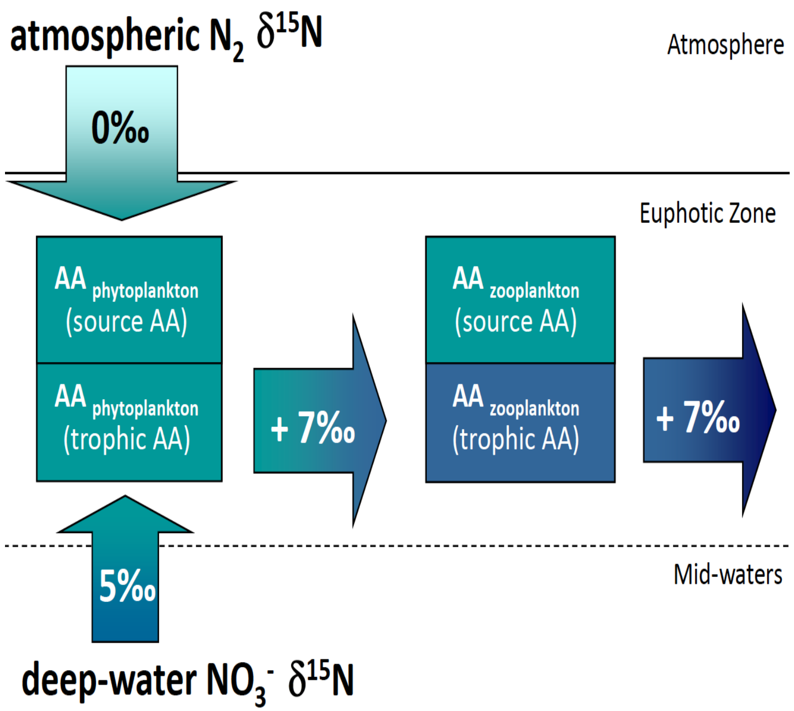
GGE = 25%

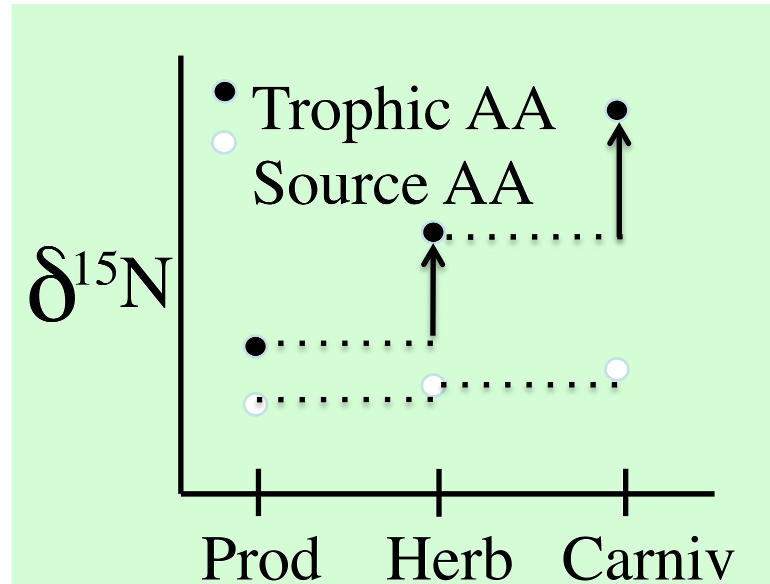
Trophic Position = 2.9

Isotopic Approach to Estimating TPs

CSIA-AA (Compound-Specific Isotopic Analyses of Amino Acids)

Trophic AAs (glutamic acid)
Source AAs (phenylalanine)



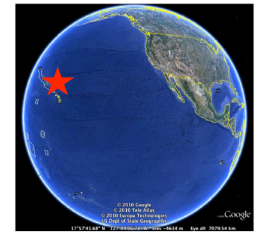


$$TP = \frac{(\delta^{15}N_{glu} - \delta^{15}N_{phe} - 3.4)}{7.6} + 1$$

McClelland & Montoya (2002)

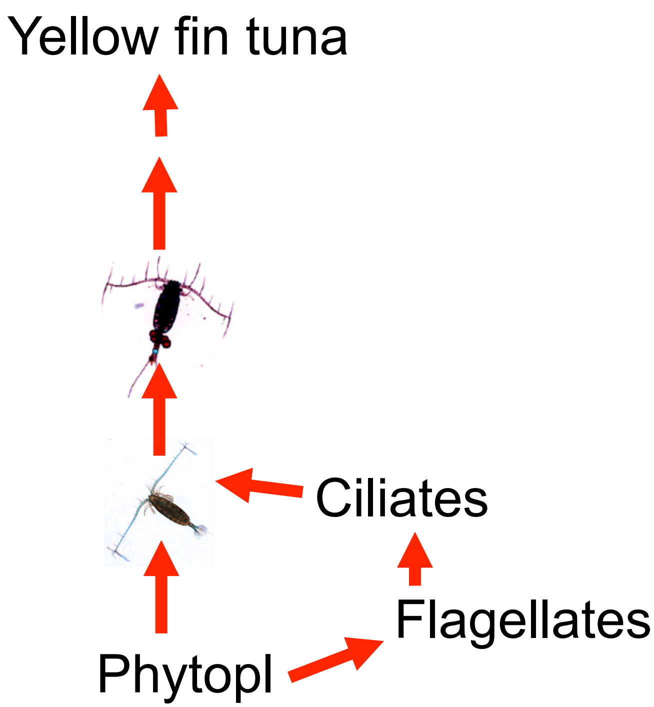
Chikaraishi et al. (2009)

CSIA-AA applied to Plankton

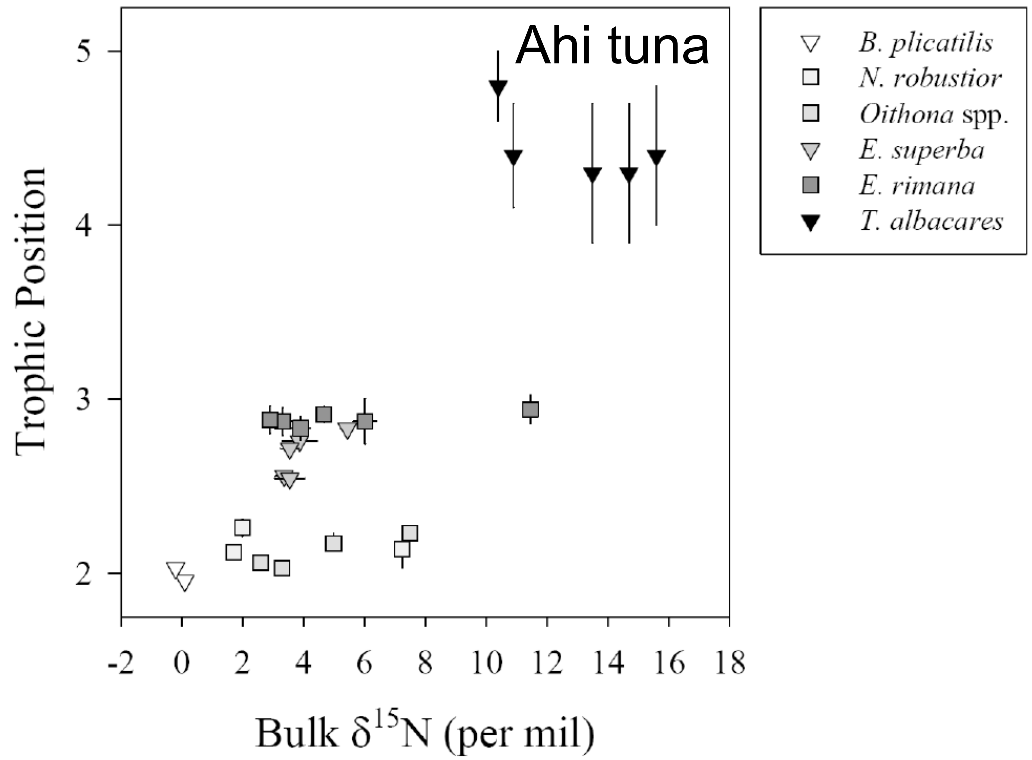


Species-specific analyses of open-ocean zooplankton

The implied food chain shows <u>no</u> trophic steps for protozoan consumers

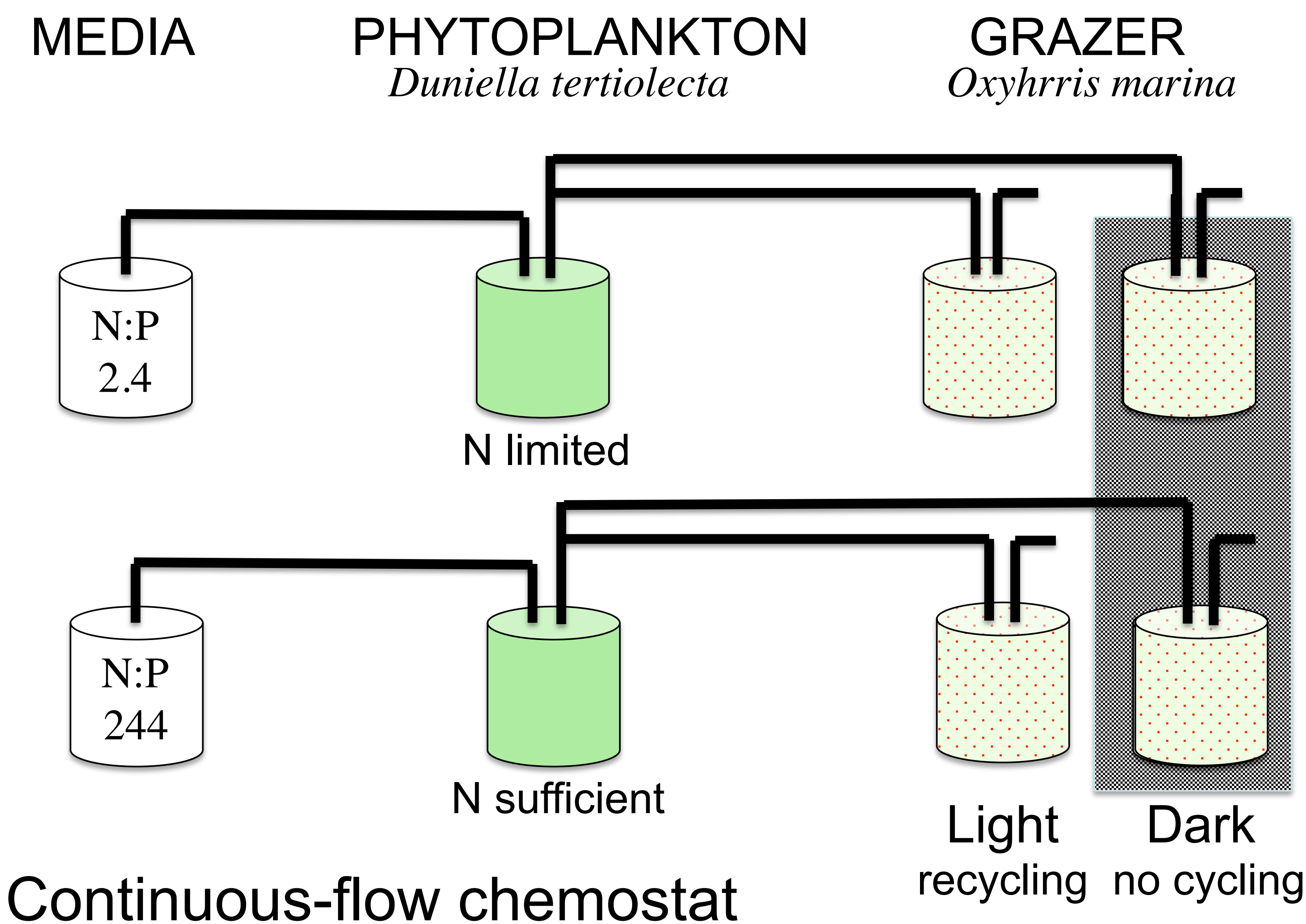


Hawaii Ocean Time-Series (HOT)
Subtropical North Pacific



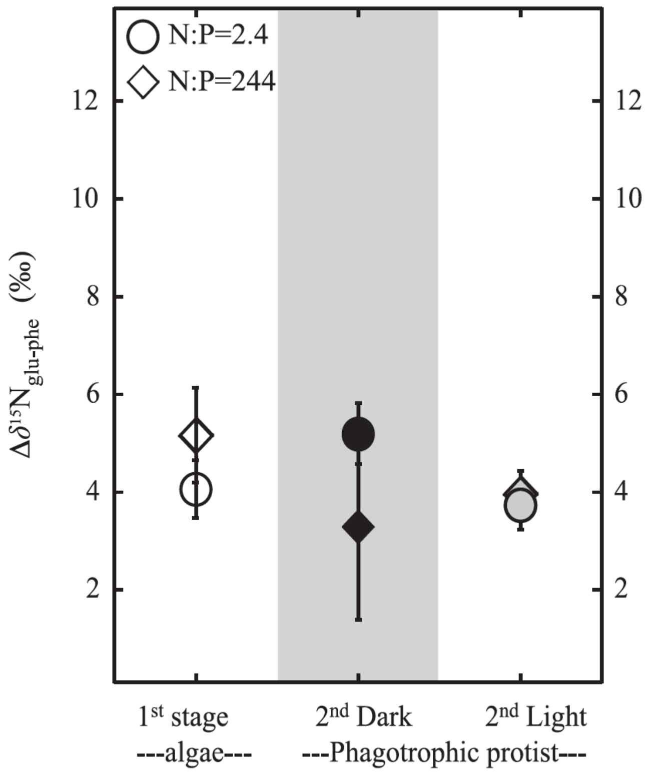
Hannides et al. (2009)

Experimental Design



Isotopic Invisibility of Protistan Trophic Steps

Trophic – Source AAs



No difference between algae and grazers, or L/D treatments

Implications

Minimal physiological transformation and isotopic discrimination of AAs absorbed from algae.

"Salvage incorporation"

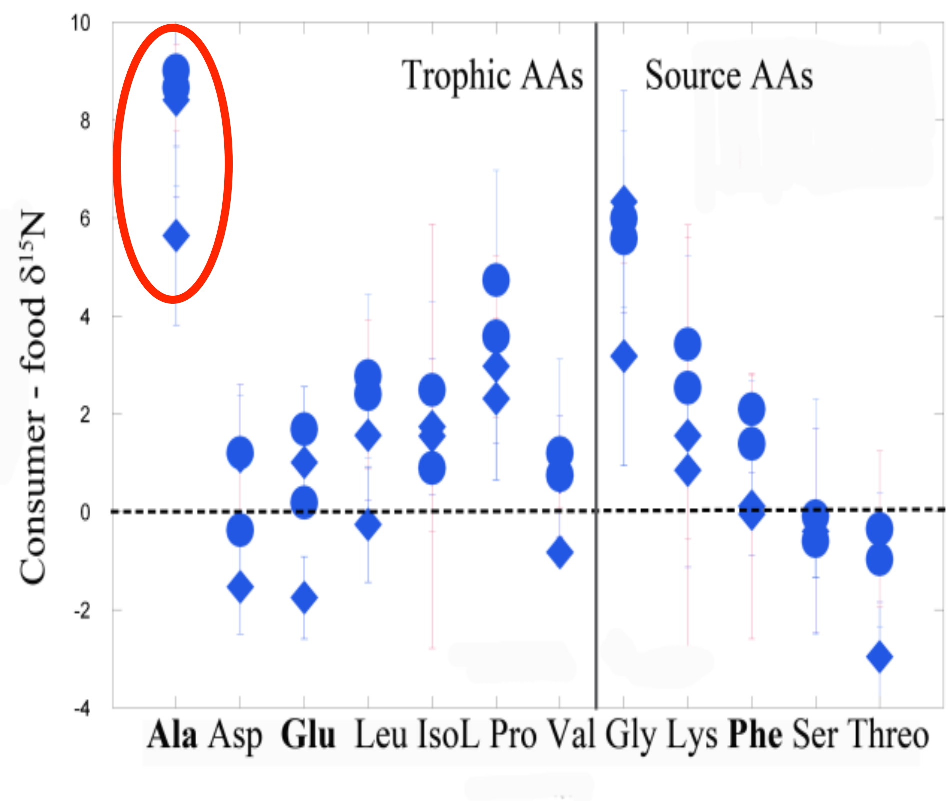
C & N skeletons of digested AAs remain intact during uptake and incorporation into protistan biomass.

Gutiérrez-Rodríguez et al. (2014)

However …

One trophic AA, ***alanine***, showed a strong enrichment between the algal food and protistan consumer.

There is evidence that **Alanine** plays a key role in synthetic pathways of protozoans, similar to glutamic acid in metazoans.

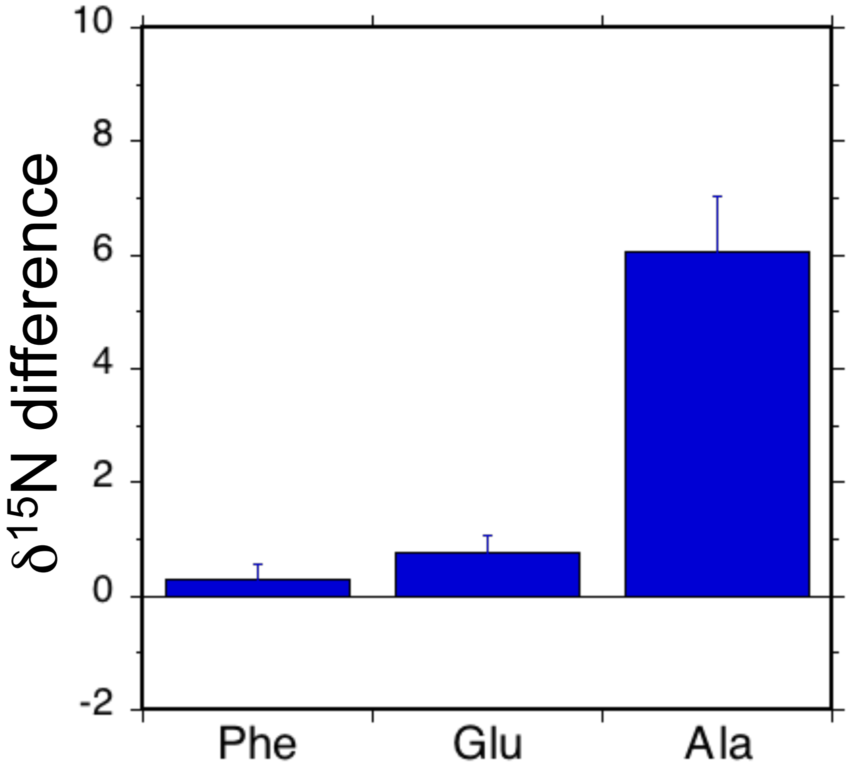


Gutiérrez-Rodríguez et al. (2014)

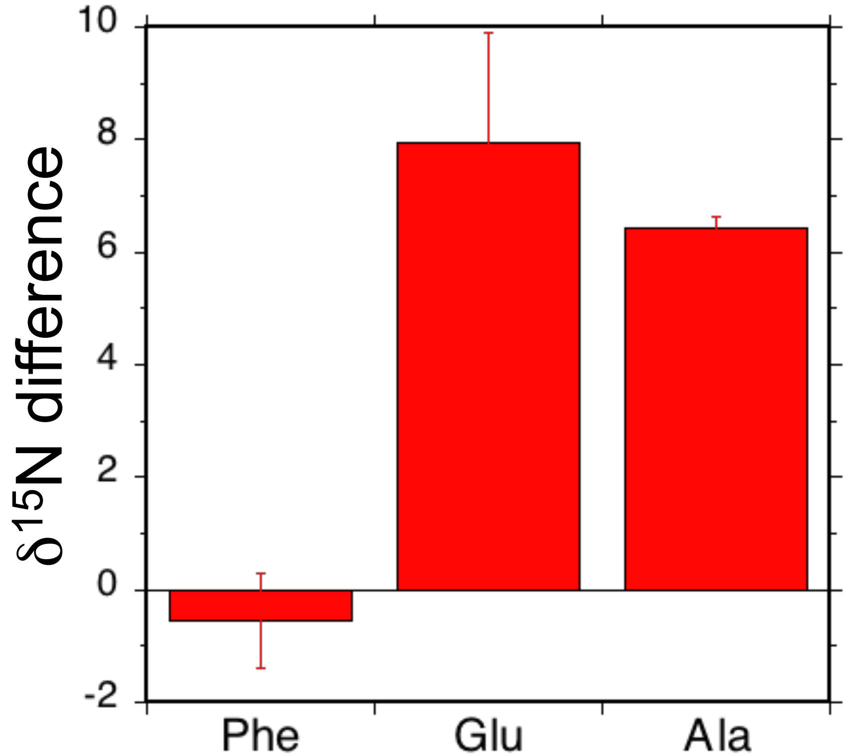
Protists & metazoans enrich **Alanine** similarly, and **Glutamic Acid** differently

Pred-Prey $\delta^{15}N$ differences, 2-stage chemostats

Favella (ciliate) feeding on *Heterocapsa triquetra* (dinoflag)



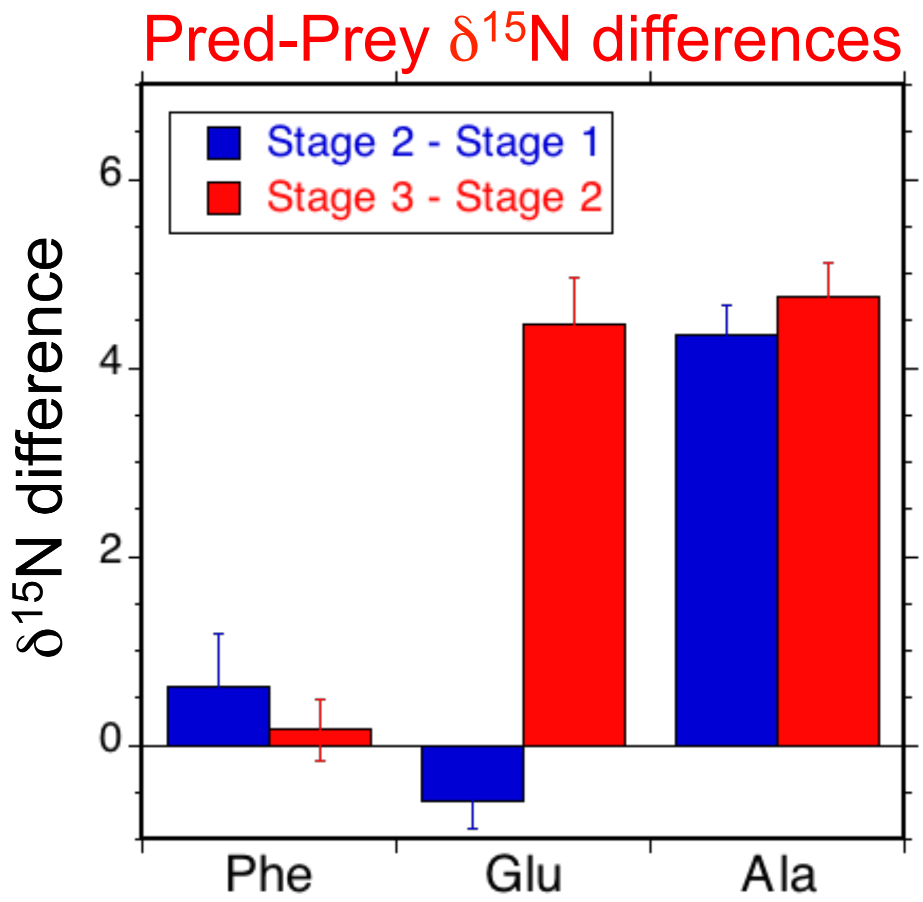
Calanus pacificus (copepod) feeding on *T. weissflogii* (diatom)



Décima et al. (ms)

Enrichment in a 3-stage chemostat

Stage 1 = *Dunaliella tertiolecta*
Stage 2 = *Oxyhrris marina*
Stage 3 = *Calanus pacificus*



Décima et al. (ms)

MesoZoo TPs with **Alanine** as the "Trophic AA"

Subtrop. N. Pacific	**TP_{Glu}**	**TP_{Ala}**	**$TP_{Ala-Glu}$**
Oithona sp.	2.11 ±0.09	3.03 ±0.22	0.91 ±0.29
Neocal. robustior	2.16 ±0.07	2.97 ±0.06	0.81 ±0.10
Thysanopoda sp.	2.29 ±0.18	3.23 ±0.26	0.94 ±0.22
1-2 mm mixed	2.52 ±0.17	3.29 ±0.13	0.76 ±0.08
Pleurom. xiphias	2.77 ±0.07	3.81 ±0.16	1.04 ±0.11
Euchaeta rimana	2.83 ±0.05	3.85 ±0.20	1.02 ±0.22
California Current			
Cal. pacificus C5	1.91 ±0.07	2.67 ±0.21	0.69 ±0.16
Cal. pacificus fem	1.99 ±0.18	2.74 ±0.33	0.75 ±0.30
Euphausia pacifica	1.93 ±0.21	2.82 ±0.32	0.89 ±0.17

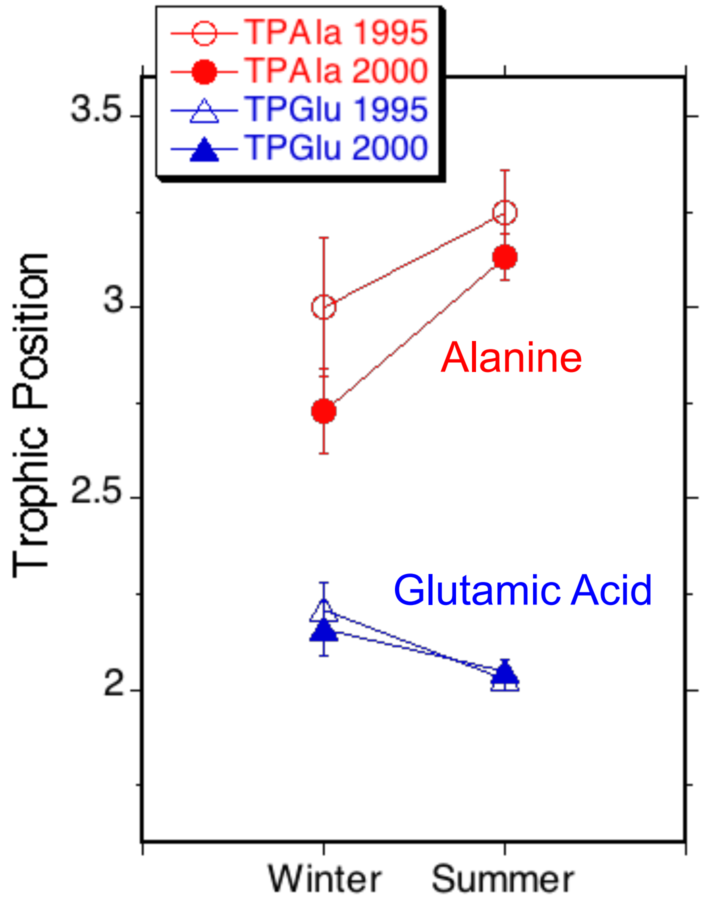
Common suspension-feeders are TP ≈ 2.7-3.0

Ala-Glu difference ≈ 0.7 - 1.0 TP

Décima et al. (ms)

Indications of temporal variability

Oithona sp., seasonal Subtropical Pacific



MesoZoo are temporal integrators of lower food-web structure and flows. δ^{15}N-AA variability provides insight into the linkages.

For *Oithona*, TP_{Ala} indicates more active feeding on H-protists in summer, while TP_{Ala} suggests modest elevation due to carnivory (predation on nauplii?) in winter.

Data from Hannides et al. (2009)

Some Take Home Thoughts

1. **Problem:** MicroZoo are major consumers, but C flows through Micro-Meso linkages are not well integrated into food-web understanding (Biol C Pump, fisheries models). Trophic steps for MicroZoo are systematically underestimated by (invisible to) traditional stable isotope methods.

2. **Emerging View**: Global carbon budgets, regional food web studies and new isotopic approaches (CSIA-Alanine) are all consistent with MicroZoo occupying ~ one full trophic step … potentially substantial regional and temporal variability.

3. **More than "Tucker":** Zoopl δ^{15}N-AA composition may hold the key to unlocking previously unseen temporal-spatial variability in structure of the lower food web, and new insights into climate sensitivities of food-web efficiencies (historical collections).

4. **Who occupies TP=4, suspension-feeding copepods or tuna?** Neither; likely "carnivorous zooplankton" – *Euchaeta*, chaetognaths … Open-ocean, suspension-feeding copepods ~ TP=3. Tuna are 2.5-3 levels higher; TP ≈ 5.5 to 6.