國立臺灣大學海洋研究所
Institute of Oceanography
National Taiwan University

Copepod community growth rates in relation to body size, temperature, and food availability in the East China Sea:
A test of Metabolic Theory

Kuan-Yu Lin, Akash Sastri, Gwo-Ching Gong, and **Chih-hao Hsieh**

Lin et al 2013 Biogeosciences 10: 1-16.

Essential factors influencing growth rates?

- Body size (M)
- Temperature (T)

$$g \propto M^{-0.25} e^{-E/kT}$$

- Metabolic Theory of Ecology (Brown et al. 2004)
- Debated both on size-scaling (−0.25?) and temperature-coefficient (E?)

g : weight-specific growth rate (day^{-1})
M : body weight (μg)
T : temperature (K)
E : activation energy (eV)
k : Boltzmann's constant (8.62×10^{-5} eV/K)

Additional factors influencing growth rates?

- Food availability
  - Important determinant (Mullin and Brook 1970)

- Still other possibilities
  - Life history (e.g. Hirst and Bunker 2003)
    - Spawning types in copepods

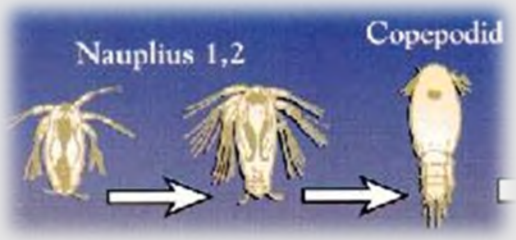

Figure origin: www.upei.ca
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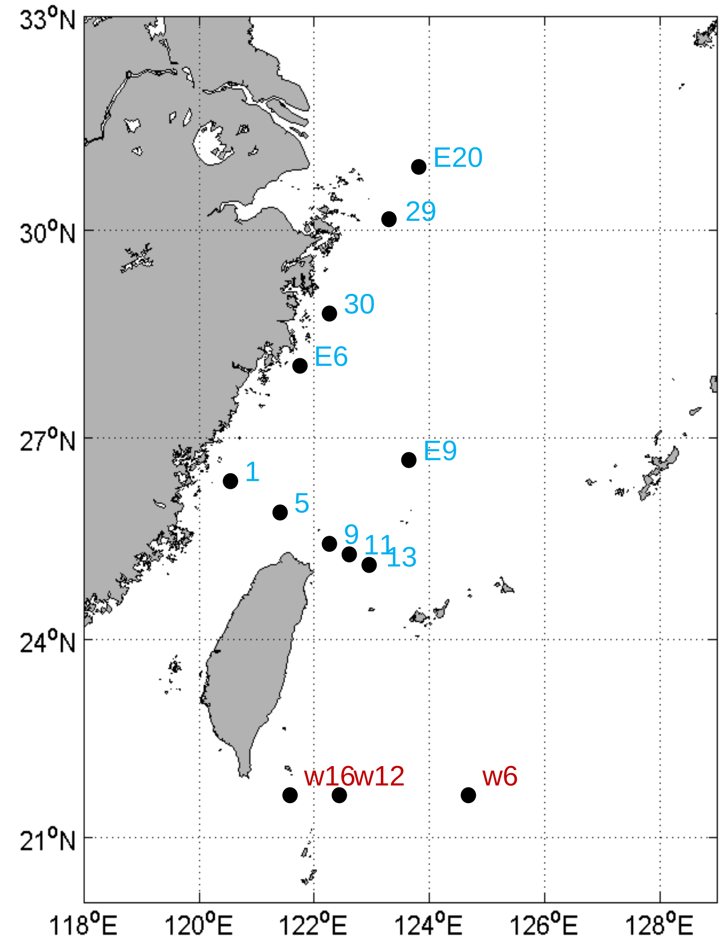
Hypothesis

- The variation of copepod community growth rate is explained by the relationship predicted by Metabolic Theory
  - $g \propto M^{-0.25} e^{-E/kT}$
  - Additional examination
    - Differences among development stages and spawning types
    - Condition of food limitation

Sampling

- Sites: the East China Sea
  - Few studies measured *in situ* copepod growth rate
  - Oceanic environment is variable spatially and temporally (e.g. Gong et al. 2003)

- Sites: Kuroshio region



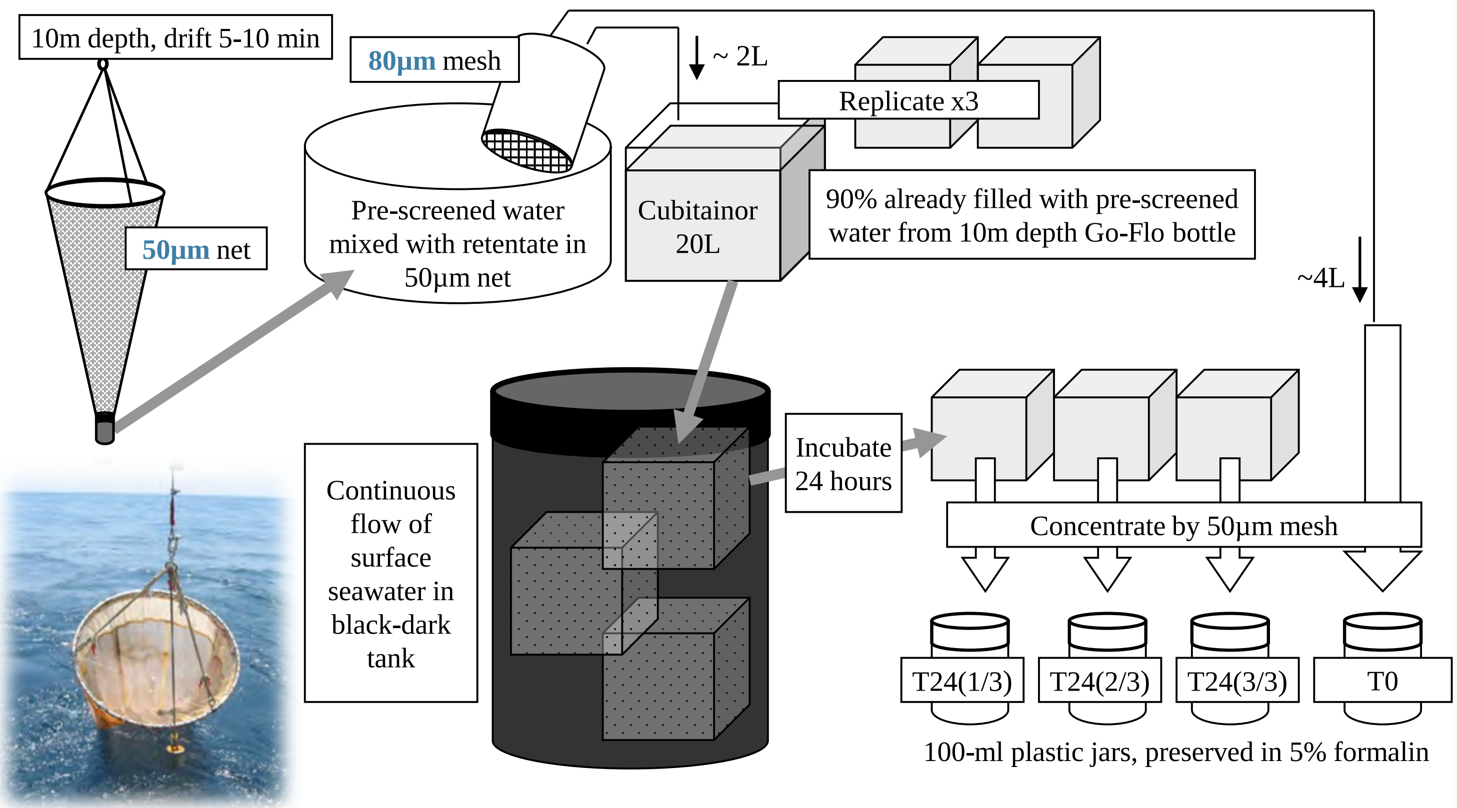
Sampling

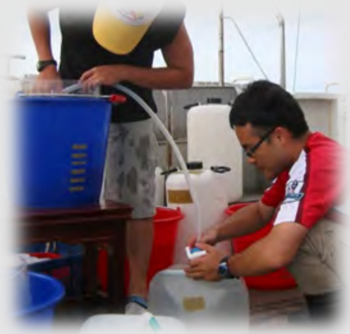
- Environmental data from CTD and Go-Flo bottle
  - Temperature
  - Salinity
  - Chlorophyll *a* concentration (a proxy of food)

- Copepods from plankton nets
  - Shipboard incubation for growth rate measurement
    - Food source: 50µm-screened seawater from Go-Flo bottles
  - Artificial Cohort method (Kimmerer and McKinnon 1987)
    - Restricted size ranges mimicking natural cohort

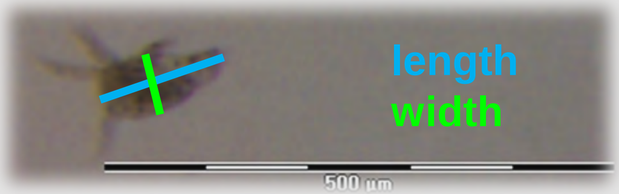
Incubation

- Artificial Cohort (50-80 μm as example)





Enumeration



$$carbon\ weight\ (M) = K \times length \times width^2$$

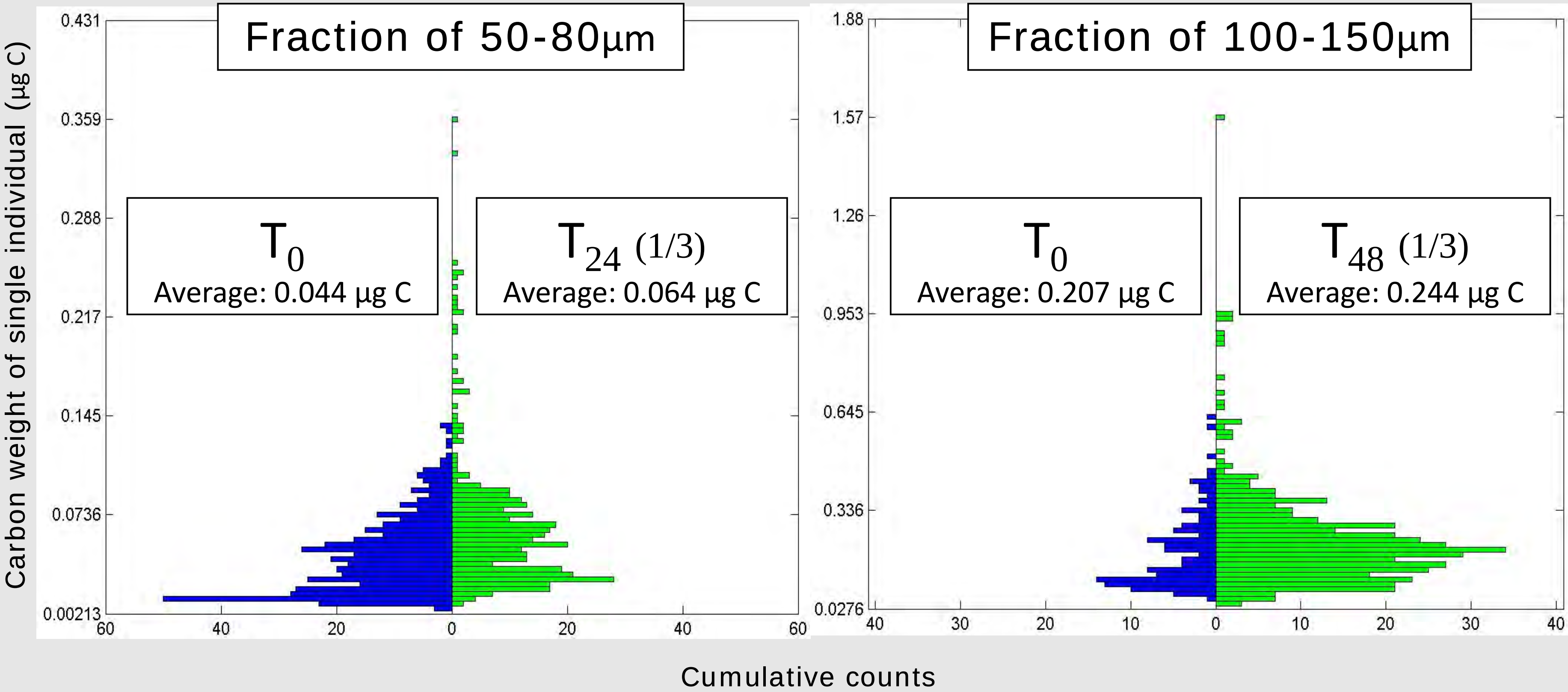
Multiple-peak consideration for representative carbon weight M_T or M_0

$$weight\text{−}specific\ growth\ rate = \ln(M_T/M_0)\ /T$$

Two size fractions:

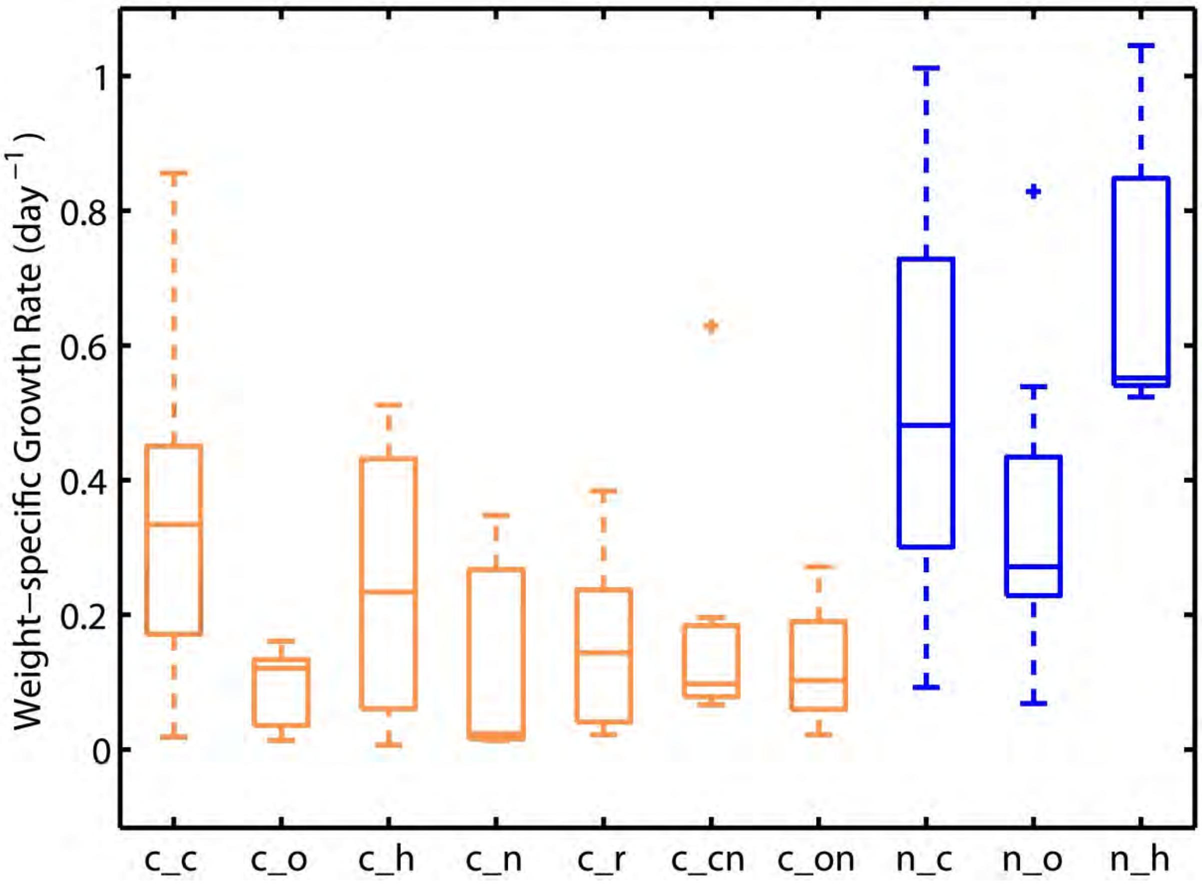
- 50-80 µm , for nauplii , T=1 day
- 100-150 µm , for copepodites , T=2 days

Example



$\ln(0.064/0.044) / 1 = 0.39\ (\text{day}^{-1})$ $\ln(0.244/0.207) / 2 = 0.08\ (\text{day}^{-1})$

Estimates of growth rate



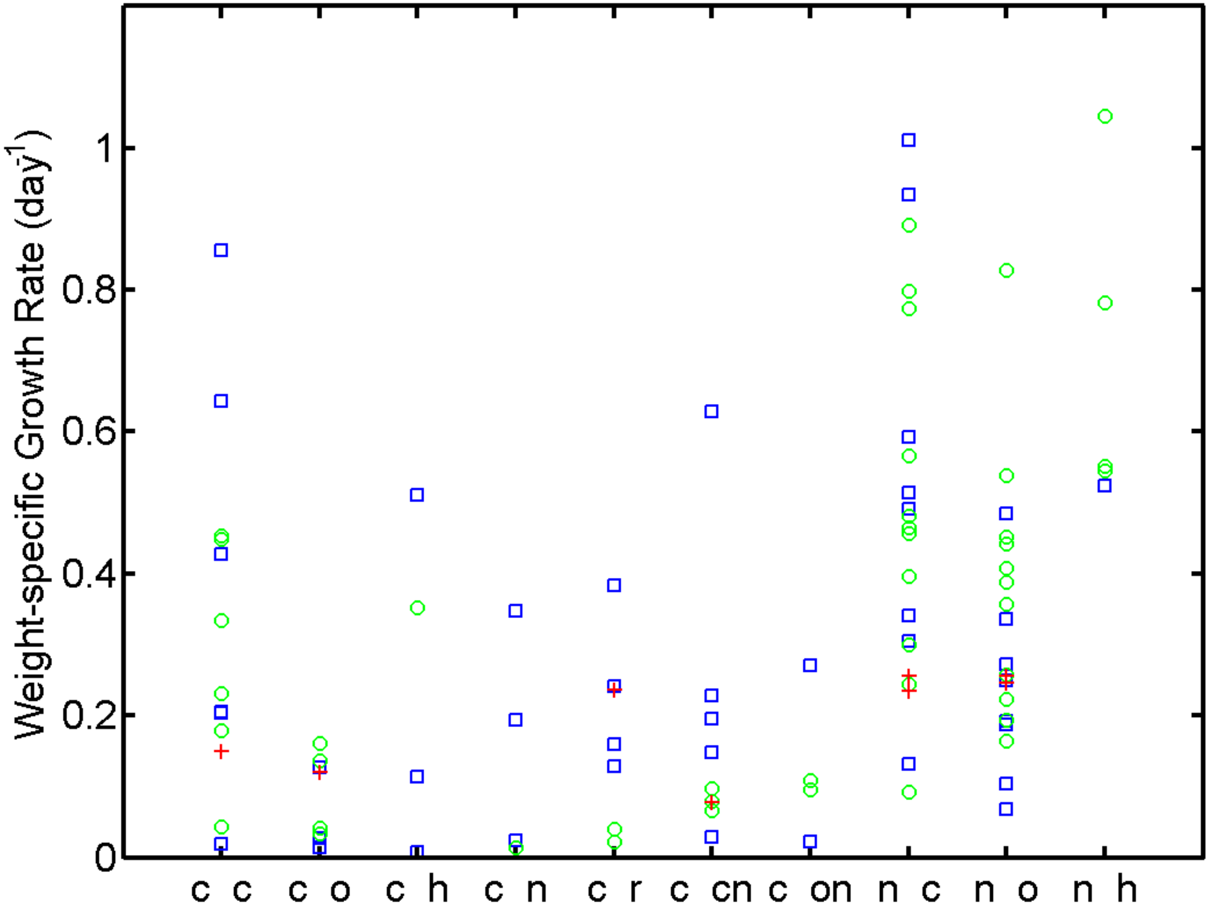
100-150 µm:

c_c	Calanoid
c_o	Oithonid
c_h	Harpacticoid
c_r	Corycaeid
c_n	Oncaeid
c_cn	Calanoid nauplii
c_on	Cyclopoid nauplii

50-80 µm:

n_c	Calanoid
n_o	Cyclopoid
n_h	Harpacticoid

Seasonal variation



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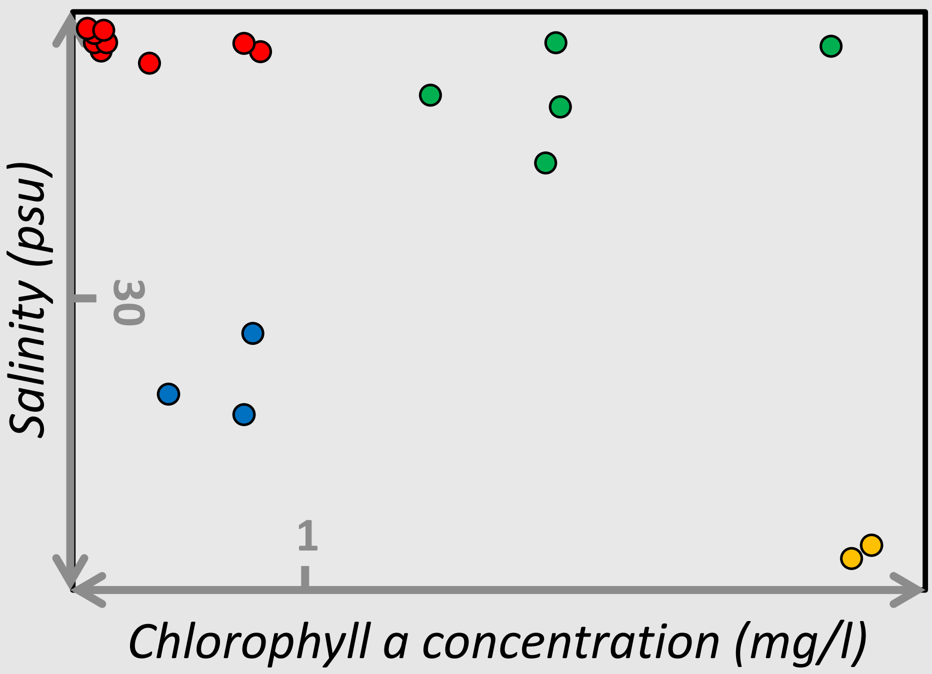
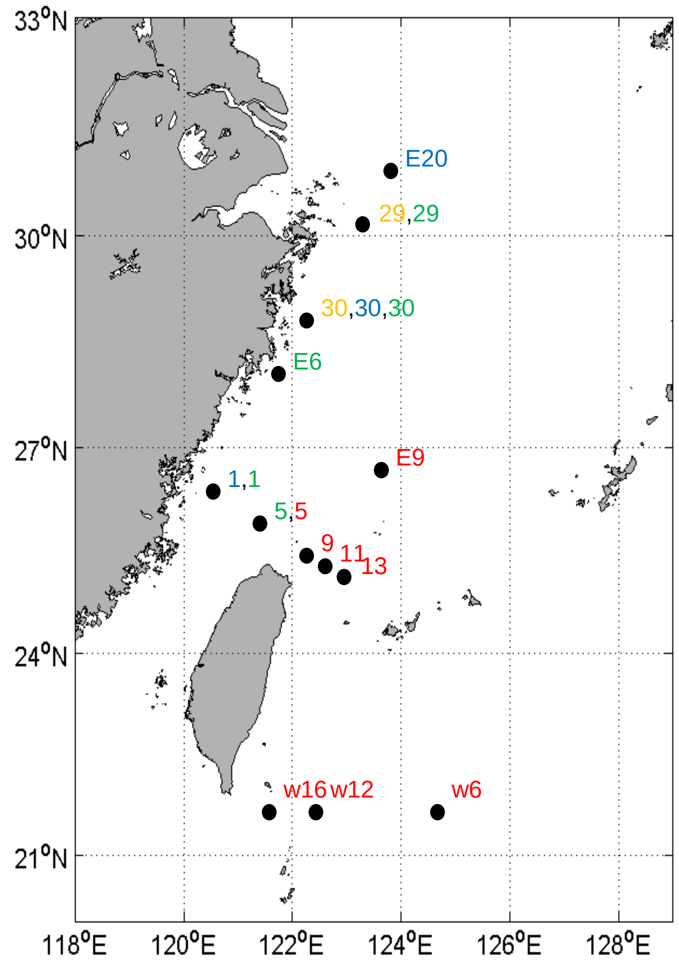
50-80 µm:

n_c	Calanoid
n_o	Cyclopoid
n_h	Harpacticoid

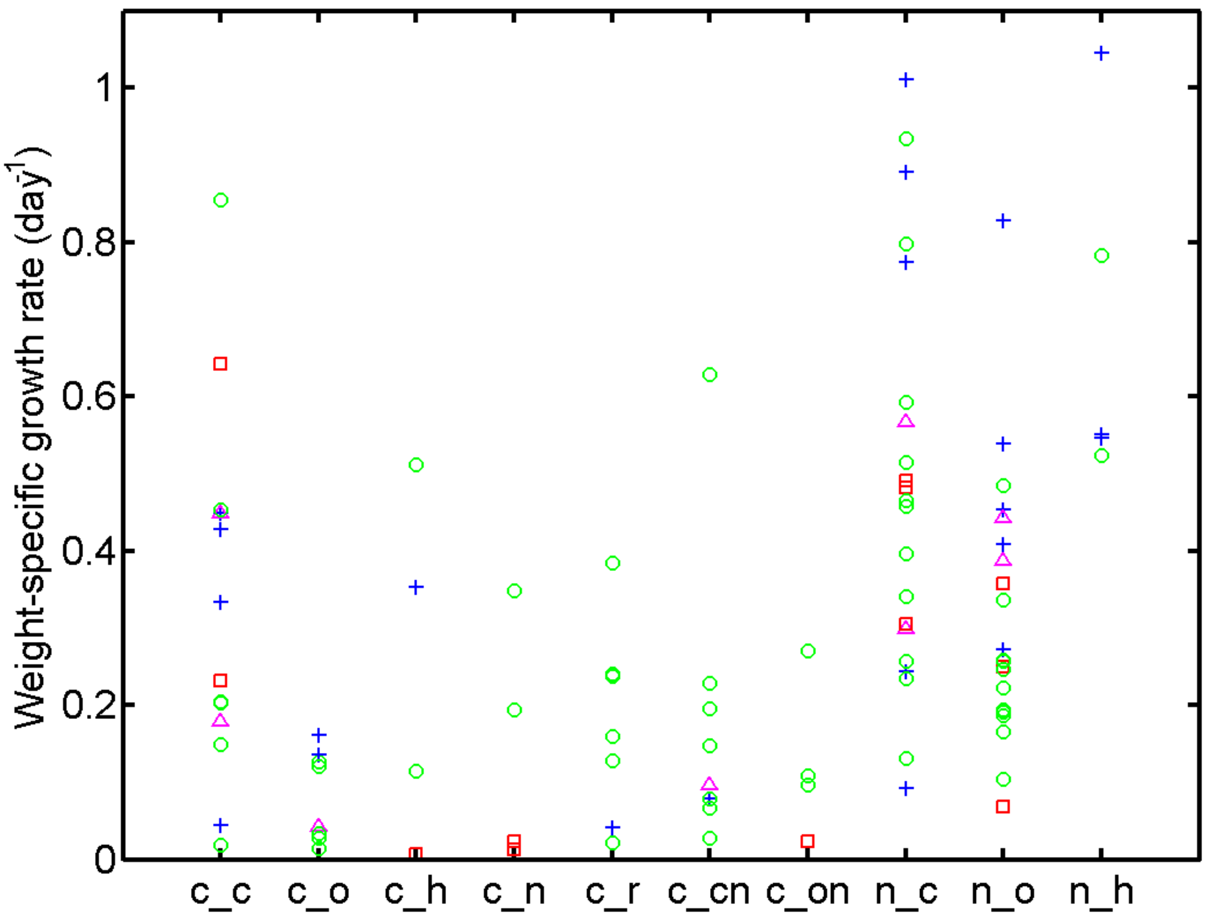
Classification of Spatial groups

K-means cluster





Spatial variation



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50-80 µm:

n_c	Calanoid
n_o	Cyclopoid
n_h	Harpacticoid

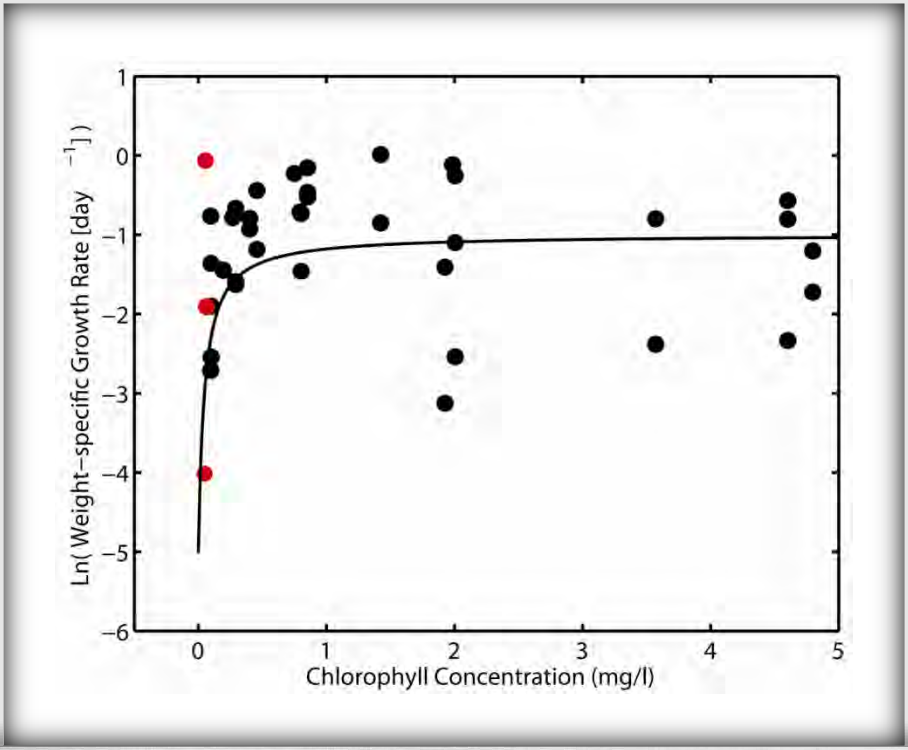
○ High S, Low Chl
+ High S, High Chl
□ Low S, Low Chl
△ Low S, High Chl

Test of Metabolic Theory

- Different groups for testing the MTE
  - All data as a whole
  - Two size fractions
    - 50-80 µm
    - 100-150 µm
  - Two spawning types
    - Broadcaster (all calanoid)
    - Sac-spawner (all cyclopoid, harpacticoid)

Test of Metabolic Theory

- Exclusion of possible "food-limited" growth
  - Fit Michaelis-Menton model $g = V_{max}[Chl]/(K_m + [Chl])$
  - Eliminate growth where $[Chl] < 2 \times K_m$



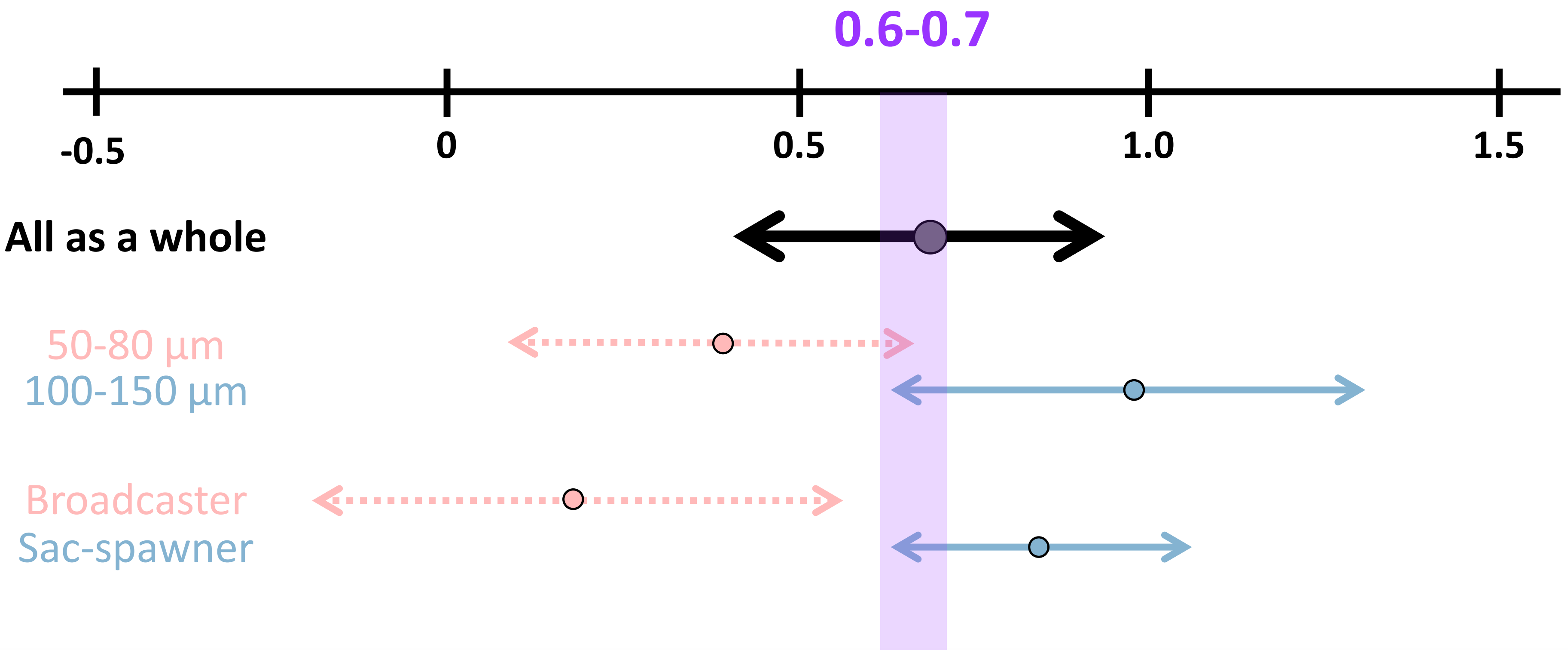
Test of Metabolic Theory

- $\ln(g) = a_0 + (-E/k)T^{-1} + a_1 \ln(M)$

	a_0	E	a_1	r^2	p
50-80 µm	9.70 (±10.24)	0.35 (±0.26)	-0.70 (±0.37)	0.13	0.08
100-150 µm	33.19 (±13.62)	0.94 (±0.35)	-0.54 (±0.52)	0.25	0.02
Broadcaster	4.00 (±13.63)	0.16 (±0.35)	-0.38 (±0.19)	0.16	0.12
Sac-spawner	27.23 (± 8.61)	0.80 (±0.22)	-0.70 (±0.15)	0.51	<0.01
All	22.11 (± 8.73)	0.66 (±0.22)	-0.66 (±0.12)	0.41	<0.01
Expectation		0.6-0.7	-0.25		

Test of Metabolic Theory – Temperature

- $\ln(g) = a_0 + (-E/k)T^{-1} + a_1 \ln(M)$



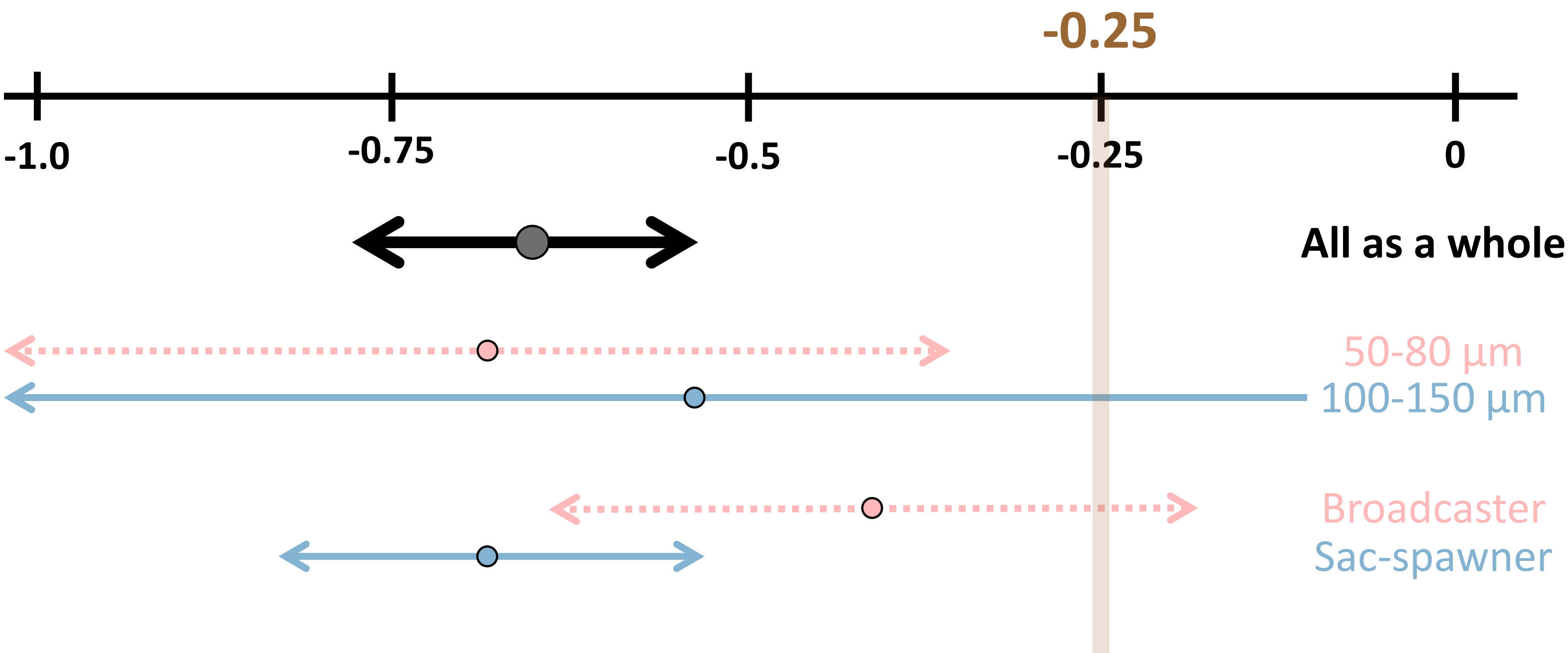
Test of Metabolic Theory – Temperature

- Reasonably consistent with MTE prediction, when considering all data.

- Smaller coefficient in smaller (50-80 µm) size fraction
  - Also found in other study (De Castro and Gaedke 2008)

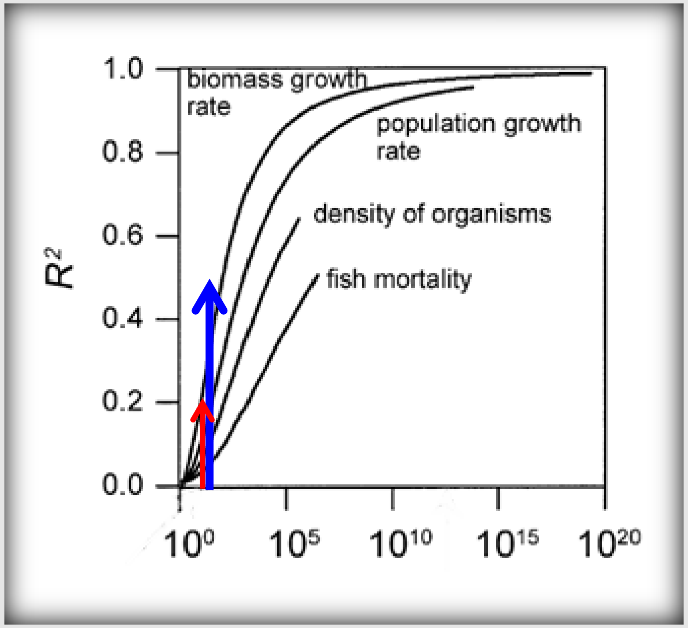
Test of Metabolic Theory – Body size

- $\ln(g) = a_0 + (-E/k)T^{-1} + a_1 \ln(M)$



Test of Metabolic Theory – Body size

- Caveat: Overall size range?



(Tilman et al, 2012)

  - Our size range: $\sim 10^{1.36}$-fold
  - But, explaining ~49% variance

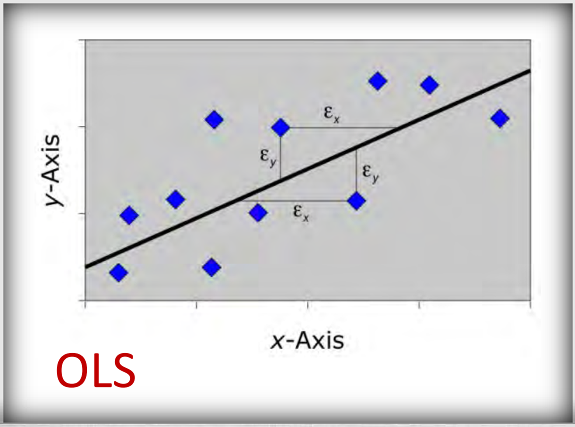
    ➔ high dependence of body size.

    ??But, why coefficient/scaling not as prediction?

Test of Metabolic Theory – Body size

- Possible reasons for deviation: Regression method
  - Ordinary least square (OLS)
  - Major axis (MA)
  - Standardized/Reduced major axis (SMA/RMA)

  - Comparative models applied to relationship between “temperature-corrected growth rate” and “body size”



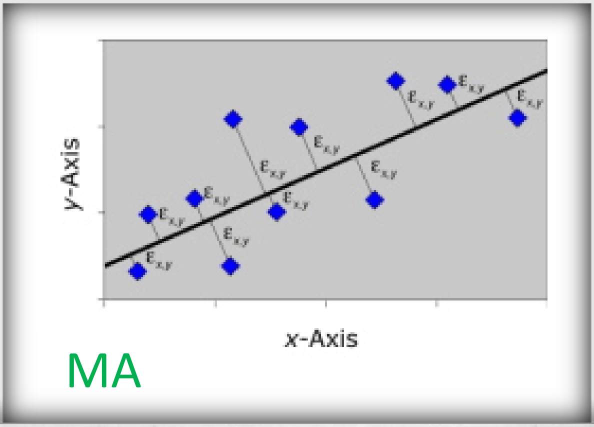
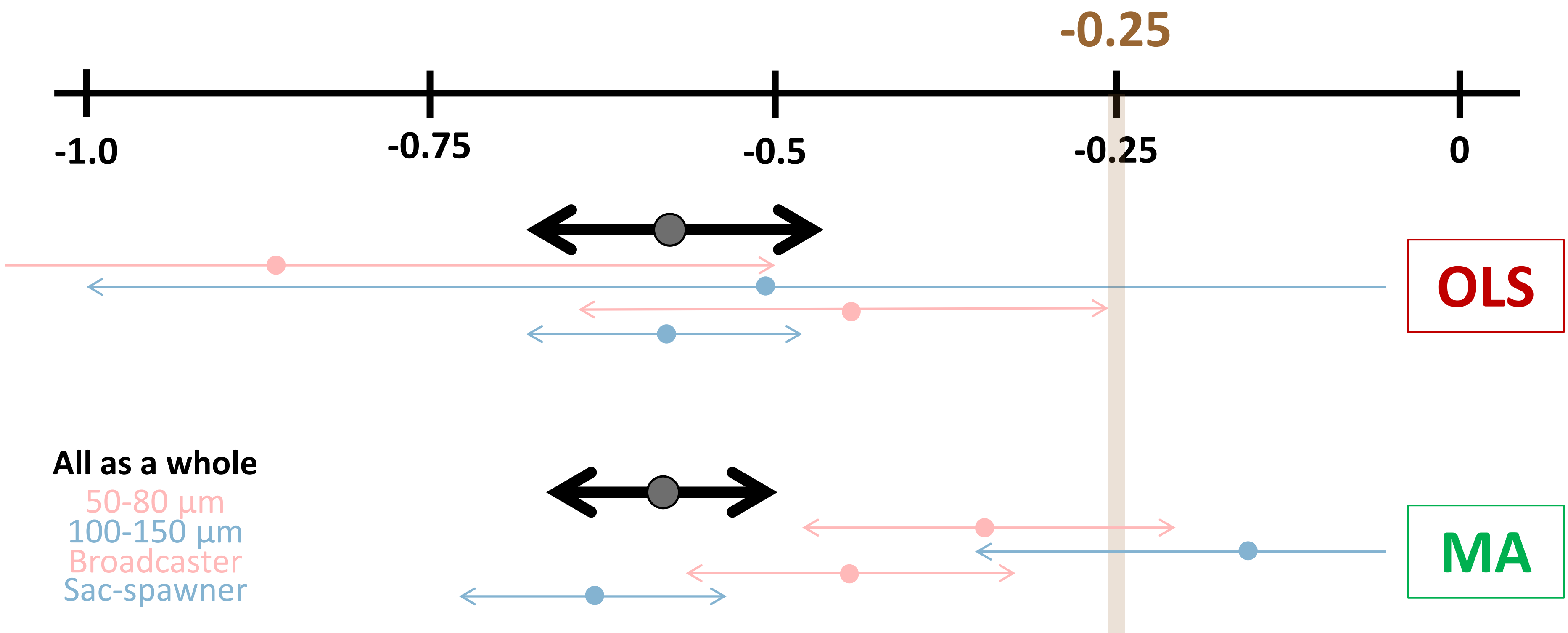


Figure origin: The Palaeontological Association

Test of Metabolic Theory – Body size

- $g' = a_0 + a_1 \ln(M)$
  - g': temperature-corrected growth rate



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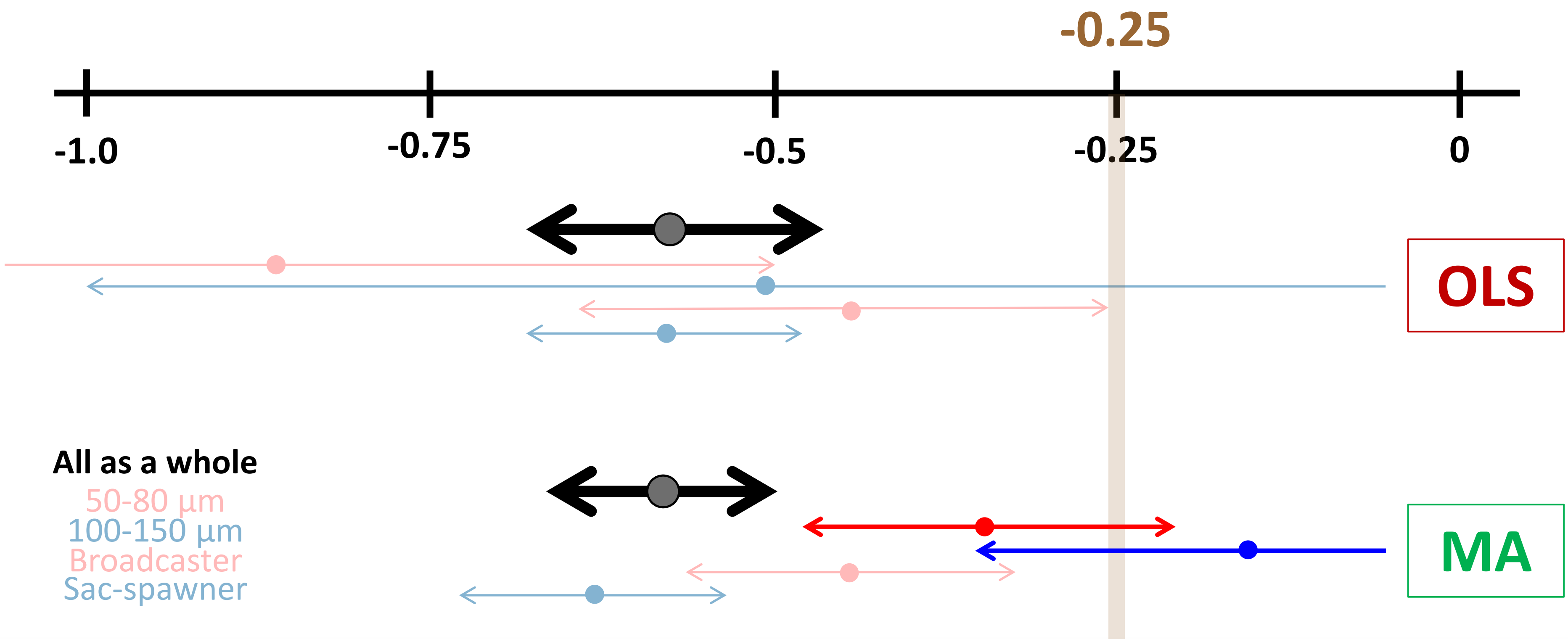


Test of Metabolic Theory – Body size

- Possible reasons for deviation: Regression method

- Possible reasons for deviation: Phylogenetic effect
  - Differences in normalized constant (a_0) and/or slope (a_1) among groups
  - Emphasized in previous studies (e.g. Ives and Zhu 2006)

- Still in lack of analytic methods incorporating both phylogenetic correction and major axis regression

Test of Metabolic Theory – Body size

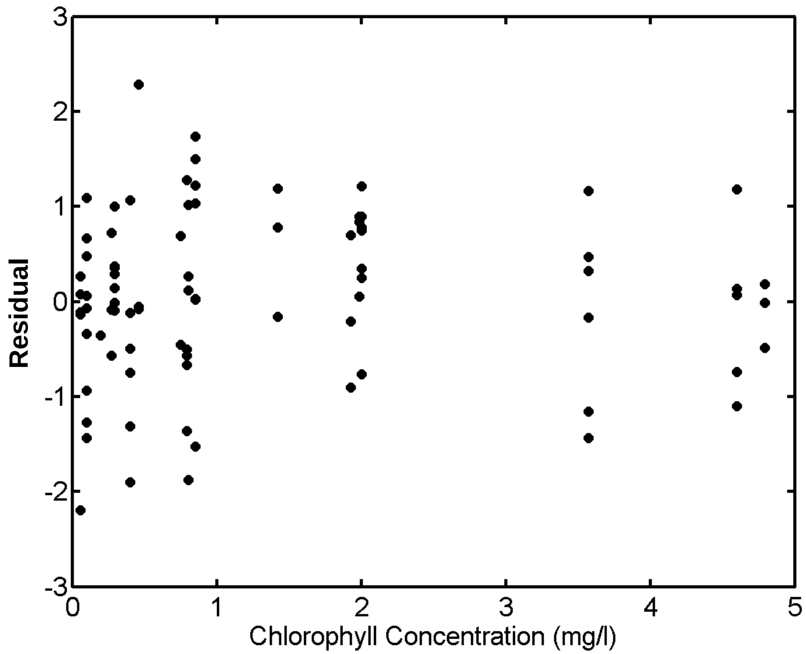
- Smaller coefficient in smaller (50-80 µm) size fraction
  - Such difference also described by others (Hopcroft et al. 1998)
  - Opposite to WBE model (West et al. 1997) prediction

- Smaller coefficient in sac-spawner group
  - Controversial observation among studies
    - Supported by Hopcroft et al. 1998
    - Opposed to Hirst and Bunker 2003
  - Opposite to cost-of-transport hypothesis (Seibel 2007)

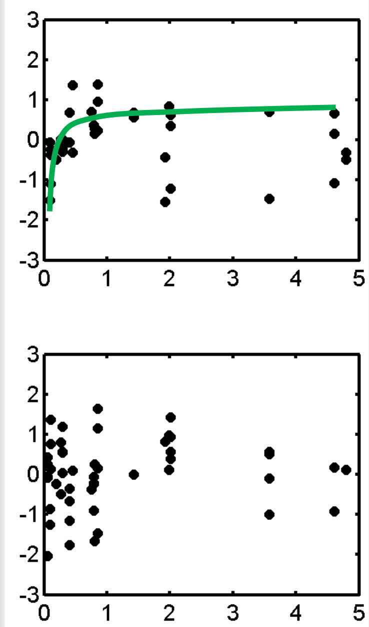
Test addition effects of food availability

- Y: residuals of $\ln(g) = a_0 + (-E/k)T^{-1} + a_1 \ln(M)$
- X: chlorophyll *a* concentration

All data included

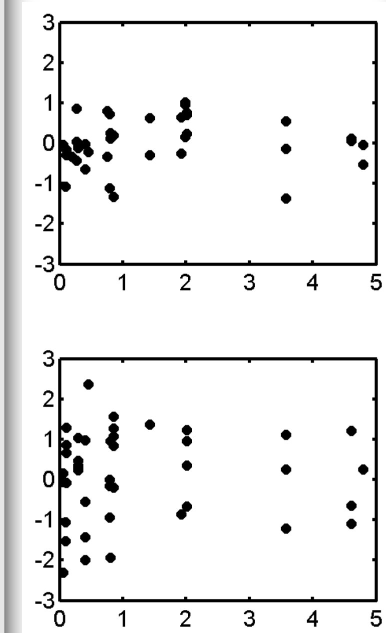


Broadcaster



Sac-spawner

50-80 µm



100-150 µm

Test of Metabolic Theory – Food availability

- Alternative models
  - Model1 : $G = a_0 \times M^{a_1}$
  - Model2 : $G = a_0 \times M^{a_1} \times [Chl]$
  - Model3 : $G = a_0 \times M^{a_1} \times \frac{[Chl]}{a_2 + [Chl]}$
  - Model4 : $G = a_0 \times M^{a_1} \times \frac{e^{[Chl]}}{a_2 + e^{[Chl]}}$

G : temperature-corrected weight-specific growth rate (day^{-1})
$[Chl]$: chlorophyll *a* concentration (mg/l)

Figure origin: Wikipedia

Test of Metabolic Theory – Food availability

- Alternative models
  - Model1 : $G = a_0 \times M^{a_1}$

    AIC= -135.7
  - Model2 : $G = a_0 \times M^{a_1} \times [Chl]$

    AIC= 1054.4
  - Model3 : $G = a_0 \times M^{a_1} \times \frac{[Chl]}{a_2 + [Chl]}$

    AIC= **-160.6**
  - Model4 : $G = a_0 \times M^{a_1} \times \frac{e^{[Chl]}}{a_2 + e^{[Chl]}}$

    AIC= -152.9

Test of Metabolic Theory – Food availability

- Alternative models
  - Model1 : $G = a_0 \times M^{a_1}$

    AIC= -135.7
  - Model2 : $G = a_0 \times M^{a_1} \times [Chl]$

    AIC= 1054.4
  - Model3 : $G = a_0 \times M^{a_1} \times \frac{[Chl]}{a_2 + [Chl]}$

    Best Model

    AIC= **-160.6**
  - Model4 : $G = a_0 \times M^{a_1} \times \frac{e^{[Chl]}}{a_2 + e^{[Chl]}}$

    AIC= -152.9

Test of Metabolic Theory – Food availability

- Other mechanisms not discussed here
  - Food preference
  - Non-phytoplankton food
  - Algal toxin (e.g. Paffenhöfer 2002)
  - Elemental composition, e.g. N:C ratio (Touratier et al. 1999)

Taxa of copepods	Food sources	References
Adults of small species, arctic *Calanus* spp., nauplii	Heterogeneous protozoan (over phytoplankton)	Turner 2004 and references therein
Oithonidae	Nauplii, protozooplankton	Turner 2004
Oithona davisae	Flagellate (over diatoms)	Uye (1994)
Oithona similis	Pellet of zooplankton	Gonzalez and Smetacek 1994
Limnoithona tetraspina	Moving prey	Gould and Kimmerer 2010
Corycaeus spp.	Nauplii	Turner et al. (1984), Landry et al. 1985
Oncaeidae	Flagellate	Turner 2004
Oncaea mediterrenea	Marine snow	Alldredge 1972, Ohtsuka and Kubo 1991
Pseudocalanus acuspes	Ciliate, flagellate, heterogenous particles, sinking particles	Peters et al. 2006, Renz and Hirche 2006
Calanus pacificus	Bacteria (~30% assimilation efficiency)	Lawrence et al. 1993
Various taxa	Bacteria, ciliates, dinoflagellates, coccolithophores, cannibalism	Mauchline 1998 and references therein

Summary

$$g \propto M^{-0.25} e^{-E/kT}$$

Summary

$$g \propto M^{-\boxed{?}} e^{-E/kT}$$

Summary

$$g \propto M^{-?} e^{-E/kT} \times \frac{[Chl]}{a + [Chl]}$$

Comparison with other empirical model predictions