Feeding Rate Measurements

OCN 621

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Methods used to Estimate Grazing Impacts

• Inferences from Natural Populations
  – no incubations
  – use natural properties to infer feeding rates

• Tracer Techniques
  – short incubations
  – uptake of labeled prey
  – relatively minor disruption of natural community

• Community Manipulations
  – long incubations (to measure significant changes in population abundances)
  – substantial disruption of natural community
Inferences from Natural Populations

• Digestive Enzyme Assay
  – activity of acid lysozyme in grazer cell lysates
  – bacterivores only (peptidoglycan-bearing cells)
  – problem: substrate specificity
  – only really useful in eutrophic environments (e.g., coastal)
  – analogous method in metazoans stymied by their ability to store digestive enzymes in their guts, so the activity doesn’t represent current food conditions

• Food Vacuole (protist) or Gut Content (metazoan)
  – assess average number of prey/predator
  – rate of prey digestion (vacuole turnover rate or gut clearance rate)
  – laborious method
Vacuole Contents

What is it?
Prey recognition

How long has it been there?
Digestion times

Useful, however, especially to reveal significant trophic pathways among dominant predators and prey

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Inferences, cont’d

• Pigment Budget
  – uses depth distribution of chl a and degradation products to infer grazing by microzooplankton
  – problem: degradation products not conservative tracers
    • photo-degradation accounted for and assumed constant
    • but, microbial activity or re-ingestion also cause degradation of pigments
  – contribution of metazoans vs. protists to pigment signature?
    • If metazoan grazers have faecal pellets that don’t sink fast, then their grazing impact will be included as if they were microzooplankton grazers
Tracer Techniques

• Radio-isotope labeled prey
  – Effective separation of prey and predator (not so hard with metazoans)
  – Very sensitive (easy to measure low amounts of radioactivity)
  – Isotope cycling causing interpretation problems

• Minicell Recovery (containing $^{35}$S-labeled protein)
  – Follow disappearance of protein after protist digestion in particulate fraction
  – Community-level (unless size fractionated) bacterivory

• Fluorescently-labeled prey (bacteria or algae)
  – Measure rate of increase of marker in predator
  – Since prey digested, can also use in longer disappearance expts.
  – Main drawback: selection for or against labeled prey
Fluorescently-labeled Prey

closed circles: FLB
open circles: microspheres

Sherr et al. 1987

tracer concentrations?
discrimination - rejection?
egestion - preservation
Community Manipulations

• Size Fractionation (separate predator & prey)
  – assumes observed rate of growth = prey $\mu$ (w/o predators)
  – potential problem with effective separation of predator and prey
  – organic enrichments from cell breakage?
  – loss of “nurturing” relationship

• Metabolic Inhibitors (group-specific)
  – assumes observed rate = prey $m_{\text{grazing}}$ (prokaryote inhibitors)
  – assumes observed rate = prey $\mu$ (eukaryote inhibitors)
  – problems with specificity and timing
  – loss of “nurturing” relationship, release of organics

• Dilution (reduce mortality relative to growth)
  – main advantage: $\mu$ and $m$ for phytoplankton community in single expt.
  – assumes prey $\mu =$ constant
  – assumes clearance rate constant
  – problems with differential enrichment or nutrient cycling
Size Fractionation: Grazer Removal

Location: Station ALOHA

Manipulation:
Bacterial net growth in a size-truncated food web

Implied Grazer Chain:
5 - 20 µm HF
2 - 5 µm HF
Bacteria

Calbet & Landry 1999

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Microzooplankton Grazing by Dilution

Principle: Reduce grazer-prey encounter rate

Phytoplankton:
- light, nutrients & temp affect growth rate,
- whereas death rate mainly due to grazing

Two key assumptions:
1) predators feeding a Fmax
2) dilution does not reduce prey density below threshold level inducing reduced grazing effort

Landry et al. 1995

\[ k = \frac{\mu_n}{1 + \frac{m}{\mu_n}} \]

\[ n = 1.4 \text{ d}^{-1}, \ m = 0.8 \text{ d}^{-1} \]

\[ n = 1.7 \text{ d}^{-1}, \ m = 1.3 \text{ d}^{-1} \]

no nutrient effect

nutrient effect
2-Bottle Dilution Experiments

\[ k = \frac{1}{t} \ln \left( \frac{P_t}{P_o} \right) \]
\[ k = \mu - m \]
\[ k' = \mu - D \cdot m \]
\[ m = \frac{(k' - k)}{(1 - D)} \]
\[ \mu = k + m \]

D = 0.33

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“Mini-Dilutions”

Growth & Grazing Rates (d⁻¹)
Based on HPLC TChla

EB04 (n = 10)

EB05 (n = 14)
References


Lecture Outline

1) Materials Balance Approach defined
2) Sloppy Feeding
3) Egestion: as relates to Assimilation efficiency
4) Metabolism: Allometric Equation
   1) Temperature dependency
   2) Activity level
   3) Specific Dynamic Action
   4) Excretion
5) Growth
Materials Balance Approach

SF = sloppy feeding
I = ingestion = E + A
A = assimilation = absorbed across gut wall
E = egestion = organic loss to defecation (DOM)
M = metabolism = loss as small MW organics (DIM)
G = growth
R = reproduction (metazoans)
Other Definitions

Ingestion (I) = E + A
Assimilation (A) = M + G + R
Assimilation Efficiency (AE) = 
\[ 100 \times \frac{A}{I} = 100 \times \frac{(I - E)}{I} \]
Heterotrophic Production = G + R
where R includes reserves, molts, mucus, etc.
Gross Growth Efficiency = \( \frac{G + R}{I} \)
Net Growth Efficiency = 
\[ \frac{(G + R)}{A} = \frac{(G + R)}{(I - E)} \]
Sloppy Feeding

Loss of prey biomass during feeding process


Note that sloppy feeding is a process associated with metazoans, not protists, since protists engulf their prey whole. Organisms that rip or tear their prey would contribute to sloppy feeding.
Egestion

Losses of non-digestable or partially digested material prior to assimilation

• This material becomes part of the detritus pool in the euphotic zone (DOM), or
• It is lost from euphotic zone as fecal transport (fecal pellets)
Crustacean Fecal Pellets

- food leaving gut is wrapped in “peritrophic membrane”

*Figure 7.10. Fecal pellets of some zooplankton species. (1) Calanus plumchrus (length of a pellet, about 0.9 mm); (2) Euphausia pacifica (about 3 mm); (3) Paraithemisto japonica (about 1.5 mm); (4) Sagitta elegans (about 1.5 mm).*
Fecal Pellets

Not all fecal pellets are created equal...

D. Steinberg, VIMS

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“Marine snow”

• amorphous marine aggregates, 0.5 mm or larger in diameter
• derived from discarded “body” material (apps, pteropod webs, fecal pellets, senescent diatoms)
• combines with other phytoplankton, fecal material, micro-organisms, inorganic particles
• forms larger particles
  – food source (copepods, fish, jellies)
  – carbon flux source (higher density)
Protist Egestion: Contribution to DOM

Protist Grazer: in all experiments, more DOC produced in presence of grazing.
16-37% of algal carbon released as DOC (30% carbohydrates)

Copepod Grazer: in 2/4 experiments, more DOC produced in presence of grazing

Strom et al. 1997
Assimilation Efficiency: \( (I - E)/I \)

- AE generally assumed to be constant at \( \sim 70\% \) of carbon for herbivorous copepods, but may be higher \( (>80\%) \) for carnivores and for nitrogen, i.e., the nutrient limiting to protein synthesis; typically \( C:N_{\text{phytopl}} > C:N_{\text{zoopl}} \).

- Protists: AE(carbon) generally assumed to be \( \sim 80\% \), whereas AE(nitrogen) may be lower if \( C:N(\text{prey}) < C:N(\text{protist}) \).
Metabolism

Defined as: *all energy transformations, chemical reactions and pathways that make possible the properties of living organisms*

Measured as: the *Respiration Rate*, assumes all organism’s energy comes from the oxidation of organic to inorganic constituents with release of chemical energy.

Products: $CO_2$, $H_2O$, and depending upon substrate: $NH_4$, $PO_4$

Excretion of inorganic nutrients or low MW organics is tied to respiration
Respiration: Allometric Relationship

Bigger organisms have higher metabolic rates than smaller organisms

\[ M = \alpha \cdot W^\beta \]

where: \(0.7 \leq \beta \leq 0.8\)

\[ \beta = 0.75 \]

Summary of published data on protozoan respiration rate per cell for growing cultures. Upper and lower lines, respectively, represent Hemmingsen's (1960) regression lines for polikilotherm metazoa and for unicellular organisms (From Fenchel & Finlay, 1983).
Specific Metabolic Rate: Organism Size

\[ M/W = \alpha \times W^{\beta-1} \]
where \(-0.3 \leq \beta-1 \leq -0.2\)

Table 14.3: Relation of Daily Basal Heat Production to Body Weight and Surface Area

<table>
<thead>
<tr>
<th></th>
<th>Body weight, kg.</th>
<th>Metabolism per kg. of body weight per day, Cal.</th>
<th>Metabolism per m.² of body surface per day, Cal.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Horse</td>
<td>441.0</td>
<td>11.3</td>
<td>948</td>
</tr>
<tr>
<td>Pig</td>
<td>128.0</td>
<td>19.1</td>
<td>1078</td>
</tr>
<tr>
<td>Man</td>
<td>64.3</td>
<td>32.1</td>
<td>1042</td>
</tr>
<tr>
<td>Dog</td>
<td>15.2</td>
<td>51.5</td>
<td>1039</td>
</tr>
<tr>
<td>Goose</td>
<td>3.5</td>
<td>66.7</td>
<td>969</td>
</tr>
<tr>
<td>Fowl</td>
<td>2.0</td>
<td>71.0</td>
<td>943</td>
</tr>
<tr>
<td>Mouse</td>
<td>0.018</td>
<td>212.0</td>
<td>1188</td>
</tr>
</tbody>
</table>

Surface:Volume vs. Metabolism: Weight

- Smaller organisms have higher surface area:volume and higher metabolic rate:weight ratios than larger organisms
- However, metabolic rates per $m^2$ of surface area is the same across organism weights/volumes
- Because -- the metabolic rate basically represents processes across membranes
Effect of Body Size
Allometric Scaling of Growth (Potential)

- Respiration scales with size of protist
  -- small organisms can grow faster than large organisms

Figure 4.2 (Left) respiration rates (at 20°C) of various species of ciliates and flagellates (filled circles) and of amoebae (open circles) during exponential growth and as a function of cell volume. The slope of the regression lines is 0.75. (Right) the maximum attainable growth rate constant (20°C) for some protozoan species; the slope of the line is −0.25. (Data from Fenchel & Finlay, 1983.)
Temperature

- As temperature increases, metabolism increases too (~3X), at a faster rate than growth (~2X).

### Table 3. Effects of temperature on bioenergetics of Tintinnopsis vasculum and Tintinnopsis acuminata grown at phytoplankton carbon concentrations (C) that supported maximum growth rates. Respiration (R) (pg C tinninid⁻¹ h⁻¹) and excretion (E) (pg N tinninid⁻¹ h⁻¹) were calculated by linear regression of changes in O₂ and NH₄⁺ concentrations over time. C.I. represents 95% confidence intervals around regression slopes. O:N is the atomic ratio of oxygen consumption : ammonium excretion. Hourly specific ingestion (I), growth (G), respiration (R), and excretion (E) were normalized to carbon and nitrogen contents in Table 1; standard deviations shown in Figs. 3, 4, and 7. Assimilation efficiency (AE) = (G + R)100/I. Gross growth efficiency (GGE) = (G/I)100.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>T. vasculum</th>
<th>T. acuminata</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>5°C</td>
<td>10°C</td>
</tr>
<tr>
<td>C(μg liter⁻¹)</td>
<td>165</td>
<td>210</td>
</tr>
<tr>
<td>R(±C.I.)</td>
<td>114(39)</td>
<td>314(51)</td>
</tr>
<tr>
<td>E(±C.I.)</td>
<td>32(8)</td>
<td>58(12)</td>
</tr>
<tr>
<td>O:N</td>
<td>4.1</td>
<td>6.3</td>
</tr>
<tr>
<td>I(h⁻¹)</td>
<td>0.04</td>
<td>0.08</td>
</tr>
<tr>
<td>G(h⁻¹)</td>
<td>0.02</td>
<td>0.04</td>
</tr>
<tr>
<td>R(h⁻¹)</td>
<td>0.01</td>
<td>0.04</td>
</tr>
<tr>
<td>E(h⁻¹)</td>
<td>0.02</td>
<td>0.03</td>
</tr>
<tr>
<td>AE(±SD) (%)</td>
<td>95(21)</td>
<td>95(10)</td>
</tr>
<tr>
<td>GGE(±SD) (%)</td>
<td>57(23)</td>
<td>46(3)</td>
</tr>
</tbody>
</table>
Temperature Dependency

• Within the normal temperature range of a species, increasing temperature enhances all enzymatic processes.

Consequences

• Lgr. organisms have higher metabolic demand because more chemical rxs need more energy, thus more evolution of CO$_2$/O$_2$ consumption

• Smlr. organisms have higher S/V ratio, so more surface reactions available to “capture” nutrients relative to somewhat lgr organisms
  – thus better competitors for dissolved scarce nutrients
  – can also grow faster because metabolic costs lower with more of food ration available for growth
Activity Level

\[ M_{\text{total}} = M_{\text{standard}} + M_{\text{active}} + M_{\text{sda}} \]

where

\[ M_{\text{standard}} = \text{basal (resting) metabolism} \]

\[ M_{\text{active}} = \text{metabolism due to active swimming & foraging} \]

\[ M_{\text{sda}} = \text{“specific dynamic action” - metabolism associated with digestion, assimilation & growth} \]
Activity Level: Metazoans

- For many macrozooplankton, $M_{std}$, $M_{act}$ and $M_{sda}$ seem to be about equal. Hence, the metabolic rates of actively swimming and feeding animals is about 2-3X that of animals at rest.

Metabolic rate may be further reduced in “diapause” by shutting down non-essential biochemical systems.

Ctenophore ammonium excretion rate as a function of starvation time (Kremer 1982)
**Cost of Activity for Crustaceans**

**Fig. 6.** Relationship between oxygen consumption rate and swimming speed for *E. pacifica* (redrawn from Torres and Childress 1983). Measurements were made at 8°C and 1 atm pressure (101.325 kPa) in the daytime, but animals were cycled to 12°C at night while held in the laboratory prior to experiments.

**Euphausia pacifica**

<table>
<thead>
<tr>
<th>Swimming Speed (cm·s⁻¹)</th>
<th>O₂ Consumption Rate (µL O₂·mg DW⁻¹·h⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>5</td>
<td>5</td>
</tr>
</tbody>
</table>

Standard metabolism = 7.5 µL O₂ mg⁻¹ dry wt h⁻¹
Routine metabolism = 13.9 µL O₂ mg⁻¹ dry wt h⁻¹
Active metabolism = 45.4 µL O₂ mg⁻¹ dry wt h⁻¹

**Fig. 2.** *Dioithona oculata.* Respiration rate as a function of swimming speed in sealed flow-through chamber. Copepods were induced to swim at different speeds by varying current speed.

**y = 2.14x + 7.50**
**r² = 0.92**
Fish Activity

- $M_{act}$ is very important for fish. May be as much as a factor of 10-20X difference between metabolic requirements for active swimming and resting states, and 100X resting metabolism for “burst” swimming.

Salmon Respiration
Cost of movement for protists?

Example: 8 \( \mu \text{m} \) flagellate (from Sleigh 1974)

Power requirement for flagellate movement = \( 3 \times 10^{-7} \) erg/sec
(assumes conversion factor of \( 2 \times 10^8 \) erg/ml \( \text{O}_2 \) used)
Therefore, power required for swimming = \( 1.5 \times 10^{-9} \) nl \( \text{O}_2/\text{sec} \)
But, Total Metabolism for flagellate = \( 1.25 \times 10^{-6} \) nl \( \text{O}_2/\text{sec} \)
(measured using respirometry)

Conclusion: Motility requires \(~0.1\%\) of Total Metabolism.
Specific Dynamic Action: Protists

Protists have a low inherent rate of basal metabolism and low activity cost, thus their metabolic rate is highly influenced by the energetic costs associated with handling and processing food (e.g., vacuole formation, digestion, biosynthesis and growth) (aka "specific dynamic action")

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**Fig. 7.** Hourly specific NH$_4^+$ excretion rate ($E$) as a function of specific respiration rate ($R$) for *Tintinnopsis vasculum* (○) and *Tintinnopsis acuminata* (●). Error bars represent 95% C.I. Geometric mean regression: $E(h^{-1}) = 0.00 + 0.84(R, h^{-1})$, $r^2 = 0.99$. 95% C.I. around slope is 0.06.

**Fig. 8.** Hourly specific respiration (○) and excretion (▲) rates as a function of ingestion rate for *Tintinnopsis vasculum* (open symbols) and *Tintinnopsis acuminata* (solid symbols). Geometric mean regressions: $E(h^{-1}) = -0.01 + 0.53(I, h^{-1})$, $r^2 = 0.99$; $R(h^{-1}) = -0.01 + 0.63(I, h^{-1})$, $r^2 = 0.99$. Verity 1985
Metabolic and Size responses to starvation

Biovolume
2-3X decline

Respiration
10-20X decline

Figure 4.3 Cell numbers, respiration per cell, and cell volume in a batch culture of the phagotrophic flagellate *Ochromonas* during exponential growth and after onset of starvation (all food bacteria have been consumed) at around 30 hours (left). To the right, the lag time before starving cells begin to divide following feeding as a function of the length of the starvation period. $T_g$ is the generation time corresponding to the food concentration. (After Fenchel, 1982c.)
Protist Metabolism: Excretion

Grazing of flagellate on diatom

- Diatom abundance
- Flagellate abundance
- Particulate nitrogen
- \( \text{NH}_4 \) & urea

Goldman & Caron 1985

Fig. 5. Grazing of *P. imperforata* on *P. tricornutum* and nitrogen regeneration in the absence (A, C) and presence (B, D) of bacteria in the dark and at 24°C. (A, B) Grazing of *P. imperforata* (\( \bullet \)) on *P. tricornutum* (\( \circ \)). (C, D) Regeneration of \( \text{NH}_4^+ \) (\( \triangle \)) and \( \text{NH}_4^+ \) + urea (\( \Delta \)) along with changes in particulate nitrogen (\( \square \)) and total nitrogen (=particulate nitrogen + \( \text{NH}_4^+ \) + urea) (\( \ast \)).
Why “waste” that food?

*Concept*: Organisms tend to retain the nutrients that are limiting to growth and excrete the nutrients that are available in excess.

*Underlying assumption*: Organisms try to maintain a constant stoichiometry of elements, such as C, N, P, in their own cells through conserving or excreting/egesting food.
## Relative Importance of Heterotrophic Organisms with regard to Remineralization

**Who are the important nutrient cyclers?**

*An example:*

<table>
<thead>
<tr>
<th>Parameter</th>
<th>DOM BACT</th>
<th>BACT ZOOFL</th>
<th>ALGAE CILIATE</th>
<th>ALGAE COPEPOD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ingestion(C)</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Respiration (C)</td>
<td>40*</td>
<td>40</td>
<td>40</td>
<td>40</td>
</tr>
<tr>
<td>AE</td>
<td>1.0</td>
<td>0.8</td>
<td>0.8</td>
<td>0.7*</td>
</tr>
<tr>
<td>GGE</td>
<td>0.6</td>
<td>0.4</td>
<td>0.4</td>
<td>0.3*</td>
</tr>
<tr>
<td>C:N(prey)</td>
<td>6.6</td>
<td>5.0</td>
<td>6.6</td>
<td>6.6</td>
</tr>
<tr>
<td>C:N(pred)</td>
<td>5.0</td>
<td>5.5</td>
<td>5.5</td>
<td>4.0</td>
</tr>
</tbody>
</table>

*Note that for Copepod, respiration includes reproduction, AE(C) = 70%, but AE(N)=80%, and GGE set at 30% but would vary over life cycle.*
DOM Uptake by Bacteria

Bacteria C:N = 5, DOM C:N = 6.6 (from algae)

Bacteria are generally not efficient recyclers of nutrients (Nitrogen).
High GGE, C:N(bact) << C:N(DOM)
Food (DOM) quality matters

Bacteria grown on substrates, ranging in C:N from 1.5 - 10

At C:N > 6 (~algal C:N),
GGE = 40-50%,
Nitrogen regeneration: 0-20%

Bacteria are significant respirers of C, but if DOM poor in N, they have little role in N remineralization.

Goldman et al. 1987 L&O 32:1239-1252
Protists feeding on bacteria

Protist C:N = 5.6, Bacteria C:N = 5

Bacterivores expected to excrete and egest a significant portion of consumed food.
Protist C:N > Bacteria C:N
Protist feeding on Algae

Protist C:N = 5.6, Algae C:N = 6.6

Protist herbivores would be expected to excrete and egest less, because their elemental ratio is closer to that of their prey.
Copepod feeding on Algae

Copepod C:N = 4, Algae C:N = 6.6

Metazoan herbivores would be expected to excrete and egest less, because their elemental ratio is lower than that of their prey and they have significant metabolic costs associated with egg and molt production.

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Summary

Role of organisms as nutrient remineralizers increases with

1) low GGE
2) low C:N( prey) relative to C:N( pred)
3) small size = high specific rates
   - because larger organisms (metazoans) also have to fuel metabolic products into reproduction
   - also, sinking velocity of fecal material decreases with small size so more remineralized in upper water column
Growth Rates

- Exponential Growth Equation:
  - \( P_t = P_0 e^{\mu t} \) (growth) and,
  - \( P_t = P_0 e^{(\mu - m)t} \) (growth with grazing)

Where:
- \( P_0 \) = initial cell concentration/biomass
- \( P_t \) = final cell concentration/biomass
- \( t \) = incubation time
- \( \mu \) = instantaneous growth rate (d)
- \( m \) = instantaneous mortality rate (d)

- Solve equation for \( \mu \) or \( (\mu - m) \):
  \[
  \ln P_t = \ln P_0 + \mu t \quad \text{OR} \quad \ln P_t = \ln P_0 + (\mu - m)t
  \]
  \[
  \frac{\ln(P_t/P_0)}{t} = \mu \quad \frac{\ln(P_t/P_0)}{t} = \mu - m
  \]
Growth Potentials

• **Metazoan zooplankton**
  – Strongly influenced by temperature
  – Generation times week to months
  – Less able to respond to increased food availability in a short time frame
    • exception: Appendicularians ~2-3 day generation time
Example: *Calanus* growth vs. [food]

*Calanus pacificus*

Relationship between weight-specific growth rate (G, % d^{-1}) and food concentration (P) for copepods of different body weights (shown in figures A & B).

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Vidal 1980
Protist Growth Potential

- Protists *Can* grow faster than autotrophic prey: can feed 24/7 (unlike autotrophs which only grow during daylight hours) and food already in reduced form.
- Most grow by binary fission (1 cell becomes 2, 2 cells become 4, and so on...)
- Maximum Growth Potential (biomass doubling = generation time): determined by temperature, size, species characteristics
  - 2 - 3 h: small flagellates
  - 10-20 h: large ciliates
  - days-weeks: large sarcodines
Net and Gross Growth Efficiency

• Definitions:
  – GGE(Yield) = G*100/I
  – NGE = G*100/A = G*100/(M+G)
    □ does not include Egestion, so NGE>GGE

• NGE and GGE “constant” in protists
  – NOT in metazoans because their basal metabolism cost high

• Caveat: Balanced growth
  – under “unbalanced” conditions, see effect with food concentration
GGE vs. Food Concentration

- GGE constancy is approached most closely for smaller protists, but even relatively large ciliates display relatively high GGE at low food
- GGEs of 30-40% (G/I) are widely accepted as an assumption for calculation of food web flows

Ciliate (Tintinnopsis sp.): Relationship between GGE (G/I) and food (C). From Verity 1985.
GGE can be assumed to be ~30% for planktonic consumers

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Fig. 2. Plots for GGE of nano/microflagellates (Fl), ciliates (Ci), cladocerans (Cl), dinoflagellates (Di), copepods (Co), and rotifers (Ro). Dots represent the mean value, the central line of the box is the median of the distributions, and the box limits the 25% and 75% quartiles of the data. The whiskers cover the 5–95 percentiles of the data.

Fig. 3. Relationship between GGE and log(F) for the different taxa. Studies that influence regression statistics regarding the selection of log(F) or [log(F)]² into the models are especially marked, other observations are represented by black dots. Only observations that reported carbon, dry weight, or energy-specific GGE are shown (see Table 3 for data sources). S&VdB refers to Santer and Van den Bosch (1994) and H&B refers to Hamburger and Boeius (1987).