The microzooplankton trophic link:

can conventional understanding of food web structure explain mesozooplankton biomass variability in the oceans?

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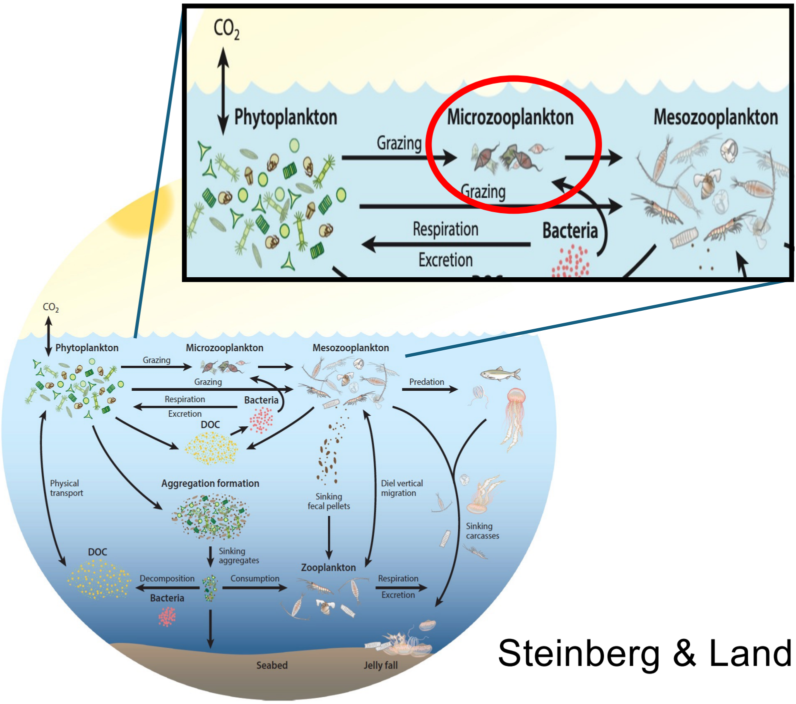
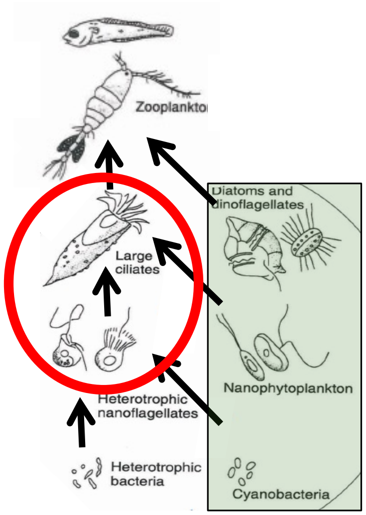
Conventional understanding of the pelagic food web envisions at least **one heterotrophic step of microzooplankton** between phytoplankton primary production and mesozooplankton

MicroZoo (<0.2 mm) are typically represented as phagotrophic protists, but also include small metazoan stages & species



Steinberg & Landry (2017)

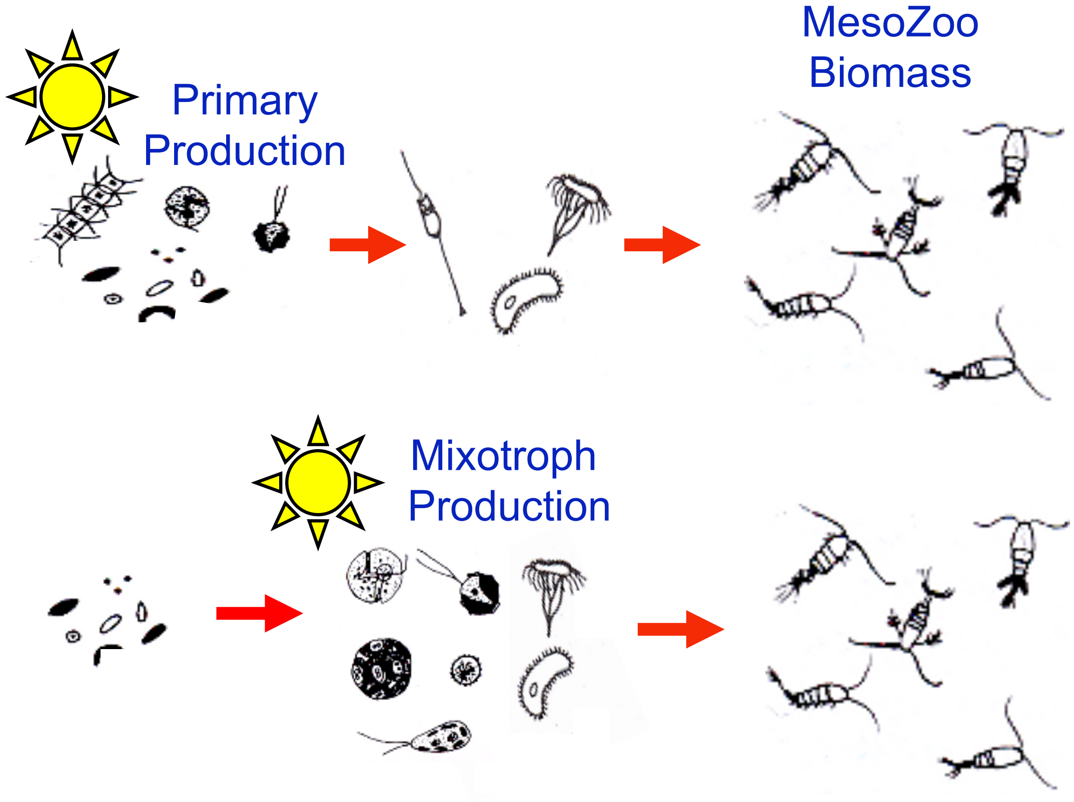


SAHFOS

The MicroZoo Link

- ➢ Major grazers in open ocean
- ➢ Major contributors to nutrient remineralization
- ➢ Food resource for mesozooplankton
- ➢ Trophic transfer intermediate to higher consumers and C export

Can conventional understanding of food web structure explain MesoZoo biomass variability?



Can measured primary production support observed MesoZoo biomass with 70% or higher energy loss through a heterotrophic MicroZoo step?

If not, we must consider a more efficient food web paradigm in which MicroZoo are mainly mixotrophic.

Data Sources

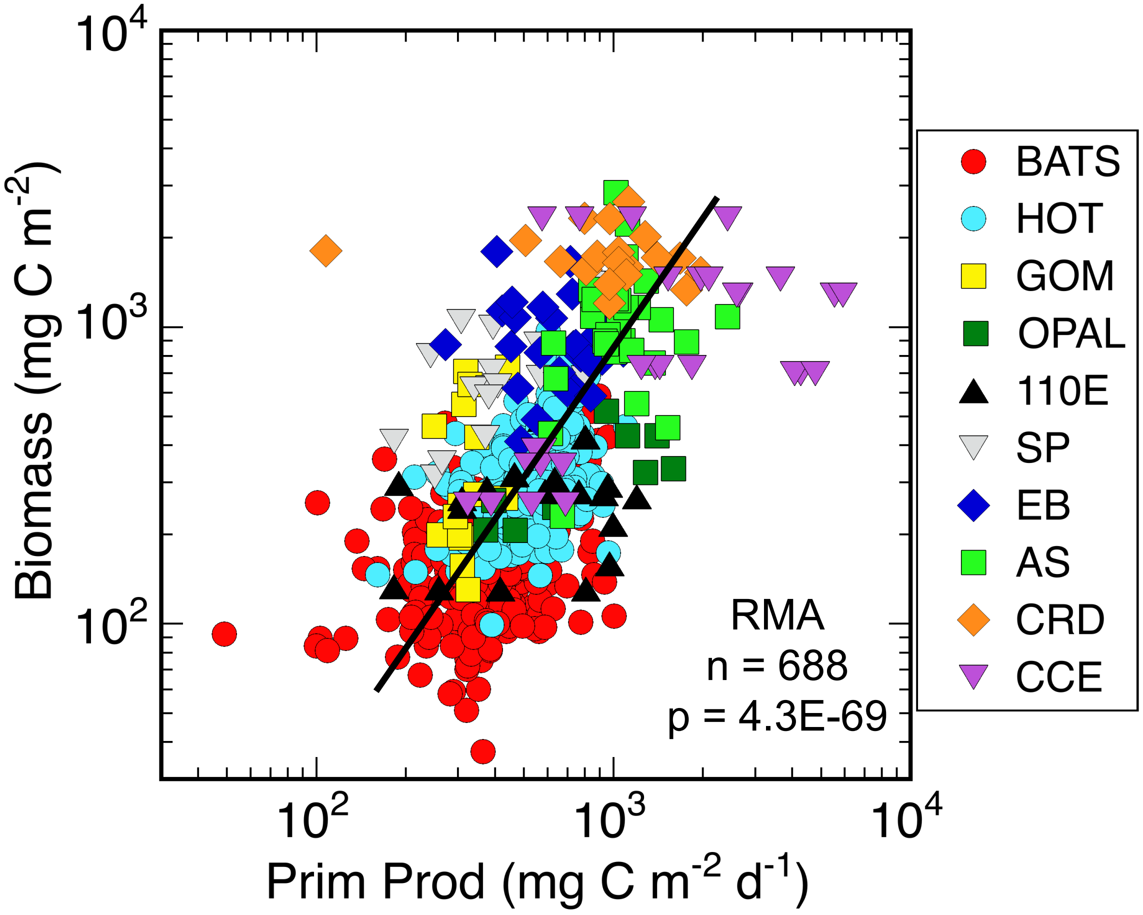
Large Datasets with contemporaneous measurements of PrimProd, Day/Night size-fractioned (0.2 to >5 mm) MesoZoo biomass, 200-µm mesh

HOT, **BATS** – about 270 cruises each

Experimental Process Studies with contemporaneous measurements of PrimProd, Day/Night size-fractioned MesoZoo biomass, MicroZoo and MesoZoo grazing rates, Phyto C or C:Chl*a*

Arabian Sea (**AS**) – US JGOFS, 4 monsoon seasons, 1995
Equatorial Pacific (**EB**) – Equatorial Biocomplexity, 2004, 2005
Cyclone OPAL (**OPAL**) – E-FLUX3, Hawaiian mesoscale eddy, 2005
California Current Ecosystem (**CCE**) – CCE-LTER, 2006, 2007
Costa Rica Dome (**CRD**) – CRD FLUZiE cruise, 2010
Gulf of Mexico (**GOM**) – BLOOFINZ-GoM, 2017, 2018
Southwest Pacific (**SP**) – SalpPOOP, Chatham Rise, *R/V Tangaroa*, 2018
Western Australia (**110°E**) – IIOE-2, *R/V Investigator*, 2019

MesoZoo biomass relationship to system PrimProd



Oligotrophic waters have lower PP and biomass:

BATS, HOT, GOM, 110E

Upwelling centers have higher PP and biomass:

EB, AS, CRD, CCE

Zoopl Carbon Requirements (ZCR) for metabolism and growth

Assumptions

MesoZoo have healthy metabolism and growth (T°C, Body Size) defined by:

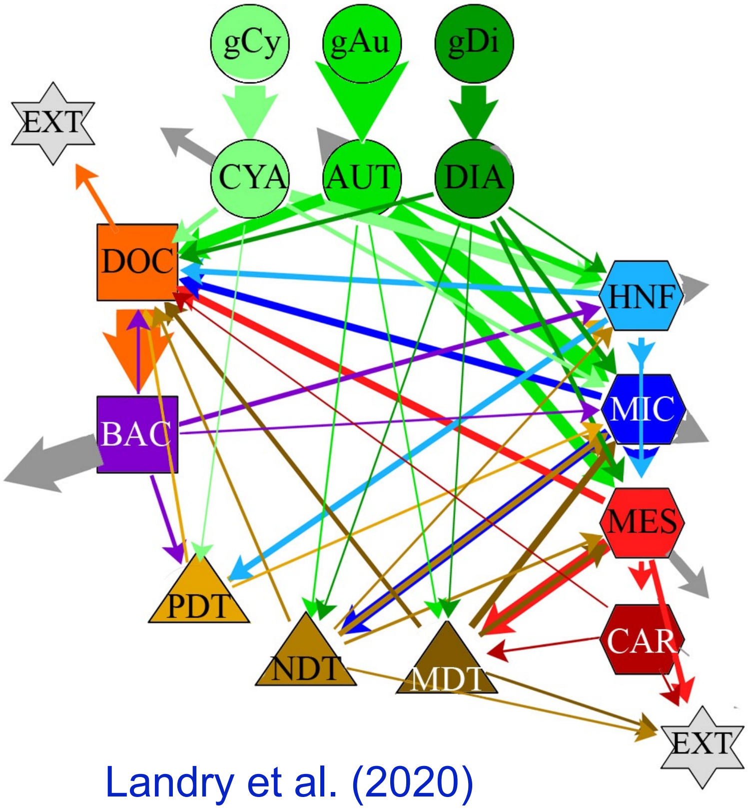
*Ikeda (1985) – 1.5X Respiration

Hirst & Sheader (1997) – Growth

Euphotic Zone feeding supports mean Day-Night EZ biomass plus metabolism and growth of diel migrants

Trophic flow analysis for EB measured rates support zooplankton consistent with these assumptions.

Equatorial Pacific network model



Landry et al. (2020)

ZCR Calculations

$$ZCR = \left[\sum_{i=1}^{5} (\text{Metabolism } f(\text{size}, T°C) + \text{Production } f(\text{size}, T°C))\right]/AE$$

where i = size fractions, AE = absorption efficiency (0.70)

Mean Day/Night size-fract biomass from upper 150-200 m, mean T°C of EZ

Migrant (Night–Day) size-fract biomass, ½ day at mean T°C of 300-500 m

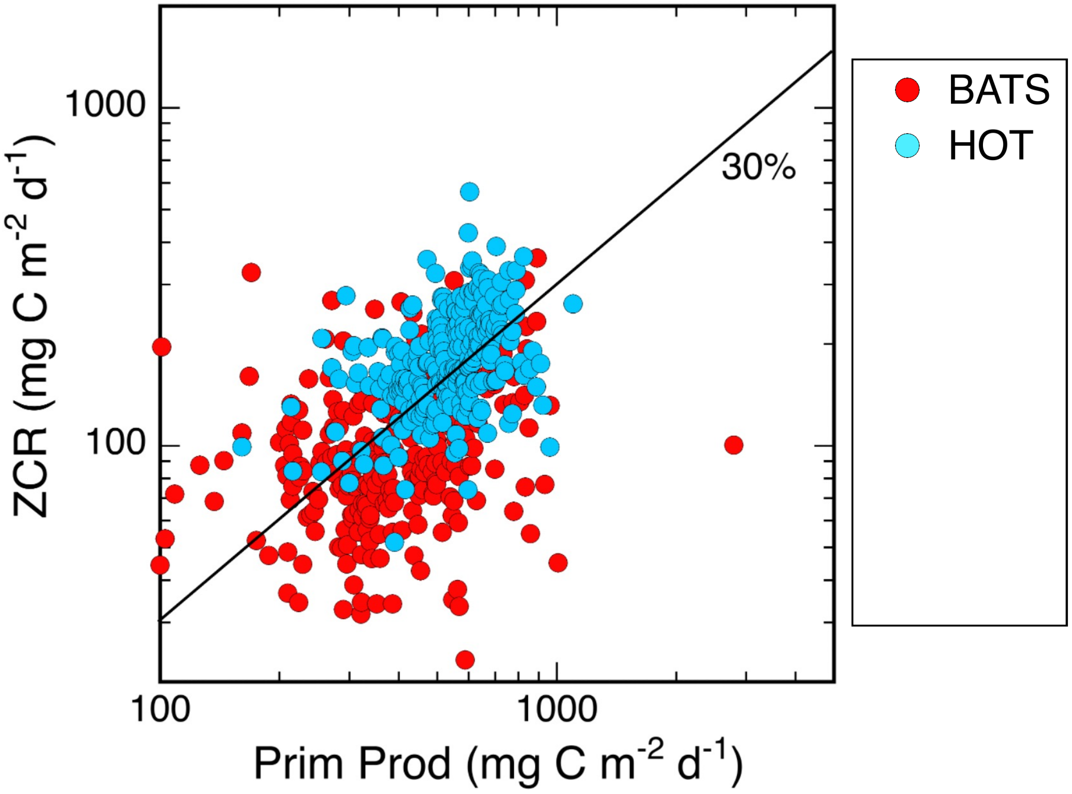
This produces MesoZoo with mean GGE = 23.6%
MesoZoo GGE Synthesis = 26% (Straile 1997)

Special Circumstance: Salp Bloom Experiments (SP)

$$ZCR_{salps} = 3X \sum (\text{Metabolism } f(\text{size}, T°C))/0.70$$

Based on Iguchi & Ikeda (2004) rates, size-binned individuals, $Q_{10} = 2.0$

ZCR estimates for different systems

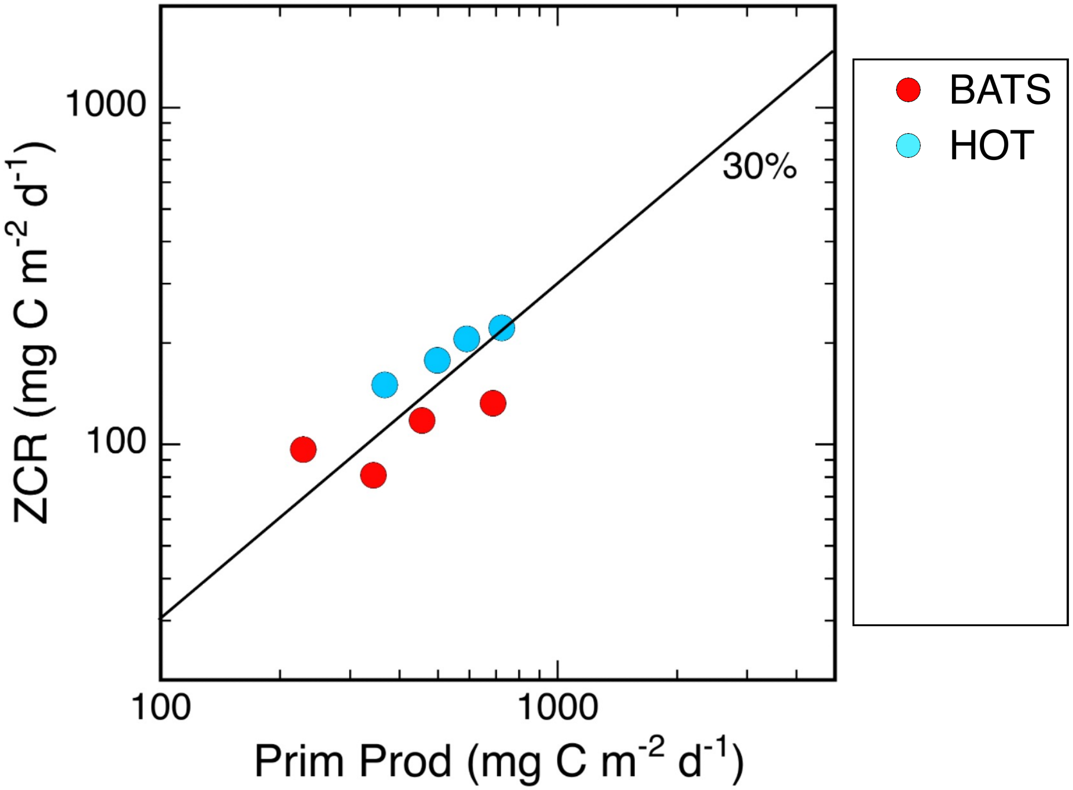


30% line would be the expected contribution of MicroZoo to ZCR if all PrimProd was consumed by heterotrophic MicroZoo and available to MezoZoo consumption with a 30% trophic transfer efficiency.

protistan GGE
(Straile1997)

ZCR estimates for different systems

BATS and HOT data divided into quartiles of lower to higher PrimProd, averaged

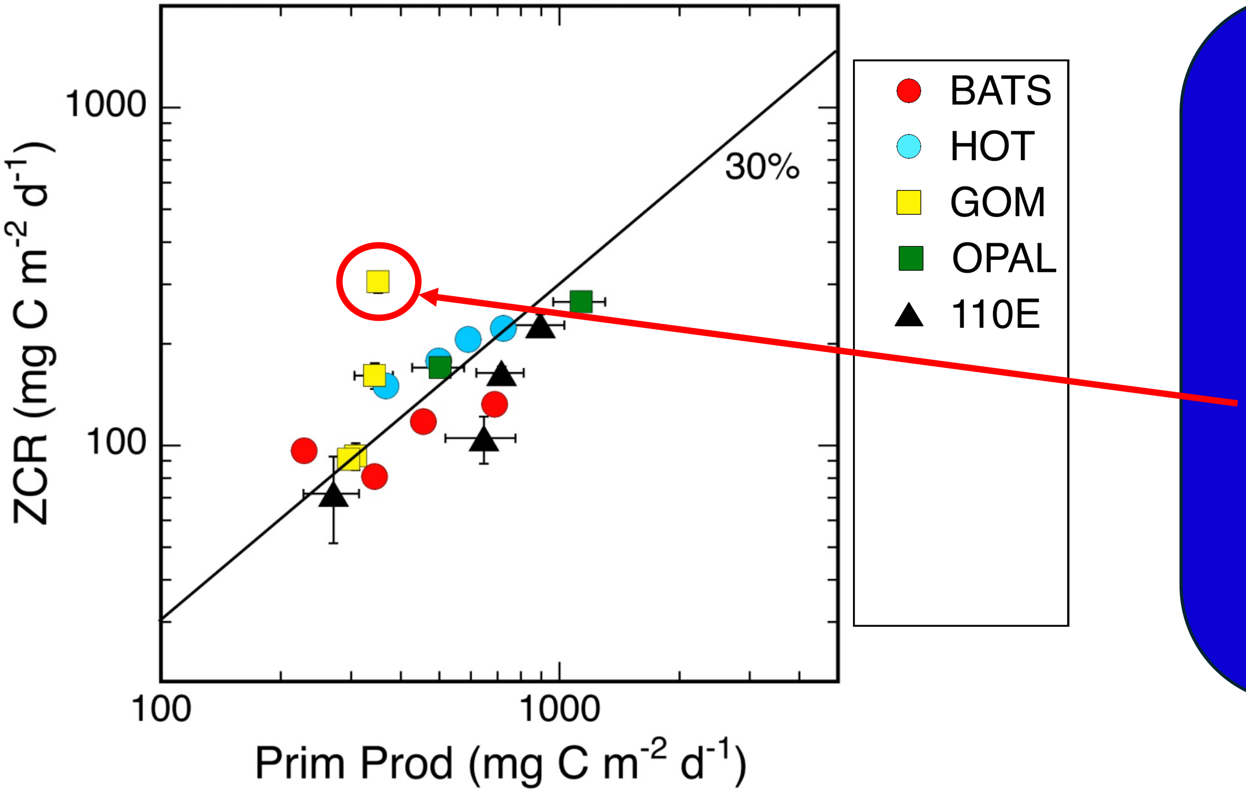


The quartiles capture the ~2X seasonal and ~2X secular MesoZoo biomass increases observed in each system

SEM uncertainties are plotted but smaller than the symbols

ZCR estimates for different systems

Three subtropical experimental sites are added to the BATS & HOT data

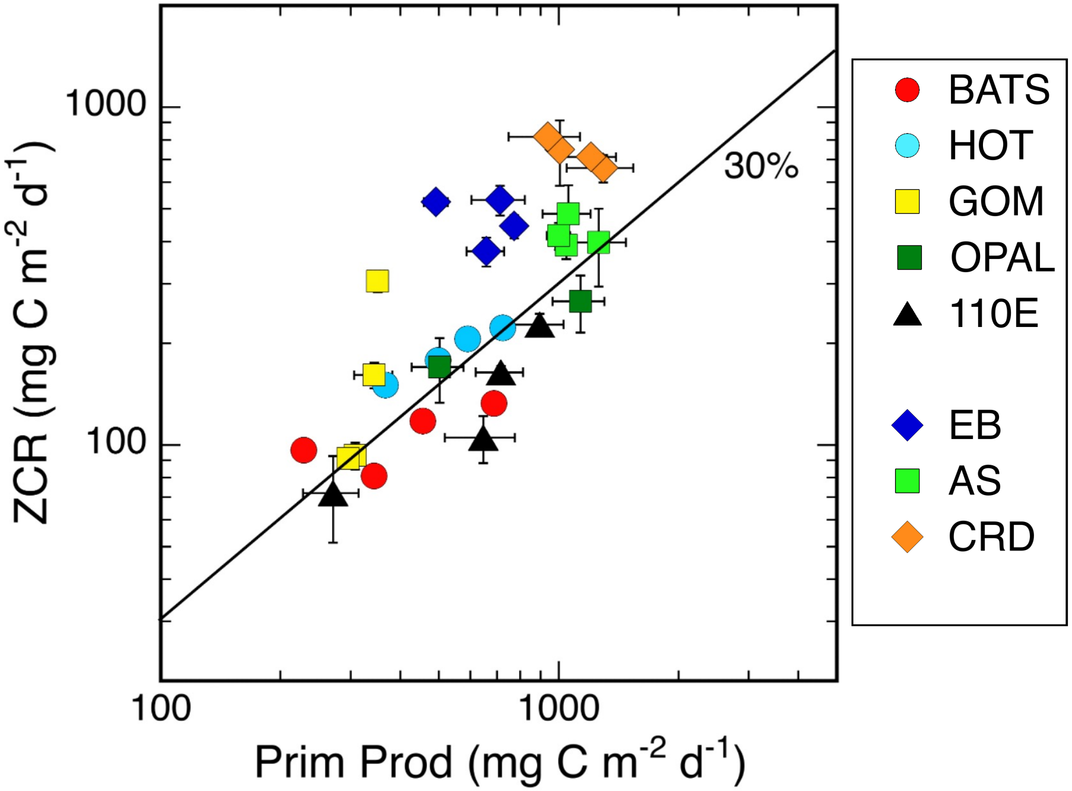


ZCR for subtropical sites are similar to BATS & HOT in relation to PrimProd

One GOM experiment received a lateral supplement from the rich continental margin (Landry & Swalethorp 2021)

ZCR estimates for different systems

Open-ocean upwelling regions are added



ZCR for open-ocean upwelling sites have higher ZCR in relation to PrimProd

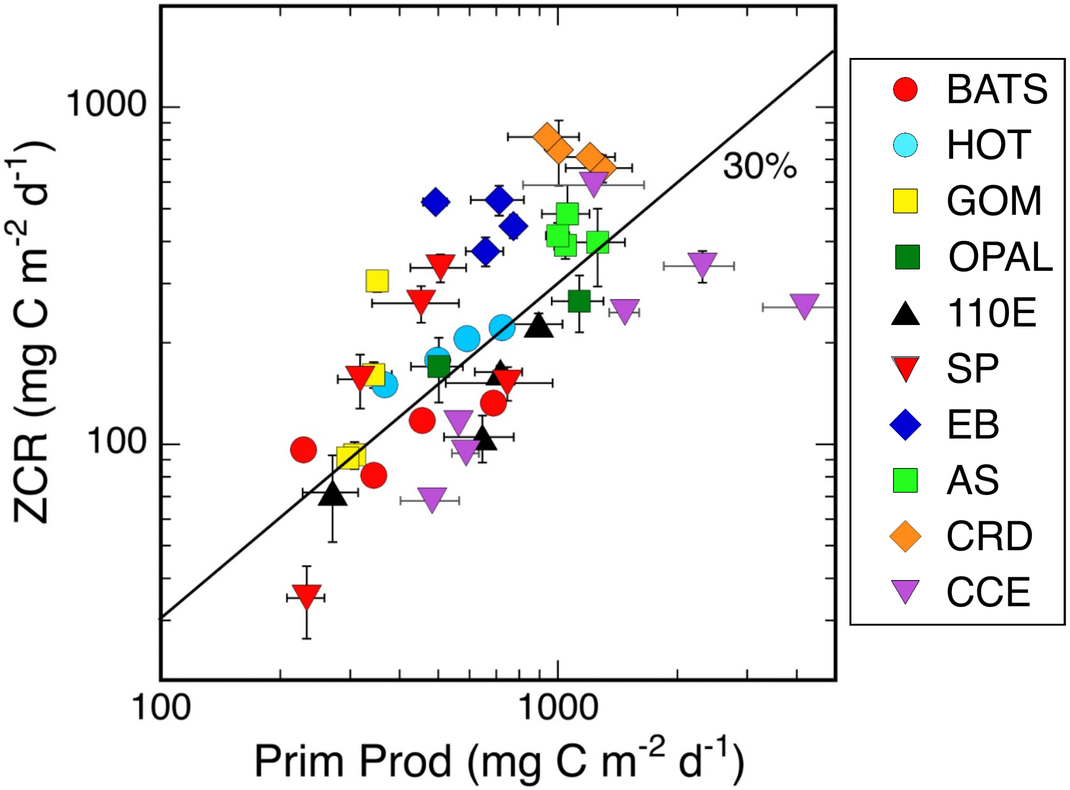
EB = 32 stns, 4 transects

AS = 30 stns, 4 seasons

CRD = 4 Lagrangian exps

ZCR estimates for different systems

The CCE captures two coastal upwelling blooms. Three of five SP experiments are salp blooms.



One CCE upwell exp with highest ZCR is bloom decline: Prod << Graz

Upwelling exps with highest PrimProd have net Phyto growth: Prod >> Graz

Salp bloom increases ZCR relative to PrimProd

Average: ZCR = 47.1 ± 2.8% PP

Can grazing rate estimates satisfy ZCR?

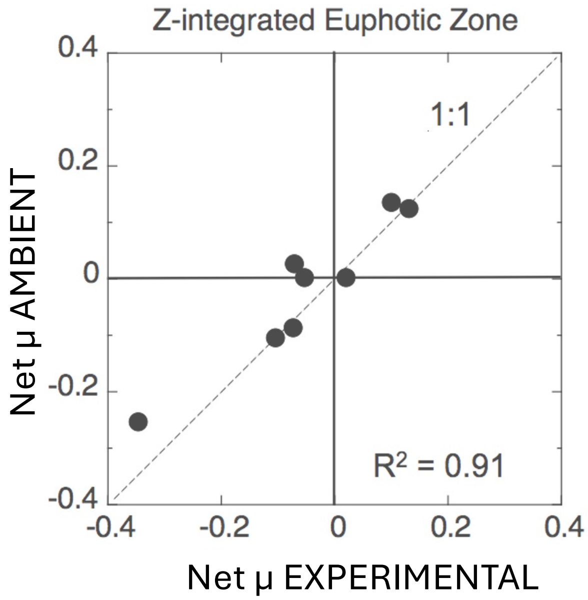
MicroZoo Graz by 2-point dilution method, 6-8 light depths, 24-h incubations, spanning EZ. Phyto growth (μ, d^{-1}) and grazing mortality rates (m, d^{-1}) measured by Chl*a*, converted to carbon with measured Phyto C:Chl*a* (microscopy, flow cytometry). Depth integrated for EZ.

MesoZoo Graz by gut fluorescence. Same net tows and size fractions as biomass. Measured as [Phaeo] x Gut Turnover Rate *f*(T°C) to get % Chl*a* consumed d^{-1}, converted to C measured Phyto C:Chl*a*.

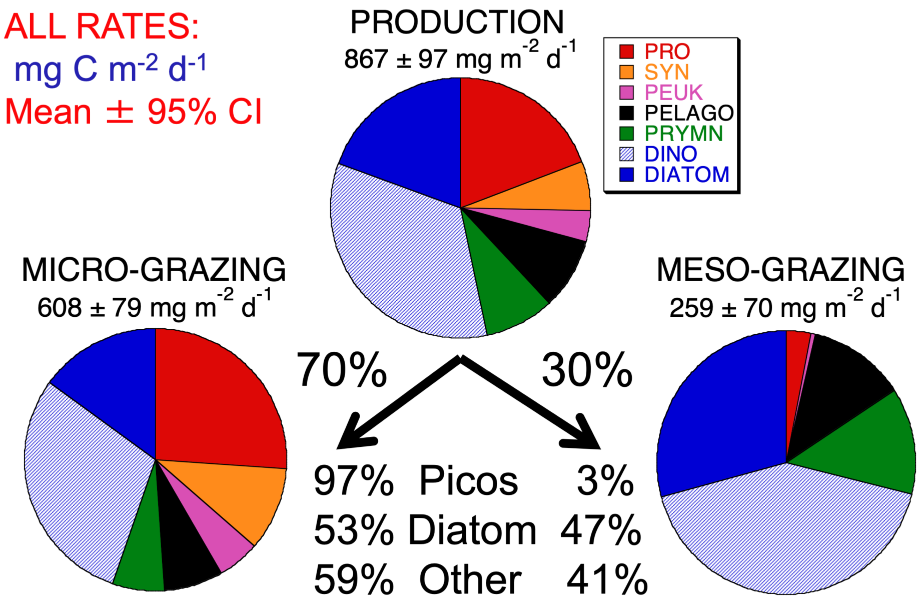
$Graz_{salps}$ = gut Chl*a*, size-binned individuals

Arabian Sea: MesoZoo grazing by ^{14}C method incubation analogous to PrimProd (Roman & Gauzens 1997)

Six of 8 process studies resolved 1) steady-state balances of phyto growth and grazing or 2) showed experimental rates consistent with observed ambient changes from Lagrangian sampling



CCE Phyto Net Change, Landry et al. (2009)



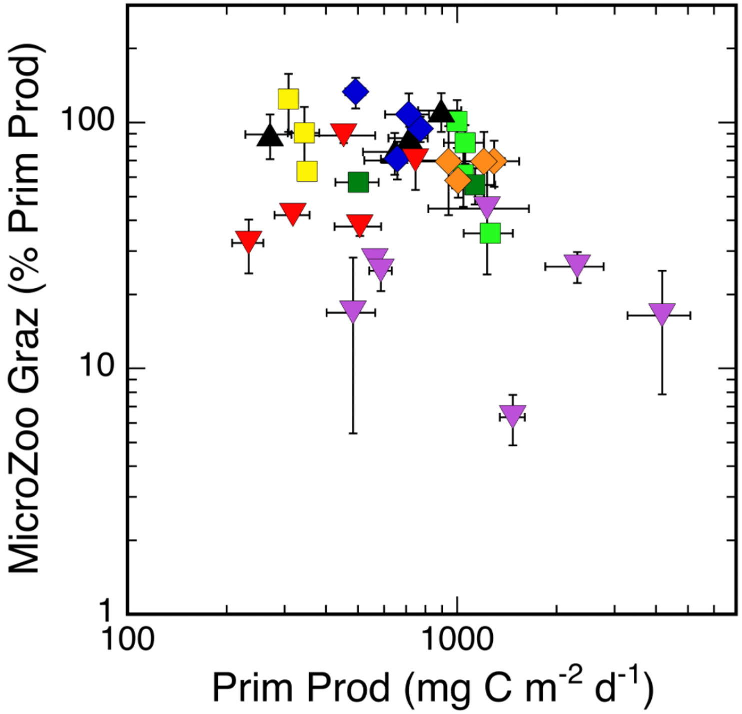
ALL RATES:
mg C m^{-2} d^{-1}
Mean ± 95% CI

70% 30%

97% Picos 3%
53% Diatom 47%
59% Other 41%

EB Steady-State Balance, Landry et al. (2011)

MicroZoo contribution to ZCR



Full data average = 70.0 ± 3.6%
Calbet & Landry (2004) = 67%

Most experiments show that MicroZoo consume a high percentage of daily Prim Prod

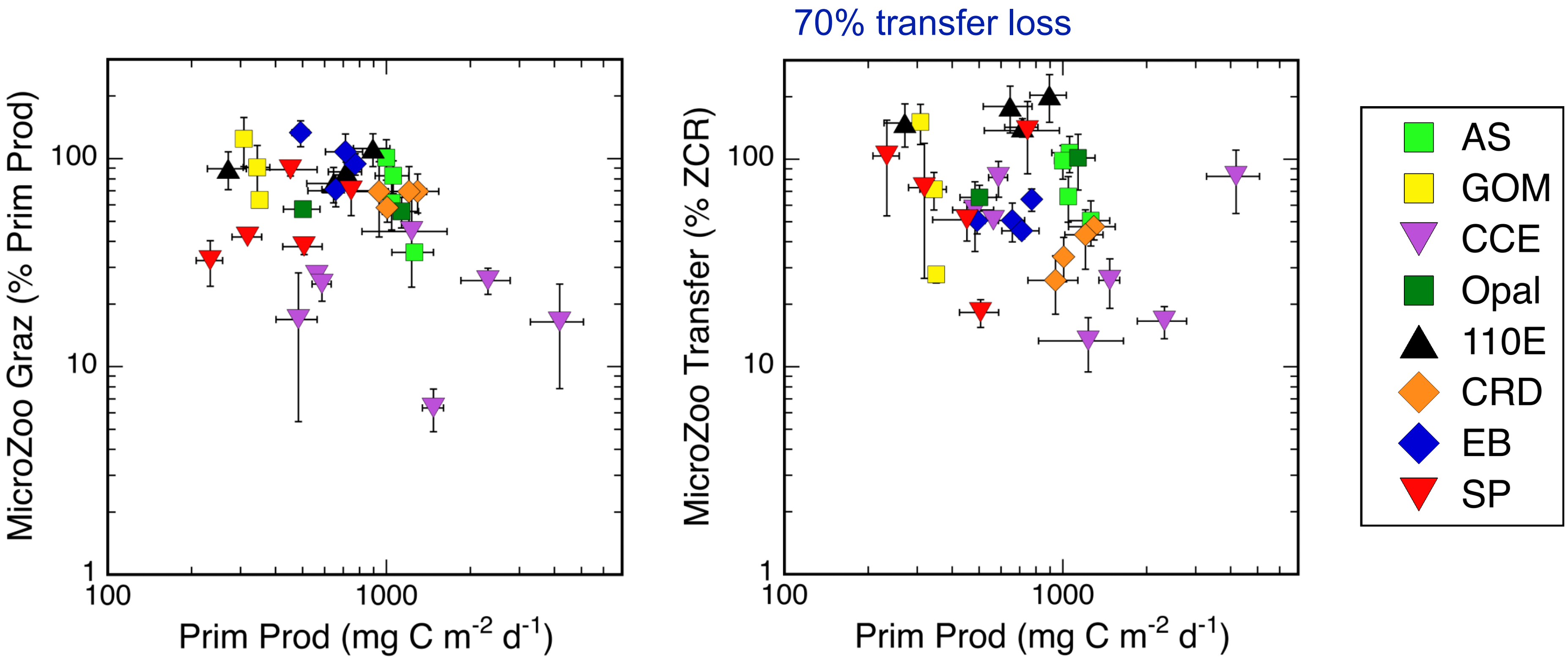
<u>Exceptions</u>:

Coastal upwelling sites, Salp bloom

MicroZoo overwhelmed, controlled by predators

- 🟩 AS
- 🟨 GOM
- ▽ CCE
- 🟩 Opal
- ▲ 110E
- ◆ CRD
- ◆ EB
- ▼ SP

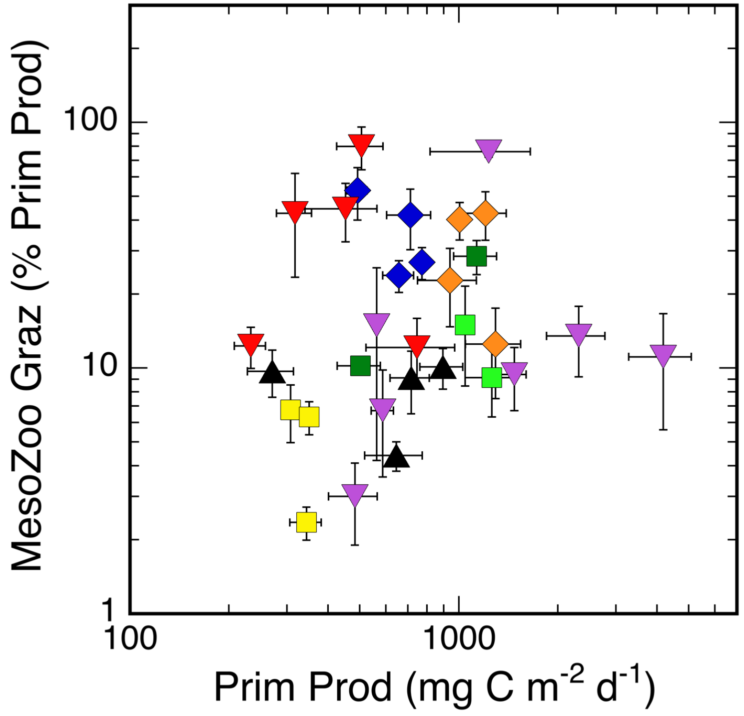
MicroZoo contribution to ZCR



Full data average = 70.0 ± 3.6%
Calbet & Landry (2004) = 67%

Full data average = 58.7 ± 4.0%

MesoZoo contribution to ZCR



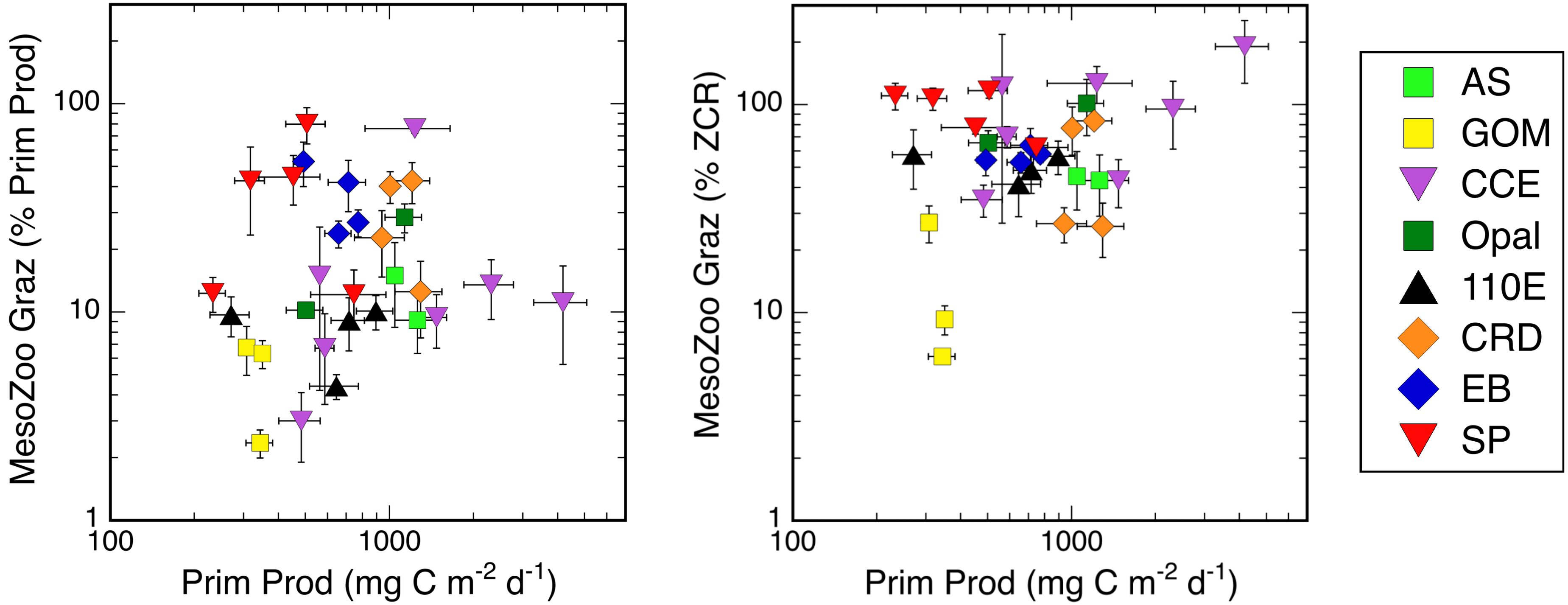
Data average = 23.9 ± 2.1%
Calbet (2001) = 23% global

MesoZoo consumption of Prim Prod is mostly low (~10%)

Elevated in upwelling bloom decline (CCE), salp bloom (SP), open-ocean upwelling (EB, CRD), eddy diatom bloom (Opal)

🟩 AS
🟨 GOM
▼ CCE
🟩 Opal
▲ 110E
🔶 CRD
🔷 EB
🔻 SP

MesoZoo contribution to ZCR

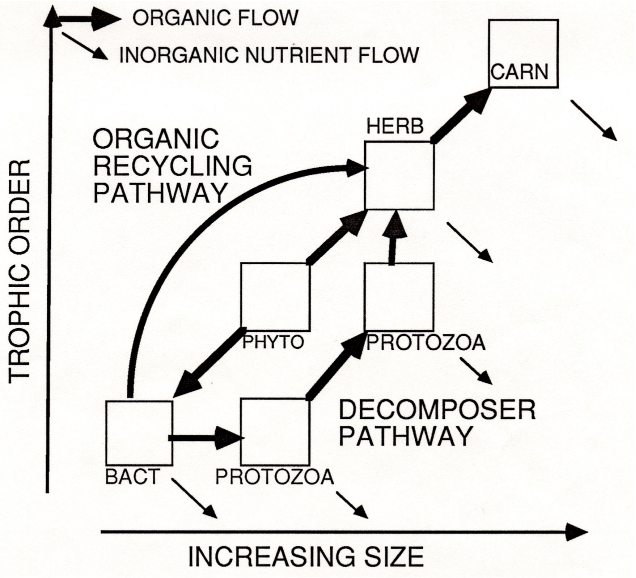


Data average = 23.9 ± 2.1%
Calbet (2001) = 23% global

Data average = 54.0 ± 3.5%

Other contributions to ZCR: Bacteria via Microbial Loop

Microbial Loop refers to the return of dissolved organics to the food web by uptake into bacterial production and subsequent grazing. Williams (1981) predicted that this would be an inefficient process unless the long food web was short circuited by a metazoan (like appendicularians) that feed directly on bacteria.



Williams (1981)

In general:

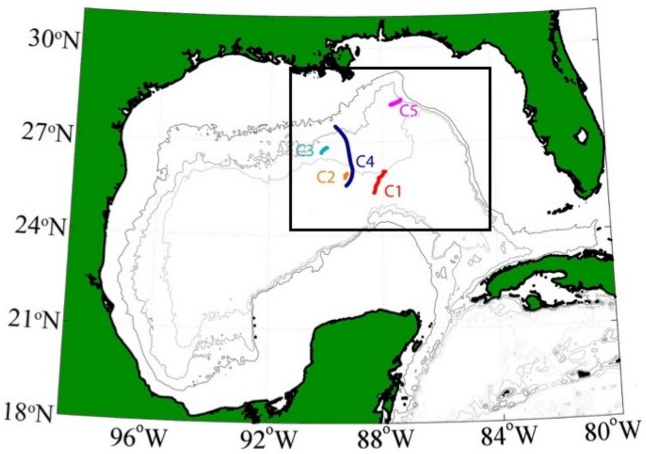
Bact Prod ≈ 10% Prim Prod

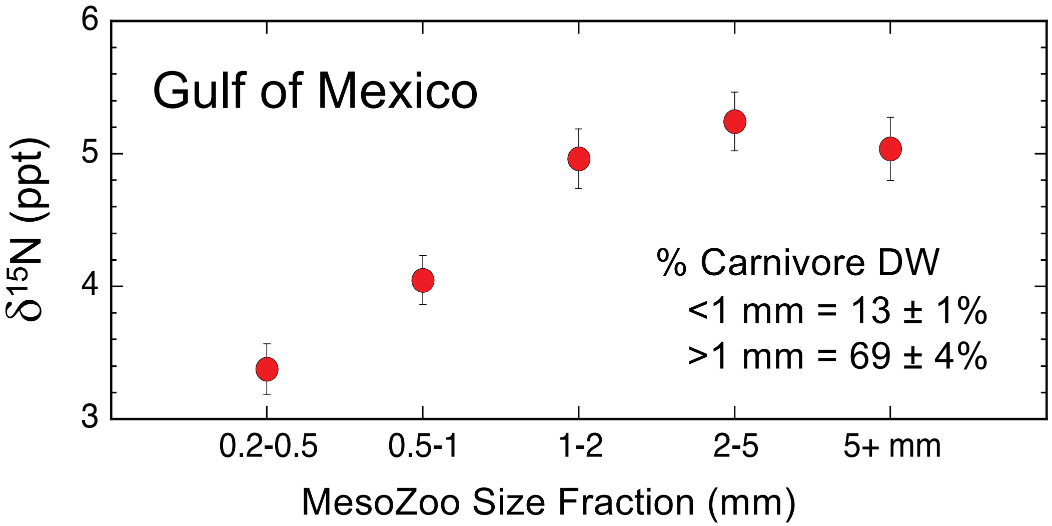
Half lost to viruses

One trophic transfer = 1.5% Prim Prod

Two trophic transfers = 0.45% Prim Prod

Other contributions to ZCR: Carnivory

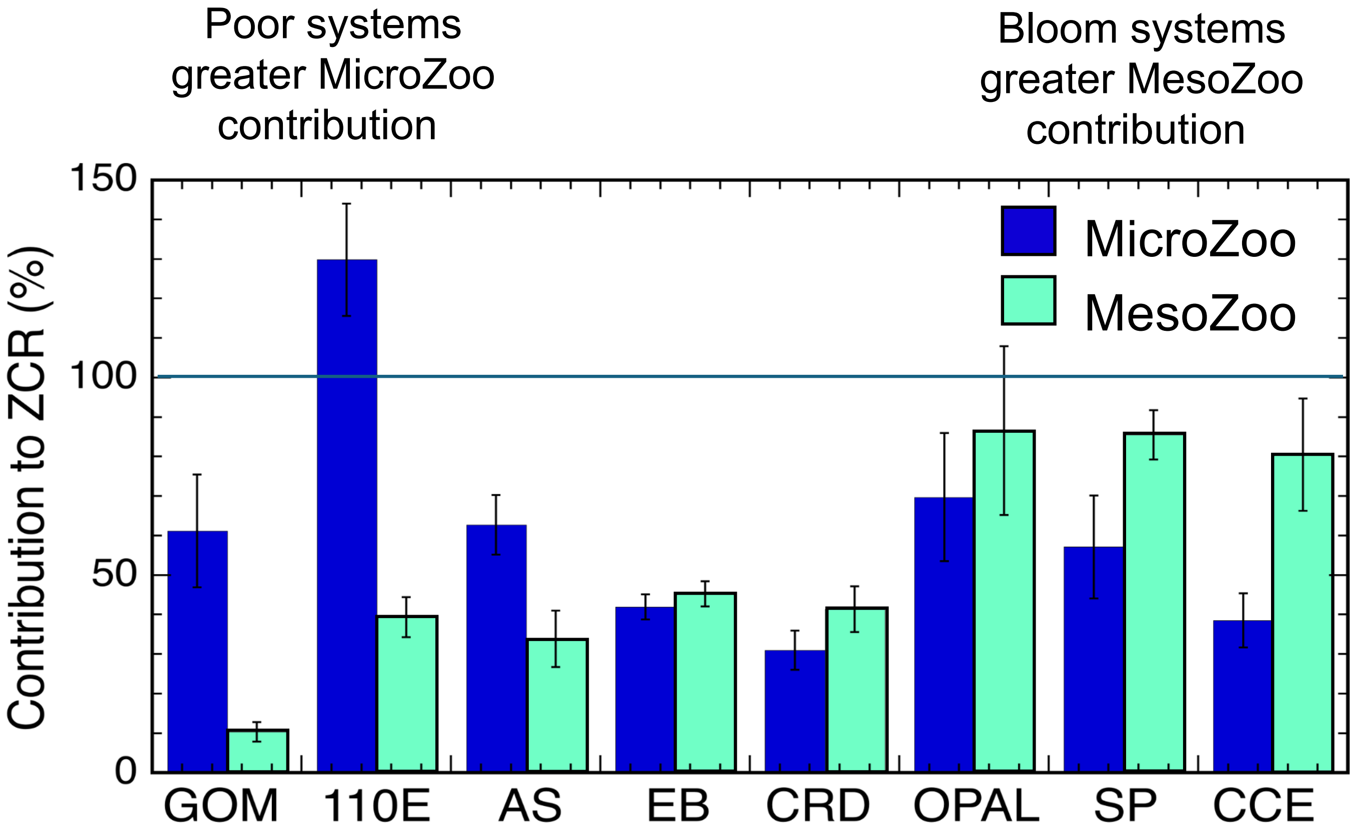




In a balanced system, carnivory cannot exceed MesoZoo production = 23.6% of ZCR, according to our growth rate calculations.

This reduces what needs to be provided by direct MesoZoo grazing and MicroZoo trophic transfer, and mainly satisfies ZCR of larger animals.

Conventional interpretation explains trophic support of MesoZoo



Five meet or exceed 100% ZCR with only Micro and MesoZoo

Others meet ZCR with carnivory

Summary Points

Liberal assumptions

- Healthy, actively growing zooplankton
- Metabolism = 1.5 X Ikeda (1985), with organic excretion
- Satisfy upper 150-200 m biomass and migrants
- No feeding on detritus

Conventional understanding satisfies ZCR

- 59% transfer from MicroZoo
- 54% direct from MesoZoo herbivory
- 24% additionally from carnivory/omnivory

Overestimates of contributions to ZCR (>100%)

- Undersampling of some MesoZoo components – smaller, larger, deeper?
- Methodological?
- Additional trophic steps for MicroZoo transfer?
- Allometric equations give mean rates, not maximal?