

# FROM LILLIPUTIANS TO WHALES: ALLOMETRY IN BIOLOGICAL OCEANOGRAPHY AND ECOLOGY

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## Assignment

### TOPIC

What physiological principles could you use to estimate the number of Lilliputian meals needed to feed Gulliver? Using similar arguments, how many *Calanus finmarchicus* would be needed to feed a Right Whale in Cape Cod Bay? Also, read the discussion of **Kenney et al. (1986)** and think about whether the Magnuson Act, which reduced the fishing intensity on planktivorous herring in the Gulf of Maine, may have had unintended consequences on the endangered right whales. Finally, we’ll discuss whether there is a physiological advantage to being big in marine systems.

### REQUIRED

Kenney, R. D. M. Hyman, R. E. Owen, G. P. Scott, and H. E. Winn. 1986. Estimation of prey densities required by Western North Atlantic Right Whales. *Marine Mammal Science* 2: 1-13. [*A wonderful back-of-the-envelope style calculation of the number of *Calanus finmarchicus* required to support the metabolic demands of Right Whales. Do such patches occur in Cape Cod Bay, a prime Right Whale feeding ground? No one knows.*]

## SUPPLEMENTAL

Banase, K. and S. Mosher. 1980. Adult body mass and annual production/biomass relationships of field populations. Ecol. Monogr. 50: 355-379. [This is the definitive review of the literature on P/B ratios, where P is the annual production and B is the mean annual population biomass.]

Fenchel, T. 1974. Intrinsic rate of natural increase: the relationship with body size. Oecologia (Berlin) 14: 317-326. [A classic paper showing that  $r_{max}$  declines as a power function of body size. The allometric equation for the relationship between  $r_m$  and body size (from viruses to whales) is:

$$\log_{10} r_{max} = a - 0.275 * \log_{10} \text{Weight.}$$

where,  $a$  = -1.9367 for unicellular organisms  
= -1.6391 for heterotherm metazoans  
= -1.4 for homeotherm metazoans

**Blueweiss et al. (1978)** and **Banase (1982b)** showed that the -0.275 slope was not significantly different from the anticipated -0.25 ]

Geider, R. J., T. Platt, and J. A. Raven. 1986. Size dependence of growth and photosynthesis in diatoms: a synthesis. Mar. Ecol. Prog. Ser. 30: 93-104. [Large cells may dominate over small cells during spring blooms, not because of physiological advantage, but because of predator release]

Gasol, J. M., P. A. del Giorgio and C. M. Duarte. 1997. Biomass distribution in marine planktonic communities. Limnol. Oceanogr. 42: 1353-1363. [They analyze the biomass distribution of autotrophs to heterotrophs in a variety of marine environments. The traditional ecological pyramid is inverted {heterotrophic dominance} in open-ocean communities]

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge. Read pages 24-44 (Metabolism), [An excellent book. Peters reviews the literature on mass-scaled growth, respiration and ingestion.]

West, G. B., J. H. Brown, and B. J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. Science 276: 122-126. [A very important paper that explains the prevalence of the 3/4 allometric scaling based on the fractal geometry of capillaries and other vessels used for exchanging gasses]

West, G. B. and J. H. Brown. 2005. The origin of allometric scaling laws in biology from genomes to ecosystems: towards a quantitative unifying theory of biological structure and organization. J. Exp. Biol. 208: 1575-1592. [A comprehensive review of the **1997 theory**, its critics, and extensions]

Zhou, M. 2006. What determines the slope of a plankton biomass spectrum? J. Plankton Res. 28: 437-448. [The biomass spectrum slope is a function of the number of trophic levels and the ecological transfer efficiency. Few trophic levels produce steep slopes (>>-1) With higher transfer efficiencies, a given slope would be associated with more trophic levels] {}

## Comments on Scaling Processes by Body Size

### THE ALLOMETRIC EQUATION

Body size and physiological processes increase at different rates. The equations which scale these different rates are called allometric equations, from the Greek *allos* (other) and *metron* (scales). Allometric equations have the form:

$$y = \alpha x^\beta. \quad (2)$$

Some processes appear to be the same at all scales. Net growth efficiency doesn't appear to differ much across body size. This scale-invariance of net growth efficiency allows the prediction that a ton of seed fed to mice should produce roughly the same biomass as a ton of seed fed to pigs. The Redfield ratio is also nearly scale invariant. Almost all plankton, regardless of size, have elemental ratios of C:N:P near Redfield proportions when growing near their optimal growth rate ( $\mu_{max}$ ). Most other processes do differ tremendously as a function of body size. These processes can be expressed using the allometric equation:

$$\text{Rate of a process} = \alpha \text{Weight}^\beta \quad (3)$$

**Peter's (1983)** Chapter 2 describes the simple algebra needed to analyze most allometric relationships. These are usually expressed using a log-log plot with the logarithm of the rate (e.g., respiration) vs. log body weight. A logarithm to any base can be used; natural logarithms (log base e),  $\log_2$ , and  $\log_{10}$  are all common in the oceanographic literature. This log-log plot usually produces a straight line with slope  $\beta$  and y-intercept  $\log(\alpha)$ :

$$\log \text{Rate} = \log \alpha + \beta \log(\text{Weight}). \quad (4)$$

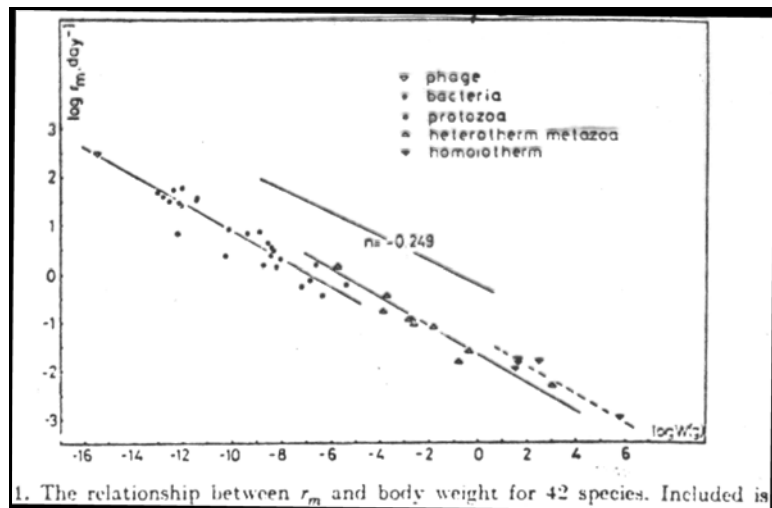
Sometimes a process is plotted on a weight-specific basis:

$$\frac{\text{Rate}}{\text{Weight}} = \alpha \text{Weight}^{\beta - 1}. \quad (5)$$

$$\log\left(\frac{\text{Rate}}{\text{Weight}}\right) = \log \alpha + (\beta - 1) \log(\text{Weight}). \quad (6)$$

Virtually all metabolic processes scale with body mass to the  $\frac{3}{4}$  power. Weight-specific metabolic rates and maximum per capita growth rate,  $r_{max}$ , scale with body mass to the  $-\frac{1}{4}$  power (**Fenchel 1974** found the exponent to be  $-0.275$ , but **Blueweiss et al. (1978)** and **Banse (1982b)** showed that  $-0.275$  was statistically indistinguishable from  $-\frac{1}{4}$ , see Fig. 1). This  $\frac{3}{4}$  allometric exponent, or  $-\frac{1}{4}$  on a weight specific basis, is as close to a universal law as exists in biology and no one really knows why. **Peters (1983)** devotes a chapter to explanations for the 0.75 exponent in body-mass scaling relationships. These explanations include:

1. The surface law. The areas of geometrically similar objects rise to the  $\frac{2}{3}$  power. This explanation fails to explain the  $\frac{3}{4}$  power law.
2. Compositional explanations. Concentrations of biochemical macromolecule pools increase to the  $\frac{3}{4}$  power. This may set a  $\frac{3}{4}$  limit on the products of cellular metabolism.



**Figure 1.**  $r_m$  as a function of body weight from Fenchel (1974).

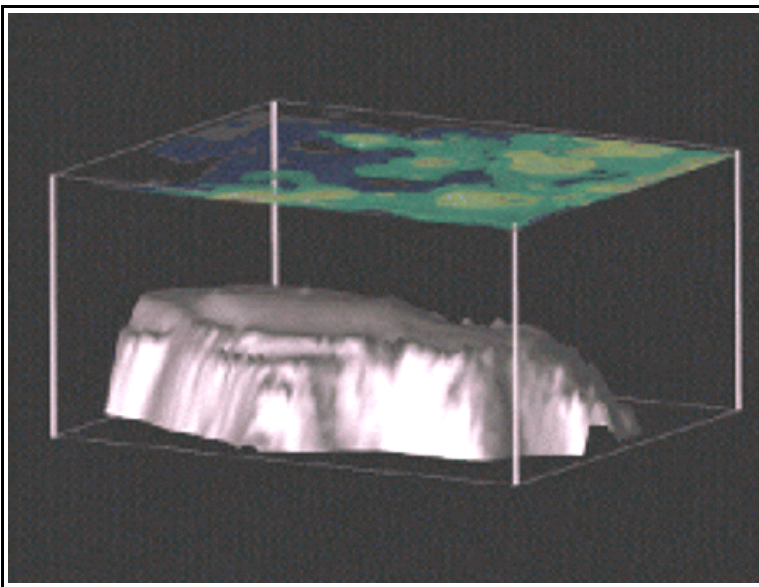
3. Tissue metabolism. An organisms metabolic rate may be genetically constrained to match the metabolic scaling of cells.
4. McMahon's structural explanation. Organisms are constructed so that loads supported by the organism are proportional to the maximum load supportable without buckling
5. Dimensional analyses: **Platt & Silvert (1981)** argued that aquatic organisms have allometric exponents of  $\frac{2}{3}$  and terrestrial organisms  $\frac{3}{4}$ . Unfortunately, Peters feels the data refute their dimensional arguments.
6. **Blum (1977)**: organisms are scaled in 4-dimensions, not 3!

**West et al. (1997)** proposed a model that is now widely regarded as **THE** likely explanation of the 0.75 allometric scaling law. This model is based on fractal geometry. The arguments in this paper don't seem applicable to protozoa. I will review Banse's work indicating that among protozoa and unicellular algae, the 0.75-allometric scaling doesn't seem to apply.

Even though ecologists and physiologists cannot explain the 0.75-weight scaling law, they must use it. In biological oceanographic models, the 0.75 scaling law is used extensively. This scaling controls the rate at which zooplankton feed on phytoplankton, the rate at which phytoplankton and zooplankton respire, and the rate at which zooplankton excrete nutrients.

Biological oceanographers deal with organisms that span at least 7 or 8 orders of magnitude in length, ranging from viruses ( $10^{-8}$  m) to fish ( $\approx 10^{-1}$  to 1 m) to whales ( $>10$  m). Even the phytoplankton span 4 orders of magnitude in width from ( $10^{-7}$  m to over  $10^{-3}$  m). Allometric scaling is essential to understanding many biological oceanographic processes.

The second required reading is a very interesting paper by **Kenney et al. (1986)**. They use a simple, but standard allometric scaling, to predict the density of calanoid copepods required by the right whale. This topic is especially important in understanding Massachusetts and Cape Cod Bays, because the Great South Channel Region outside of Cape Cod Bay is one of the most important right whale feeding grounds.



When reading **Kenney et al. (1986)**, pay attention not only to the allometric scaling arguments, but also consider some of the ecological factors that determine why right whales feed in Cape Cod Bay. This could be a key area for future research. Charles Greene at Cornell University, describes in a world wide web page a model that shows how aggregated patches of zooplankton can result from the interaction of zooplankton vertical migration patterns with submarine topography: (URL: <http://www.tc.cornell.edu/Research/Articles/GEO/OCE/Greene/greene.html>). Large zooplankton of the size required by baleen-feeding whales usually vertically migrate (down during the day, up at night). In areas with bottom depths shallower than the 1% light depth, this vertical migration pattern is disrupted. Copepods can be concentrated in dense patches because there is insufficient water depth for them to vertically migrate. Green & Wiebe have documented this process and provide a number of movies (in mpeg format) showing zooplankton patch development due to the interaction of topography, vertical migration and currents. Figure 1 is a frame from one of their movies.

## PHYTOPLANKTON

**Banse (1982a)** concluded that the mass-scaling of phytoplankton specific growth rate is one of the few areas where allometric scaling breaks down. There is

**Figure 1** A frame from C. Greene's web page <http://www.tc.cornell.edu/Research/Articles/GEO/OCE/Greene/greene.html>, showing zooplankton patches forming due to the interaction of submarine topography and zooplankton vertical migration. Each patch is formed on a daily time scale as zooplankton which could not vertically migrate to depth are focused near the surface. These patches are then advected away from the submarine feature.

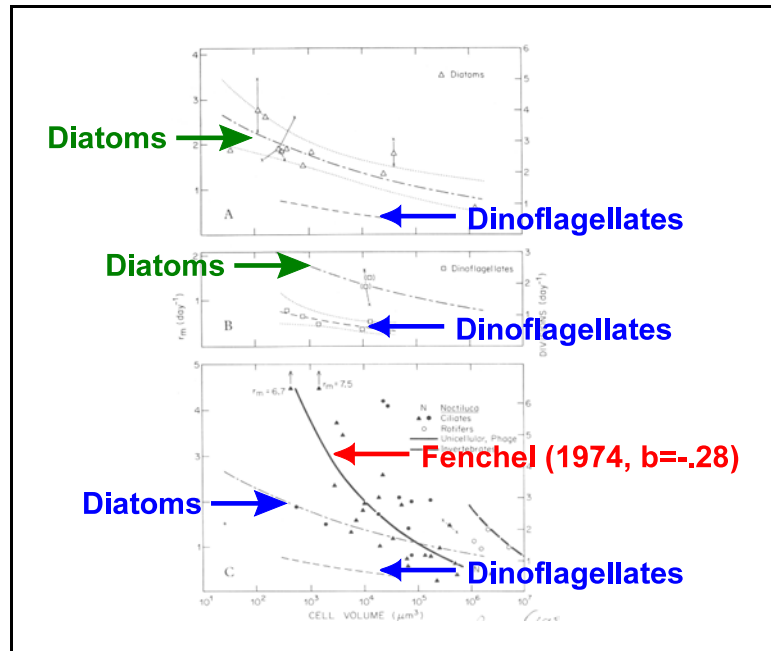
only a very weak mass dependence of phytoplankton  $\mu_{\max}$ . Taxonomic differences among phytoplanktonic groups of similar size often outweigh any simple scaling based on size. As shown in Fig. 2, **Banse (1982a)** showed that diatoms appear to have the highest  $\mu_{\max}$  for their size and dinoflagellates the lowest. Dinoflagellates of a given size tend to grow at a much lower  $\mu_{\max}$  than diatoms and other algal groups fall in between these 2 extremes. **Banse (1982a)** also showed the heterotrophic protozoa have  $r_{\max}$  values much higher than similarly sized phytoplankton. One cannot assume that small phytoplankton cells have a  $\mu_{\max}$  that is intrinsically greater than a larger phytoplankton cell.

There are several problems relating to the scaling of body size of phytoplankton. The first is why is there such a tremendous range in body size in phytoplankton. Hutchinson posed his paradox of the plankton which asks why are there so many species of phytoplankton when all are competing for a limited number of resources? There is a rich literature on solutions to the paradox. The most compelling explanation is Hutchinson's solution: competitive exclusion rarely occurs because the pelagic environment does not remain constant enough for long enough for one phytoplankton species to consistently have the competitive edge over another. A second compelling explanation is that there are a wide variety of pelagic niches in space and time. That is, the resource spectrum is not as simple as Hutchinson suggested.

Still ecosystem modelers have faced the problem of creating conditions under which the size or taxonomic diversity of phytoplankton can be maintained. For example, **Steele & Frost (1977)** gave large phytoplankton cells an edge over small by giving large phytoplankton an edge in the uptake of nutrients ( $V_{\max}$ ) and with lower weight-specific metabolic costs. Large cells had a higher mortality rate from sinking from the euphotic zone. Most ecosystem models have adopted this approach. Large cells are given an edge through higher  $V_{\max}$  for nutrient uptake and small cells are given the competitive edge at low nutrient concentrations by having a lower  $K_s$  or half-saturation constant for nutrient uptake or growth at low.

**Malone (1980)** predicted that large phytoplankton cells do better than small when nitrate is the predominant form of nitrogen. **Turpin & Harrison (1979, 1980)** and **Turpin et al. (1981)** showed that large phytoplankton cells increase their proportionate representation in a community under conditions of higher nutrient patchiness (see references on the nutrient handout). Large cells can take up larger amounts of an ephemeral, patchy nutrient supply. **Harrison & Wood (1988)**

Unfortunately, the physiological correlates of large and small body size in phytoplankton are not as simple as the ecosystem modelers suppose. **Fogg (1986)** and **Raven (1986)** review the physiological consequence of extremely small body size in phytoplankton. They can grow faster than large cells, but they experience very high metabolic costs due to the short diffusion pathways. Large phytoplankton cells can compartmentalize the site of carbon fixation, allowing them to better maintain a high  $\text{CO}_2$  to  $\text{O}_2$  ratios at the Rubisco active site. **Geider et al. (1986)** reviewed the physiological data on phytoplankton photosynthesis and respiration. They argue that the only advantage of large phytoplankton cells over small is that they suffer less grazing mortality from microzooplanktonic grazing. [Please note how **Geider et al.'s (1986)** equation relating the assimilation number, C:Chl a ratio and  $\mu$  differs from **Eppley's (1972)** Equation 5.]



**Figure 2.** Banse (1982) showed only a weak allometric scaling between diatom & dinoflagellate specific growth vs. body size. For a given size, diatoms have a much higher specific growth rate. The exponent is -0.13 instead of -0.25. The above graph shows the Fenchel relationship plotted vs. the best fit diatom and dinoflagellate regressions.

Large phytoplankton cells may be selectively ingested by the macrozooplankton. Indeed, George **Jackson (1987)** used equations for molecular diffusion and phytoplankton growth to predict that small phytoplankton cells ( $<5 \mu\text{m}$ ) do not produce the chemical plumes that macrozooplankton use to detect food. *<Fall 2000 note some recent work indicates that macrozooplankton may detect deviations in the flow rather than chemical plumes for detecting phytoplankton cells.>* However, large mesozooplanktonic grazers, like calanoid copepods, are rarely the most important grazers in oceanic pelagic ecosystems. The dominant grazers in most of the world's oceans are small heterotrophic nanoflagellates and ciliates. These small grazers don't need to detect chemical plumes to feed. They are probably 'contact feeders', ingesting particles that they directly contact (*i.e.*, no detection at a distance). Even in neritic ecosystems, primary production may be dominated by nano- and picoplanktonic sized phytoplankton that are grazed ineffectively by the large calanoid copepods.

## ZOOPLANKTON

The days are past when biological oceanographers can model planktonic production using one species of calanoid copepod, like *Calanus finmarchicus*, feeding on large diatoms. Biological oceanographers must be able to view primary and secondary producers and the trophic interactions among these groups at a variety of size scales from the pico- to macrozooplankton.

### *The size-efficiency hypothesis*

**Brooks & Dodson's (1965)** size-efficiency hypothesis was one of the first attempts to analyze the interactions among different sizes of phytoplankton and zooplankton. Unfortunately, their hypothesis is wrong in almost every essential feature. One especially glaring error is their assumption that large body size confers **competitive** advantages in the exploitative competition for scarce food resources. In exploitative competition for scarce resources, large body size confers few if any advantages. **Hall et al. (1976)** applied allometric scaling relationships to model the size-efficiency hypothesis. Their conclusion was that there was no clear competitive advantage in large size except at low food concentrations. At intermediate or high food concentrations, the higher  $r_{\text{max}}$  of the smaller species (see **Fenchel 1974**), would lead to their competitive dominance. Their work and especially the demographic models of Lynch showed that there could be tremendous advantages to large body size if predation rates were lower on larger zooplankton. A recast version of the size-efficiency hypothesis would have to emphasize that the key correlates of body size in lake systems and the ocean is vulnerability to predation. Invertebrate predators are strongly constrained to eat only those organisms that they can capture and ingest. Visual predators virtually always capture organisms that they detect, their ingestion rates are controlled by their ability to see prey. Visibility is a strong function of organism size.

### *Species vs. size categories*

Some modelers have proposed that size should replace traditional taxonomic categories. **Sheldon & Parsons (1967)** found that the biomass in each  $\log_2$  size class in pelagic systems was roughly constant. This has come to be known as **the linear-biomass hypothesis**. Based on this earlier work, recent models have handled the energy transfer among biomass size classes, not taxonomic groups.

**Frost (1980)** addressed this issue for copepods in his important paper, "The inadequacy of body size as an indicator of niches in the plankton." He pointed out that while all copepods seem to obey the same allometric power functions and the exponents are close to  $\frac{3}{4}$ , the y-intercepts,  $a$  in equation (1), differ tremendously among groups. Small copepods like *Pseudocalanus*, *Acartia* and *Oithona* have ingestion and growth rates that cannot be modeled using an allometric scaling appropriate for a large *Calanus*.

## BIOMASS SPECTRA IN THE PLANKTON AND THE LINEAR BIOMASS HYPOTHESIS

**Marquet et al. (2005)** provide a recent review of biomass spectra and the linear biomass hypothesis in ecology. Platt & Silvert had defined the normalized biomass spectrum, reviewed in **Zhou (2006)**

## BENTHOS

**Schwinghamer (1981)** examined the biomass spectrum of organisms in sediments, finding it to be very different from the pelagic linear biomass spectrum. Schwinghamer (1981, 1983) found that the biomass spectrum of benthic communities was bimodal in unpolluted communities, and unimodal in polluted communities. **Schwinghamer (1983)** used path analysis to analyze the biological interactions among size groups of primary and secondary producers in the benthos.

## LIMITATIONS OF ALLOMETRY

It is important to note the limitations of the  $\frac{3}{4}$  scaling law. Within different groups of organisms, the scaling law may work, but the y-intercepts differ. Unicellular organisms have a lower y-intercept ( $\alpha$  in the above equations) for metabolism than metazoans. **Peters (1983)** notes that a picophytoplankton cell respiring with a mammalian respiration y-intercept wouldn't be able to survive the night. Meiofauna tend to have much lower intrinsic growth and metabolic rates than similarly sized zooplankton species. **Banse (1982b)** argued that ciliates had a lower weight-specific metabolic rate than other macrozooplankton. Among benthic organisms, **Banse et al. (1971)** showed that large subsurface deposit feeders not only have a lower weight-specific respiration rate due to their larger body size, but they may also have a lower y-intercept as well.

Thus, there is a limit to the allometric scaling of biological oceanographic processes. While there is an almost universal  $\frac{3}{4}$  scaling for most physiological processes, the y-intercepts of these physiological processes differ widely among groups. For example, dinoflagellates tend to have lower specific growth rates than similarly sized diatoms (**Banse 1982a**). Benthic harpacticoid copepods have much lower metabolic and population growth rates than do similarly-sized pelagic calanoid copepods (**Banse & Mosher 1980**). **Frost (1980)** documents that generation times in calanoid copepods cannot be scaled as a simple allometric function of body size; small and large copepods, differing by more than 50-fold in body mass have similar generation times.

## Terms and concepts

### Efficiencies

Assimilation efficiency = assimilation/ingestion [**Handout 2**]

Fenchel '82 II: 60% assimilation efficiency for protozoa.

**Kenney et al. (1986)**: 80% assimilation efficiency assumed for cetaceans.

Ecological efficiency:

P:B ratios: Total annual production to mean population biomass, proportional to specific mortality rate

Zooplankton P:B ratios 10-36. Meiofauna 4.6 or lower, oligochaetes 0.85

Meiofaunal oligochaete P:B ratios: *Paranais litoralis* and *Amphichaeta sannio* 18.1 (**Giere & Pfankuche 1982**)

Net growth efficiency = somatic growth/(Growth + Respiration) [**Handout 2**]

a independent of mass if the exponents are the same

b see **Sebens (1987)**, **Banse (1979)**

**Predation refuge hypothesis:** **Banse & Mosher (1980)** and **Banse (1982b)** propose that the relatively low mass-scaled P:B ratio of small organisms, especially meiofauna is due to limited predation lower mortality of developmental stages (*e.g.*, nauplii)

## Outline of Ideas on Allometry

- I. History of Allometry (from Dr. K. Banse's UW 'Allometry' course)
  - A. 1726: J. Swift Gulliver's travels.



Swift's length scaling in Lilliput is consistently 12:1, in Brobdingnag 1:12.  
 The King of Lilliput strikes a contract granting...

*"The said Man-Mountain shall have a daily allowance of meat and drink sufficient for the support of 1728 of our subjects ... The reader may please to observe, that in the last article for the recovery of my liberty, the Emperor stipulates to allow me a quantity of meat and drink sufficient for the support of 1728 Lilliputians. Some time after, asking a friend at court how they came to fix on that determinate number, he told me, that his Majesty's mathematicians, having taken the height of my body by the help of a quadrant, and finding it to exceed theirs in the proportion of twelve to one, they concluded from the similarity of their bodies, that mine must contain at least 1728 of theirs, and consequently would require as much food as was necessary to support that number of Lilliputians. By which the reader may conceive an idea of the ingenuity of that people, as well as the prudent and exact economy of so great a prince."* (p. 59).

1. Swift scaled biomass according to volume, a cubed function of body length
  2. Swift assumed that food intake was linearly proportional to biomass
    - a. Note that the proper scaling if the above  $\text{Mass}_1/\text{Mass}_2=(L_1/L_2)^3$  scaling is correct would be  $\text{Ration} = 1728^{0.75}$  power = **268 rations**, not **1728!**
    - b. Gulliver would have been give **144 rations** with an exponent of  $2/3$  instead of 1728 rations
- B. 1847: Bergman's rule  
 size of appendages decreases with latitude (ears decrease with latitude)
- C. Cope's rule: increasing body size with phylogeny (see Peters 1983)
- D. Rubner
  1. 1883, experimental study on dog metabolism.  $\text{Resp}=a*W^{2/5}$
  2. 1888: found that same respiration rule applies to fish
- E. 1932: Kleiber, mammals.  $\text{Respiration}=a*W^{0.75}$ , different from  $2/5$
- F. 1934: Brody- expanded relationship from mice to elephants.
- G. 1960: Hemmingsen: extended basal metabolism relationships to include plants.
  1. different intercepts for unicellular, poikilotherms and homeotherms
  2. slope =0.75
- H. **Fenchel (1974)** applies allometric scaling to the maximum instantaneous rate of increase,  $r_m$ , finding a slope close to -0.25
- I. **West et al. (1997)** explain the allometric exponent in terms of fractal geometry.
- II. Metabolism:
  - A. Metabolic balance:  
 Ingestion = somatic or individual growth + reproductive growth + respiration + egestion + excretion.
  - B. Ingestion and each of the terms in the metabolic equation scales with biomass to the 0.75 power.
- III. Ingestion & Substrate uptake:
  - A. For macrophages.
    1. Prey size: Predator size. There is a characteristic scaling of food size to predator size.
      - a. This plays a large role in the **Azam et al. (1983)** microbial loop hypothesis.
        - (1) picoplankton are fed on by heterotrophic microflagellates
        - (2) ciliates feed on small microplankton. They do not feed well on bacterioplankton.
        - (3) calanoid copepods feed on phytoplankton larger than 8-10 $\mu\text{m}$  size.
      - b. Modified size-efficiency hypothesis.
        - (1) Invertebrate predators (e.g., *Sagitta*, *Euchaeta*) feed poorly on prey very much smaller than themselves or larger.
        - (2) Visually feeding predators must detect zooplankton in order to feed on them. Detection is a function of light intensity and body size (cubed)
    2. large predators more variable in choice of prey
  - B. Microphages
    1. Phytoplankton
      - a. Uptake of nutrients dependent on surface:volume ratio

- b. Leakage of DOM and DIC dependent on algal size, with smaller cells having proportionately higher loss rates (**Geider *et al.* 1986**). Up to 40% of the CO<sub>2</sub> converted from HCO<sub>3</sub><sup>-</sup> in cyanobacteria make leak from picoplanktonic sized cells.
  - c. Presence of detectable chemical plumes by chemotactic zooplankton strongly dependent on algal size. **Jackson (1987)** modeled that actively growing small algal cells (< 10 μm) do not have chemical plumes that extend more than 1 cell radius away from the cell.
  - d. **Malone (1980)** proposed that large cells depend on new N and nanoplankton on regenerated nitrogen.
  - e. Turpin and Harrison (**1979, 1980**) and **Turpin *et al.* (1981)** could switch the relative proportions of large and small diatoms in chemostats by increasing the variance in NH<sub>4</sub><sup>+</sup> supply. Large diatoms do better with increased nutrient patchiness.
2. Zooplankton
- a. zooplankton ingestion scales according to W<sup>0.75</sup>
  - b. However, different zooplankton groups have different Y intercepts. See Frost (1980), the inadequacy of body size as an indicator of niches in the plankton!
    - (1) Ciliates
      - Banse ('82a)**: Mass-scaled ciliate grazing lower than that for copepods; also mass-scaled excretion lower. Ciliate mass-scaled respiration (hence excretion is) less than copepods. Hence their biomass would have to be much higher to have a similar ingestion rate.
    - (2) **Fenchel (1980)**
      - (a) ciliates can be important grazers on phytoplankton
      - (b) dominant grazers in project SUPER (**Frost 1988**)
      - (c) ciliates can be important in sediments as bacterial grazers.
  - c. Heterotrophic microflagellates may control bacterial standing stocks (**Azam *et al.* 1983**)
    - (1) numerous other papers on Microbial loop handout
    - (2) Fenchel '82 II.
      - (a) 60% assimilation efficiency for protozoa.
      - (b) heterotrophic microflagellates can control bacterial standing stocks.
    - (3) Fenchel '82 IV
      - (a) 16-day predator prey cycle between bacteria and heterotrophic microflagellates
      - (b) heterotrophic microflagellates can filter 20% of water/day
  - d. Calanoid copepods
    - Steele & Frost (1977)**: scaled ingestion to size of animals
    - (a) feeding electivity a function of body size
    - (b) allometric ingestion.
- C. Benthos.
1. Micro- and meiofauna.
- a. Fenchel (1969?) Qualitative and quantitative significance of the microfauna, especially ciliates in benthic ecosystems. page 165.
    - (1) Bacteria most important
    - (2) Fenchel's macrofauna includes oligochaetes. (>0.10 mg)
    - (3) in non-capillary sediment, only nematodes represent the microfauna
    - (4) Fine sand in 10 m depth. Smith-McIntyre grab.
    - (5) weight category 10<sup>-5</sup> to 10<sup>-4</sup> g (.01 to .1 mg) seems lacking at 10 m. Hiatus between macrofauna and interstitial fauna
    - (6) microfauna accounts for 40% of respiration and ciliates 25% (note bacteria left out)

- (7) Niva Bay: no size hiatus.
- (a) many oligochaetes, *Hydrobia* ( $10^{-3}$  to  $10^{-2}$  g), small polychaetes.
- (b) macro:micro:ciliates = 1:10:50 numbers  
 = 170:10:1 weight  
 = 4:2:1 metabolism
- (c) ciliates account for 14% and microfauna more than 40% of animal respiration.
- b. Fenchel 1978 review:
- (1) metabolic rate per unit weight increases by 1.77 for a reduction in body weight by a factor of 10
- (2) **Gerlach (1978)** meiobenthos have 5 x the mass-specific metabolic rate of the macrofauna.
- (a) metazoan carbon flow = 15% \* macrofauna
- (b) Vernberg & Coull ciliates: metazoan meiofauna: macrofauna
- i) = 1:0.5:2.1 for a sandy sublittoral
- ii) = 1:3.4:1.9 for estuarine sediment
- iii) = 1:0.54:0.04 for an exposed beach
- c. **Fenchel (1980)**
- (1) ciliates can be important in sediments as bacterial grazers.
- (2) ciliates can control bacterial abundances in aquatic sediments
- d. **Banse (1982b)**: Because of differences in slope of P:B with weight, nematode importance has been overestimated in many studies (*E.g.*, Gerlach)
2. Macrofauna
- a. **Cammen (1980)**

$$C = 0.381 * W^{0.742}$$

where,  $C = \text{organic matter ingestion} \left[ \frac{\text{mg organic C}}{\text{day}} \right]$

$W = \text{individual weight} [\text{mg dry weight}]$ .

**Fig. 1:**

log body weight linearly correlated with log dry weight ingested.

**Fig. 2:**

log body weight linearly correlated with log organic matter ingested

**Fig. 3:**

log body weight inversely correlated with log organic matter in food

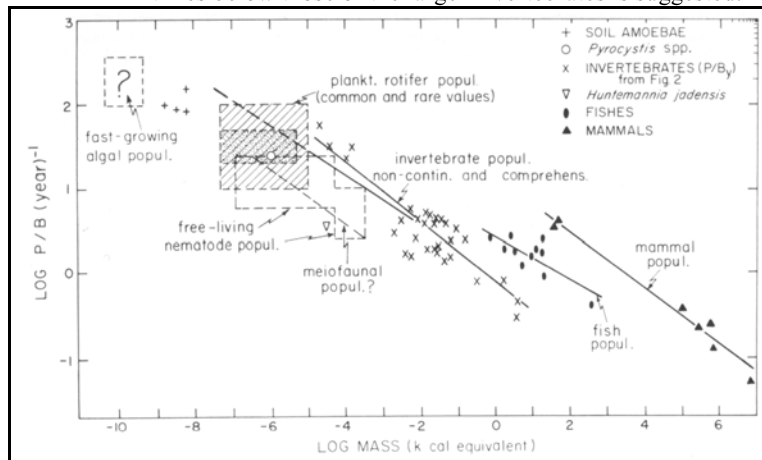
- (1) aquatic detritivores ingest more substrate when organic content is low
- (2) large detritivores feed on less rich material and therefore pass more material
- (3) Forbes: organic matter ingestion scales with body weight to the 0.74 power
- (4) Hypotheses
- (a) organisms can adjust ingestion rate in response to **food quality**
- (b) the relation shown here may represent the end result of long-term adaptation by the various species populations.
- b. **Peters (1983, p. 116)**: content of organic matter in detritivores declines as  $W^{-2.5}$
- (a) achieved through selection of sites.
- (b) Case finds that large African ungulates feed on poorer food
- (c) smaller species feed at richer sites.
- (2) Taghon predicted that ingestion rate should increase with increasing organic content. Neil Phillips showed that if the minimum food ration is achieved, ingestion rate should decline.
- (3) **Forbes & Lopez (1987)**:
- (a) pellet weight to body weight to the 0.7 power
- (b) pellet production (number) independent of body size
- (c) egestion scales with body weight to the 0.7 power, *i.e.*, larger Capitellids process less sediment than smaller capitellids per unit weight

- IV. Respiration
- A. Respiration scales allometrically to  $W^{0.75}$   
-differences in intercept among major groups: unicellular, poikilotherms, heterotherms
- B. **Peters (1983)** basal Metabolism:
1. basal metabolism = respiration.
  2. Peters. Fig. 3.2 (p. 32). unicells have a lower mass-scaled metabolism than poikilotherms, less than homeotherms. Slope the same (-.25)
    - a. homeotherms draw more power than poikilotherms of the same body size.  
- dinosaur example.
    - b. metabolic rate rises more slowly than body size.
    - c. the energy flow to support one half-ton moose would only maintain about 40kg of 20 g-mice (Peters p. 33)
    - d. **Turnover time:** time to respire energy in all tissues:  
Table 3.3 p. 34 7.3 d for a mouse. 91 d for a moose.
  3. Big animals are more resistant to food shortages than small (p.34)
  4. cold blooded animals resist starvation better (p.35)
  5. an active algal cell, if scaled like a mammal could not survive the night. (p, 35)
- C. Phytoplankton: **Geider et al. (1986)** argue that larger cells may not have much of a reduced weight-specific respiration.
- D. Benthos:  
**Banse et al., (1971):**
1. The following equation was used:  $\log r = a \log t + b \log W + c$ , in which r is respiration in microliters of oxygen per hour, t is temperature (Celsius) and W is the ash-free dry weight (in mg).
  2. *Lumbrineris zonata*, a subsurface deposit feeder, has a very low respiration rate for its size. The exponent for polychaete regression relationships is slightly less than 0.75"
  3. False Bay work. Subsurface deposit feeders have a lower specific respiration cost than surface deposit feeding polychaetes.
  4. spionids have higher respiration costs, relatively (*Pseudopolydora kempji japonica*)
- V. Defecation
- A. Cammen and Hargrave found that egested feces rise almost as fast as body size  
- Forbes found a 0.7 slope
- B. Larger benthic detritivores ingest and defecate large amounts of material but have normal rates of energy consumption.
- C. the defecation rate of smaller poikilotherms might be overestimated from the linear relation observed by Cammen and Hargrave. (**Peters 1983**)
- VI. Growth & Reproduction
- A. Peters '83:
1. Isochronal rule: regardless of size, a given developmental stage requires a constant proportion of an animals life.
  2. Somatic growth curves: Table 8.1 p. 123. Gompertz, logistic, Von Bertalanffy.
  3. poikilotherms can have indeterminate growth
    - a. somatic growth is sigmoid
    - b. see Sebens model for optimum body size.
  4. Total clutch mass/size doesn't vary between groups: total investment in a single reproductive event is a conservative property.  
absolute investment rises as  $W^{0.75}$
- VII. Nutrient release
- A. **Peters 1983**
1. nutrient flux scales with metabolic rate
  2. nutrient release rises as  $W^{0.75}$  (Peters. p. 159)
- B. Caron (1988) proposes differences in chemical composition to account for excretion by microzooplankton. If bacterial carbon source is nitrogen rich, then and only then can they excrete N.
- C. Chemical composition: no apparent trends in Redfield ratios as a function of body size (**Banse 1982a**)
- D. Excretion: must scale with respiration (Banse 1972)

- VIII. Ecological efficiencies
- A. PTH p. 243. Herbivores lowest efficiency, carnivores highest (Humphreys 1979)
  - B. Net Growth efficiency (Sebens)
    1.  $g/(g+q)$ , where  $g$  is growth and  $q$  is respiration
    2. independent of mass if the exponents are the same
    3. see Sebens
- IX. Size and specific growth
- A. Sheldon *et al.* 1973:
 

$\log_{10} T_D = 0.64 + 0.8 \log_{10} L$   
 where,  $T_D$  = doubling time  
 $L$  = length in mm.
  - B. **Fenchel, T. 1974. Intrinsic rate of natural increase: the relationship with body size. *Oecologia (Berlin) 14: 317-326.*** “*This classic paper presents an allometric equation for the relationship between  $r_m$  and body size, with body size ranging from viruses to whales.  $\log_{10} r_m = a - 0.275 \log_{10} \text{Weight}$ , where  $a$  is  $-1.9367, -1.6391$ , and  $-1.4$  for unicellular, heterotherm metazoan and homeotherms metazoans respectively.*”
    1. Exponent not greater than 0.75
      - a. **Banse (1982b)**
      - b. **Blueweiss *et al.* (1978)** reanalyzed data, exponent not different from 0.75
  - C. Phytoplankton: no clear allometric scaling
    1. Mass dependence not clear in phytoplankton: drastic differences among phylogenetic groups
    2. Eppley (1972) found maximum diatom growth of  $2.1 \text{ d}^{-1}$ , cited by Banse
    3. dinoflagellates have lower  $r_m$  relative to diatoms
      - a. some exceptions, in **Banse ‘82a**
      - b. low mass dependence in dinoflagellates (**Banse 1982a**)
    4. **Geider *et al.* 1986** review effects of size on phytoplankton physiology
  - D. Zooplankton: no clear allometric scaling among microcrustacea
    1. Complete lack of mass dependence of  $r$  in Cladocerans (**Banse 1982b**)
    2. J. D. Allan (1976)
      - a. uses Lewontin’s figure to estimates  $A$ ,  $T$ ,  $W$  and  $S$  (the  $l_x m_x$  triangle)
      - b. rotifers > cladocera > Copepoda
      - c. ability to overwinter may confer an advantage to copepods. see **Peters 1983** on the amount of time a species reserves can last. Small species at a disadvantage.
    3. **Hall *et al.* (1976):**
      - a. lower respiration costs are a key assumption of the size-efficiency hypothesis.
      - b. Fig. 1: optimum body size increases as food supply decreases.  
 “*Mathematical and graphical models are presented for **Brooks & Dodson’s (1965)** size-efficiency hypothesis. The cornerstone of the models is the assumed allometric relationship for weight specific respiration and ingestion, giving larger species an energetic advantage at low food concentrations. At high food concentrations, smaller body sizes have an advantage (due to higher  $r_m$ )*”
  - E. Meiofauna (Banse)
    1. meiobenthic nematodes have a lower mass-scaled growth ( $<0.12 \text{ d}^{-1}$ )
    2. meiobenthic rates may be lower than protozoa of the same mass
    3. **Banse 1982b** Fig. 4. Meiofauna have lower specific growth rates.
- X. Size and P:B ratios = Turnover Ratio.
- A. Definition of P:B ratio: Total annual production to mean population biomass
    1. On average, specific production rates of all members of the population weighted for their temporal duration or to the sum of all productivity terms associated with the life history again biased according to the number and duration of the population’s members at each ontogenetic stage (**Peters (1983 p. 133)**)
    2. Waters found that within a lifespan TR ranges from 2.5 to 6 with a mode at 3.5. Annual TR’s are multiplied by the generations per year to obtain annual P:B ratios.  
 $\log_{10} \text{P:B} = 0.69 - 0.14 T_D$ , where  $T_D$  = generation time
      - (1) accounts for 60% of the variance
      - (2) if  $t=1$ , then value = 3.55, the modal value

- (3) Marine macrobenthos (lifespan > 1 year)  $\log_{10} P:B = 0.66 - 0.73 t$ , where  $t$  = generation time
3. Zooplankton have P:B ratios between 10 and 36
  4. P:B ratio of macroinfauna=2 (Gerlach 1978)
  5. Ankar & Elmgren found P:B ratios for meiofauna =4.6 (relatively slow ostracods and juvenile molluscs)
- B. General: **Banse and Mosher (1980)**
1. from copepods to clams,  $10^5$  range in body mass,  $10^2$  range in production
  2. Production: biomass declines with individual biomass to the  $-0.37$  power.
    - a. lower P:B ratios have low P/R ratios (0.1)
    - b. twice the predicted P/B ratios have P/R ratios of 1
    - c. annual specific mortality rate scales as P:B ratio
    - d. For meiofauna, a power function of mass dependence of P/B with average rates 3-5 times below those of the larger invertebrates is suggested.



**Figure 2.** P:B ratio declines with body weight to the  $-0.37$  power, from Banse & Mosher (1980).

3. P:B declines as  $W^{-0.37}$ , not  $-0.25$  as one might expect.
    - a. slopes differ between groups, steep slope for inverts. slope near  $-0.25$  for fish
    - b. Production: respiration ratios key.
    - c. small Metazoa have a lower mass scaled P:B ratio than the relationship suggests.
  4. In stable populations specific mortality rate equals P/B, and hence this also declines as  $0.65 * M^{-0.37}$ 
    - a. since intercepts differ, the Metazoa have a predation refuge.
    - b. thus Metazoa have a lower specific mortality rate.
  5. Predation refuge hypothesis
    - a. **Banse & Mosher (1980)** and **Banse (1982b)** propose that the relatively low mass-scaled P:B ratio of small organisms, especially meiofauna is due to limited predation
    - b. lower mortality of developmental stages (e.g., nauplii Banse 1982)
- C. Bagheri and McLuskey (1984):
1. used 3 methods: Gibson respirometer,  $O_2$  electrode and Cartesian diver.
  2. Uses Humphrey's relation  $\log$  production =  $0.942 \log$  respiration  $-0.252$
  3. annual production ranges from 0.84 to 3.33 g ash free dry weight  $m^{-2} yr^{-1}$  in the Forth estuary
  4. Mean P:B ratio is 0.85:1.
    - a. lower than most values in the literature
    - b. P:B ratio of *Manayunkia aestuarina* = 2.34 in the Forth, 5.5 reported by Warwick for *Ampharete acutifrons*.
    - c. P:B ratio for *Paranais litoralis* and *Amphichaeta sannio* is 18.1 (**Giere & Pfankuche 1982**)

- d. "Small polychaetes and oligochaetes may comprise 49% of total invertebrate secondary production."
  - e. total production is  $16.9 \text{ g m}^{-2} \text{ yr}^{-1}$
  - f. *Manayunkia* and *Tubificoides* dominant
  - g. *Manayunkia* production is  $3.67 \text{ g m}^{-2} \text{ y}^{-1}$
  - h. In some areas, small polychaetes account for 90% of the production.
- XI. Temperature and biomass
- A. Animal size can increase with temperature (Corkett & McLaren, McLaren)
  - B. Forbes shows an exponential increase in temperature with development
  - C. isochronal rule: development time lengthens with decreasing temperature, but the % of time spent in each demographically discrete stage remains the same.
  - D. Parsons et al. (1984). p. 245: Brinkhurst 1971
    - 1.  $P:B = \text{Turnover Ratio} = T^2/10$ , where T is in degrees Celsius
    - 2. annual production =  $P = B*[T/10]$
- XII. Animal abundance and size:
- A. Pelagial
    - 1. The linear size hypothesis.
    - 2. Sheldon *et al.* ATP measured in different size classes **Sheldon & Parsons 67**
      - a. base 2 log scale
      - b. no trend in biomass with size.
      - c. reviewed by PARSONS ET AL. (1984) (p.278):
        - (1) roughly similar amounts of biomass in log equal size intervals from 1 to  $10^6 \mu\text{m}$  (plankton fish to whales).
        - (2) fish standing stock can be estimated from zooplankton.
        - (3) estimated total PP and estimated 10 size classes (wet weight) for phytoplankton 8-80 micrometers (see PARSONS ET AL. (1984) table 41, p. 279)
        - (4) herring occupy 2 size grades and cod 4
        - (5) estimated that maximum amount of fish already being harvested.
        - (6) theoretically treated by **Platt & Denman 1978**.
        - (7) predicting the biomass of the Loch Ness monster and mermaids (Banse)
    - 3. Banse: ciliates consume little food relative to post-naupliar copepods because their food supply is too low (Banse 1982, L&O)
      - a. predation refuge for ciliates (Banse 82)
      - b. Banse disagrees with Sheldon & Kerr
  - B. Size spectra of the benthos:
    - 1. **Gerlach 1978** . A model 30-m subtidal station.
      - a. Parsons et al. (1984) summary. 242
      - b. 30 m deep silty sand station
      - c. Meiofauna and Foraminifera contribute 30 and 12% of biomass
      - d. bacteria are the main food of macro, meio- and microfauna
      - e. meiofauna and macrofauna don't compete because meiofauna stimulate bacterial productivity
      - f.  $10 \text{ gm}^{-2}$  organic matter of macrofauna =  $200 \mu\text{g/ml}$
      - g. meiofauna 40 micron to 500 micrometers
      - h. microfauna:
        - (1) Foraminifera and nematodes
        - (2) ciliates
      - i. bacteria
        - (1) biomass in doubt
        - (2) Gerlach assumes  $100 \mu\text{g/ml}$
        - (3) Moriarity calculates 0.4 to 2.6 mg bacterial carbon per g
      - j. energy flow
        - (1) 36% to 50% of spring bloom may sediment to the bottom
        - (2) epifaunal predators (*e.g.*, *Crangon*) can't hunt meiofauna efficiently
        - (3) ciliates, flagellates and small nematodes are digested by *Abarenicola*, but only constitute a small fraction of its food (Hylleberg 1975).
        - (4) P:B ratio of macroinfauna=2

- (5) Ankar & Elmgren found P:B ratios for meiofauna =4.6 (relatively slow ostracods and juvenile molluscs)
  - (6) Meiofauna account for only 18% of macroinfaunal food demand
  - (7) annual bacterial P:B ratios of only 30
  - (8) benthic activity stimulates bacterial production
2. **Schwinghamer, P. 1981.**
- a. Characteristic size distributions of integral benthic communities. *Can. J. Fish. Aquat. Sci.* 38: 1255-1263. "Documents a bimodal distribution of benthic organism sizes."
  - b. 1983. *Mar. Ecol. Prog. Ser.* 13: 151-166.
    - (1) Size spectra for different areas and different seasons are produced
    - (2) **Schwinghamer (1983)** found 3 biomass peaks
      - (a) bacteria,
      - (b) meiofauna
      - (c) macrofauna.
    - (3) 32 µm size class dominated the microalgae
    - (4) analyzed data with Sewall Wright's path analysis. Indirect evidence is offered for competition between juvenile macrofauna and permanent meiofauna for microalgae
  - c. 1985. 19th European *Mar. Biol. Symposium.*
    - (1) size spectra of benthic food chains mirror images of pelagic food chains.
    - (2) Harris: herbivorous zooplankton graze the nanoplankton, the larger phytoplankton sediment. Thus, there is an explanation for the larger size of benthic grazers.
3. Gerlach, S. A., A. E. Hahn. and M. Schrage. 1985.
- a. Trough in biomass at about 5 µg weight, between meiofauna and macrofauna
  - b. Fenchel '69, organisms in trough to large to move between sand grains.
  - c. Confirms Schwinghamer's finding of a trough in the juvenile macrofauna size classes.
  - d. Metabolism dominated by the meiofauna.
4. Warwick, R. M, N. R. Collins, J. M. Gee and C. L George. 1986. *Mar. Ecol. Prog. Ser.* 34: 63-68.  
Standard bimodal distribution
- a. meiofaunal mode at .63 µg dry weight
  - b. macrofaunal mode at 2.03 mg
  - c. trough at 60 µg
  - d. planktrophic larvae avoid competition with the meiobenthos but settle when they reach the size of the holoplankton
5. Thiel, H. 1975. The size structure of the deep-sea benthos. *Int. Rev. Ges. Hydrobiol.* 60: 575-606. Thiel found deep-sea benthos dominated by small organisms
- a. Reduced level of resource supply accounts for this
  - b. Proposes that the small body size of deep-sea organisms is due to the low energy flux to the bottom.
  - c. **Cammen's (1980)** empirical regression might suggest that larger deposit feeder body sizes might result under such conditions. The paradox remains unresolved."
- C. Diversity. (**Peters 1983, p. 179**), uses May's relationship
1. species number falls as  $W^{-.67}$
  2. Fig. 10.5 overestimates the number of small species at a site.

## Outline of papers

### REQUIRED



**Kenney, R. D., M. A. M. Hyman, R. E. Owen, G. P. Scott, H. E. Winn. 1986. Estimation of prey densities required by Western North Atlantic Right Whales. Marine Mammal Science 2: 1-13. [2, 5, 8]**

I. Abstract

- A. Lack of recovery may be related to prey availability
- B. This paper provides estimates of prey density required
- C. Estimate requires
  - 1. Body weight
  - 2. Metabolic rate
  - 3. Assimilation efficiency
  - 4. Time spent feeding
  - 5. Mouth size
  - 6. Swimming speed.
- D. Estimated food requirements
  - 1. 7.57 to 2394 kcal m<sup>-3</sup> (3.17 x 10<sup>4</sup> to 10<sup>7</sup> joule m<sup>-3</sup>)
  - 2. Estimates are 1 to 3 orders of magnitude greater than the densest concentrations of zooplankton sampled near right whales.
- E. Right whales must seek out dense aggregations of prey.

II. Introduction

- A. Right whale (*Eubalaena glacialis*) is the most endangered whale species inhabiting continental US waters.
  - 1. Numbers drastically reduced by whaling
  - 2. Little recovery in numbers
  - 3. Current estimates of numbers: a few hundred concentrated
    - a. Great S. Channel region east of Cape Cod in spring and early summer
    - b. Mouth of Browns Bank off SW Nova Scotia in summer and early fall.
- B. Food of right whales
  - 1. Calanoid copepods and juvenile euphausiids\
  - 2. *Calanus finmarchicus* a preferred right whale prey.
- C. Hypotheses: insufficient prey densities (the mean), or right whales seek out aggregated patches (variance:mean)

III. Methods and Results

- A. Allometric scaling,
  - 1. Brody's (1968) equation (Q is metabolic rate in kilocalories per day, and W is body weight in kilograms)

$$Q = 70.5W^{0.7325}$$

- 2. Average body weight: 40,000 kg
- 3. Basal metabolic requirement: 1.66 x 10<sup>5</sup> kcal d<sup>-1</sup>
- 4. Feeding Rate:
  - a. Assume 80% assimilation efficiency
  - b. Feeding rate=2.07 x 10<sup>5</sup> kcal d<sup>-1</sup>.
- 5. Filtering rate
  - a. Mouth cross section x swimming speed
  - b. Filtering rate=6.25 x 10<sup>3</sup> m<sup>3</sup> h<sup>-1</sup>.
- 6. Time spent filtering: 15.8 h d<sup>-1</sup>.
- 7. Minimum required concentration of prey:  
2.07 x 10<sup>5</sup> kcal d<sup>-1</sup>/9.90 x 10<sup>4</sup> m<sup>3</sup> d<sup>-1</sup> =1.67 kcal m<sup>-3</sup>.
- 8. Caveats
  - a. Only basal metabolism
  - b. Mouth hydrodynamics
  - c. Reduced feeding or fasting
  - d. Mouth cross section
  - e. Swimming speed
  - f. 100 % filtration efficiency
  - g. Feeding time shorter than 15.8 h d<sup>-1</sup>.
- 9. Actual required prey are 4.5 to 1431 times the density we calculated. New estimate: 7.57-2394 kcal m<sup>-3</sup>.

- B. Results
1. May 1981 sampling near right whales
  2. Densest sample 93.3% *Calanus finmarchicus* (6182 zooplankton m<sup>-3</sup>, 5768 *C. finmarchicus* m<sup>-3</sup>)
  3. Zooplankton energy content (by bomb calorimetry): 0.72 kcal m<sup>-3</sup>.
  4. Food requirements are 5.5-3325 times the maximum estimated zooplankton food content and 18.9-5985 times the average.
  5. Required zooplankton densities:  $3.54 \times 10^4$  to  $1.12 \times 10^7$  m<sup>-3</sup>.
  6. Required densities of stage V *Calanus*:  $4.67 \times 10^3$  to  $1.48 \times 10^6$  m<sup>-3</sup>. (Sei whale estimate was  $1.8 - 5.0 \times 10^4$  m<sup>-3</sup>.)

IV. Discussion

- A. Allometry & basal metabolism
- B. Observed prey densities too low to meet energetic needs.
1. MARMAP data contain only a few samples with copepod densities higher than 5000 m<sup>-3</sup>.
  2. MARMAP data based on oblique tows, but whales don't feed in this fashion
- C. Are right whales starving to death, and why not?
1. Emaciated whales **are not** washing up on beaches.
  2. Prey densities not being properly estimated with zooplankton nets and towing schemes.
    - a. Year-to-year predictability of prey patches may play a role
    - b. Prey patch formation may depend on tidally influenced currents and vertical migration of the copepods.
  3. Competition with sei whales
    - a. Sei whales have identical prey preferences
    - b. Not important in US waters since there is little sympatry
  4. Competition with planktivorous fishes
    - a. Sand lance (*Ammodytes americanus*) also feed on copepods
    - b. Sand lance abundances have increased due to depletion of herring and mackerel by commercial fishing
    - c. Sand lance preyed on by other cetaceans
- D. Overall conclusions
1. Right whales require high densities of prey
  2. *Calanus* densities might be very much higher than current estimates.
  3. These high density *Calanus* patches are what make the Great South Channel in Cape Cod, the Bay of Fundy and Browns Bank areas the principal western North Atlantic feeding grounds of the right whale.
  4. More data needed.

**Stormy Mayo (March 2000 OMSAP):**

Based on research at the Center of Coastal Studies (CCS), we have identified a feeding threshold, i.e. the number of zooplankton at which right whales begin feeding. We originally calculated **3900 organisms per cubic meter**, with a correction factor for the varied calorie content of different species, however, this calculation has been revised to about **3750 organisms per cubic meter**. This threshold is based on 3000-4000 samples collected near feeding right whales. The mean density within the path of feeding right whales in Cape Cod Bay is around **26,700 organisms per cubic meter**. Since we have researched the filtering abilities of right whales, these values are based on what the right whale can capture in its baleen. **The maximum integrated density of zooplankton is about 250,000 organisms per cubic meter**. He then showed calculations of caloric intake and a model of the density of a surface patch from southeastern Cape Cod Bay in 1999.

West, G. B, J. H. Brown, and B. J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. *Science* 276: 122-126. [A general model based on organisms being 'space-filling fractal networks' proposed to explain the  $3/4$  power scaling law.] [3, 5, 9, 26]

## SUPPLEMENTAL

**Banse, K. and S. Mosher. 1980. Adult body mass and annual production/biomass relationships of field populations. *Ecol. Monogr.* 50: 355-379. [This is the definitive review of the literature on P/B ratios, where P is the annual production and B is the mean annual population biomass.]**

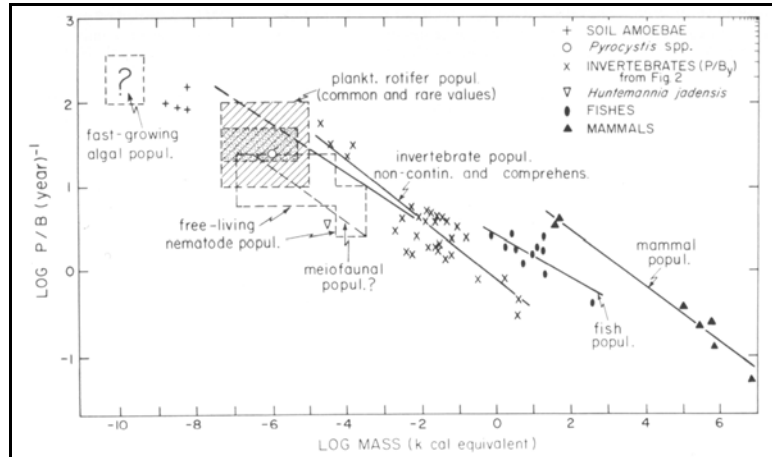
**Fenchel, T. 1974. Intrinsic rate of natural increase: the relationship with body size. *Oecologia (Berlin)* 14: 317-326.**  
 After Fenchel: The exponent in the allometric equation was found by Banse (1982) and **Bluewiss et al. (1978)** to be no different than -0.25

**Marquet, P. A., R. Q. Quiñones, S. Abades, F. Labra, M. Tognelli, M. Arim, and M. Rivadeneira. 2005. Scaling and power-laws in ecological systems. *J. Exp. Biology* 208: 1749-1769.**

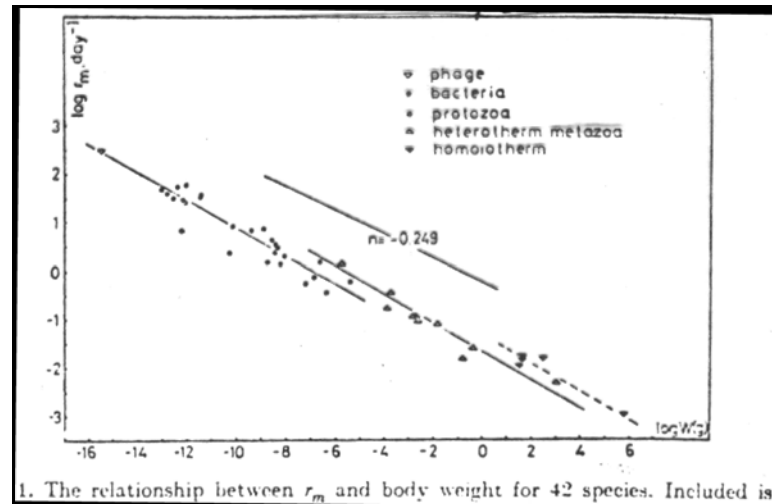
- I. Summary. Biomass spectra and linear biomass hypothesis to be reviewed
- II. Introduction

A.  $Y = BX^\alpha$

1. Allometric if  $\alpha \neq 1$ , isometric if 1
2. Power law relations:
  - a. Frequency of earthquakes of different magnitudes: Gutenberg-Richter law
  - b. Incomes Pareto's Law
  - c. Zipf's laws for words in language and people in cities
- B. Why bother with scalings and power laws
  1. Scale invariance (shape retained)
  2. Universality
- C. Scaling in ecology
  1. Two recent research programs:
    - a. Macroecology
    - b. Brown's 'metabolic theory of ecology'



**Figure 2.** P:B ratio declines with body weight to the -0.37 power, from Banse & Mosher (1980).



**Figure 2.**  $r_m$  as a function of body weight from Fenchel (1974).

- D. Individual and population level scaling  
 1. Relation between animal density and biomass is roughly  $M^{-3/4}$

$$N = \dot{R}/\dot{B}.$$

$$\dot{B} = C_o M^{3/4}.$$

$$N = C_1 M^{-3/4}.$$

2. Home range

$$H = N^{-1} \propto \dot{B}/\dot{R} \propto M^{3/4}.$$

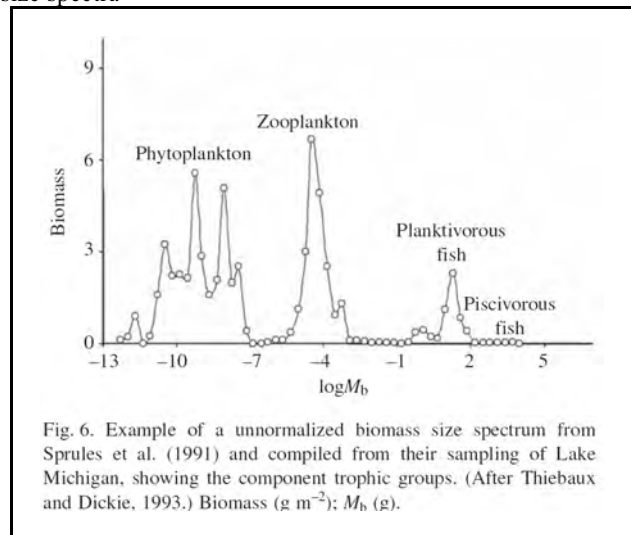
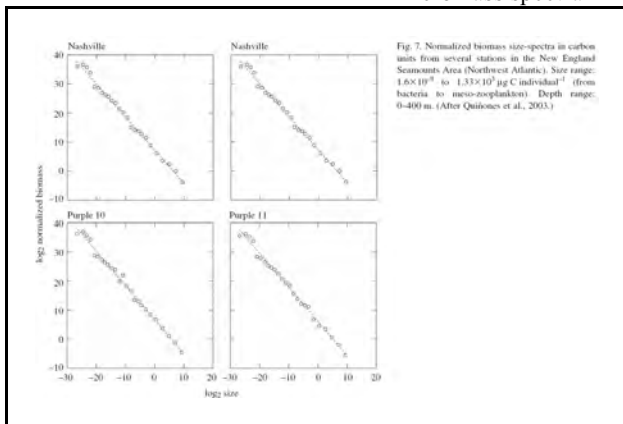
3. Ecological invariants  
 a. Sheldon's linear biomass hypothesis

$$Z(s) \propto s^0.$$

*Normalized*

$$Z(s) \propto s^{-1}.$$

4. Ecological scaling and biomass size spectra  
 a. Fig. 6  
 Unnormalized  
 biomass spectra



- b. Fig. 7 Normalized  
 biomass spectra

- c. Dickie et al.'s analysis of specific production (based on Banse & Mosher!) T Fig. 8
- d.

**Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge.** Read pages 10-23 (Math), 24-43 (Metabolism), 100-106 (Ingestion), 133-146 (Production, P:B ratios, P:R ratios), 213-226 (Explanations) [*An excellent book. Peters reviews the literature on mass-scaled growth, respiration and ingestion.*][4, 8, 9, 11, 12, 13, 16, 32]

1. A philosophical introduction
  - a.  $Y=aW^b$
  - b. Nature of scientific theory [*Pure instrumentalism - Theories as tools!*] [*Peters has the gall to quote Popper to justify his instrumentalist approach*]
  - c. Theoretical status of body size relations.
  - d. The acceptability of body size relations.'
  - e. **Scientific crisis in ecology.**
2. **A mathematical primer: logarithms, power curves, and correlations (10-23)**
  - a. Basic tools
    - i. Logarithms
    - ii. Power formulas
    - iii. Transformation
    - iv. Regression analysis
    - v. Indexes of fit
    - vi. Limits of confidence
    - vii. Problems in regression analysis
3. **Metabolism p. 24-42**
  - a. The balanced growth equation  
 Ingestion=somatic or individual growth + reproductive growth + respiration + egestion + excretion
  - b. Respiration
    - i. Units
    - ii. Metabolic typology
    - iii. Standard metabolic rate

Table 3.1 "mass-specific" or "specific" rates of respiration

Fig. 3.2 Specific metabolic rates of homeotherms, poikilotherms and unicells. Note difference in Y intercept

Table 3.2 Calculations of the effect of size on metabolic rates.

Table 3.3 Metabolic power output and internal energy reserves in homeotherms, poikilotherms and unicells.

Fig. 3.3 Biomass supported per unit energy flow.

- iv. Maximum metabolic rate
- v. The average realized metabolic rate

c. Interpretations and implications

Table 3.4 Effects of fasting on birds and poikilotherms.

- i. Birds burn 0.14% of body mass hourly.
- ii. Larger birds take longer to starve than small birds
- iii. Smaller birds more adversely affected by low temperatures.
- iv. poikilotherms are more resistant to starvation than homeotherms.

Fig. 3.4 Survival times for fasting birds.

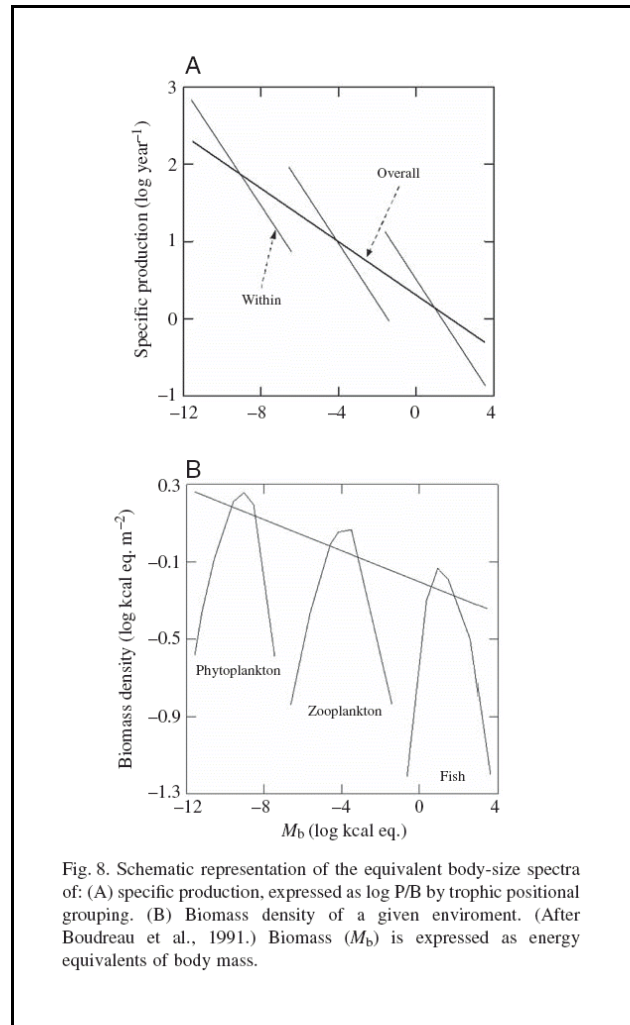


Fig. 8. Schematic representation of the equivalent body-size spectra of: (A) specific production, expressed as log P/B by trophic positional grouping. (B) Biomass density of a given environment. (After Boudreau et al., 1991.) Biomass ( $M_b$ ) is expressed as energy equivalents of body mass.

4. Physiological correlates of size
5. Temperature and metabolic rate
6. Locomotion
7. **Ingestion** read 100-106

- a. Some basic properties
  - i. ingestion rate
  - ii. scaling ingestion rate to size  
- power curves with slopes from .63 to 0.75
  - iii. comparison of ingestion and other rates

Table 7.1 Ratio of ingestion to basal metabolic rates: **All animals eat 2-4 times their basal metabolic rate.**

- iv. Specific dynamic action, the metabolic cost of processing food. Metabolism increased 30% to 100% (carnivores eating protein) over basal metabolic rate

8. Production: growth and reproduction 118-146 read pp. 133-146.

- a. **The scaling of life history**
  - i. *An eutherian model*
    - (1) *The timing of ontogeny*
    - (2) *Size in ontogeny*
    - (3) *Somatic growth rates*

Table 8.1 Three equations that describe individual body mass ( $W_t$ ) at age  $t$  as a function of maximum body mass ( $W_\infty$ )

Growth curves	
<b>Gompertz:</b>	$W_t = W_0 \exp(G(1 - \exp(-t)))$
<b>Logistic:</b>	$W_t = W_\infty W_0 \exp(t) / (W_\infty - W_0 + W_0 \exp(t))$
<b>Von Bertalanffy:</b>	$W_t = W_\infty (1 - \exp(-t))^3$
Curves from early growth	
<b>Exponential</b>	$W_t = W_0 e^{kt}$
<b>Power</b>	$W_t = W_0 t^k$
Growth rates	
<b>Gompertz</b>	$dW/dt = W_0 \exp(G(1 - \exp(-t))) + G(1 - \exp(-t))$
<b>Logistic</b>	$dW/dt = g W_t (W_\infty - W_t) / W_\infty$
<b>Von Bertalanffy</b>	$dW/dt = W_\infty (b g e^{-t})^3$
<b>Exponential</b>	$dW/dt = W_0 k e^{kt}$
<b>Power</b>	$dW/dt = W_0 k t^{k-1}$

- ii. Reproductive growth and reproductive effort
- b. The allometry of life history in other homeotherms
- c. *Poikilotherms and eutherian model.*
  - i. Somatic growth in poikilotherms appears sigmoid and can be described by the growth models in Table 8.1. This S shape reflects a marked decline in somatic growth once sexual maturity is achieved.
  - ii. Regardless of taxonomic affiliation, animals invest similar amounts of tissue in each reproductive bout....Different organisms do differ remarkably in the amount of this investment directed to each offspring.
  - iii. Higher fecundity in larger poikilotherms implies higher mortalities (Table 8.3)

**Table 8.3** The effect of adult size on mortality as suggested by the scaling of fecundity and generation time to size.

<b>FOR POIKILOTHERMS</b>	
<b>Process</b>	<b>Proportional to:</b>
fecundity	$W^{0.5}$
generation time	$W^{0.25}$
birth rate	fecundity/generation time
<b>Therefore,</b>	
birth rate per generation	$W^{0.5}$
birth rate per unit time	$W^{0.25}$
<b>If population numbers are stable:</b>	
natality=mortality	
death per generation	$W^{0.5}$
death rate per unit time	$W^{0.25}$
<b>Mortality rates rise with poikilotherm body mass.</b>	

<b>For homeotherms</b>	
<b>Process</b>	<b>Proportional to:</b>
fecundity	$W^0$
generation time	$W^{0.25}$
birth rate	fecundity/generation time
<b>Therefore,</b>	
birth rate per generation	$W^0$
birth rate per unit time	$W^{-0.25}$
<b>If population numbers are stable, natality=mortality</b>	
death per generation	$W^{0.5}$
death rate per unit time	$W^{0.25}$
<b>∴ Mortality rates decline with homeotherm body mass.</b>	

- d. **Population production**
- i. P/B ratio definition. It is equivalent to the average specific production rates of all members in the population weighted for their temporal duration or to the sum of all productivity terms associated with the life history again biased according to the number and duration of the population's members at each ontogenetic stage. The bias of production by populations size structure and survivorship may lead to departures from the typical allometric exponent of size in equations describing specific rates,  $-1/4$ .
  - ii. *Some contradictory relations.*  
 Discussion of Banse & Mosher P:B curves  
 (1) P/B declines as  $W_a^{-0.37}$  (Fig. 8.4)  
*"Apparently, populations of small invertebrates are dominated by highly productive juveniles and those of larger animals by less productive adults and subadults."*  
 (2) Fenchel's 1974  $r_{max} \approx$  maximum P/B; see Appendix VIIIc) which scaled with slope of  $-0.27$   
 (3) Other workers found slopes of  $-1/4$
  - iii. *Some applications for production relationships*  
 (1) *Harvesting our natural resources*  
 (a) Fig. 8.5. Harvesting of elk-deer predicted from Farlow's P/B vs B equation  
 (b) "The apparent predictive power of the mammalian equation contrast with the doubtful nature of relations describing the scaling of P/B for invertebrates."  
 (2) *The scaling of population dynamics*  
 (a) Fig. 8.6  
 (b) population dropped to  $1 \text{ g km}^{-2}$   
 (c) Used **Bluweiss et al. 1978** equation to show rates of increase until population biomass was  $100 \text{ kg/km}^{-2}$  (see chapter 10) 100,000-fold increase in biomass.
- Fig. 8.6. The effect of body size on the potential duration of maximum rates of population growth. Time to expand 100,000 fold in biomass =  $2,500W^{0.26}$
- (d) **Biological time scales as  $W^{1/4}$ . This fundamental relationship should be remembered in planning programs of ecological research that involve populations of different-sized organisms.**
- e. **An individual production term for the balanced growth equation**
- i. The allometry of individual production: an interim solution.
  - ii. Ecological efficiencies (P. 142)

**Table 8.5** A comparison of various ecological efficiencies calculated as the ratios of allometric equations for rates of respiration (R), growth (G), defecation (D), assimilation (A), and ingestion (I).

TERM	DEFINITION	POIKILOTHERM	HOMEOTHERM
Respiration efficiency	R/I	$0.48W^{-0.06}$	$0.77W^{0.05}$
Growth efficiency	G/I	$0.21W^{-0.05}$	$0.019W^{0.03}$
[Defecation efficiency]	D/I	$\approx 0.31W^{-0.03}$	$\approx 0.22W^{0.01}$
Assimilation efficiency	A/I	$\approx 0.69W^{-0.06}$	$\approx 0.78W^{0.04}$
	R/A	$\approx 0.70$	$\approx 0.98$
Tissue growth efficiency	G/A	$\approx 0.30$	$\approx 0.024W^{-0.02}$

- f. Table 8.5 indicates that there exist marked differences among the major metabolic groups. Within these groups, size has a negligible effect on all energetic efficiencies. Homeotherms of all sizes produce much less for each unit of energy ingested or assimilated than do poikilotherms. This is primarily because homeotherms burn most of their food to maintain their high metabolic rates.



*“Kleiber (1961) has given these efficiencies more reality with a practical example. If one feeds 10 tons of hay to two half-ton steers and an equal amount to five hundred 2-kg rabbits, both will reduce their food resource to 6 tons of manure while producing 0.2 ton of new tissue. In other words, assimilation efficiency and production efficiencies are independent of size. The remaining 38% of the energy in the feed will be lost as respiration. The major difference in the two species is that 1 ton of rabbits will eat all their food and produce all their growth in only 3 months, whereas 1 ton of cattle will require 14 months. If this analysis were extended to poikilotherms, Table 8.5 suggests that 109 tons of hay could support a population of 1 million 1-g grasshoppers for 9 months, but at the end of that time they would produce 2 tons of new grasshoppers, leaving behind 6 tons of manure and burning off the energy in only 2 tons of the food.”*

9. Mass flow

a. **The autecology of material flows**

i. Ingestion and nutrient requirements

ii. A comment on defecation

“I have found only two equations describing the allometry of defecation.”

(1) Hargrave

(2) Cammen

iii. Water economy

b. **Nutrients and nutrient turnover**

i. Estimation of nutrient release rates.

ii. Nutrient turnover in lakes.

10. Animal abundance

**The numerical density of individual species**

*Patterns in animal abundance*

Mean density

Ghilarov (1967) noted that the density of soil animals falls with animal length.

*“In general, these analyses show highly significant trends despite substantial residual variance. Body size relations provide one of the most general tools for the prediction of animal abundance. It is a tool that should be more widely available.”*  
p. 166

**Sieburth, J. McN., V. Smetacek and J. Lenz. 1978. Pelagic ecosystem structure: heterotrophic compartments of the plankton and their relationship to plankton size fractions. *Limnol. Oceanogr.* 23: 1256-1263.**

*[Classifies the plankton using a log scale: femto- $\{0.02-0.2\mu\text{m}\}$ , pico- $\{0.2-2\mu\text{m}\}$ , nano- $\{2-20\mu\text{m}\}$ , micro- $\{20-200\mu\text{m}\}$ , and mesoplankton  $\{0.2-20\text{ mm}\}$ ]*

**West, G. B. and J. H. Brown. 2005. The origin of allometric scaling laws in biology from genomes to ecosystems: towards a quantitative unifying theory of biological structure and organization. *J. Exp. Biol.* 208: 1575-1592.**

I. Abstract

II.

## References

### GENERAL ALLOMETRY BOOKS AND ARTICLES

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- Brown, J. H. and P. F. Nicoletto. 1991. Spatial scaling of species composition: body masses of North American land mammals. *Amer. Natur.* 138: 1478-1512. [The number of species vs  $\log_2$  size classes are given for N. American mammals in general and those inhabiting 21 biomes. 3 hypotheses are invoked to explain the patterns: 1) competitive exclusion of similar-sized species, 2) differential extinction of large species and 3) allometric energetic constraints causes modal sized species to be more specialized for food than large species]
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- Enquist, B. J., E. P. Economo, T. E. Huxman, A. P. Allen, D. D. Ignace, and J. F. Gillooly. 2003. Scaling metabolism from organisms to ecosystems. *Nature* 423: 639-642. [Abstract: Here we derive a general model of ecosystem respiration based on the kinetics of metabolic reactions and the scaling of resource use by individual organisms. The model predicts that fluxes of CO<sub>2</sub> and energy are invariant of ecosystem biomass, but are strongly influenced by temperature, variation in cellular metabolism and rates of supply of limiting resources (water and/or nutrients). Variation in ecosystem respiration within sites, as calculated from a network of CO<sub>2</sub> flux towers provides robust support for the model's predictions. However, data indicate that variation in annual flux between sites is not strongly dependent on average site temperature or latitude.]
- Fenchel, T. 1974. Intrinsic rate of natural increase: the relationship with body size. *Oecologia* (Berlin) 14: 317-326. [This classic paper presents an allometric equation for the relationship between  $r_m$  and body size, with body size ranging from viruses to whales.  $\log_{10} r_m = a - 0.275 \log_{10} \text{Weight}$ , where  $a$  is -1.94, -1.64, and -1.4 for unicellular, heterotherm metazoan and homeotherms metazoans respectively. Fenchel noted that the exponent (-.275) was greater than Hemmingsen's exponent for mass-scaled respiration (-.25), and attributed the difference to greater structural complexity in larger organisms. Later workers have found that the data cannot be used to distinguish between -.275 and -.25 (the standard allometric exponent)] [4, 7, 9, 13, 24]
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- Williams, N. 1997. Fractal geometry gets the measure of life's scales. *Science* 276: 34. [A 1-p summary of the importance of West et al. 1997]

Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005. Body size in ecological networks. *Trends in Ecology and Evolution* 20: 402-409.[]{}

## SIZE STRUCTURE & ALLOMETRY OF THE BENTHOS AND PLANKTON

- Allan, J. D. 1976. Life history patterns in zooplankton. *Amer. Natur.* 110: 165-180. [*Zooplankton ranked according to  $r_m$ : rotifers > Cladocera > Copepoda. The ability to overwinter may confer an advantage to copepods in marine waters. The rotifer: copepod growth rates predicted by the model are not realized in the field.*]
- Azam, F., T. Fenchel, J. G. Field, J. S. Gray, L. A. Meyer-Reil, and F. Thingstad. 1983. The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser.* 10: 257-263. [*Note the alphabetical authorship. Fenchel experimentally demonstrated the importance of flagellate grazing in controlling bacterial standing stocks*] [9, 10]
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- Banse, K. 1982a. Cell volumes, maximal growth rates of unicellular algae and ciliates, and the role of ciliates in the marine pelagial. *Limnol. Oceanogr.* 27: 1059-1071. [*A major paper, well before its time. Ciliates have maximal growth rates as fast or faster than their algal food*] [5, 6, 8, 12]
- Banse, K. 1982b. Mass-scaled rates of respiration and intrinsic growth in very small invertebrates. *Mar. Ecol. Prog. Ser.* 9: 281-297. [*Allometric equations for small invertebrates are developed. The mass scaled respiration rate for larger invertebrates is greater for larger inverts, less for small invertebrates and less still for unicellular eukaryotes. Specific growth rates for the meiobenthos are considerably below similarly sized pelagic populations*] [3, 4, 8, 11, 13, 14]

- Banse, K., F. H. Nichols, and D. R. May. 1971. Oxygen consumption by the seabed. III. On the role of macrofauna at three stations. *Vie et Milieu, Suppl* 22: 31-52. [*The following equation was used:  $\log r = a \log t + b \log W + c$ , in which  $r$  is respiration in  $\mu\text{l}$  of  $\text{O}_2$  per hour,  $t$  is temperature (Celsius) and  $W$  is the ash-free dry weight. *Lumbrineris zonata*, a subsurface deposit feeder, has an anomalously low respiration rate for its size. The exponent for polychaete regression relationships is slightly less than 0.75*] [8, 12]
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- Brooks, J. L. and S. I. Dodson. 1965. Predation, body size, and composition of the plankton. *Science* 150: 28-35. [*B & D proposed that large zooplankton are superior competitors and dominate in lakes lacking visually feeding fish. This size-efficiency hypothesis has been greatly modified since. The key modification was the introduction of invertebrate predation by Dodson in 1970.*] {7, 13}
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- Hall, D. J., S. T. Threlkeld, C. W. Burns and P. H. Crowley. 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. *Ann. Rev. Ecol. System.* 7: 177-208. [Mathematical and graphical models are presented for Brooks and Dodson's size-efficiency hypothesis. The cornerstone of the models is the assumed allometric relationship for weight specific respiration and ingestion, giving larger species an energetic advantage at low food concentrations. At high food concentrations, smaller body sizes have an advantage (due to higher  $r_m$ )] {7, 13}
- Hansen, P. J., P. K. Bjørnsen, and B. W. Hansen. 1997. Zooplankton grazing and growth: scaling within the 2-2,000- $\mu$ m body size range. *Limnol. Oceanogr.* 42: 687-704. [Lit. review from 60 species shows specific ingestion declines with volume to the -.23 power [ $\pm 0.12$ ] ciliate ingestion higher than het. dinos and calanoid clearance rates higher than cladocera and meroplankton by 10x]

- Harrison, W. G. and L. J. E. Wood. 1988. Inorganic nitrogen uptake by marine picoplankton: evidence for size partitioning. *Limnol. Oceanogr.* 33: 468-475. [More  $NH_4^+$  used by picoplankton fraction {pico- <1  $\mu m$ }. **Malone (1980)** proposed that large cells depend on new N and large and nanoplankton on regenerated nitrogen. Picoplankton make up >50% of the biomass and >30% of the productivity of coastal communities] [?]
- Huntley, M. E. and M. D. G. Lopez. 1992. Temperature-dependent production of marine copepods: a global synthesis. *Amer. Natur.* 140: 201-242. [Expands on **McLaren's (1978)** on Pseudocalanus to global copepods] [?]
- Huntley, M. 1996. Temperature and copepod production in the sea: a reply. *Amer. Natur.* 148: 407-420. [?]
- Huntley, M. and C. Boyd. 1984. Food-limited growth of marine zooplankton. *Amer. Natur.* 124: 455-478. [Reviews **McLaren's (1978)** argument that copepods are rarely food limited. Huntley & Boyd's analysis is reviewed by **Miller (2004)**] [?]
- Jackson, G. A. 1987. Simulating chemosensory responses of marine microorganisms. *Limnol. Oceanogr.* 32: 1253-1266. [A diffusion model is used to show that algae smaller than about 2-5  $\mu m$  can not be sensed by either bacteria or zooplankton] [7, 10]
- Joint, I. R. 1991. The allometric determination of pelagic production rates. *J. Plankton Res.* 13 (Suppl.): 69-81. [Allometry is an accurate predictor of production for cells >5  $\mu m$  in size. Here, the results are extended to estimate picophytoplankton productivity. Production scales to the -0.15 power, not -0.25]
- Joint, I. R. and A. J. Pomeroy. 1988. Allometric estimation of the productivity of phytoplankton assemblages. *Mar. Ecol. Prog. Ser.* 47: 161-168.
- Kerr, S. R. 1974. Theory of size distribution in ecological communities. *J. Fish. Res. Bd. Can.* 31: 1859-1862. [An empirical model predicts standing stocks of prey should be 1.2 x that of their predators.]
- Kjørboe, T. 1993. Turbulence, phytoplankton cell size and the structure of pelagic food webs. *Advances in Marine Biology* 29: 1-72.
- Kjørboe, T. and M. Sabatini. 1995. Scaling of fecundity, growth and development in marine planktonic copepods. *Mar. Ecol. Prog. Ser.* 120: 285-290.
- Laws, E. A. 1975. The importance of respiration losses in controlling the size distribution of marine phytoplankton. *Ecology* 56: 419-426.
- Lehman, J. T. 1988. Ecological principles affecting community structure and secondary production by zooplankton in marine and freshwater environments. *Limnol. Oceanogr.* 33(pt. 2):931-945. [A devastating critique of models based on size alone. Thresholds do not vary with regularly with organism size]
- Levinton, J. S. and S. Stewart. 1988. Effects of sediment organics, detrital input and temperature on demography, production and body size of a deposit feeder. *Mar. Ecol. Prog. Ser.* 49: 259-266.
- Li, W. K. W., D. V. Subba Rao, W. G. Harrison, J. C. Smith, J. J. Cullen, B. Irwin and T. Platt. 1983. Autotrophic picoplankton in the tropical ocean. *Science* 219: 292-295. [20-80% of primary production from particles < 1  $\mu m$ ]
- Li, W. K. W. and A. M. Wood. 1988. Vertical distribution of North Atlantic ultraphytoplankton: analysis by flow cytometry and epifluorescence microscopy. *Deep-Sea Res.* 35: 1615-1638.
- López-Urrutia, Á, E. San Martín, R. P. Harris, and X. Irigoien. 2006. Scaling the metabolic balance of the oceans. *Proc. Natl. Acad. Sci. USA* 103: 8739-8744. [Based on ] [?]
- Lynch, M. 1977. Fitness and optimal body size in zooplankton populations. *Ecology* 58: 763-774.

- Mackas, D. L., R. Goldblatt and A. G. Lewis. 1998. Interdecadal variation in developmental timing of *Neocalanus plumchrus* populations at Ocean Station P in the subarctic North Pacific. *Can. J. Fish. Aquat. Sci.* 55: 1878-1893. [Abstract: *A single copepod species, Neocalanus plumchrus (Marukawa), makes up much of the mesozooplankton biomass in the subarctic Pacific....At Ocean Station P (50°N, 145°W), seasonal phasing of this annual maximum has shifted dramatically between 1956 and the present....The changes in timing are strongly correlated with large-scale year-to-year and decade-to-decade ocean climate fluctuations, as reflected by spring season temperature anomalies in the surface mixed layer within which the juvenile copepodites feed and grow... But the change in developmental timing is too large to be explained solely by physiological acceleration of individual development rate. We suggest instead that the cause is interannual differences in survival among early versus late portions of the annual copepodite cohort.*]
- Malone, T. C. 1980. Size-fractionated primary productivity of marine phytoplankton. *Brookhaven Symp. Biol.* 31: 301-319. [Large phytoplankton (e.g., diatoms take up  $NO_3^-$ ); small phytoplankton utilize regenerated production][6, 10, 29]
- Marquet, P. A., S. A. Naverete, and J. C. Castilla. 1990. Scaling population density to body size in rocky intertidal communities. *Science* 250: 1125-1127.
- McLaren, I. A. 1978. Generation lengths of some temperate marine copepods: estimation, prediction, and implications. *J. Fish. Res. Board Can.* 35: 1330-1342. [Zooplankton are apparently not food-limited (according to I.A.M., anyway). They may be limited by predation. Thus, energetic arguments based on increased food gathering abilities would not work.]{29}
- McLaren, I. A. and C. J. Corkett. 1984. Singular, mass-specific P/B ratios cannot be used to estimate copepod production. *Can. J. Fish. Aquat. Sci.* 41: 828-830.
- Miller, C. B. 2004. *Biological Oceanography*. Blackwell Publishing, Malden MA. 402 pp. [ ]{29}
- Patterson, M. R. 1992. A mass transfer explanation for metabolic scaling relations in some aquatic invertebrates. *Science* 255: 1421-1423.
- Peters, R. H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge. [An excellent book. Peters reviews the literature on mass-scaled growth, respiration and ingestion.][4, 8, 9, 11, 12, 13, 16, 32]
- Polloni, P., R. Haedrich, G. Rowe and C. H. Clifford. 1979. The size-depth relationship in deep ocean animals. *Int. Revue ges. Hydrobiol.* 64: 39-46. [A commentary on Thiel.]
- Raven, J. A. 1986. Physiological consequences of extremely small size for autotrophic organisms in the sea. *Can. Bull. Fish. Aquat. Sci.* 214: 1-70. [Small phytoplankton have an advantage in acquiring nutrients and eliminating  $O_2$ , a photosynthetic inhibitor, but are at a disadvantage in the heavy excretion losses of DOM] [6]
- Reiss, M. J. 1989. *Allometry of growth and reproduction*. Cambridge Univ. Press, Cambridge.
- Robertson, A. I. 1979. The relationship between annual production: biomass ratios and lifespans for marine macrobenthos. *Oecologia* 38: 193-202.
- Sanders, H. L. and J. A. Allen. 1973. Studies on deep-sea Protobranchia; Prologue and the Pristiglomidae. *Bull. Mus. Comp. Zool.* 145: 237-261. [Describes the reduction in body size with depth]
- Sebens, K. P. 1987. The ecology of indeterminate growth in animals. *Ann. Rev. Ecol. Syst.* 18: 371-407. [Sebens divides growth curves into 7 types, 4 determinate and 3 indeterminate. Sebens classifies indeterminate growth as the ability to modify body size throughout an organisms life in response to environmental conditions. Sebens reviews the literature on indeterminate growth and describes his model for predicting optimal body size as a function of environmental conditions and allometric energetic cost and benefit exponents. The 'optimum' body size predicted by Sebens model may not be achieved due to size-selective predation or opportunistic life history strategies in a variable environment.]
- Shuter, B. J. 1978. Size dependence of phosphorous and nitrogen subsistence quotas in unicellular microorganisms. *Limnol. Oceanogr.* 23: 1248-1255. [The Droop equation is fit to 45 data sets.  $k_q$  increases allometrically with cell volume and carbon content, but the later exponent is almost 1.0.]

- Sieburth, J. McN. 1979. Sea Microbes. Oxford University Press, New York 491 pp. [*Superb scanning E.M. 's*]
- Sieburth, J. McN., V. Smetacek and J. Lenz. 1978. Pelagic ecosystem structure: heterotrophic compartments of the plankton and their relationship to plankton size fractions. *Limnol. Oceanogr.* 23: 1256-1263. [*Classifies the plankton using a log scale: femto- $\{0.02-0.2\mu\text{m}\}$ , pico- $\{0.2-2\mu\text{m}\}$ , nano- $\{2-20\mu\text{m}\}$ , micro- $\{20-200\mu\text{m}\}$ , and mesoplankton  $\{0.2-20\text{ mm}\}$ ]*
- Sokolova, N. N. 1990. On the size of the deep-sea macrobenthic invertebrates. *Prog. Oceanogr.* 24: 251-252.
- Sprules, W. G. and M. Munawar. 1986. Plankton size spectra in relation to ecosystem productivity, size, and perturbation. *Can. J. Fish. Aquat. Sci.* 43: 1789-1794.
- Steele, J. H. and B. W. Frost. 1977. The structure of plankton communities. *Phil. Trans. Roy. Soc. London (B)* 280: 485-534. [*Most processes in the ecosystem are scaled according to organism size (e.g., phytoplankton respiration, nutrient uptake and sinking, zooplankton feeding electivity & ingestion, and predation rates. The size structure of an ecosystem can be controlled from the top (e.g., visually feeding fish) or the bottom (e.g., physical factors altering phytoplankton size composition)*] [6, 10]
- Straile, D. 1997. Gross growth efficiencies of protozoan and metazooplankton and their dependence on food concentration, predator-prey weight ratio, and taxonomic group. *Limnol. Oceanogr.* 42: 1375-1385.
- Strayer, D. 1986. The size structure of a lacustrine zoobenthic community. *Oecologia (Berlin)* 69: 513-516. [*The distribution is unimodal in contrast to bimodal marine benthic communities.*]
- Taghon, G. L. 1981. Beyond selection: optimal ingestion rate as a function of food value. *Amer. Natur.* 118: 202-214. [*This theoretical model does not deal with size per se. It is interesting in that it conflicts with **Cammen's (1980)** empirical model so strikingly. Taghon's model predicts that ingestion rate should rise monotonically with 'food quality', but Cammen's model found just the opposite. The key difference to my mind, is that Cammen's data include a strong covariate (animal size or functional group). Large subsurface deposit feeders have a low weight-specific ingestion rate and are found in areas of low organic content.*]
- Tessier, A. J., A. Young, and M. Leibold. 1992. Population dynamics and body-size selection in *Daphnia*. *Limnol. Oceanogr.* 37: 1-13.
- Thiel, H. 1975. The size structure of the deep-sea benthos. *Int. Rev. Ges. Hydrobiol.* 60: 575-606. [*Proposes that the small body size of deep-sea organisms is due to the low energy flux to the bottom. **Cammen's (1980)** empirical regression might suggest that larger deposit feeder body sizes might result under such conditions. The paradox remains unresolved.*]
- Thiel, H. 1979. Structural aspects of the deep-sea benthos. *Ambio Spec. Rep.* 6: 25-31.
- Turpin, D. H. and P. J. Harrison. 1979. Limiting nutrient patchiness and its role in phytoplankton ecology. *J. exp. mar. Biol. Ecol.* 39: 151-166. [*Pulsed  $\text{NH}_4^+$  additions lead to increased abundance of *Skeletonema* and populations with higher  $V_{max}$  for nutrient uptake*] [6, 10]
- Turpin, D. H. and P. J. Harrison. 1980. Cell size manipulation in natural marine planktonic diatom communities. *Can. J. Fish. Aquat. Sci.* 37: 1193-1195. [*Pulsed additions of ammonium leads to larger diatom species*] [6, 10]
- Turpin, D. H., J. S. Parslow, and P. J. Harrison. 1981. On limiting nutrient patchiness and phytoplankton growth: a conceptual approach. *J. Plankton Research* 3: 421-431. [*A model based on the Droop equation is proposed to explicate the role of patch nutrients on  $\mu$* ] [6, 10]

Vernberg, W. B. and B. C. Coull. 1974. Respiration of an interstitial ciliate and benthic relationships. *Oecologia* (Berlin) 16: 259-264. [Using Fenchel's 1969 relationships, predicted the metabolic rates of ciliates: metazoan meiofauna: macrofauna, which were a) 1:0.5:2.1 for a sandy sublittoral, b) 1:3.4:1.9 for estuarine sediment, and c) 1:0.54:0.04 for an exposed beach]

Weber, L. H., S. Z. El Sayed 1987. Contributions of the net, nano- and picoplankton to the phytoplankton standing crop and primary productivity in the Southern Ocean. *J. Plankton Res.* 9: 973-994. [Nanoplankton (39-98%, and picoplankton (0-32%) comprise a major fraction of the energy flow. The diatom->krill->whale pathway is relatively minor]

Wen, Y. H., A. Vézina and R. H. Peters. 1997. Allometric scaling of compartmental fluxes of phosphorus in freshwater algae. *Limnol. Oceanogr.* 42: 45-56. [PO<sub>4</sub> uptake scales allometrically to cell size]

### Biomass Spectra of Plankton

Brown, J. H. and J. F. Gillooly. 2003. Ecological food webs: high quality data permit theoretical unification. *Proc. Natl. Acad. Sci. USA* 100: 1467-1468. [Commentary on **Cohen et al. (2003)**]

Cohen, J. E., T. Jonsson, and S. R. Carpenter. 2003. Ecological community description using the food web, species abundance, and body size. *Proc. Natl. Acad. Sci. USA* 100: 1781-1786. [ ]

Fry, B. and R. B. Quiñones. 1994. Biomass spectra and stable isotope indicators of trophic level in zooplankton of the northwest Atlantic. *Mar. Ecol. Prog. Ser.* 112: 201-204. [Using <sup>13</sup>C and <sup>15</sup>N tracers to document trophic levels, they found small changes in trophic level across 7 zooplankton size fractions ranging from 64 to 8000 μm. <sup>13</sup>C showed strong regional differences, with isotopically heavy <sup>13</sup>C (-18) found in Georges Bank in small size classes. Little change in <sup>15</sup>N across size groups indicating that there are no clear-cut trophic levels in zooplankton, with consumers feeding opportunistically in unstructured food webs.]

Gasol, J. M., P. A. del Giorgio and C. M. Duarte. 1997. Biomass distribution in marine planktonic communities. *Limnol. Oceanogr.* 42: 1353-1363. [They analyze the biomass distribution of autotrophs:heterotrophs in a variety of marine

*environments. The traditional ecological pyramid is inverted {heterotroph dominance} in open-ocean communities]*

Jennings, S., T. A. Dinmore, D. E. Duplisea, K. J. Warr, and J. E. Lancaster. 2001. Trawling disturbances can modify benthic production processes. *J. Animal Ecology* 70: 459-475. [Benthic biomass spectra] [ ]

Jennings, S. and J. L. Blanchard. 2004. Fish abundance with no fishing: predictions based on macroecological theory. *J. Animal Ecology* 73: 632-642. [The abundance of large fish in the North Sea is 97-99% less than predicted by the biomass spectra for unexploited populations] [ ]

Marquet, P. A., R. Q. Quiñones, S. Abades, F. Labra, M. Tognelli, M. Arim, and M. Rivadeneira. 2005. Scaling and power-laws in ecological systems. *J. Exp. Biology* 208: 1749-1769. [ ] [ ]

Platt, T. and K. Denman. 1978. The structure of pelagic marine ecosystems. *Rapp. P. Re'un. Comm. int. explor. Mer* 173: 60-65. [Provides theoretical justification for **Sheldon & Parsons' (1967) linear biomass hypothesis and defines the normalized biomass spectrum**] [15]

Platt, T. and W. Silvert. 1981. Ecology, physiology, allometry and dimensionality. *J. Theor. Biol.* 93: 855-860. [5]

Sheldon, R. W. and T. R. Parsons. 1967. A continuous size spectrum for particulate matter in the sea. *J. Fish. Res. Bd. Canada* 24: 909-915. [The linear biomass hypothesis is proposed. When organism size is scaled by organism radius, there is a near constant biomass in each logarithmic class (base 2 logarithms are used) here but are not necessary [Peters 1983].] [7, 32]

Sheldon, R. W. and S. R. Kerr. 1972. The population density of monsters in Loch Ness. *Limnol. Oceanogr.* 17: 796-798. [An application of the linear biomass hypothesis] [15]

Sheldon, R. W., W. H. Sutcliffe, and A. Prakash. 1973. The production of particles in the surface waters of the ocean with particular reference to the Sargasso Sea. *Limnol. Oceanogr.* 18: 719-733. [Population doubling time (t) is related to body length (mm) using log<sub>10</sub> t = 0.64 + 0.80 log<sub>10</sub> L.] [ ]



- Sheldon, R. W., W. H. Sutcliffe, and M. A. Paranjape. 1977. Structure of pelagic food chain and relationship between plankton and fish production. *J. Fish. Res. Bd. Can.* 34: 2344-2353. [?]
- Sheldon, R. W., P. Nival, and F. Rassoulzadegan. 1986. An experimental investigation of a flagellate-ciliate-copepod food chain with some observations relevant to the linear biomass hypothesis. *Limnol. Oceanogr.* 31: 184-188. [?]
- Zhou, M. 2006. What determines the slope of a plankton biomass spectrum? *J. Plankton Res.* 28: 437-448. [The biomass spectrum slope is a function of the number of trophic levels and the ecological transfer efficiency. Few trophic levels produce steep slopes ( $\gg -1$ ) With higher transfer efficiencies, a given slope would be associated with more trophic levels] {}
- Zhou, M and M. E. Huntley. 1997. Population dynamics theory of plankton based on biomass spectra. *Mar. Ecol. Prog. Ser.* 159: 61-73. [Measurements of biomass spectra used to infer individual growth rate in intrinsic rate of increase]

### **Biomass Spectra of Benthos**

- Schwinghamer, P. 1981. Characteristic size distributions of integral benthic communities. *Can. J. Fish. Aquat. Sci.* 38: 1255-1263. [Documents a bimodal distribution of benthic organism sizes.]
- Schwinghamer, P. 1983. Generating ecological hypotheses from biomass spectra using causal analysis. *Mar. Ecol. Prog. Ser.* 13: 151-166. [Size spectra for different areas and different seasons are produced and analyzed with Sewall Wright's path analysis. Indirect evidence is offered for competition between juvenile macrofauna and permanent meiofauna for microalgae.]
- Schwinghamer, P. 1985. Observations on size-structure and pelagic coupling of some shelf and abyssal benthic communities. Pp. 347-360 in P. E. Gibbs, ed. *Proc. 19th European Mar. Biol. Symposium*. Cambridge University Press, Cambridge.
- Schwinghamer, P. 1985. Influence of pollution along a natural gradient and in a mesocosm experiment on biomass-size spectra of benthic communities. *Mar. Ecol. Prog. Ser.* 46: 199-206.

- Schwinghamer, P. 1988. Influence of pollution along a natural gradient and in a mesocosm experiment on biomass - size spectra of benthic communities. *Mar. Ecol. Prog. Ser.* 46: 199-206.
- Schwinghamer, P., B. Hargrave, D. Peer and C. M. Hawkins. 1986. Partitioning production and respiration among size groups of organisms in an intertidal benthic community. *Mar. Ecol. Prog. Ser.* 31: 131-142. [They use **Banse & Mosher's (1980)** allometric scaling of P:B ratio to estimate secondary production of bacteria, meiofauna and macrofauna. The bacterial secondary production dominates, but the rate of bacterial production is heavily dependent on the %-active (now known to be quite low). They conclude the microalgal production is insufficient to support secondary production.]
- Warwick, R. M. 1984. Species size distributions in marine benthic communities. *Oecologia* 61: 32-41.
- Warwick, R. M, N. R. Collins, J. M. Gee and C. L. George. 1986. Species size distributions of benthic and pelagic Metazoa: evidence for interactions? *Mar. Ecol. Prog. Ser.* 34: 63-68. [The trough in the benthic biomass spectrum corresponds to a crest in the pelagic biomass spectrum. Competition between the meroplankton and holoplankton is proposed.]

### **RIGHT WHALES**

- Baumgartner, M. F., T. V. N. Cole, P. J. Clapham, and B. R. Mate. 2003. North Atlantic Right Whale Habitat in the Northern Bay of Fundy and on the SW Scotian Shelf during 1999-2001. *Mar. Ecol. Prog. Ser.* 264: 137-154.
- Baumgartner, M. F., T. V. N. Cole, R. G. Campbell, G. J. Teegarden, and E. G. Durbin. 2003. Associations between North Atlantic Right Whales and their prey, *Calanus finmarchicus*, over diel and tidal time scales. *Mar. Ecol. Prog. Ser.* 264: 155-164.
- Costa, A. D., E. G. Durbin, C. A. Mayo, and E. G. Lyman. 2006. Environmental factors affecting zooplankton in Cape Cod Bay: implications for right whale dynamics. *Mar. Ecol. Prog. Ser.* 323: 281-298. [ANOSIM and Cluster analysis]
- Doucette, G. J., A. D. Cembella, J. L. Martin, J. Michaud, T. V. N. Cole, and R. M. Rolland. 2006. Paralytic shellfish poisoning (PSP) toxins in

- North Atlantic Right Whales (*Eubalena glacialis*) and their zooplankton prey in the Bay of Fundy, Canada. *Mar. Ecol. Prog. Ser.* 306: 303-313. [*Reproductive disfunction in the late 1990s. Whale feces positive for PSP at levels similar to that found in C. finmarchicus*]
- Durbin, E. G., R. G. Campbell, S. L. Gilman, A. G. Durbin. 1995. Diel feeding-behavior and ingestion rate in the copepod *Calanus finmarchicus* in the southern Gulf of Maine during late spring. *Continental Shelf Research* 15: 539-570. [*Abstract: "In situ feeding was measured on late stage C. finmarchicus in S. Gulf Maine... a spring feeding ground for the planktivorous right whale... ingestion rates ranged from 30.2% body C d<sup>-1</sup> at a spring bloom station to 0.6% body C d<sup>-1</sup> after stratification.... C. finmarchicus food-limited after stratification. ...Diel feeding rhythms and vertical migration absent during the bloom, but developed as the bloom declined. During the post-bloom stratified conditions, diel feeding rhythms continued but vertical migration ceased. ...a small population of nonmigratory individuals resided at depth feeding upon sedimented spring bloom diatoms. At the spring bloom station C. finmarchicus ingested only a small proportion of the phytoplankton standing stock in the >7 μm size fraction (2.9% d<sup>-1</sup>), reflecting the high biomass of phytoplankton and the stage composition of the C. finmarchicus population, dominated by early copepodite states with low biomass...at the post-bloom stations, dense surface aggregations of [late copepodite] C. finmarchicus consumed a significantly larger fraction of the >7 μm phytoplankton standing crop (up to 62.5% d<sup>-1</sup>." ]*]
- Fujiwara, M. and H. Caswell. 2001. Demography of the endangered North Atlantic Right Whale *Nature* 414: 537-541. [*Mortality is the major cause of low numbers and saving 2 whales per year could lead to the survival of the species*]
- Kenney, R. D. M. Hyman, R. E. Owen, G. P. Scott, and H. E. Winn. 1986. Estimation of prey densities required by Western North Atlantic Right Whales. *Marine Mammal Science* 2: 1-13. [*A wonderful back-of-the-envelope style calculation of the number of Calanus finmarchicus required to support the metabolic demands of Right Whales. Do such patches occur in Cape Cod Bay, a prime Right Whale feeding ground? No one knows.*]
- Kraus, S. D., M. W. Brown, H. Caswell, C. W. Clark, M. Fujiwara, P. K. Hamilton, R. D. Kenney, A. R. Knowlton, S. Landry, C. A. Mayo, W. A. McLellan, M. J. Moore, D. P. Nowacek, D. A. Pabst, A. J. Read, R. M. Rolland. 2005. North Atlantic Right Whales in Crisis. *Science* 309: 561-562. [*Right Whale investigators urge immediate steps to reduce human-caused whale mortality*]
- NAO, Calanus finmarchicus and Right Whales**
- Beaugrand, G., P. C. Reid, F. Ibañez, J. A. Lindlay, and M. Edwards. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 296: 1692-1694. [*NAO with positive trend in the last 20 years leading to more C. finmarchicus in the Gulf of Maine and fewer off the North Sea*]
- Conversi, A., S. Piontkovski, and S. Hameed. 2001. Seasonal and interannual dynamics of *Calanus finmarchicus* in the Gulf of Maine (Northeastern US Shelf) with reference to the North Atlantic Oscillation. *Deep-Sea Res. II* 48: 519-530. [*C. finmarchicus abundance coupled to the NAO with a lag*]
- Greene, C. H. and A. J. Pershing. 2001. The response of *Calanus finmarchicus* populations to climate variability in the Northwest Atlantic: Basin-scale forcing associated with the North Atlantic Oscillation (NAO). *ICES J. Mar. Sci.* 57: 1536-1544. [{}]
- Greene, C. H., A. J. Pershing, A. Conversi, B. Planque, C. Hannah, D. Sameoto, E. Head, P. C. Smith, P. C. Reid, J. Jossi, D. Mountain, M. C. Benfield, P. H. Wiebe, and E. Durbin. 2003. Trans-Atlantic responses of *Calanus finmarchicus* populations to basin-scale forcing associated with the North Atlantic Oscillation. *Progress Oceanography* 58: 301-312. [*North Sea C. finmarchicus negatively correlated with the NAO, but Gulf of Maine C. finmarchicus are positively associated with the NAO.*]
- Greene, C. H., A. J. Pershing, R. D. Kenney, and J. W. Jossi. 2003. Impact of climate variability on the recovery of endangered North Atlantic Right Whales. *Oceanography* 16: 96-101. [*A speculative stage-based model for right whales couples calving to C. finmarchicus abundance which is coupled to the NAO*]
- Jossi, J. W., A. W. G. John and D. Sameoto. 2003. Continuous plankton recorder sampling off the

east coast of North America: history and status. *Progress Oceanography* 58: 313-325. [Documents decadal increasing abundance of *C. finmarchicus* and *Pseudocalanus* in the Gulf of Maine] {}

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K.-S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. *Science* 297: 1292-1296. [Interesting general discussion of the effects of the NAO on ecological processes]

Thomas, A. C., D. W. Townsend, and R. Weatherbee. 2003. Satellite-measured variability in the Gulf of Maine. *Continental Shelf Research* 23: 971-989. [The lack of a bloom in 1998 probably due to intrusion of Labrador slope water associated with Negative NAO event. Note that 1998 was a bad year for *Calanus* in Turner et al. (2006)] {}

Turner, J. T., D. G. Borkman, and C. D. Hunt. 2006. Zooplankton of Massachusetts Bay, USA, 1992-2003: relationships between the copepod *Calanus finmarchicus* and the North Atlantic Oscillation. *Mar. Ecol. Prog. Ser.* 311: 115-124. [They document a negative (not Greene's positive) correlation between NAO and *C. finmarchicus* abundance with no lags. The copepods are affected negatively by wind mixing which is correlated with NAO. Implications for right whale feeding discussed.] {}

## BENTHIC METABOLISM

### Comment on metabolic papers

This collection of papers is a potpourri of references involving measurements of total community metabolism. Many of the topics covered are also dealt with in references dealing with estimates of microbial production. If there is an underlying theme to these papers, it is the effort to measure the utilization of organic matter in benthic communities by measuring the flux of terminal electron acceptors (*i.e.*, O<sub>2</sub> or SO<sub>4</sub>) into the sediment.

Anderson, L. G., P. O. J. Hall, A. Iverfeldt, M. M. Rutgers van der Loeff, B. Sundby, and S. F. G. Westerland. 1986. Benthic respiration measured by total carbonate production. *Limnol. Oceanogr.* 31: 319-329.

Bagheri, E. A. and D. S. McLuskey. 1984. The oxygen consumption of *Tubificoides benedeni* (Udekam) in relation to temperature, and its application to production biology. *J. exp. mar. Biol. Ecol.* 78: 187-197. [Used 3 methods: Gibson respirometer, O<sub>2</sub> electrode and Cartesian diver. Calculated field production using: log production = 0.942 log respiration - 0.252. Annual production ranges from 0.84 to 3.33 g ash free dry weight m<sup>-2</sup> yr<sup>-1</sup> in the Forth estuary. The mean P:B ratio is a low 0.85:1. Small polychaetes and oligochaetes may comprise 49% of invertebrate secondary production.]

Banse, K., F. H. Nichols, and D. R. May. 1971. Oxygen consumption by the seabed. III. On the role of macrofauna at three stations. *Vie Milieu Suppl.* 22: 31-52. [Respiration scales allometrically with body size. Noted the lower weight-specific respiration rates of the subsurface deposit feeders relative to surface deposit feeders] [8, 12]

Cammen, L. M. 1980. Ingestion rate: an empirical model for aquatic deposit feeders and detritivores. *Oecologia (Berl)* 44: 303-310. [An empirical allometric relationship between organic matter content of sediments, body size and ingestion rate is proposed] [11, 16, 31, 36]

Cammen, L. M. 1985. Metabolic loss of organic carbon by the polychaete *Capitella capitata* (Fabricius) estimated from initial weight decrease during starvation, oxygen uptake, and release of <sup>14</sup>C by uniformly-labeled animals. *Mar. Ecol. Prog. Ser.* 21: 163-167. [*Capitella* loses 5-8%, 8-9% and 9-16% of their body weight per day at 10, 20 and 30°C respectively. These rates of loss are higher than one would expect from basal metabolic allometric equations.]

Grant, J. and B. T. Hargrave. 1987. Benthic metabolism and the quality of sediment organic carbon. *Biological Oceanography* 4: 243-264.

Hargrave, B. T. and G. A. Phillips. 1986. Dynamics of the benthic food web in St. George's Bay, southern Gulf of St. Lawrence. *Mar. Ecol. Prog. Ser.* 31: 277-294.

Pamatmat, M. M. 1977. Benthic community metabolism: a review and assessment of present status and outlook. Pp. 89-111 in B. C. Coull, *ed.*, Ecology of Marine Benthos. U. South Carolina Press, Columbia.

Smith, K. L. 1973. Respiration of a sublittoral community. *Ecology* 54: 1065-1075.

Smith, K. L. and R. J. Baldwin. 1984. Seasonal fluctuations in deep-sea sediment community oxygen consumption: central and eastern North Pacific. *Nature* 307: 624-625.

Stamhuis, E. J., J. J. Videler, P. A. W. J. de Wilde. 1998. Optimal foraging in the thalassinidean shrimp *Callinassa subterranea*. Improving food quality by grain size selection. *J. Exp. Mar. Biol. Ecol.* 228: 197-208. [*This North Sea deposit feeder selectively ingests small organic-rich particles, as Taghon et al. (1978), Taghon (1981) model predictions. The ingestion of about 1 body*

*weight per day increases with AFDW to the 0.9 power, a slightly higher exponent than Cammen (1980)]{?}*

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Eppley, R. W. 1972. Temperature and phytoplankton growth in the sea. *Fish. Bull.* 70: 1063-1065. [6]

Mayo, C. A. and M. K. Marx. 1990. Surface foraging behavior of the North Atlantic right whale, *Eubalaena glacialis*, and associated zooplankton characteristics. *Can. J. Zool.* 68: 2214-2220. [*Tracking of feeding tracks of whales in Cape Cod Bay — dominated by C. finmarchicus & Pseudocalanus minutus, Centropages and larval barnacles.*]

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