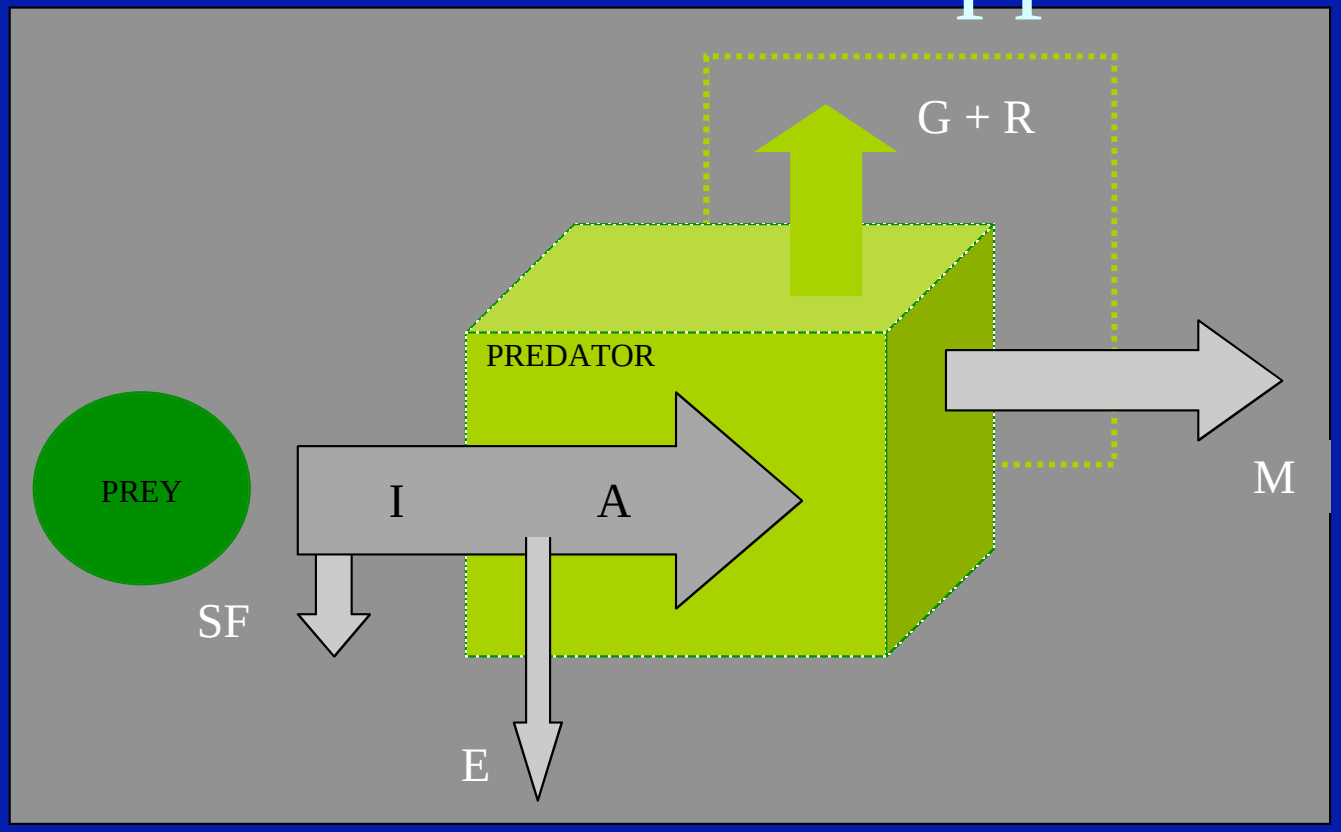
Carbon & Energy Utilization

OCN 621

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) =

$$100 * A/I = 100 * (I - E) / I$$

Heterotrophic Production = G + R

where R includes reserves, molts, mucus, etc.

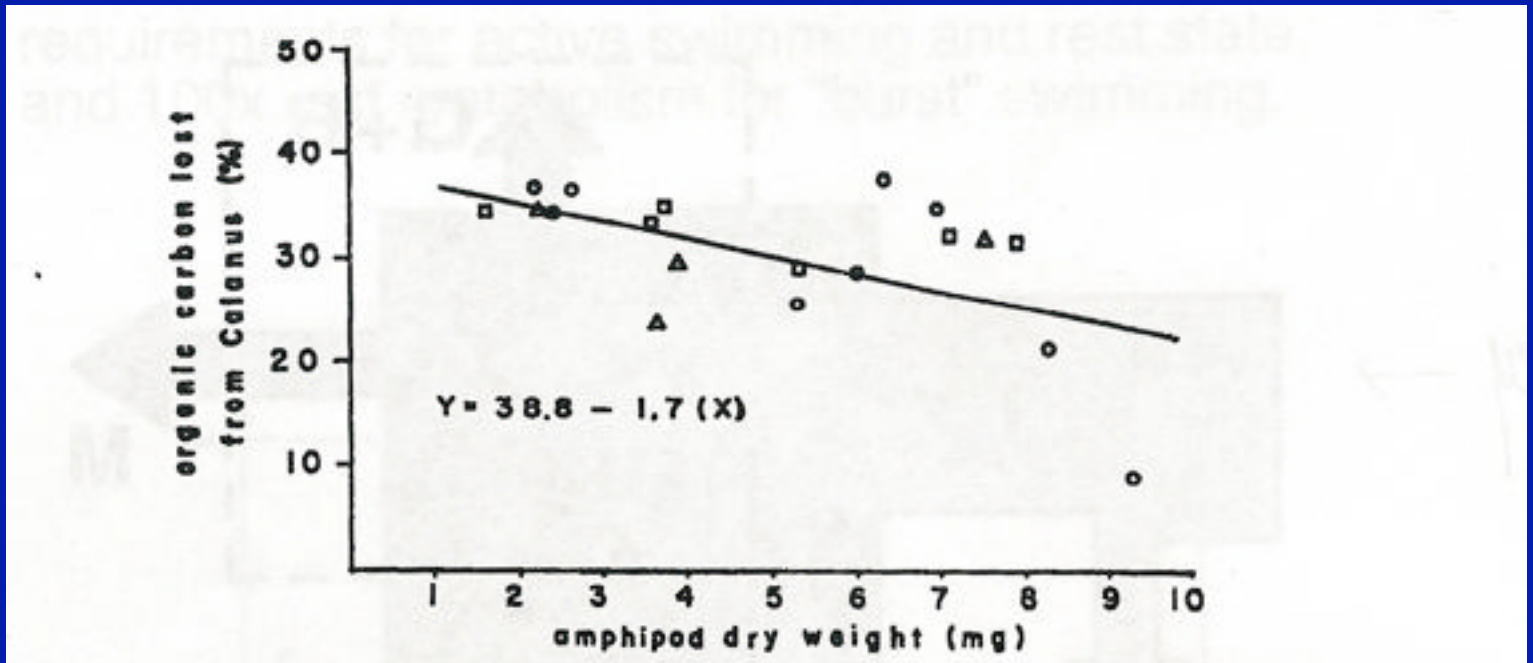
Gross Growth Efficiency = (G + R)/ I

Net Growth Efficiency =

$$(G + R) / A = (G + R) / (I - E)$$

Sloppy Feeding

Loss of prey biomass during feeding process



The relationship between the proportion of the prey's organic carbon lost while being eaten and the dry weight of the predator. Triangles, 8° C; circles, 12° C; squares, 15° C. (From Dagg. 1974. Loss of prey body contents during feeding by an aquatic predator. Ecology 55: 903-906).

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.

Sloppy Feeding, continued

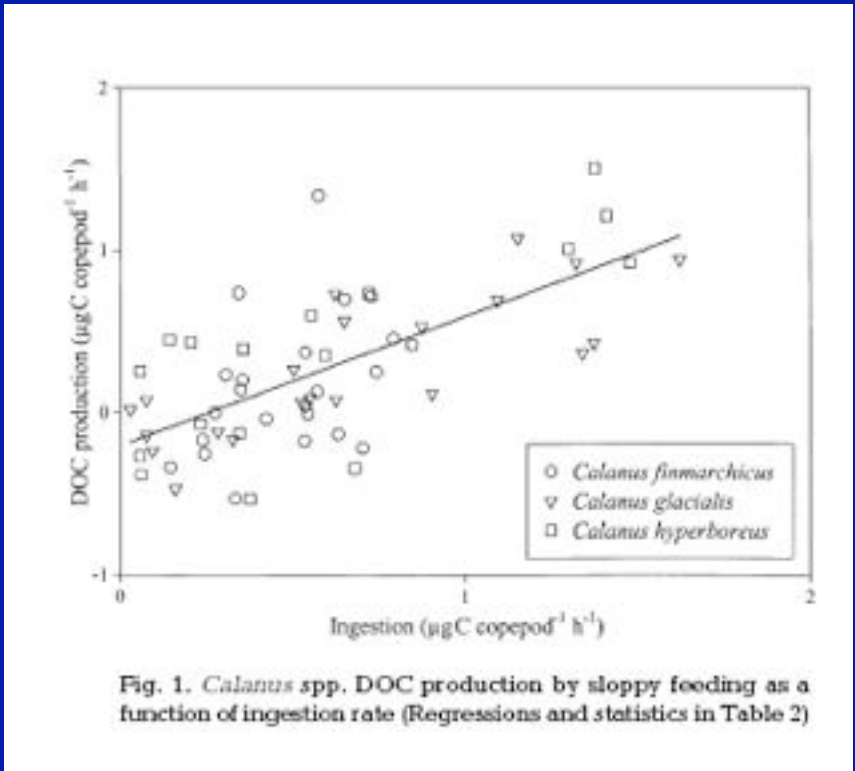


Fig. 1. *Calanus* spp. DOC production by sloppy feeding as a function of ingestion rate (Regressions and statistics in Table 2)

^{14}C-labeled algae

larger prey lead to more losses to DOC

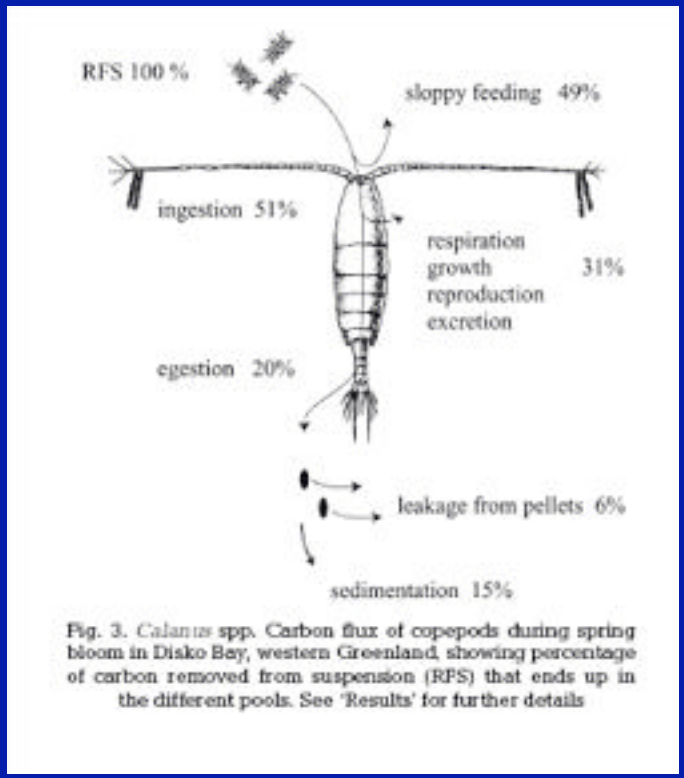


Fig. 3. *Calanus* spp. Carbon flux of copepods during spring bloom in Disko Bay, western Greenland, showing percentage of carbon removed from suspension (RFS) that ends up in the different pools. See 'Results' for further details

Møller et al. 2003

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"

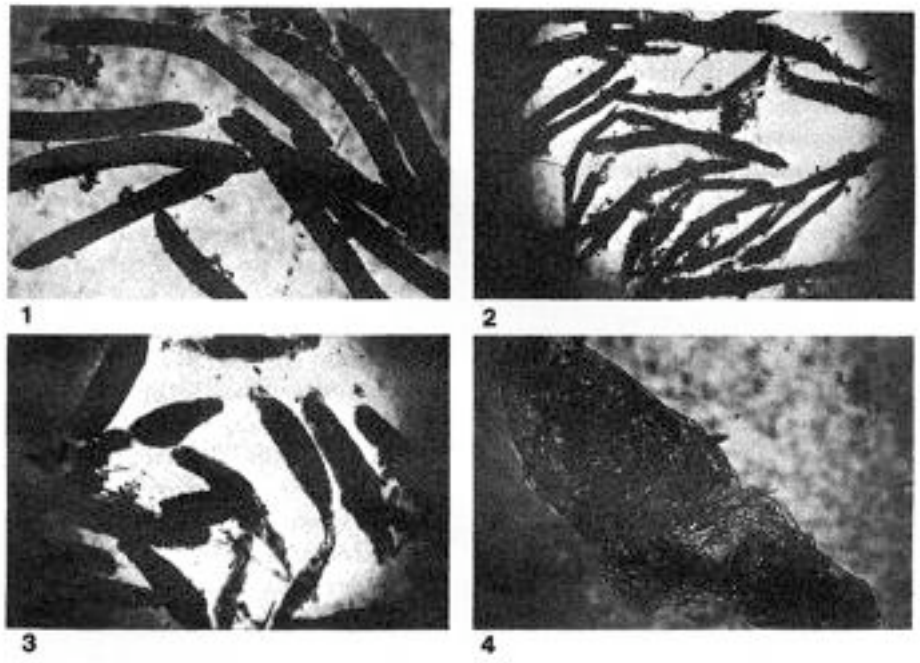
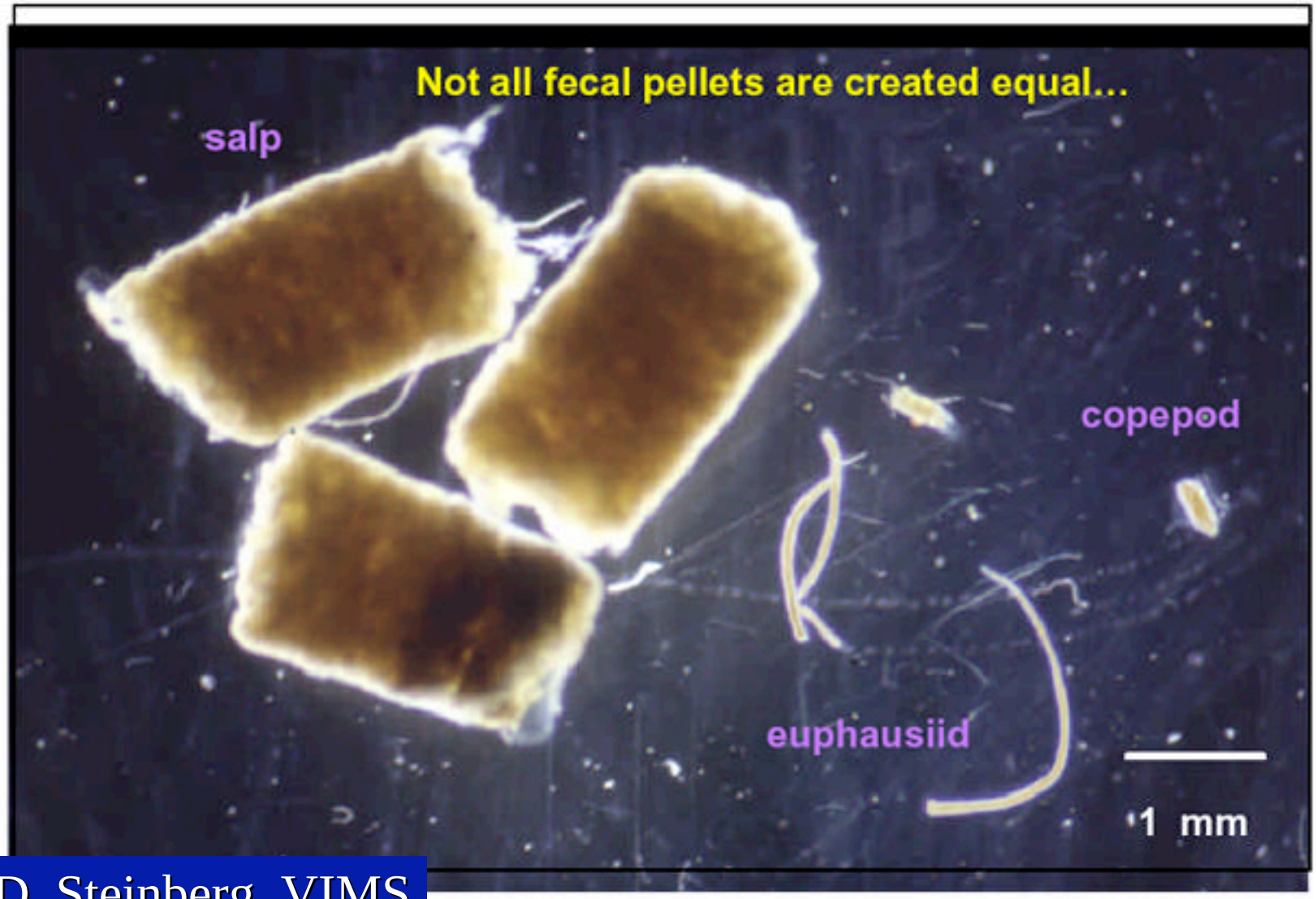


Figure 7.10. Fecal pellets of some zooplankton species. (1) *Calanus plumchrus* (length of a pellet, about 0.9 mm); (2) *Euphausia pacifica* (about 3 mm); (3) *Parathemisto japonica* (about 1.5 mm); (4) *Sagitta elegans* (about 1.5 mm).

Omori & Ikeda 1984

Fecal Pellets



D. Steinberg, VIMS

“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

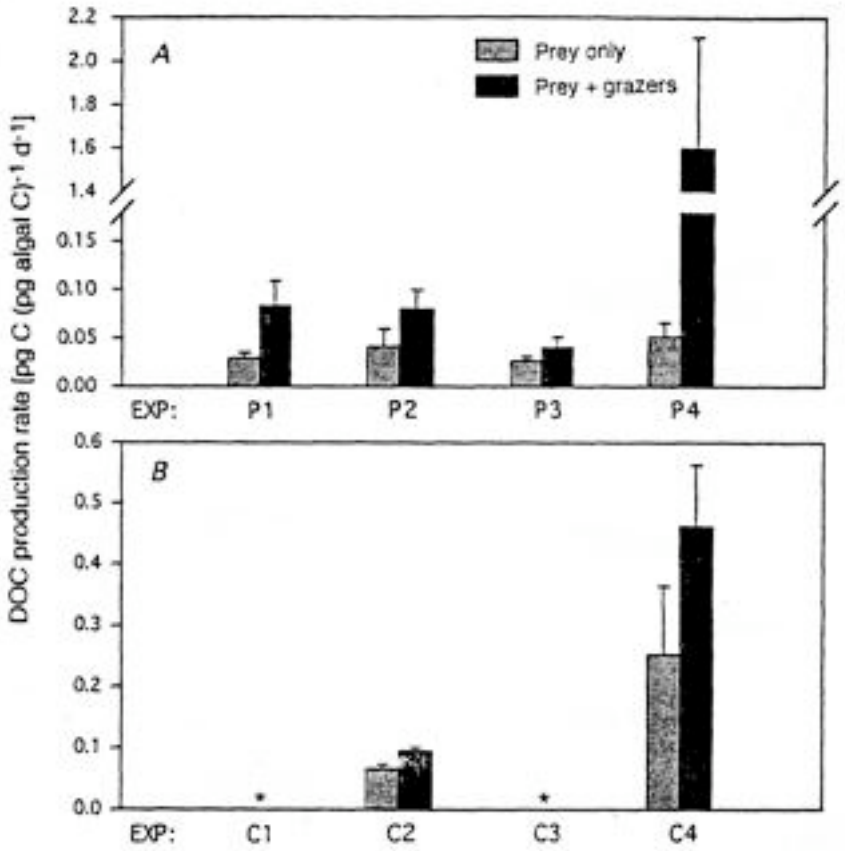


Fig. 2. DOC production rates normalized to algal cell C content for (A) protist grazer experiments (pooled data from days 1 and 2) and (B) copepod grazer experiments. Rates calculated assuming bacterial growth efficiency of 0.5. Symbols as for Fig. 1. *, no measurable DOC production in these experiments.

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

Flagellate fed bacteria: carbon budget

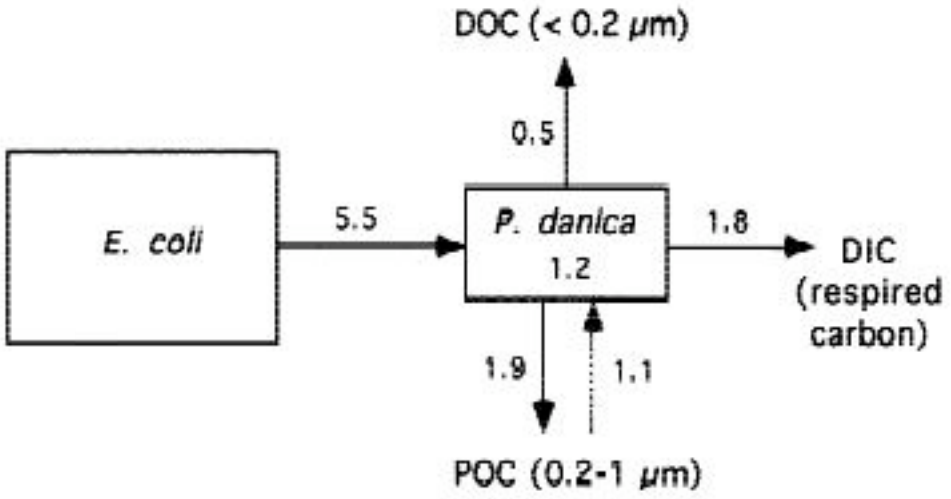


Fig. 4. Starved *Pteridomonas danica* growing on *Escherichia coli*. Simplified carbon budget of *P. danica* grazing activity during 17 h incubation: dissolved organic carbon (DOC) egestion, particulate organic carbon (POC) 0.2–1 μm egestion, and dissolved inorganic carbon (DIC) respiration. Part of the egested POC could have been reingested by *E. coli* (dotted arrow). Organic carbon units are in mg C L^{-1}.

Egested: 34% POC

Excreted/Respired: 9%/34%

Growth: 22%

Pelegri et al. 1999

Assimilation Efficiency: (I - E)/I

- AE generally assumed to be constant at ~ 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 $C:N_{phytopl} > C:N_{zoopl}$.

- Protists: AE(carbon) generally assumed to be ~80%, whereas AE(nitrogen) may be lower if C:N(prey) < C:N(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*

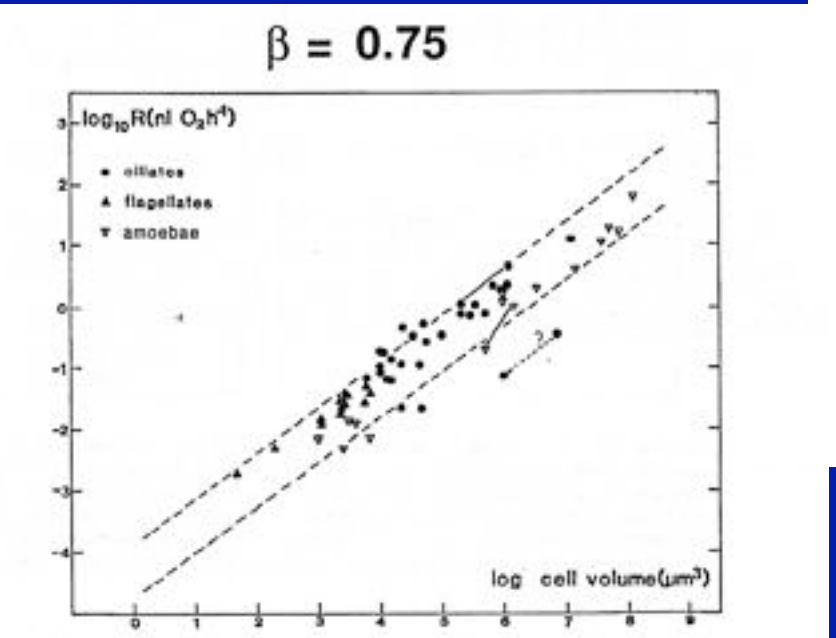
Excretion *of inorganic nutrients or low MW organics is tied to respiration*

Respiration: Allometric Relationship

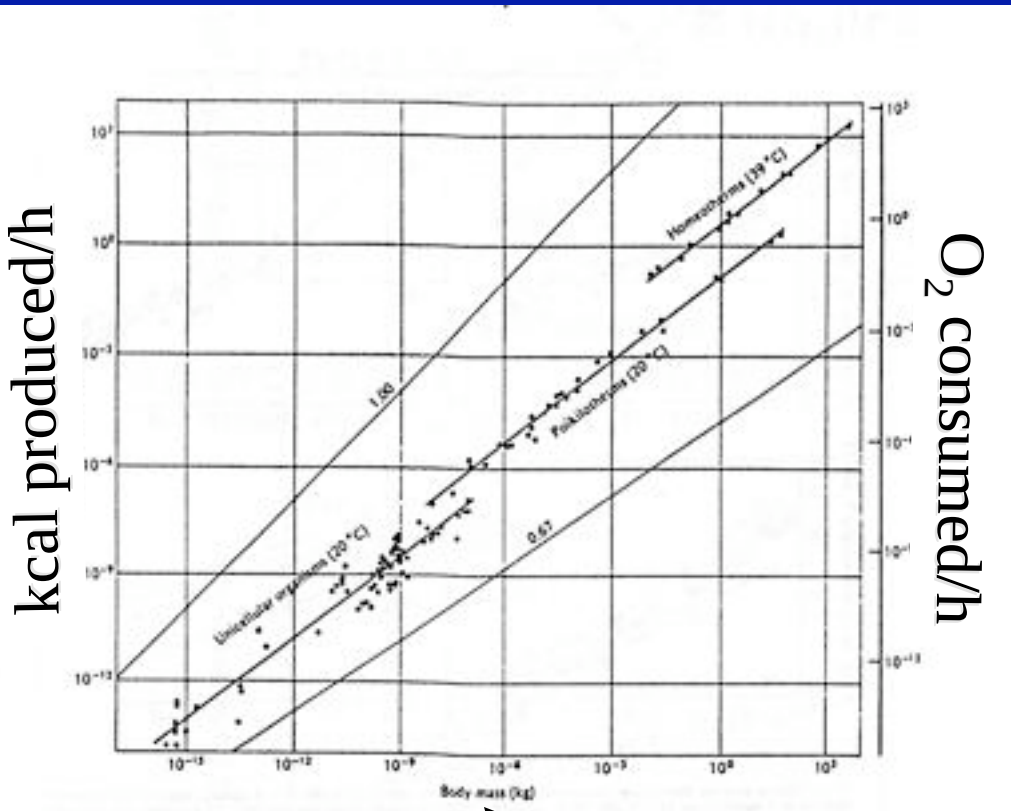
Bigger organisms have higher metabolic rates than smaller organisms

$M = \alpha * W^{\beta}$

where: $0.7 \leq \beta \leq 0.8$



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 poikilotherm metazoa and for unicellular organisms (From Fenchel & Finlay, 1983).



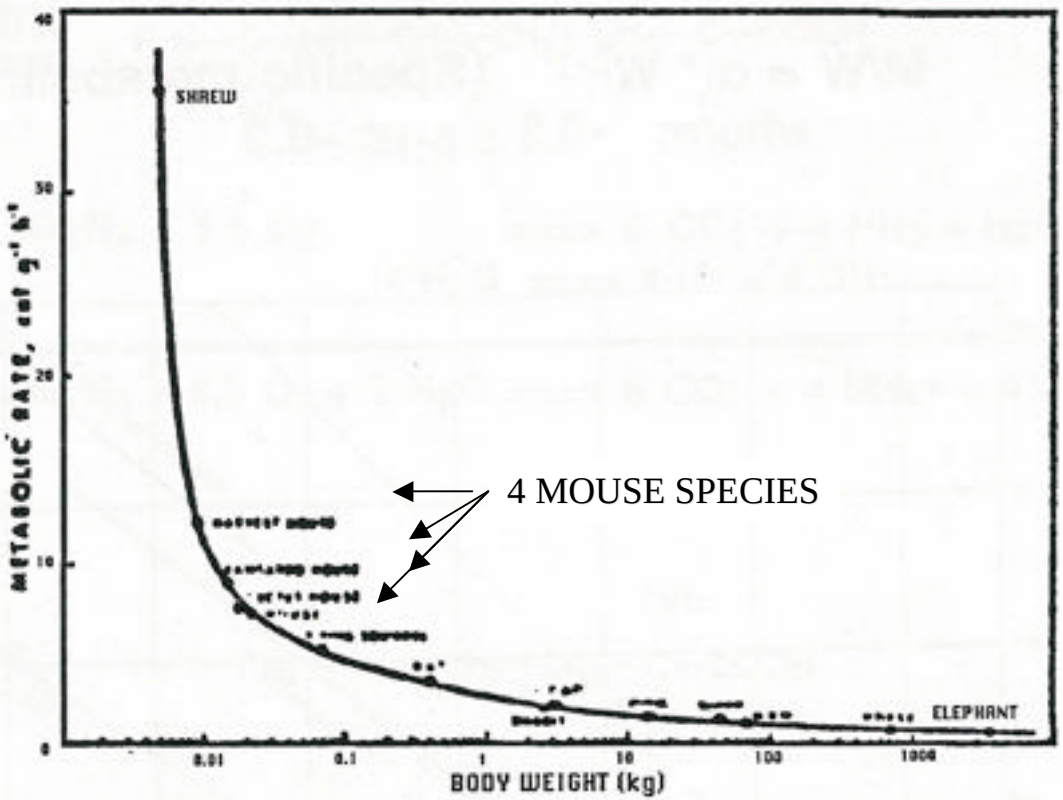
Metabolic rates of various organisms in relation to body weight (grams). Note that each mark on the weight axis denotes a 1000-fold change in magnitude (From Hemmingsen, 1960).

Body Weight (kg)

Specific Metabolic Rate: Organism Size

$M/W = \alpha * W^{\beta-1}$

where $-0.3 \leq \beta-1 \leq -0.2$



Observed metabolic rates of mammals per gram body weight plotted against body weight (kg) (From Hemmingsen, 1960).

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

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

Source: After G. Lusk, "The Elements of the Science of Nutrition," 4th ed, W. B. Saunders Company, Philadelphia, 1928.

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

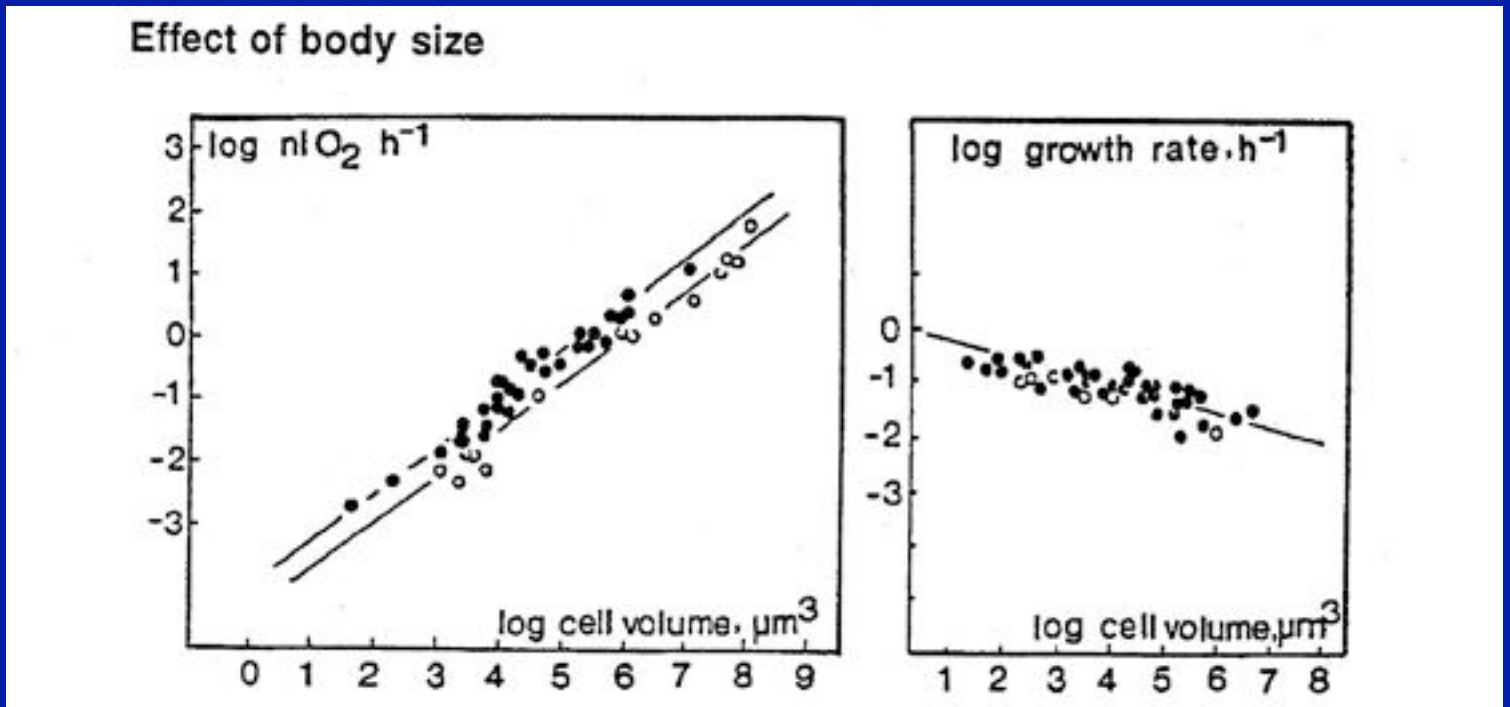


Figure 4.2 (Left) respiration rates (at 20°C) of various species of ciliates and flagellates (filled circles) and of amoebae (open circles) during exponential growth and as a function of cell volume. The slope of the regression lines is 0.75. (Right) the maximum attainable growth rate constant (20°C) 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 tintinnid^{-1} h^{-1}) and excretion (*E*) (pg N tintinnid^{-1} h^{-1}) were calculated by linear regression of changes in O_2 and NH_4^+ 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) = $(G/I)100$.

Parameter	*T. vasculum*			*T. acuminata*		
	5°C	10°C	15°C	15°C	20°C	25°C
C(μg liter^{-1})	165	210	193	184	202	240
R(±C.I.)	114(39)	314(51)	462(35)	43(7)	78(11)	114(14)
E(±C.I.)	32(8)	58(12)	82(23)	9(0)	13(0)	21(1)
O:N	4.1	6.3	6.6	5.4	6.7	6.3
I(h^{-1})	0.04	0.08	0.10	0.11	0.17	0.24
G(h^{-1})	0.02	0.04	0.04	0.05	0.06	0.08
R(h^{-1})	0.01	0.04	0.06	0.05	0.09	0.14
E(h^{-1})	0.02	0.03	0.05	0.05	0.08	0.12
AE(±SD) (%)	95(31)	95(10)	100(8)	94(9)	91(19)	94(13)
GGE(±SD) (%)	57(23)	46(5)	44(2)	49(3)	38(7)	35(4)

Verity 1985

Temperature Dependency

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

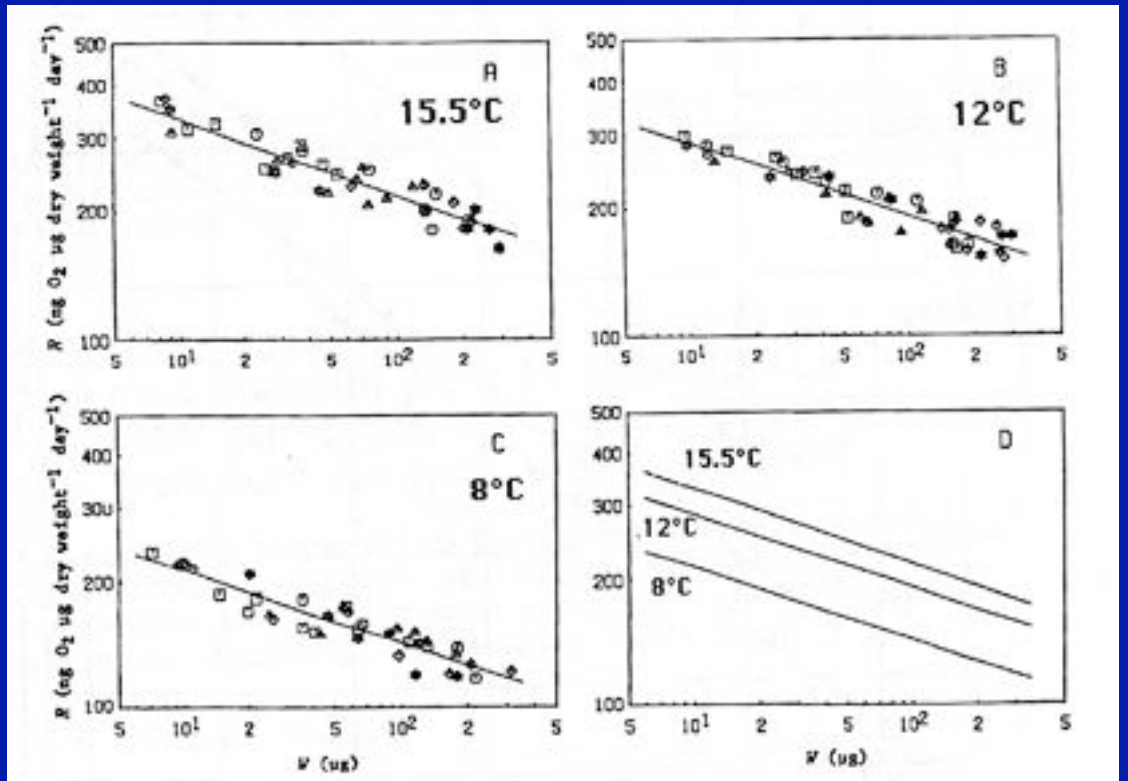


Fig. 2. *Calanus pacificus*. Relationship between weight-specific rate of oxygen consumption (R) and dry body weight (W) for copepods cultured at 3 temperatures: 15.5 °C (A), 12 °C (B), and 8 °C (C); and various food concentrations: 0.5 ppm (squares), 1.35 ppm (triangles), 2.75 ppm (circles), 6.50 ppm (diamonds), and 12.0 ppm (stars). Lines fit using Eq. (1) are shown in (A)–(C) and those using Eq. (3) in (D)

(From: Vidal. 1980. Mar. Biol. 56: 195-202)

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

$M_{total} = M_{standard} + M_{active} + M_{sda}$

where

$M_{standard}$ = basal (resting) metabolism

M_{active} = metabolism due to active swimming & foraging

M_{sda} = “specific dynamic action” - metabolism associated with digestion, assimilation & growth

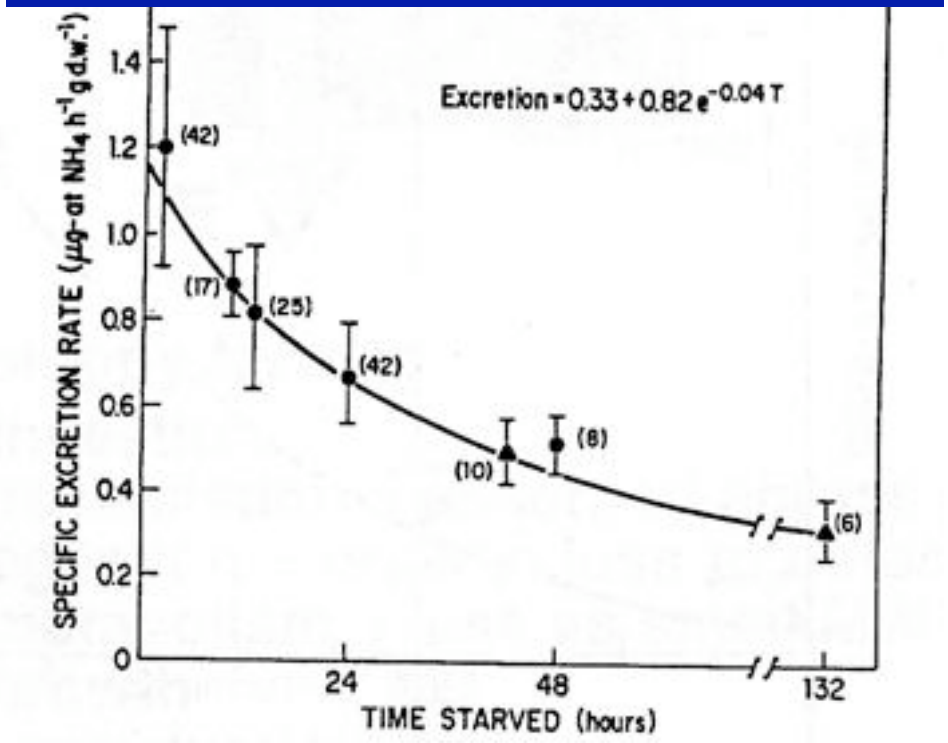
Activity Level: Metazoans

- 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.

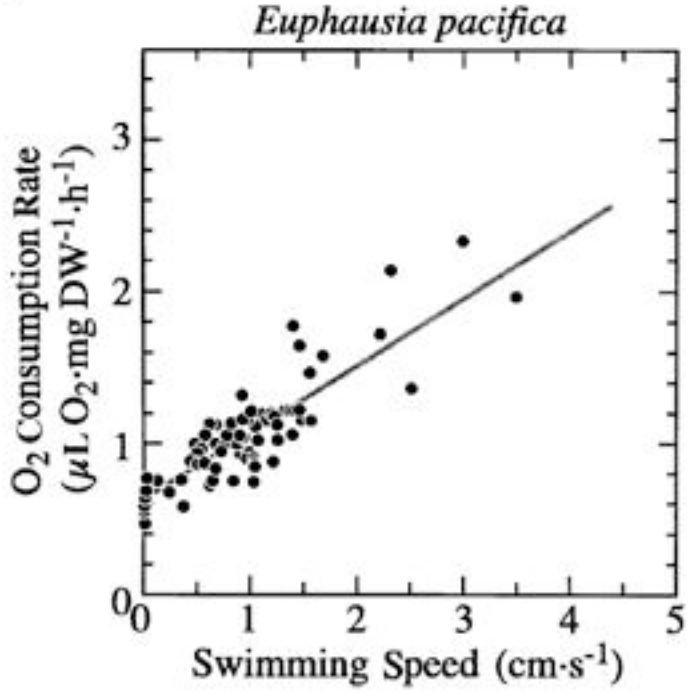
Ctenophore ammonium excretion rate as a function of starvation time (Kremer 1982)

Active → Starved 2 days



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.



Buskey 1998

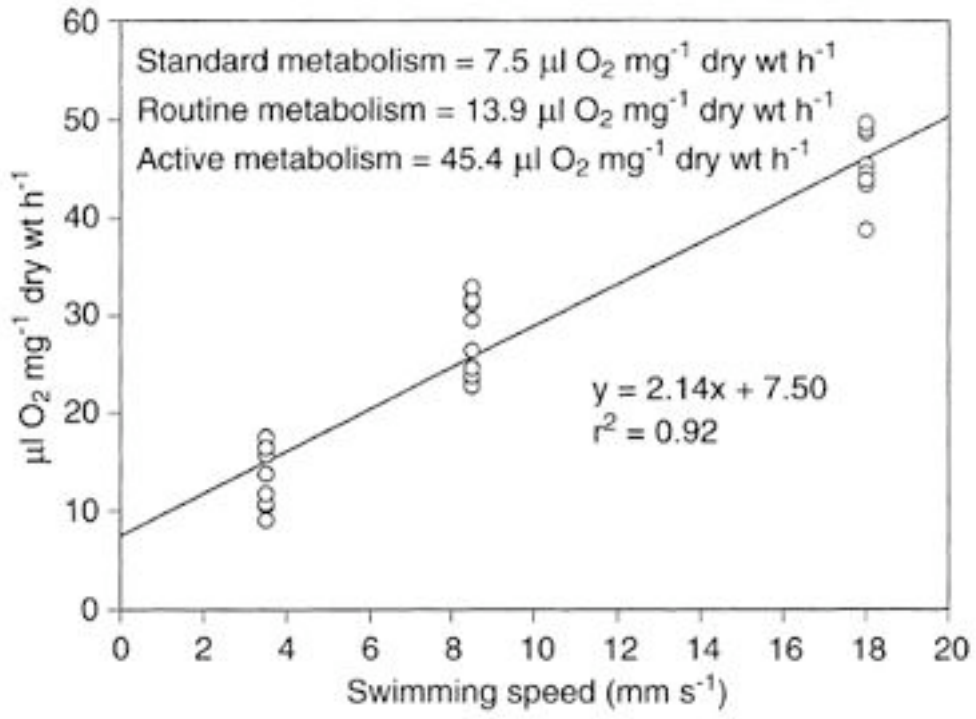


Fig. 2 *Dioithona oculata.* Respiration rate as a function of swimming speed in sealed flow-through chamber. Copepods were induced to swim at different speeds by varying current speed

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

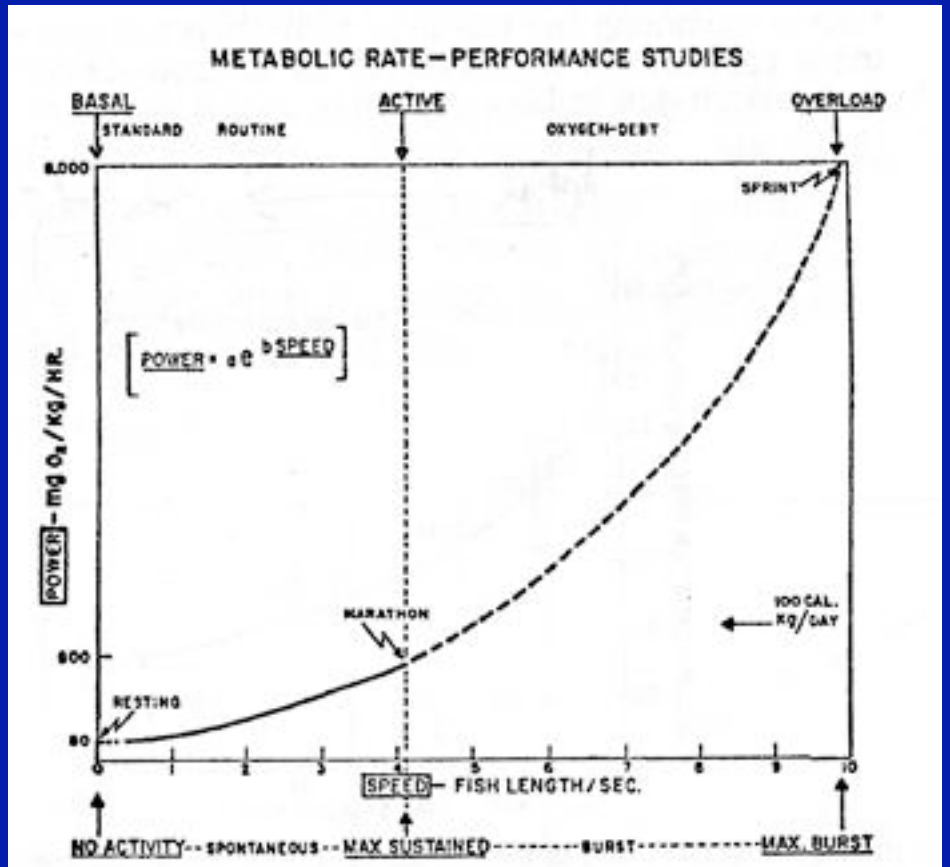


FIGURE 3. Relation between power (metabolic rate) and speed showing the energy demand associated with typical levels of performance such as "marathon" (sustained maximum) and "spring" (burst maximum). Basic curve extrapolated to indicate the equivalent oxygen requirements for burst speeds which produce an oxygen-debt.

Cost of movement for protists?

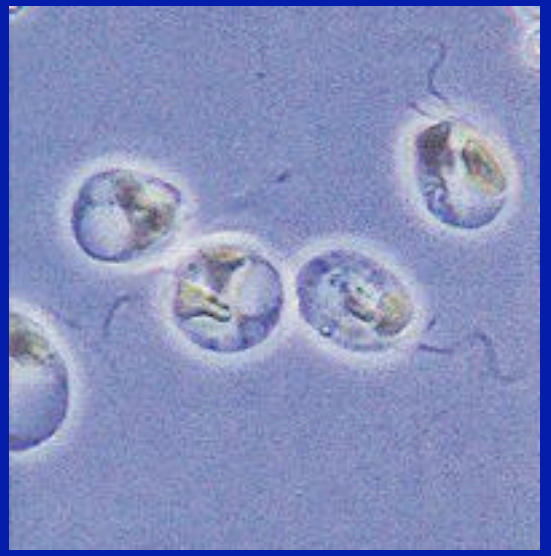
Example: 8 µm flagellate (*from Sleigh 1974*)

Power requirement for flagellate movement = 3×10^{-7} erg/sec
(assumes conversion factor of 2×10^{8} erg/ml O_2 used)

Therefore, power required for swimming = 1.5×10^{-9} nl O_2/sec

But, Total Metabolism for flagellate = 1.25×10^{-6} nl O_2/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*")

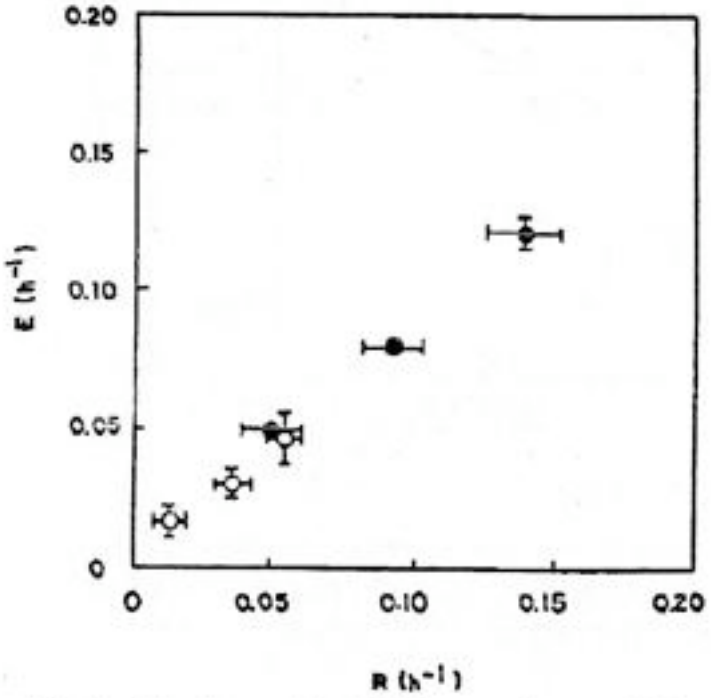


Fig. 7. Hourly specific NH_4^+ excretion rate (E) as a function of specific respiration rate (R) for *Tintinnopsis vasculum* (○) and *Tintinnopsis acuminata* (●). Error bars represent 95% C.I. Geometric mean regression: $E(h^{-1}) = 0.00 + 0.84(R, h^{-1})$, $r^2 = 0.99$. 95% C.I. around slope is 0.06.

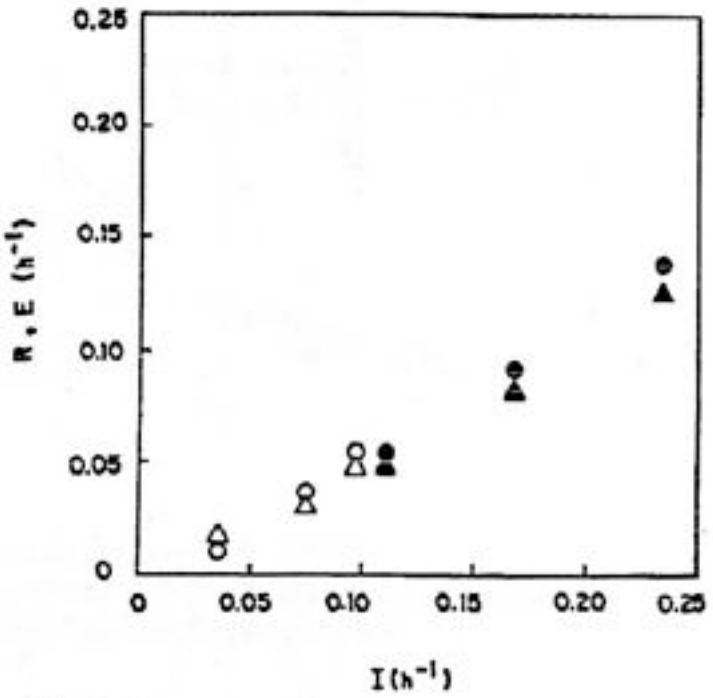


Fig. 8. Hourly specific respiration (○) and excretion (△) rates as a function of ingestion rate for *Tintinnopsis vasculum* (open symbols) and *Tintinnopsis acuminata* (solid symbols). Geometric mean regressions: $E(h^{-1}) = -0.01 + 0.53(I, h^{-1})$, $r^2 = 0.99$; $R(h^{-1}) = -0.01 + 0.63(I, h^{-1})$,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

Verity 1985

Metabolic and Size responses to starvation

all bacteria consumed

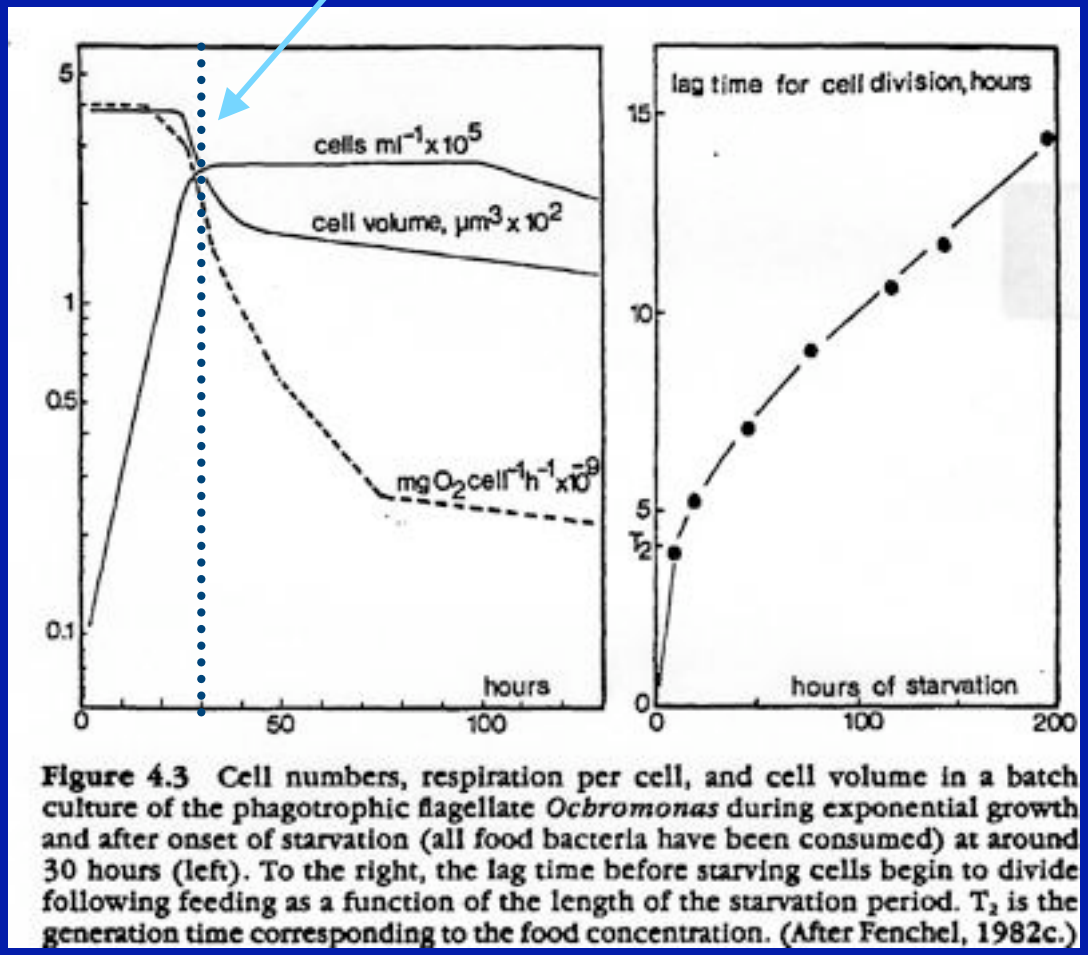


Figure 4.3 Cell numbers, respiration per cell, and cell volume in a batch culture of the phagotrophic flagellate *Ochromonas* during exponential growth and after onset of starvation (all food bacteria have been consumed) at around 30 hours (left). To the right, the lag time before starving cells begin to divide following feeding as a function of the length of the starvation period. T_2 is the generation time corresponding to the food concentration. (After Fenchel, 1982c.)

Biovolume
2-3X decline

Respiration
10-20X decline

Protist Metabolism: Excretion

Grazing of flagellate on diatom

diatom abundance

flagellate abundance

particulate nitrogen

NH_4 & urea

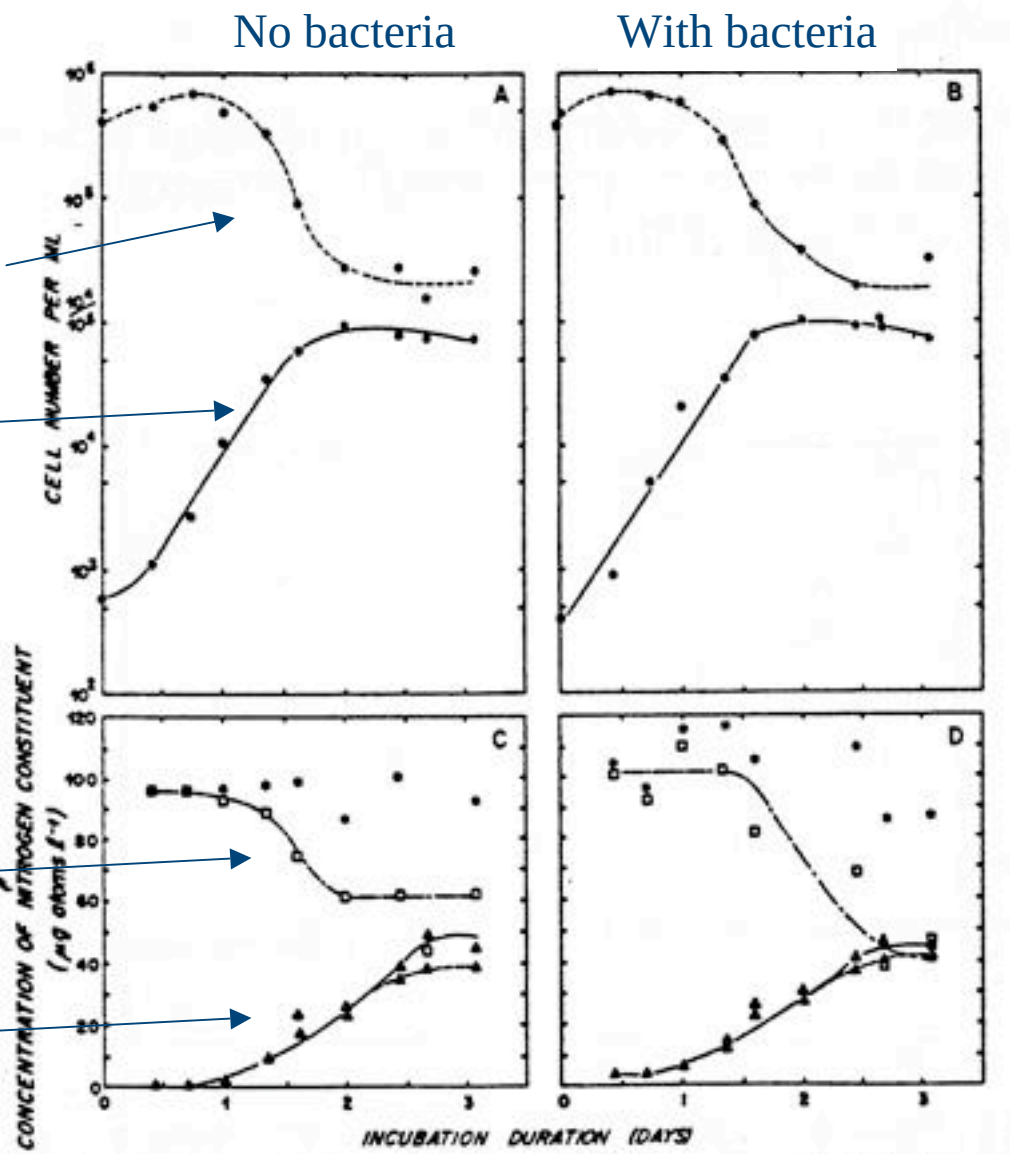


Fig. 5. Grazing of *P. imperforata* on *P. tricornutum* and nitrogen regeneration in the absence (A,C) and presence (B,D) of bacteria in the dark and at 24°C. (A,B) Grazing of *P. imperforata* (●) on *P. tricornutum* (○). (C, D) Regeneration of NH_4^+ (△) and NH_4^+ + urea (▲) along with changes in particulate nitrogen (□) and total nitrogen (=particulate nitrogen + NH_4^+ + urea) (★).

Goldman & Caron 1985

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?

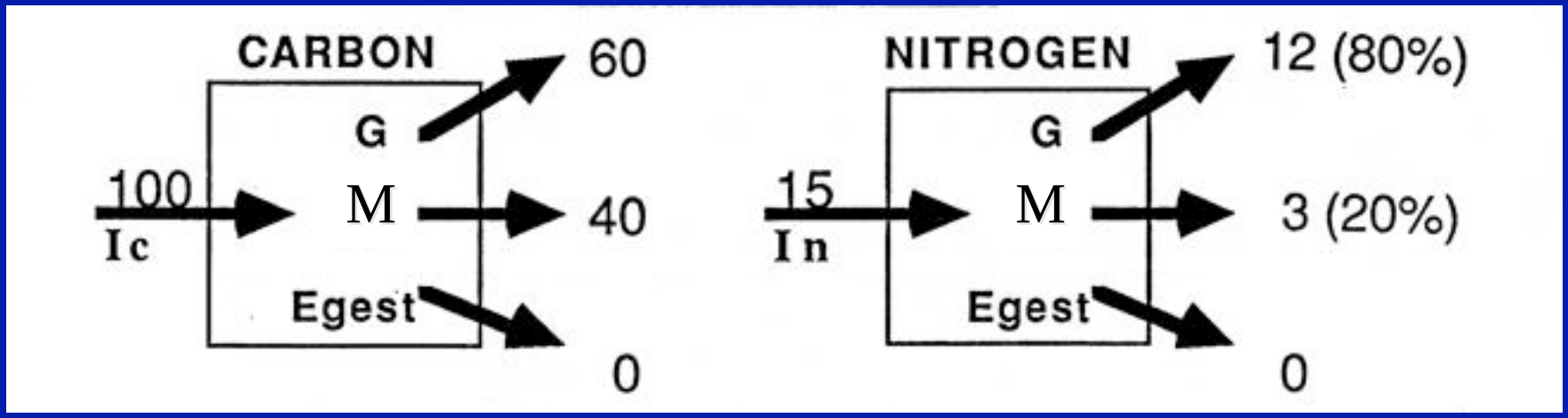
An example:

Parameter	DOM → BACT	BACT → ZOOFL	ALGAE → CILIATE	ALGAE → COPEPOD
Ingestion(C)	100	100	100	100
Respiration (C)	40	40	40	40*
AE	1.0	0.8	0.8	0.7*
GGE	0.6	0.4	0.4	0.3*
C:N(prey)	6.6	5.0	6.6	6.6
C:N(pred)	5.0	5.5	5.5	4.0

*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)

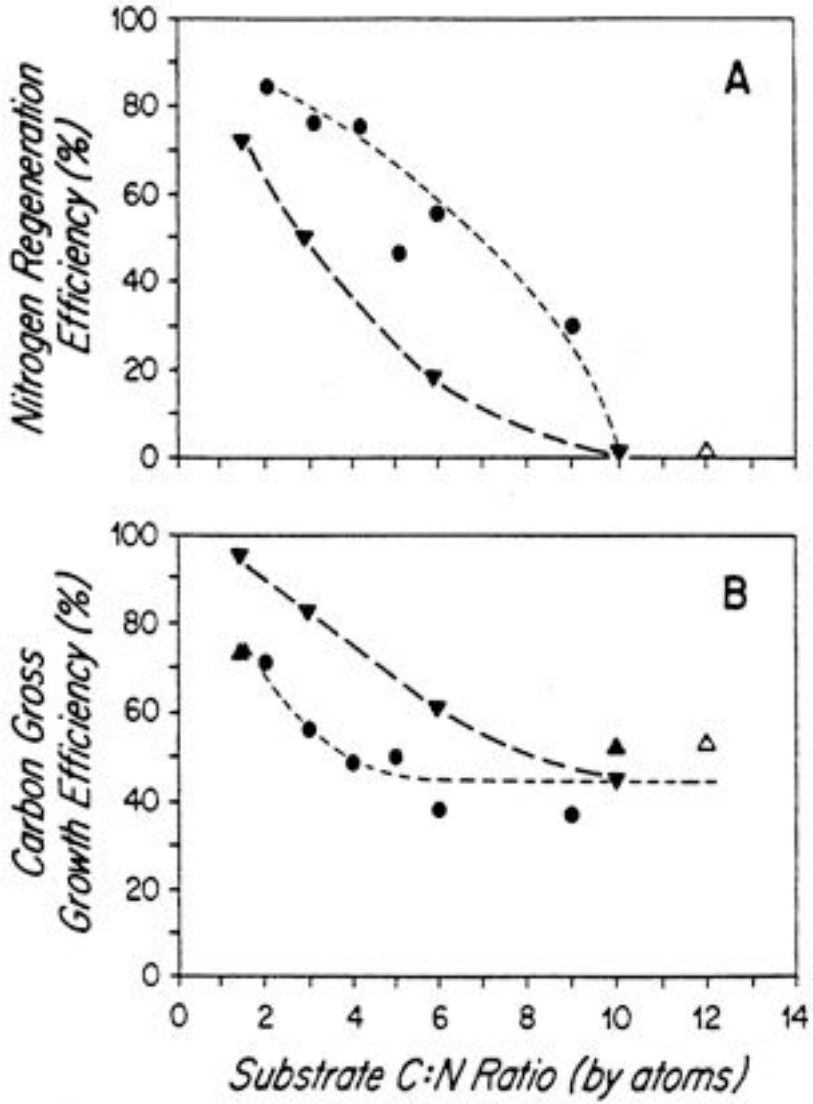


Fig. 4. Effect of substrate C:N_s ratio on nitrogen regeneration efficiency and carbon gross growth efficiency at time when maximum biomass was attained. Experiment A—▼; experiment B, amino acids—●, NH_4^+—▲; data from Goldman et al. 1985—△.

Food (DOM) quality matters

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

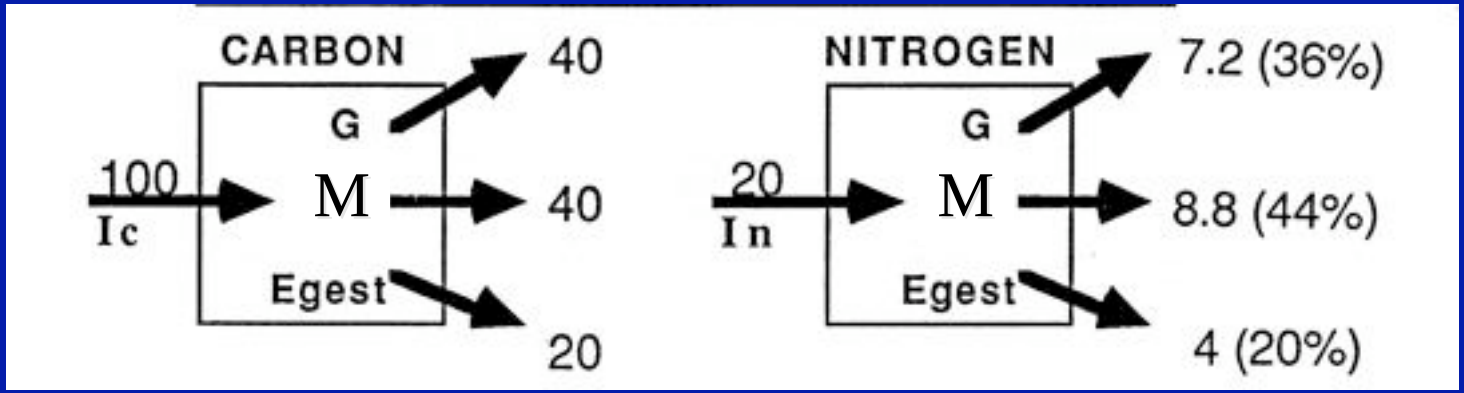
At C:N > 6 (~algal C:N),
GGE = 40-50%,
Nitrogen regeneration: 0-20%

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

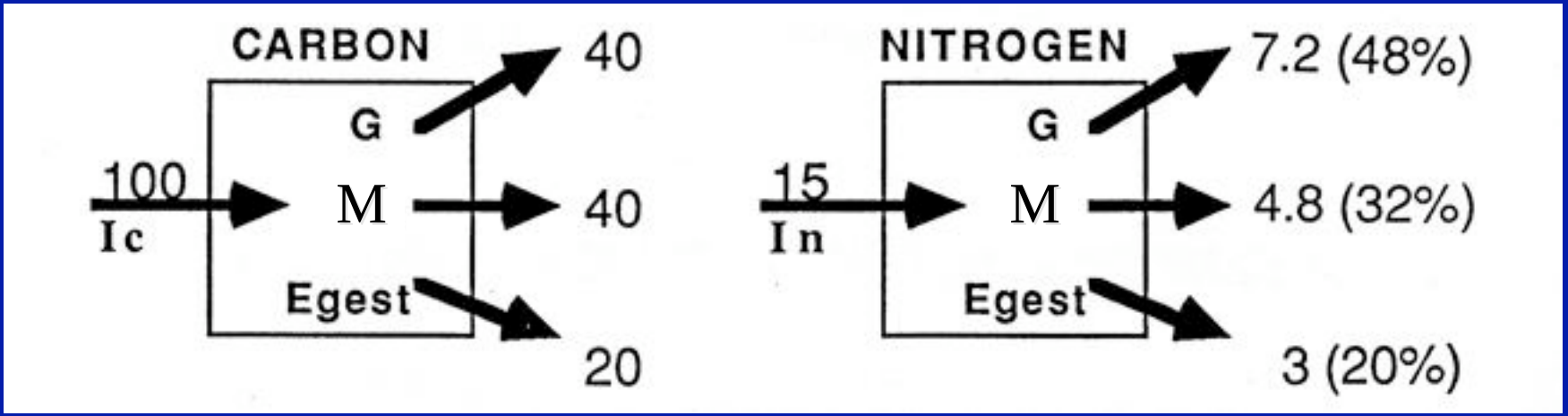
Protist C:N = 5.6, Bacteria C:N = 5



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

Protist feeding on Algae

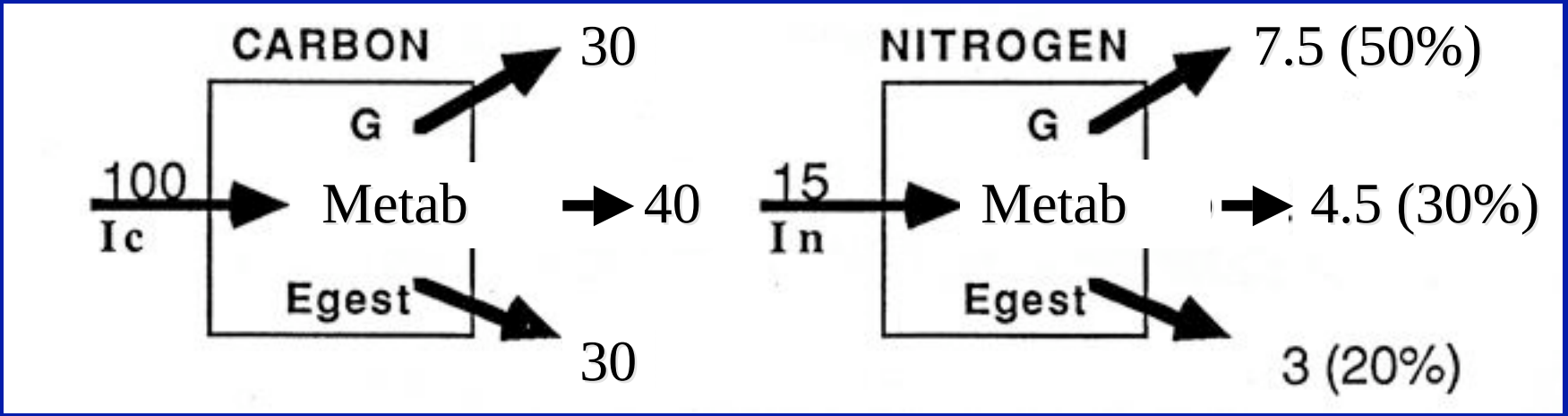
Protist C:N = 5.6, Algae C:N = 6.6



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.

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

    μ = instantaneous growth rate (d)

    m= instantaneous mortality rate (d)
  - Solve equation for μ or (μ-m):

    $\ln P_t = \ln P_0 + \mu t$ OR $\ln P_t = \ln P_0 + (\mu - m)t$

    $\frac{\ln(P_t/P_0)}{t} = \mu$ $\frac{\ln(P_t/P_0)}{t} = \mu - m$

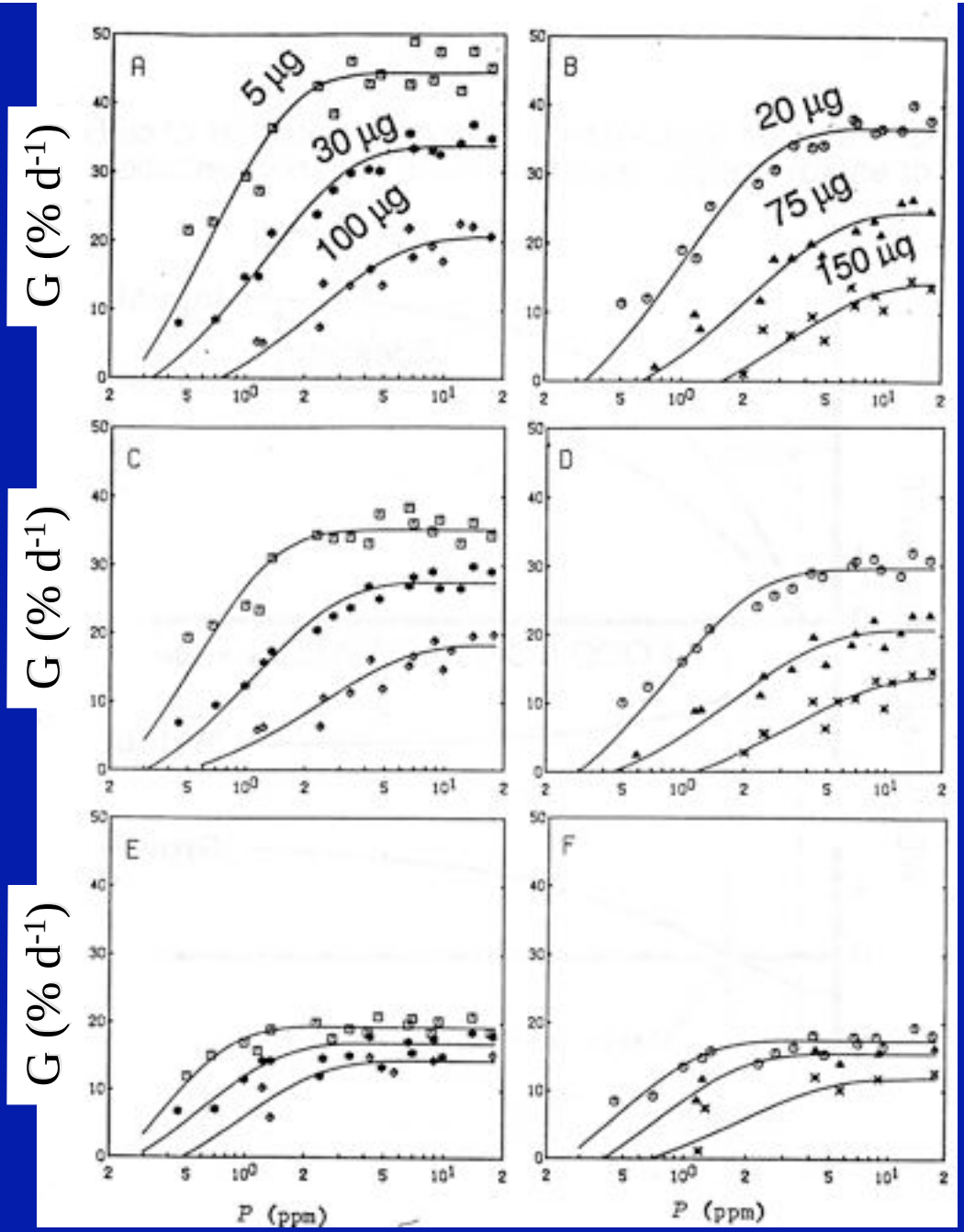
Growth Potentials

- 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).



Vidal 1980

Protist Growth Potential

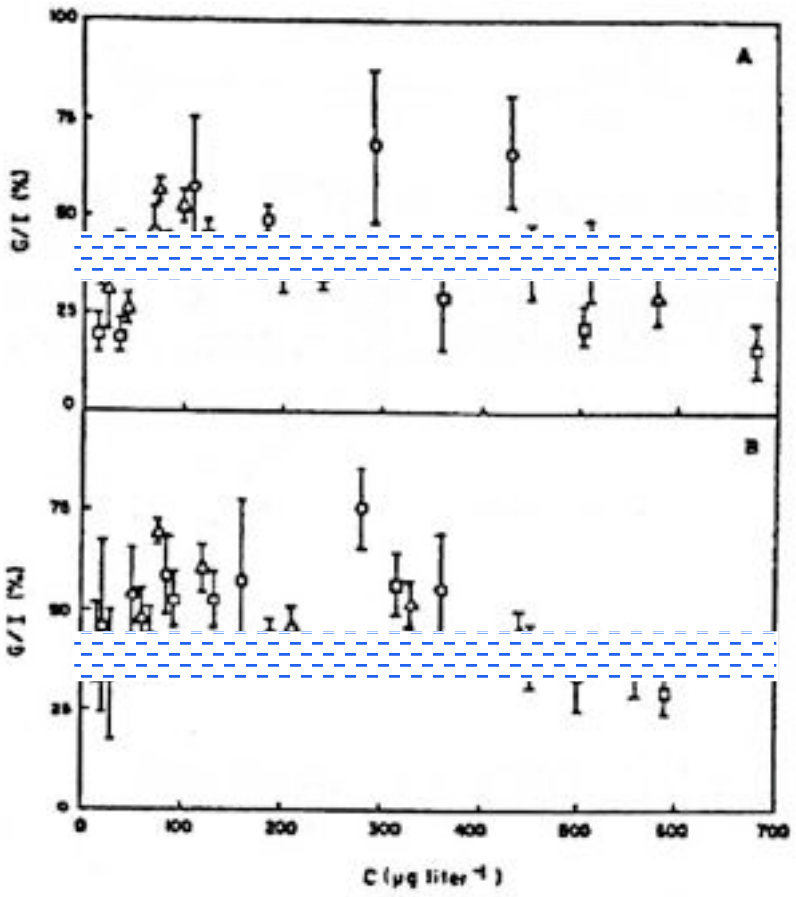
- Protists *Can* grow faster than autotrophic prey: can feed 24/7 (unlike autotrophs which only grow during daylight hours) and food already in reduced form.
- Most grow by binary fission (1 cell becomes 2, 2 cells become 4, and so on...)
- Maximum Growth Potential (biomass doubling = generation time): 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 across groups

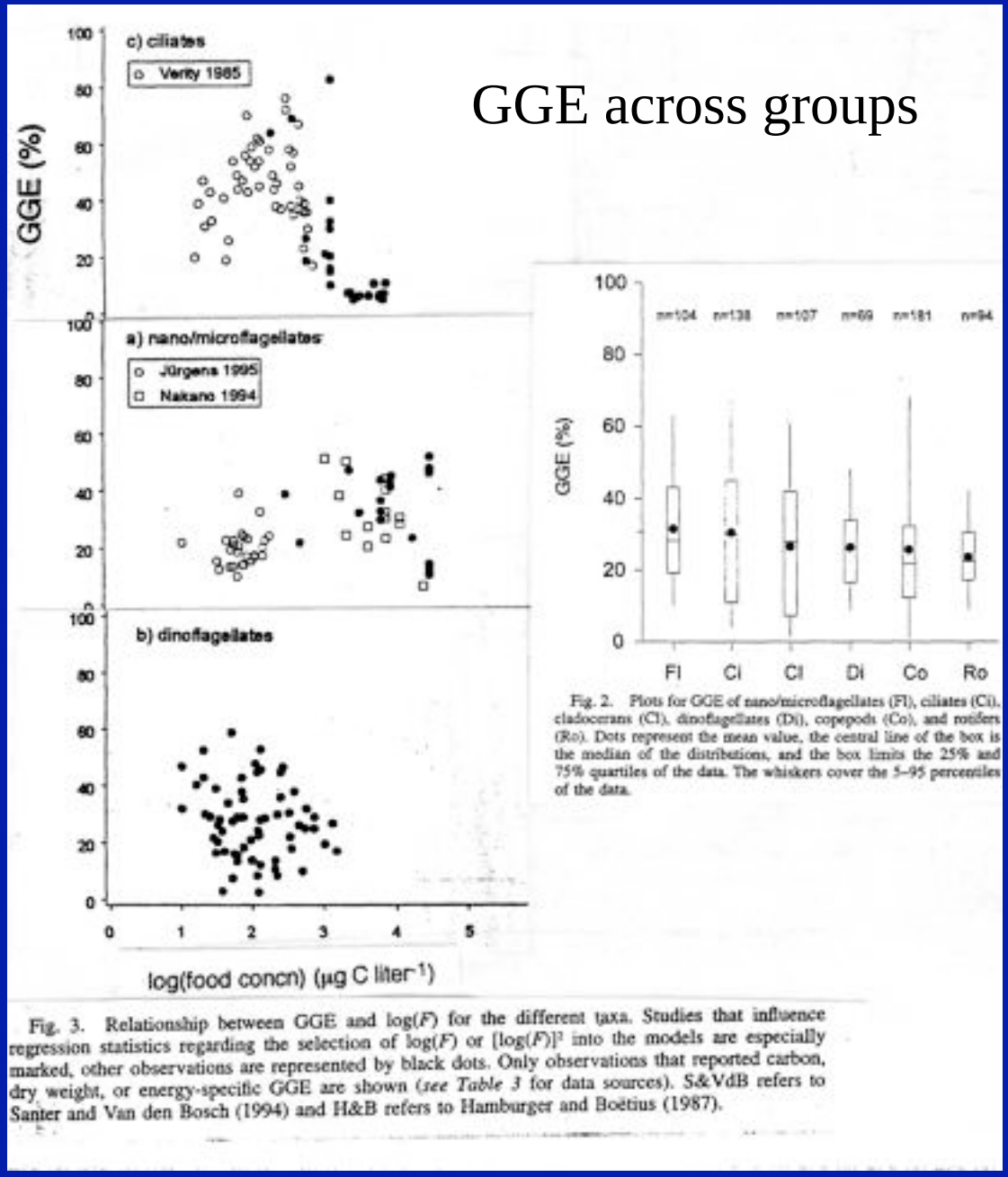


Fig. 2. Plots for GGE of nano/microflagellates (Fl), ciliates (Ci), cladocerans (Cl), dinoflagellates (Di), copepods (Co), and rotifers (Ro). Dots represent the mean value, the central line of the box is the median of the distributions, and the box limits the 25% and 75% quartiles of the data. The whiskers 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 Boëtius (1987).

GGE can be assumed to be ~30% for planktonic consumers

Straile 1997