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

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Essential factors influencing growth rates?

- **Body size** \((M)\)
- **Temperature** \((T)\)

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

- Debated both on size-scaling \((-0.25?)\) and temperature-coefficient \((E?)\)

\(g\) : weight-specific growth rate \((\text{day}^{-1})\)

\(M\) : body weight \((\mu g)\)

\(T\) : temperature \((K)\)

\(E\) : activation energy \((\text{eV})\)

\(k\) : Boltzmann’s constant \((8.62 \times 10^{-5} \text{ eV/K})\)
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
Figure origin: www.icm.csic.es
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)

- Pre-screened water mixed with retentate in 50µm net
- Cubitainer 20L
- 90% already filled with pre-screened water from 10m depth Go-Flo bottle
- Continuous flow of surface seawater in black-dark tank
- Incubate 24 hours
- Concentrate by 50µm mesh
- T24(1/3), T24(2/3), T24(3/3), T0

100-ml plastic jars, preserved in 5% formalin
Enumeration

\[ \text{carbon weight (}M\text{)} = K \times \text{length} \times \text{width}^2 \]

Multiple-peak consideration for representative carbon weight \(M_T\) or \(M_0\)

\[ \text{weight–specific growth rate} = \frac{\ln(M_T/M_0)}{T} \]

Two size fractions:
- 50-80 µm, for nauplii, \(T=1\) day
- 100-150 µm, for copepodites, \(T=2\) days
Example

<table>
<thead>
<tr>
<th>Fraction of 50-80µm</th>
<th>Fraction of 100-150µm</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_0$</td>
<td>$T_0$</td>
</tr>
<tr>
<td>Average: 0.044 µg C</td>
<td>Average: 0.064 µg C</td>
</tr>
<tr>
<td>$T_{24}$ (1/3)</td>
<td>$T_{48}$ (1/3)</td>
</tr>
<tr>
<td>Average: 0.207 µg C</td>
<td>Average: 0.244 µg C</td>
</tr>
</tbody>
</table>

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

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

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 nauplii
- n_o Cyclopoid nauplii
- n_h Harpacticoid

□ Spring
○ Summer
+ Winter
Classification of Spatial groups

K-means cluster

Salinity (psu) vs Chlorophyll a concentration (mg/l)
Spatial variation

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

- □ Low S, Low 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-Menten model \( g = \frac{V_{max}[Chl]}{(K_m + [Chl])} \)
  - Eliminate growth where \([Chl] < 2 \times K_m\)
Test of Metabolic Theory

\[ \ln(g) = a_0 + \left(-\frac{E}{k}\right)T^{-1} + a_1 \ln(M) \]

<table>
<thead>
<tr>
<th></th>
<th>(a_0)</th>
<th>(E)</th>
<th>(a_1)</th>
<th>(r^2)</th>
<th>(p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>50-80 µm</td>
<td>9.70 (±10.24)</td>
<td>0.35 (±0.26)</td>
<td>-0.70 (±0.37)</td>
<td>0.13</td>
<td>0.08</td>
</tr>
<tr>
<td>100-150 µm</td>
<td>33.19 (±13.62)</td>
<td>0.94 (±0.35)</td>
<td>-0.54 (±0.52)</td>
<td>0.25</td>
<td>0.02</td>
</tr>
<tr>
<td>Broadcaster</td>
<td>4.00 (±13.63)</td>
<td>0.16 (±0.35)</td>
<td>-0.38 (±0.19)</td>
<td>0.16</td>
<td>0.12</td>
</tr>
<tr>
<td>Sac-spawner</td>
<td>27.23 (±8.61)</td>
<td>0.80 (±0.22)</td>
<td>-0.70 (±0.15)</td>
<td>0.51</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>All</td>
<td>22.11 (±8.73)</td>
<td>0.66 (±0.22)</td>
<td>-0.66 (±0.12)</td>
<td>0.41</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Expectation</td>
<td>0.6-0.7</td>
<td>-0.25</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Test of Metabolic Theory – Temperature

\[ \ln(g) = a_0 + (-\frac{E}{k})T^{-1} + a_1 \ln(M) \]
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**

\[ \ln(g) = a_0 + \left( -\frac{E}{k} \right) T^{-1} + a_1 \ln(M) \]
Caveat: Overall size range?

- Our size range: $\sim 10^{1.36}$-fold
- But, explaining $\sim 49\%$ variance ➔ high dependence of body size.
  ??But, why coefficient/scaling not as prediction?

(Tilman et al, 2012)
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

All as a whole
50-80 µm
100-150 µm
Broadcaster
Sac-spawner

OLS

MA
Test of Metabolic Theory – Body size

\[ g' = a_0 + a_1 \ln(M) \]

\( g' \): temperature-corrected growth rate
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
Test of Metabolic Theory – Food availability

Alternative models

- **Model 1**: \( G = a_0 \times M^{a_1} \)

- **Model 2**: \( G = a_0 \times M^{a_1} \times [Chl] \)

- **Model 3**: \( G = a_0 \times M^{a_1} \times \frac{[Chl]}{a_2 + [Chl]} \)

- **Model 4**: \( G = a_0 \times M^{a_1} \times \frac{e^{[Chl]}}{a_2 + e^{[Chl]}} \)

\( G \) : temperature-corrected weight-specific growth rate (day\(^{-1}\))

\([Chl]\) : chlorophyll \( a \) concentration (mg/l)
Test of Metabolic Theory – Food availability

Alternative models

Model 1: \( G = a_0 \times M^{a_1} \)  
AIC = -135.7

Model 2: \( G = a_0 \times M^{a_1} \times [Chl] \)  
AIC = 1054.4

Model 3: \( G = a_0 \times M^{a_1} \times \frac{[Chl]}{a_2 + [Chl]} \)  
AIC = -160.6

Model 4: \( G = a_0 \times M^{a_1} \times \frac{e^{[Chl]}}{a_2 + e^{[Chl]}} \)  
AIC = -152.9
Test of Metabolic Theory – Food availability

Alternative models

- Model 1: \( G = a_0 \times M^{a_1} \)
- Model 2: \( G = a_0 \times M^{a_1} \times [Chl] \)
- Model 3 (Best Model): \( G = a_0 \times M^{a_1} \times \frac{[Chl]}{a_2+[Chl]} \)
- Model 4: \( G = a_0 \times M^{a_1} \times \frac{e^[Chl]}{a_2+e^[Chl]} \)

AIC values:
- Model 1: -135.7
- Model 2: 1054.4
- Model 3: -160.6
- Model 4: -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)

<table>
<thead>
<tr>
<th>Taxa of copepods</th>
<th>Food sources</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults of small species, arctic</td>
<td>Heterogeneous protozoan (over phytoplankton)</td>
<td>Turner 2004 and references therein</td>
</tr>
<tr>
<td><em>Calanus</em> spp., nauplii</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oithonidae</td>
<td>Nauplii, protozooplankton</td>
<td>Turner 2004</td>
</tr>
<tr>
<td><em>Oithona davisae</em></td>
<td>Flagellate (over diatoms)</td>
<td>Uye (1994)</td>
</tr>
<tr>
<td><em>Oithona similis</em></td>
<td>Pellet of zooplankton</td>
<td>Gonzalez and Smetacek 1994</td>
</tr>
<tr>
<td><em>Limnoithona tetraspina</em></td>
<td>Moving prey</td>
<td>Gould and Kimmerer 2010</td>
</tr>
<tr>
<td>Corycaeus spp.</td>
<td>Nauplii</td>
<td>Turner et al. (1984), Landry et al. 1985</td>
</tr>
<tr>
<td>Oncaeidae</td>
<td>Flagellate</td>
<td>Turner 2004</td>
</tr>
<tr>
<td><em>Pseudocalanus acuspes</em></td>
<td>Ciliate, flagellate, heterogenous particles, sinking particles</td>
<td>Peters et al. 2006, Renz and Hirche 2006</td>
</tr>
<tr>
<td><em>Calanus pacificus</em></td>
<td>Bacteria (~30% assimilation efficiency)</td>
<td>Lawrence et al. 1993</td>
</tr>
<tr>
<td>Various taxa</td>
<td>Bacteria, ciliates, dinoflagellates, coccolithophores, cannibalism</td>
<td>Mauchline 1998 and references therein</td>
</tr>
</tbody>
</table>
Summary

\[ g \propto M^{-0.25} e^{-E/kT} \]
Summary

\[ g \propto M^{-?} e^{-E/kT} \]
Summary

$$g \propto M^{-?} e^{-E/kT} \times \frac{[Chl]}{\alpha + [Chl]}$$
Comparison with other empirical model predictions

Method 1  artificial cohort method in this study
Method 2  model by Huntley and Lopez (1992)
Method 3  model by Hirst and Sheader (1997)
Method 4  model by Hirst and Lampitt (1998)
Method 5  model by Hirst and Bunker (2003)