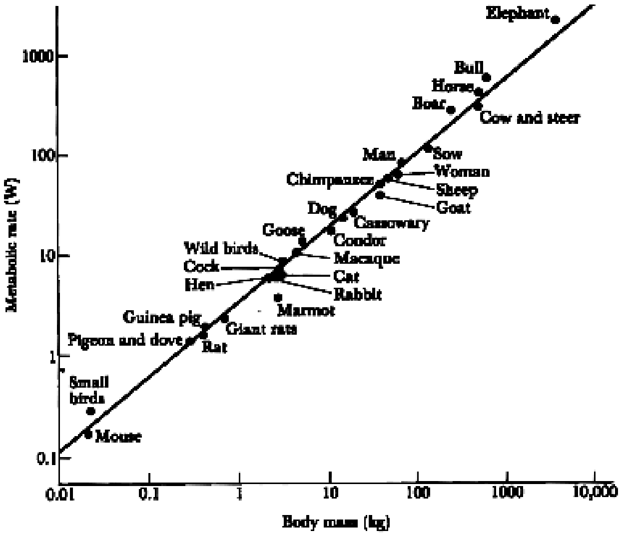
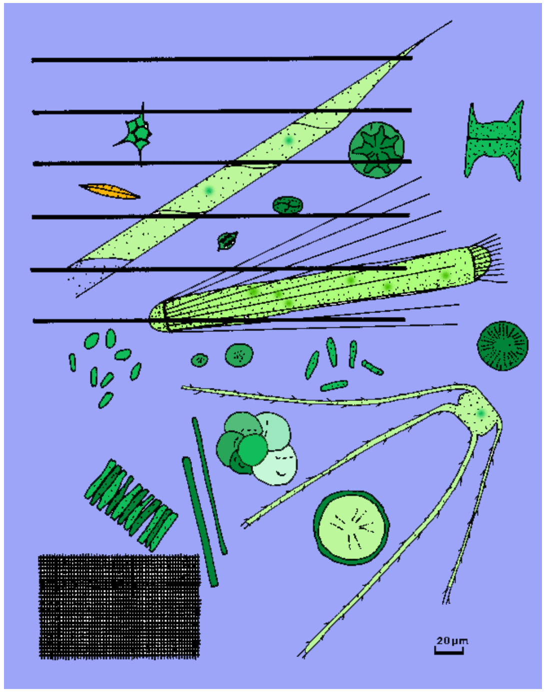
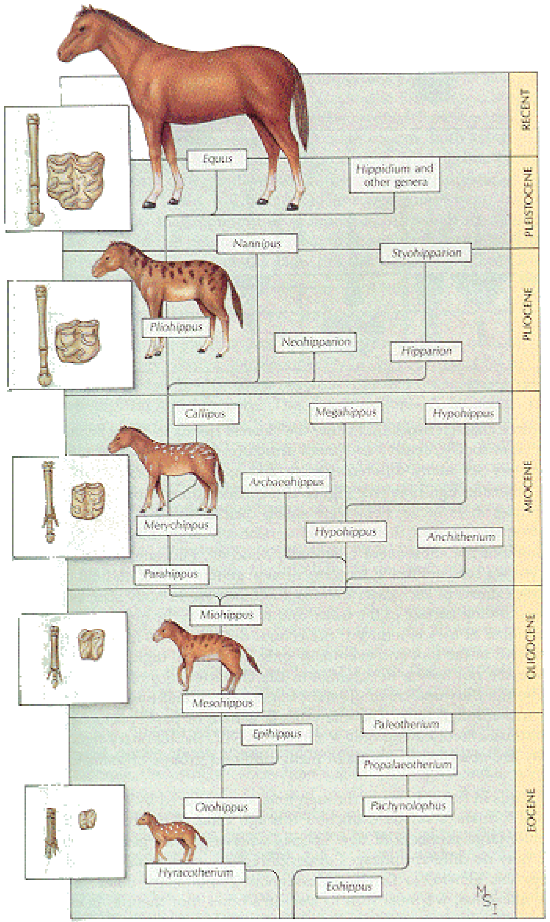
Why size matters



Physiological rates



Community composition



Evolutionary patterns

Outline

1. What is allometry?
2. Why should you care?
3. Physiological bases of size scaling of metabolism
4. Ecological consequences of size-dependent physiology
5. Size-dependent selection: evolutionary patterns in body size
6. Some environmental consequences of changes in the body size of critters.

1. **What is Allometry?**

Merriam-Webster defn: relative growth of a part in relation to an entire organism or to a standard; *also* **:** the measure and study of such growth
- **al·lo·me·tric** /"a-l&-'me-trik/ *adjective*

SJ Gould (1966) Allometry - the study of size and its consequences.

2. Why should you care

- Body size has an influence on organisms on physiological, ecological and evolutionary scales.

- Changes in size, and the adaptations associated with these changes, often define the differences between higher taxonomic groupings (Gould 1966).

- Change in body size can have environmental consequences.

The importance of scale

- Our understanding of nature is limited by our perception of our surroundings
- We often forget that other organisms perceive the world differently from the way we do
- A flea can jump a hundred times its length - But the flea is not actually performing athletic miracles
- *"You can drop a mouse down a thousand-yard mine shaft and, on arriving at the bottom, it gets a slight shock and walks away. A rat would probably be killed, though it can fall safely from the eleventh story of a building, a man is broken, a horse splashes." -- J. B. S. Haldane*

Reading I: JBS Haldane (1929) On being the right size. From The World’s best essays: from Confucius to Meneken. HapperCollins

JBS HALDANE

- **John Burdon Sanderson** , 1892–1964, British geneticist, biologist, and popularizer of science.
- One of the most influential scientists of the 20th cent.
- Studied relationships among different disciplines and problems, including the consequence of Mendelian genetics on evolutionary theory, the relationship between enzymology and genetics, and the application of mathematics and statistics to the study of biology.

An organism assumes a form best adapted to its size

- Body size dictates the morphology, ecology, physiology and evolution of an organism

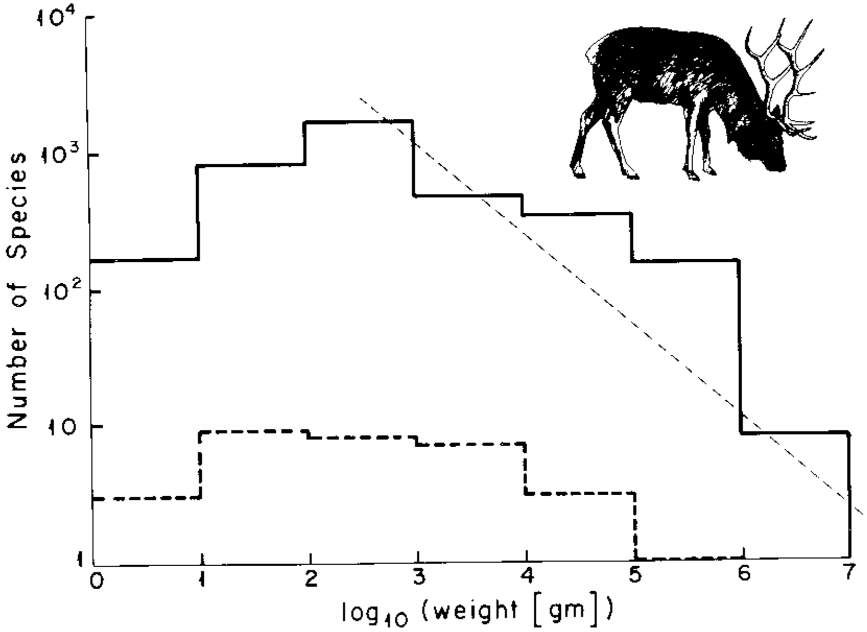
- "*Size increase permits the expression of new potentiality*" - S.J. Gould (1966)
- "*Comparative anatomy is largely the story of the struggle to increase surface in proportion to volume*" – Haldane (1929)

- This is based on physical constraints – a larger building must be made wider or out of stronger materials!

Optimal size

- We often define different groups by different sizes
- Each physiological/morphological strategy then has a size distribution
- Many groups have right-skewed log-normal distributions where there are a few species smaller than the mode and many larger

Size frequency distributions



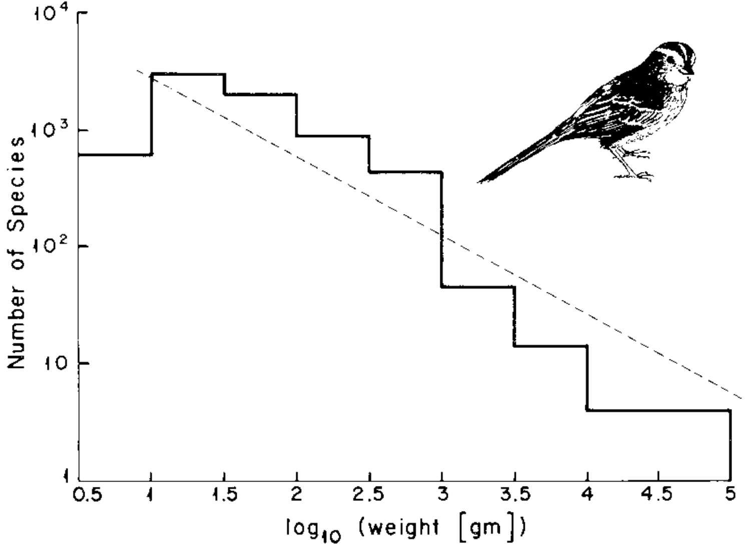
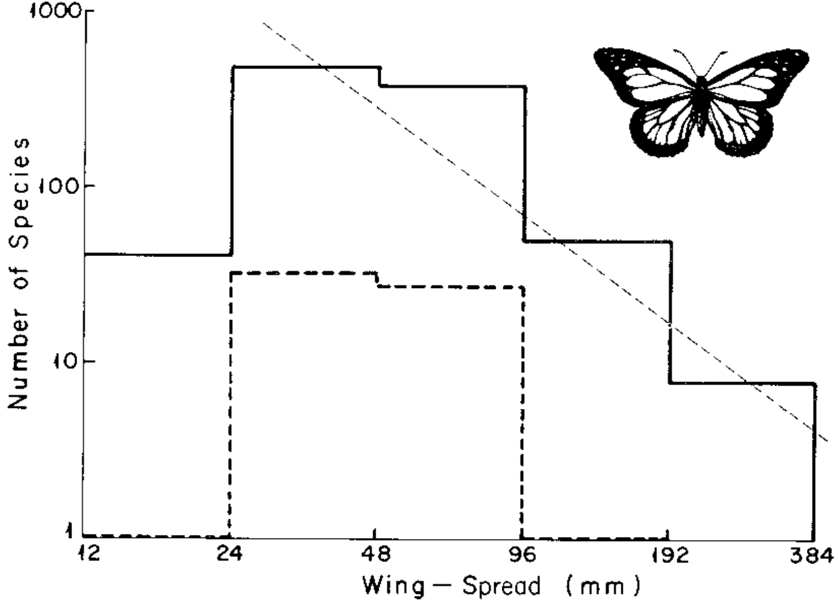
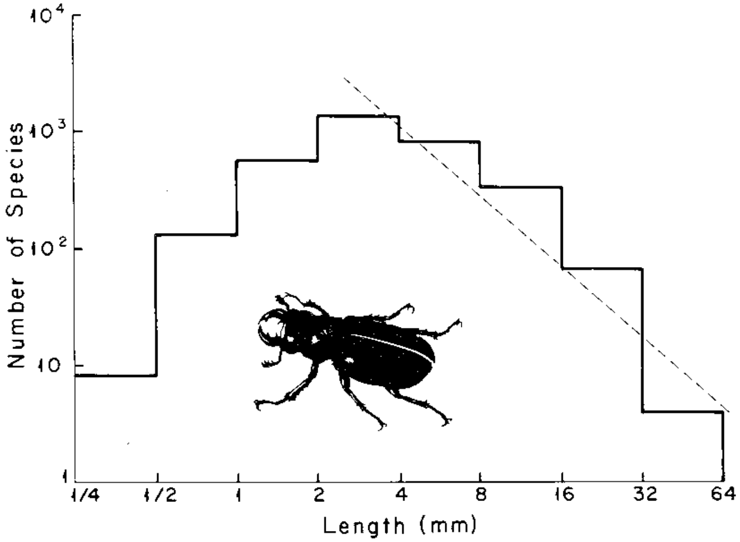


FIG. 12.2. The number of species of non-aquatic birds, classified according to weight. The dashed line is as in Fig. 12.1. (Data compiled by Van Valen, 1973).





th.
the

(May, 1978)

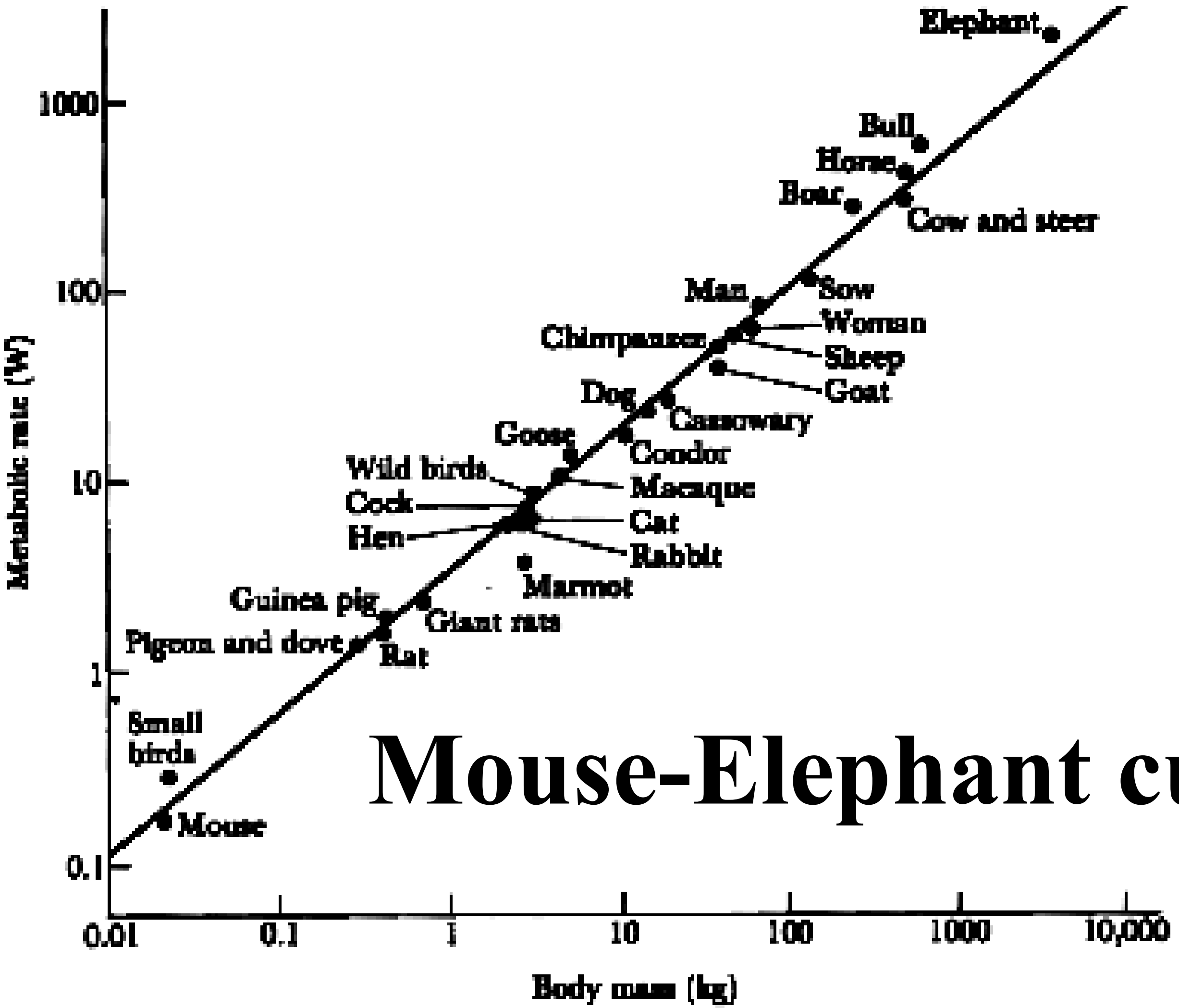
Optimal size associated with basic strategies

- Insects aerate their bodies through diffusion via tubes called tracheae with openings on the body surface
- Diffusion is very slow – becomes v. slow at ¼ inch thick
- Hardly any insects are more than ½ inch thick
- Vertebrates have gills or lungs and circulatory systems – they can be much thicker

3. Physiological bases of size scaling of metabolism

- Size-dependence of metabolic rates
- The surface rule
- The ¾ rule
- Theories for the ¾ rule
- Physiological bases for variation in ¾ rule
- Advantages and disadvantages of large versus small size

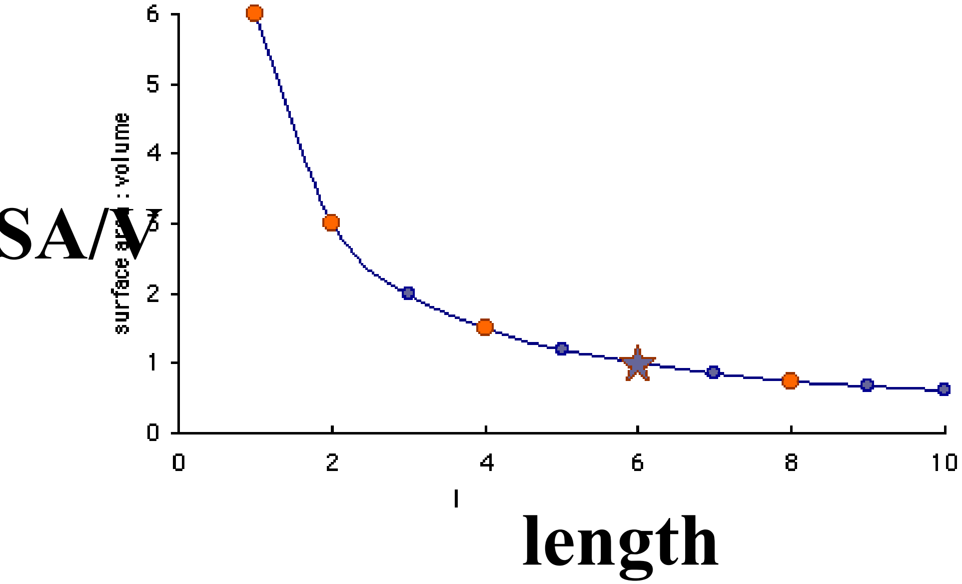
Size scaling of metabolism
One of the few laws in biology

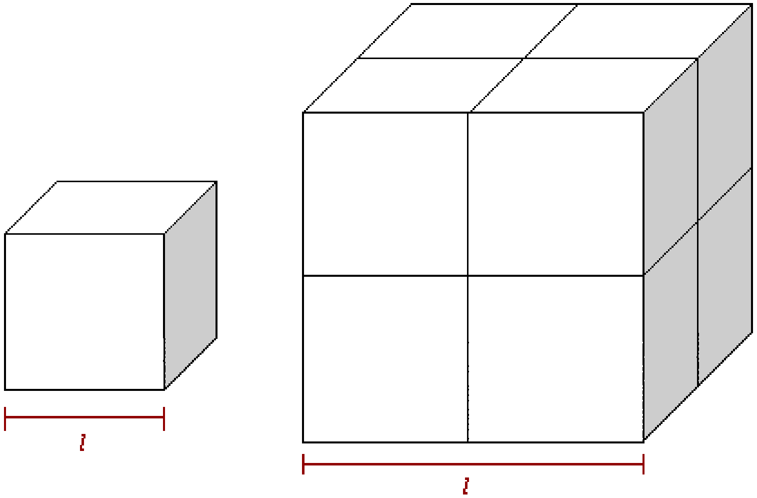


Mouse-Elephant curve

Surface rule (Rubner's rule)

Metabolic rate $\propto V^{2/3}$

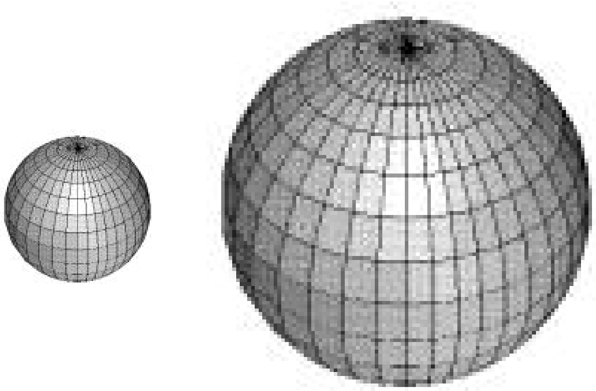




$$SA=4\pi r^2$$

$$V=4/3\pi r^3$$

$$SA/V = 3/r \propto V^{-1/3}$$



Some algebra

Metabolic rate per unit volume:
$SA/V = 3/r \propto V^{-1/3}$

Metabolic rate per individual:
$SA/V \cdot V \propto V^{-1/3} \cdot V^{1} \propto V^{2/3}$

Remember when you multiply or divide, you add or subtract the exponents, respectively!

Why is this important to animals?

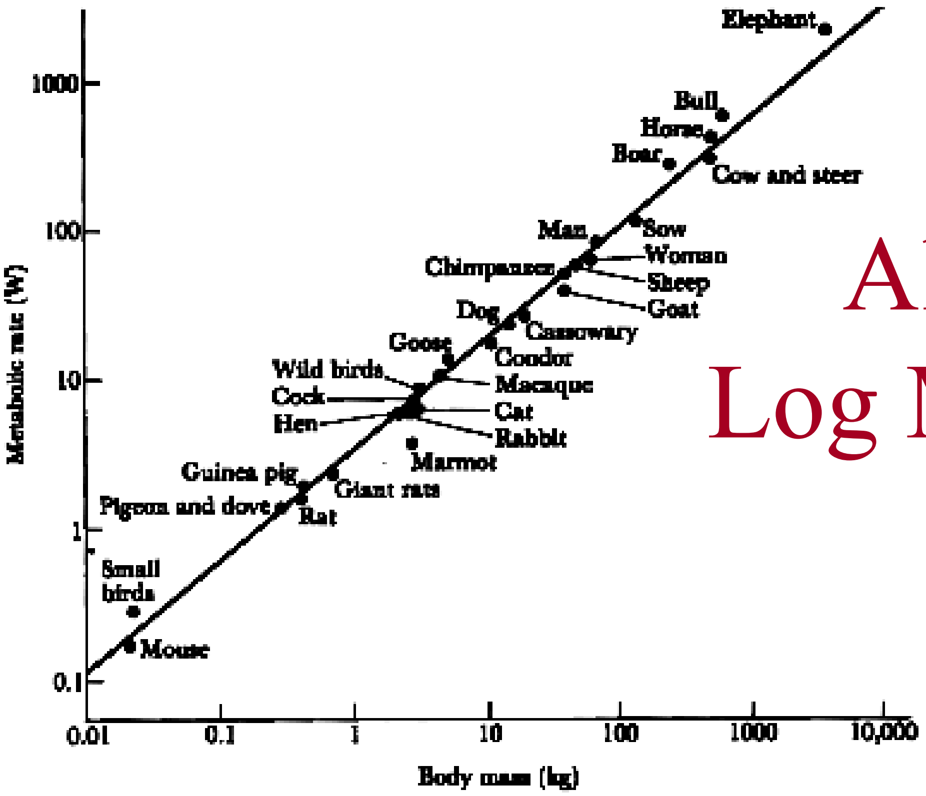
- Many functions that depend upon surface must serve the entire volume of the body

- One solution to decreasing surface has been the development of internal organs

Why is there a size scaling of metabolic rate?

- A change in size results in a change in SA/V, diffusion of nutrient through a surface area fueling a volume.
- The source of an animal’s body heat is metabolic processes. Thus, the larger the volume, the greater the total amount of heat energy required.
- In contrast, the path for heat loss from an organism is through the outer surface.
- Consequently, the higher the surface area to volume ratio the easier it is to keep cool, harder to keep warm.

Max Kleiber Quantifying the Mouse-Elephant Relationship



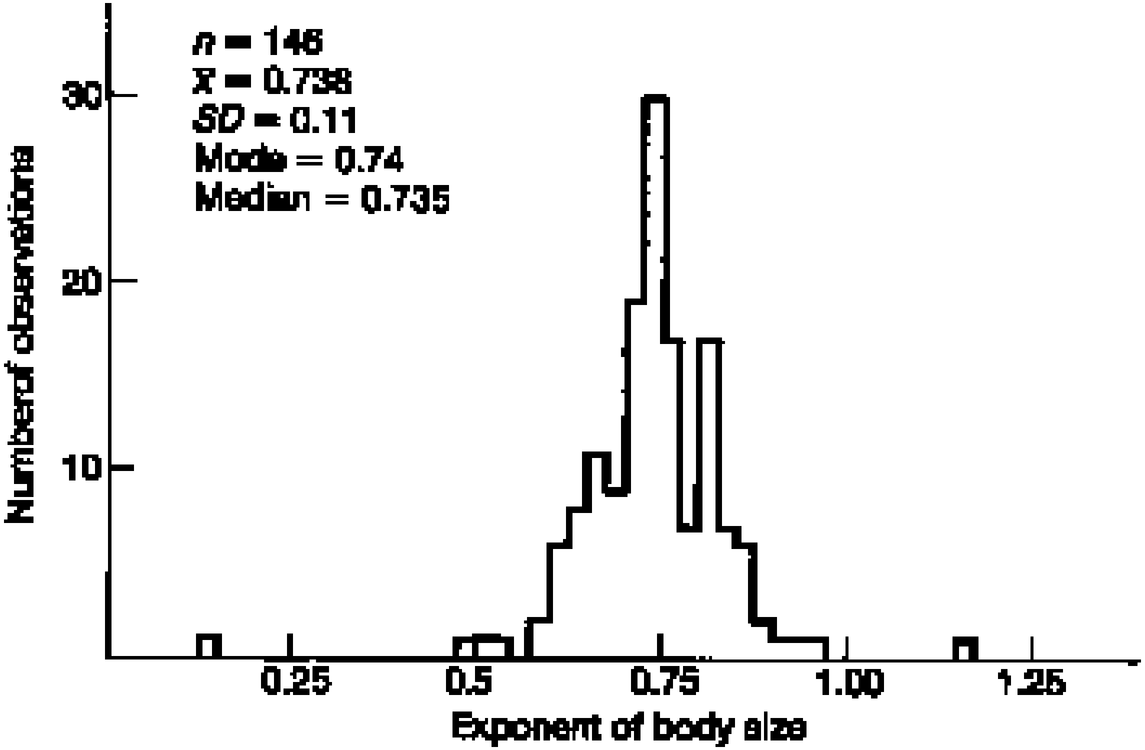
Allometric equation:

$$\text{Log Met} = \log a + b \log \text{Vol}$$

$$\text{Met} = a\text{Vol}^{b}$$

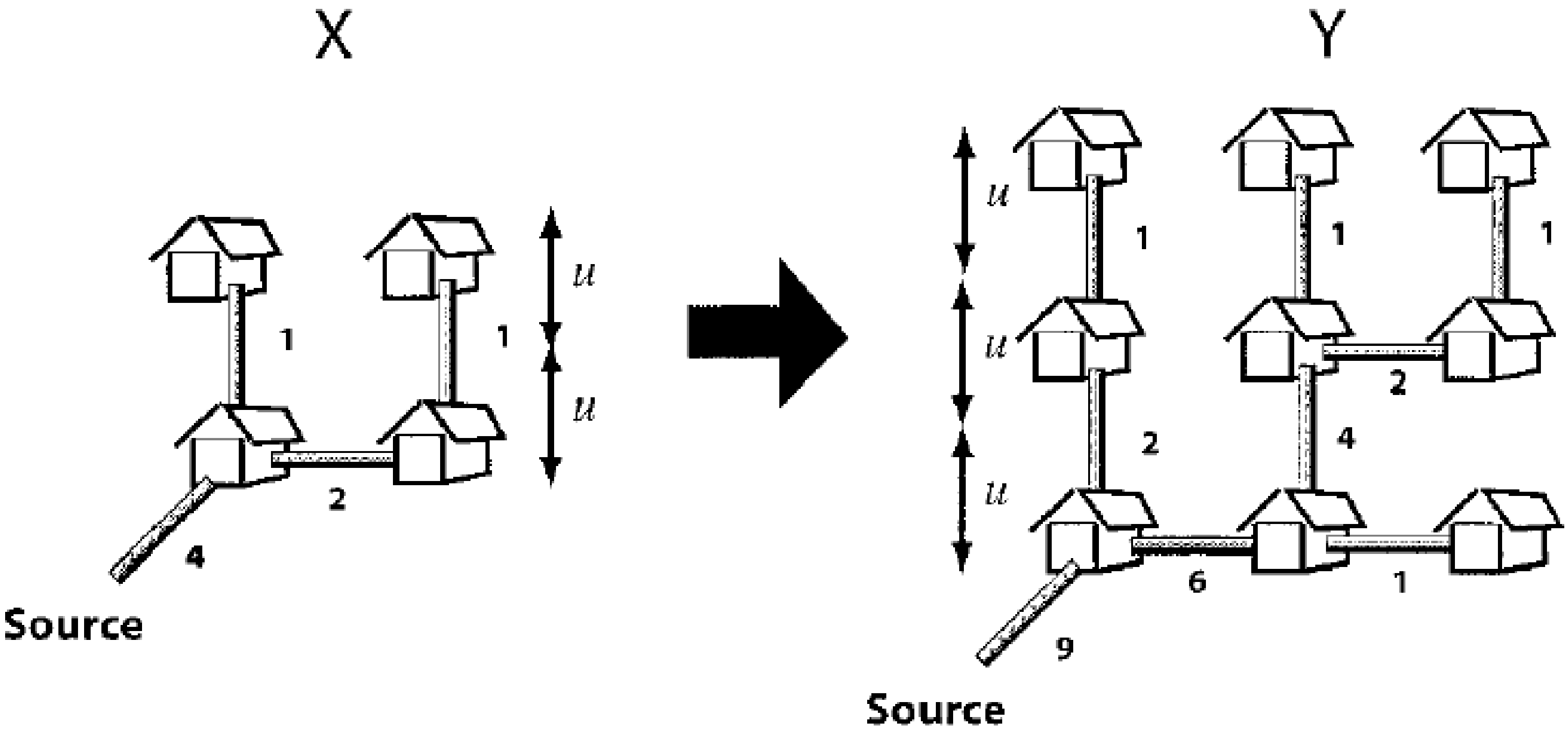
Surface rule: $b = 2/3$

Kleiber’s contribution:
¾ rule of metabolic scaling



Theories for the ¾ rule

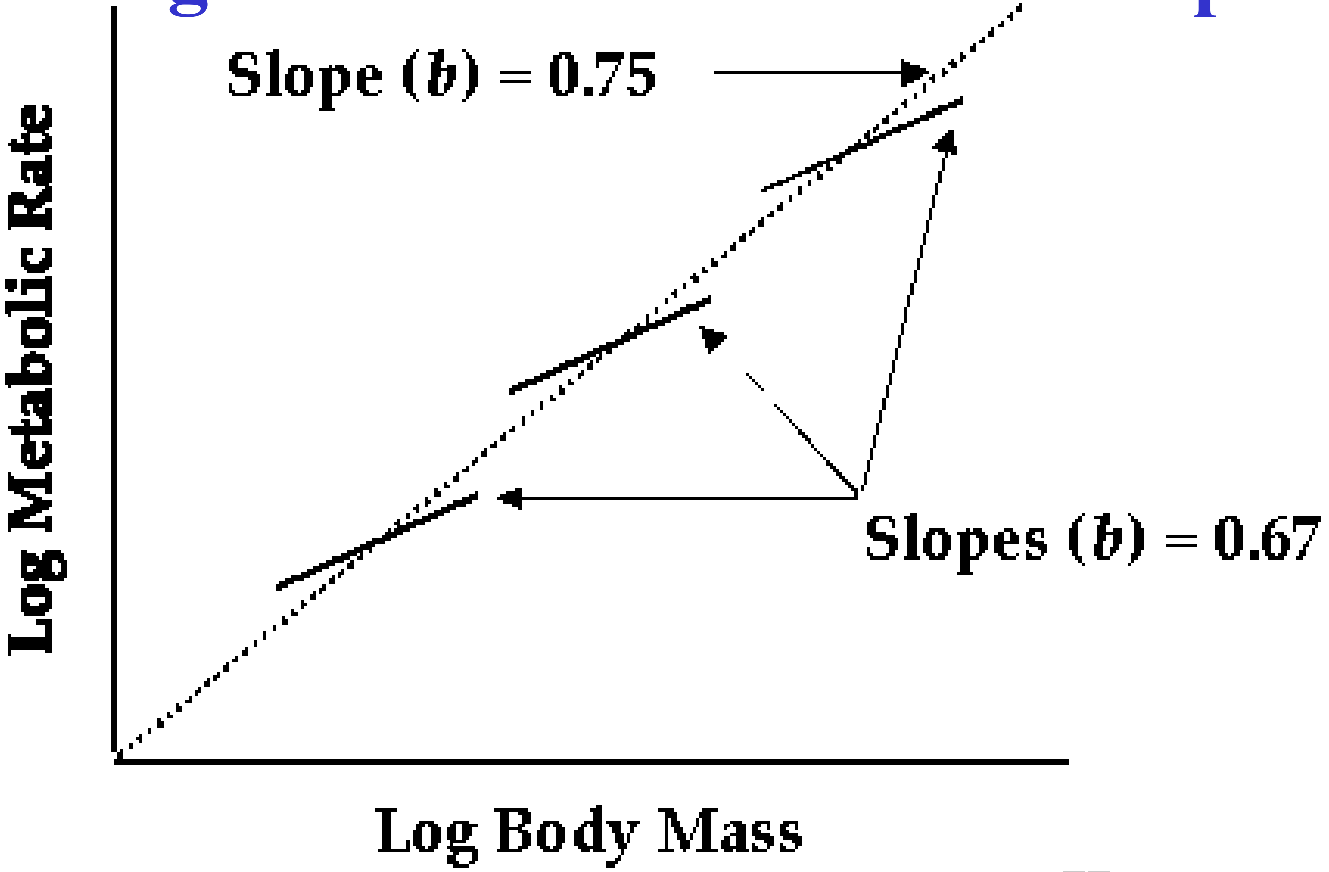
a) General scaling properties of directed transportation networks



Banavar *et al.* (2002): Supply-demand balance and metabolic scaling. PNAS 99(16): 10506-10509.

Theories for the ¾ rule

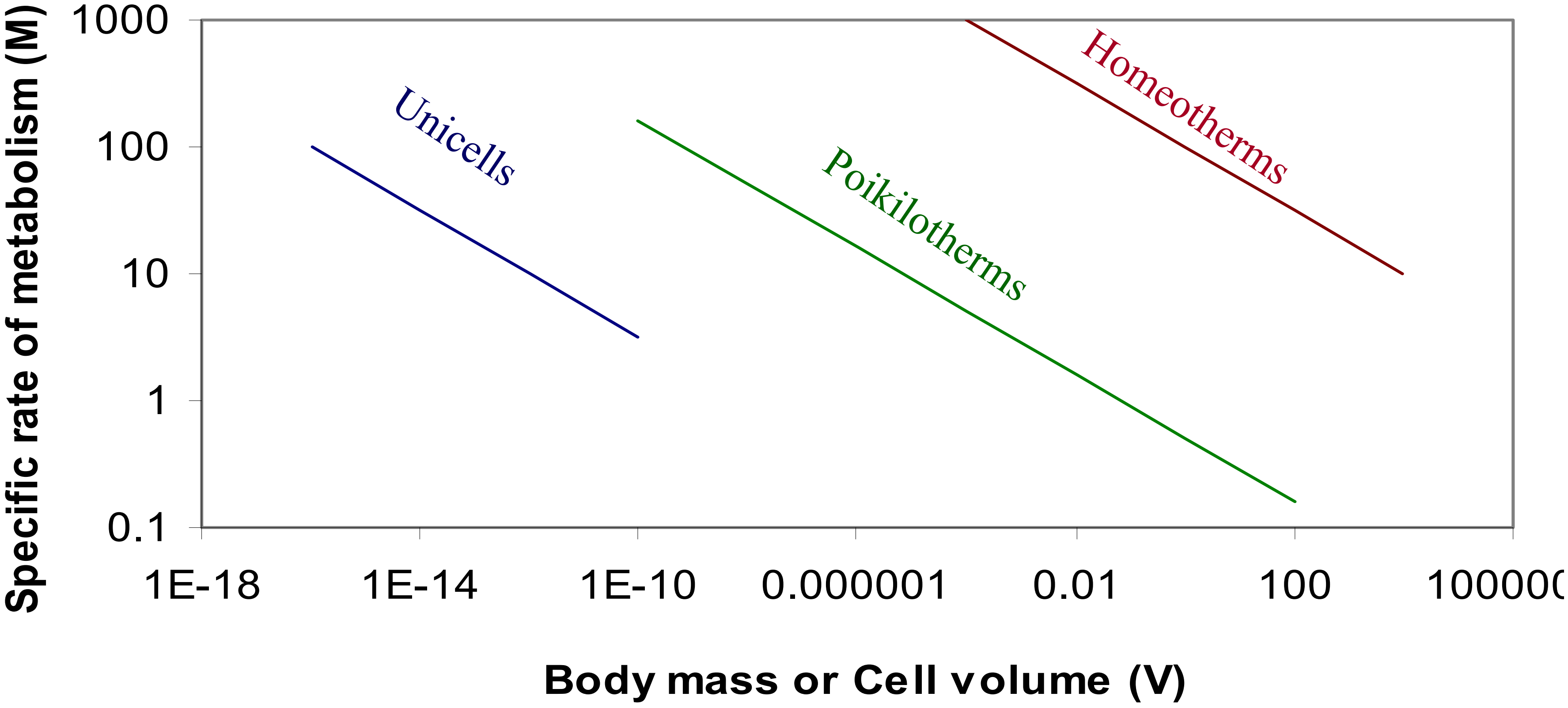
b) Artifact of mixing different groups together with different intercepts?



Huesner, 1982

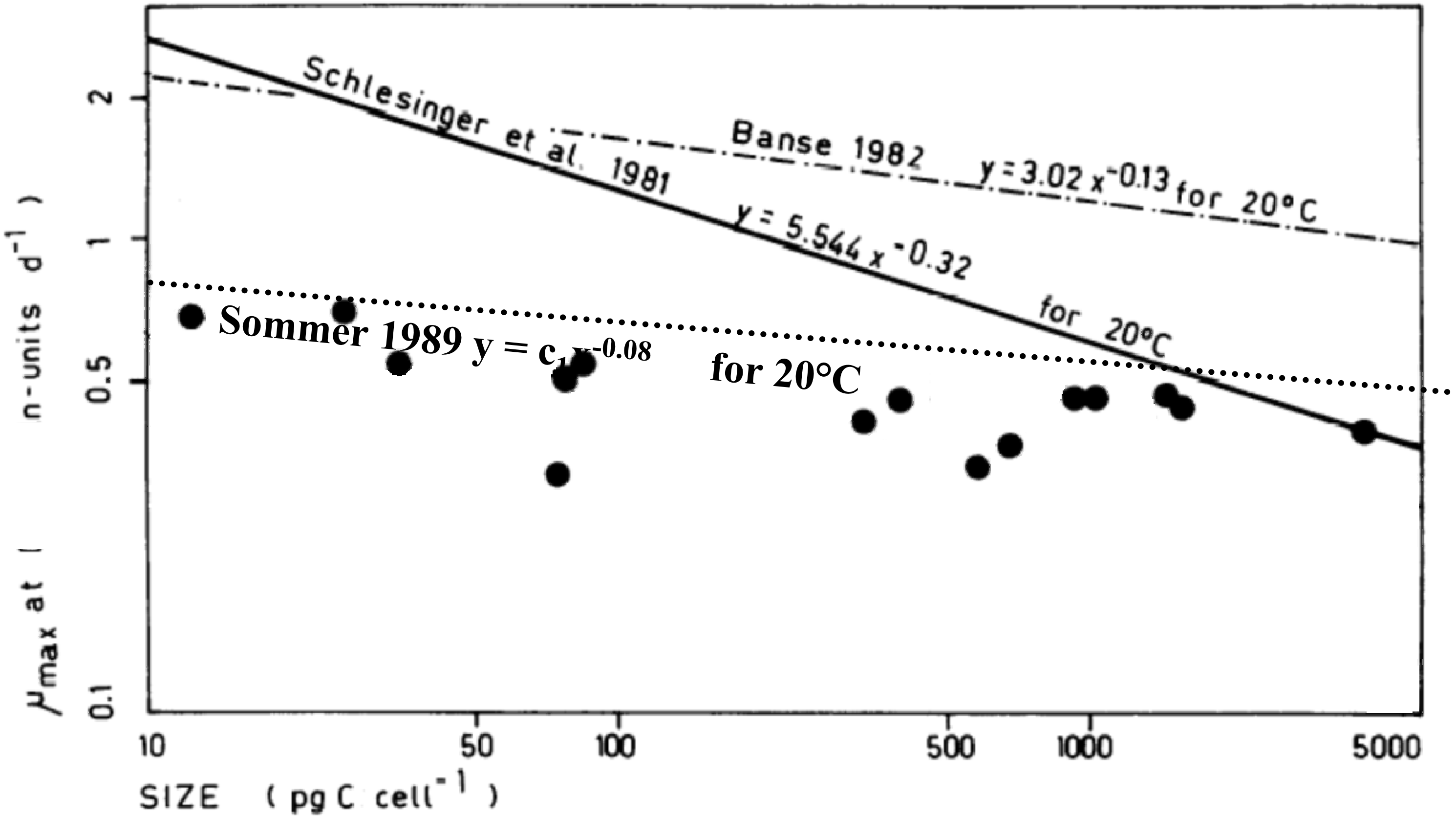
Different types of organisms have different intercepts:

$M=aV^b$



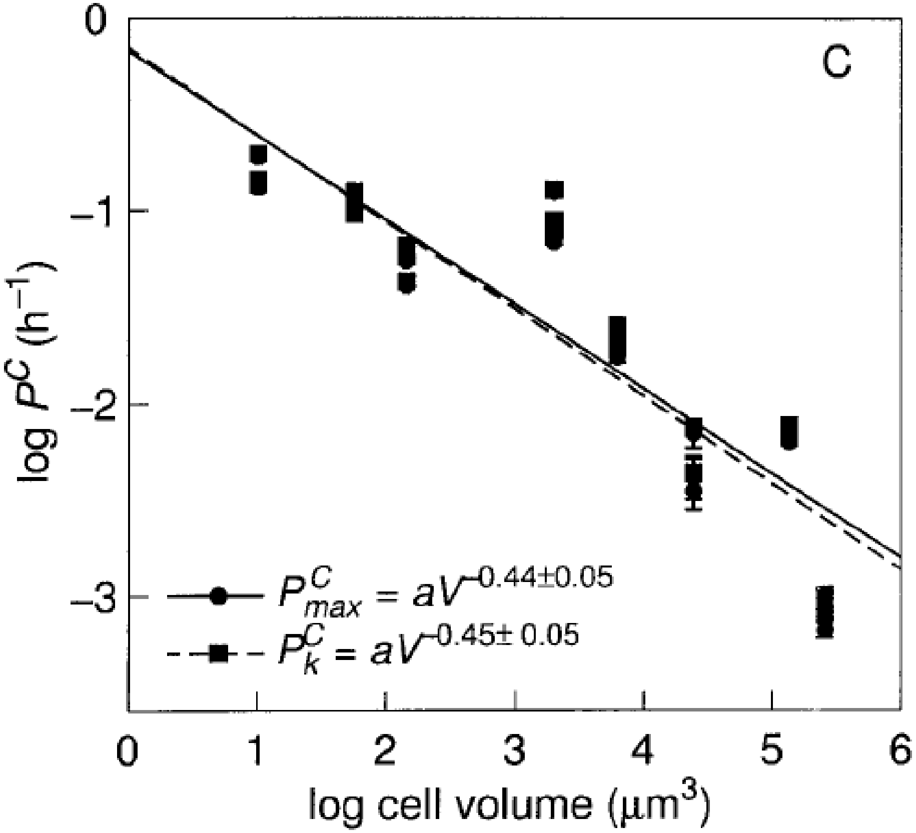
(Adapted from Peters 1983)

Physiological basis for reported deviations from the ¾ rule:



Modified from Sommer 1989

Exceptions to the ¾ rule: Light-limited photosynthesis

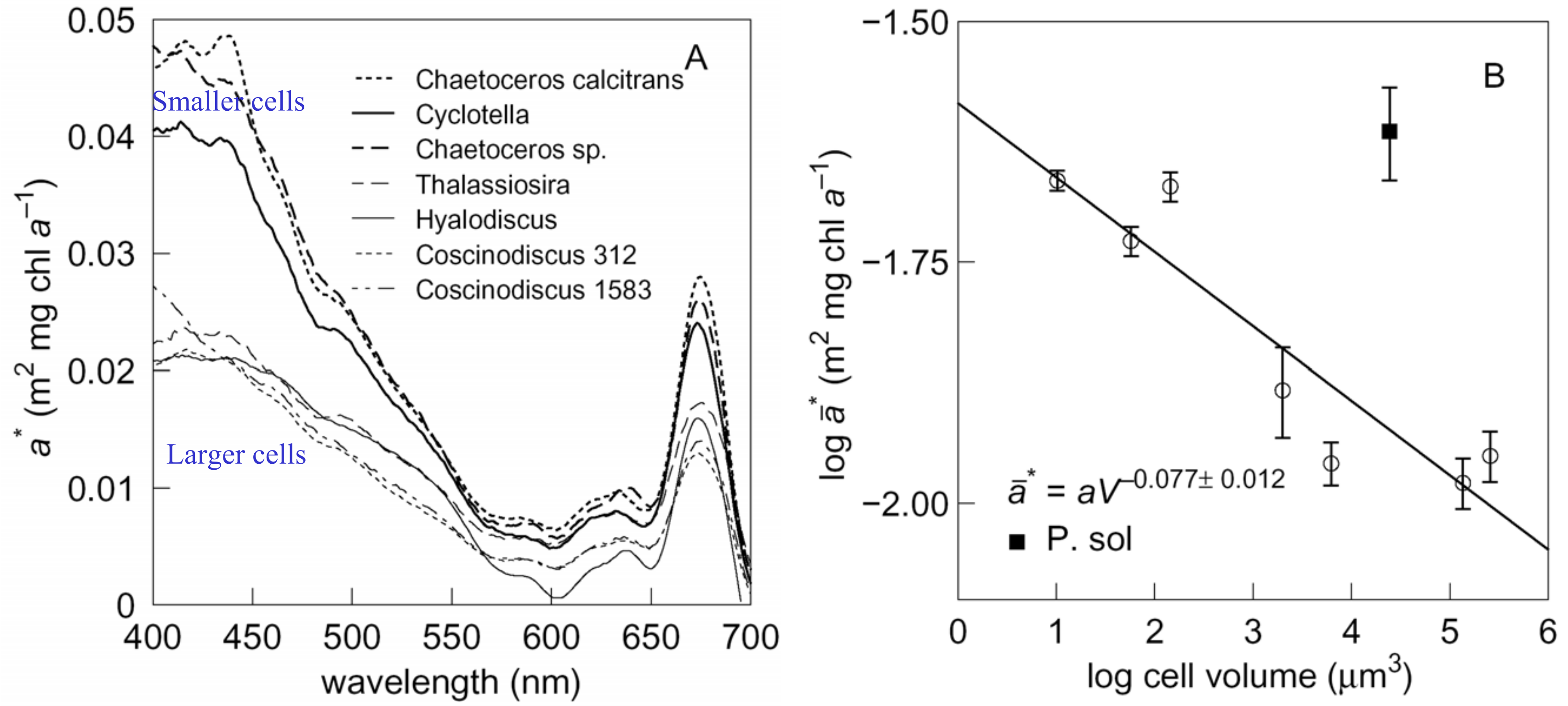


(Finkel 2001)

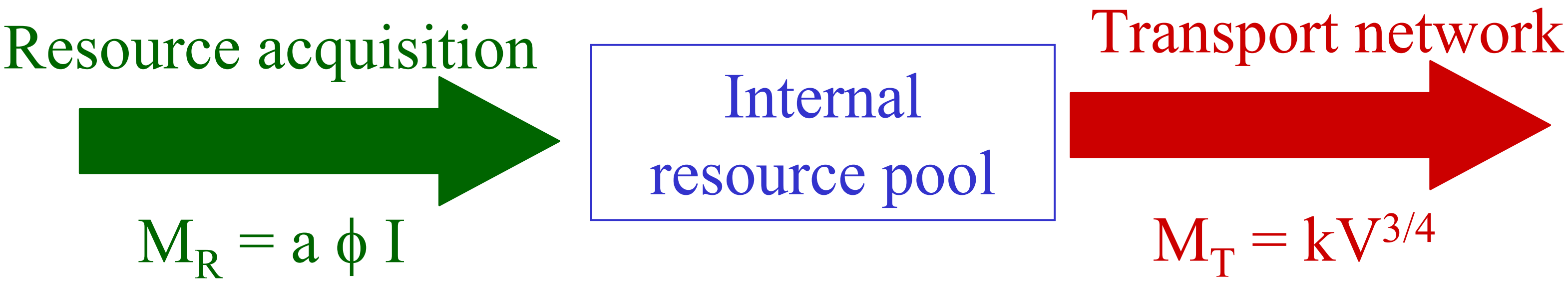
Resource acquisition

If acquisition of resources is size-dependent then there will be a change in the size scaling exponent associated with growth under resource-limiting versus saturating conditions.

Specific example: Light harvesting



(Finkel 2001)



Resource acquisition

Internal resource pool

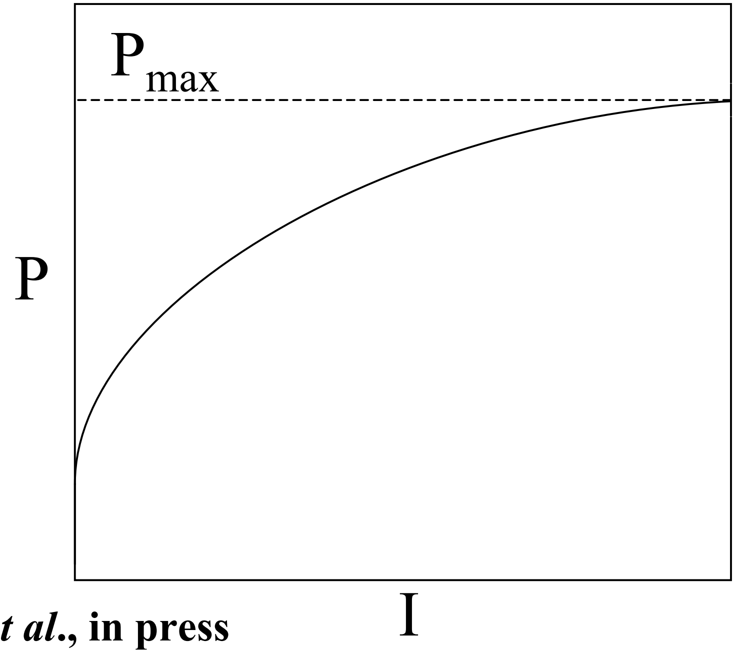
Transport network

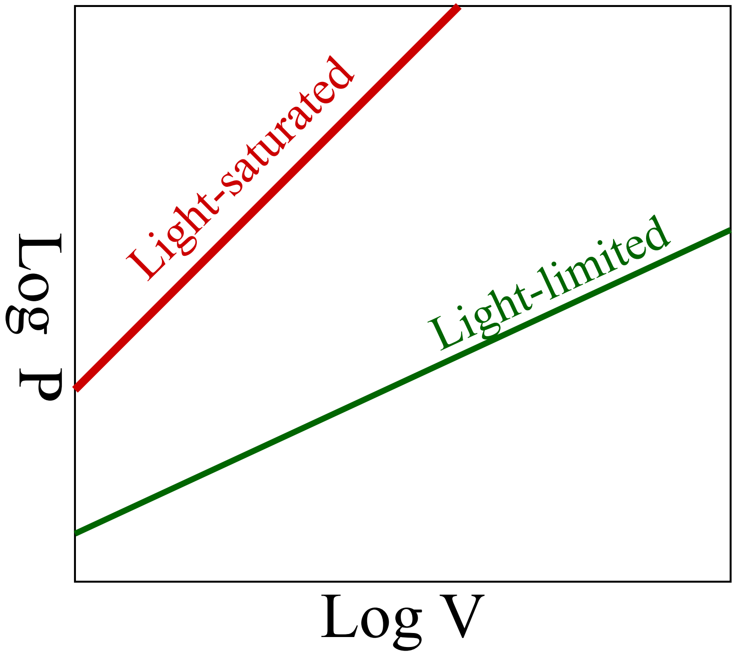
$M_R = a \phi I$

$M_T = kV^{3/4}$

$M = \mathrm{minimum}\ [M_R, M_T]$

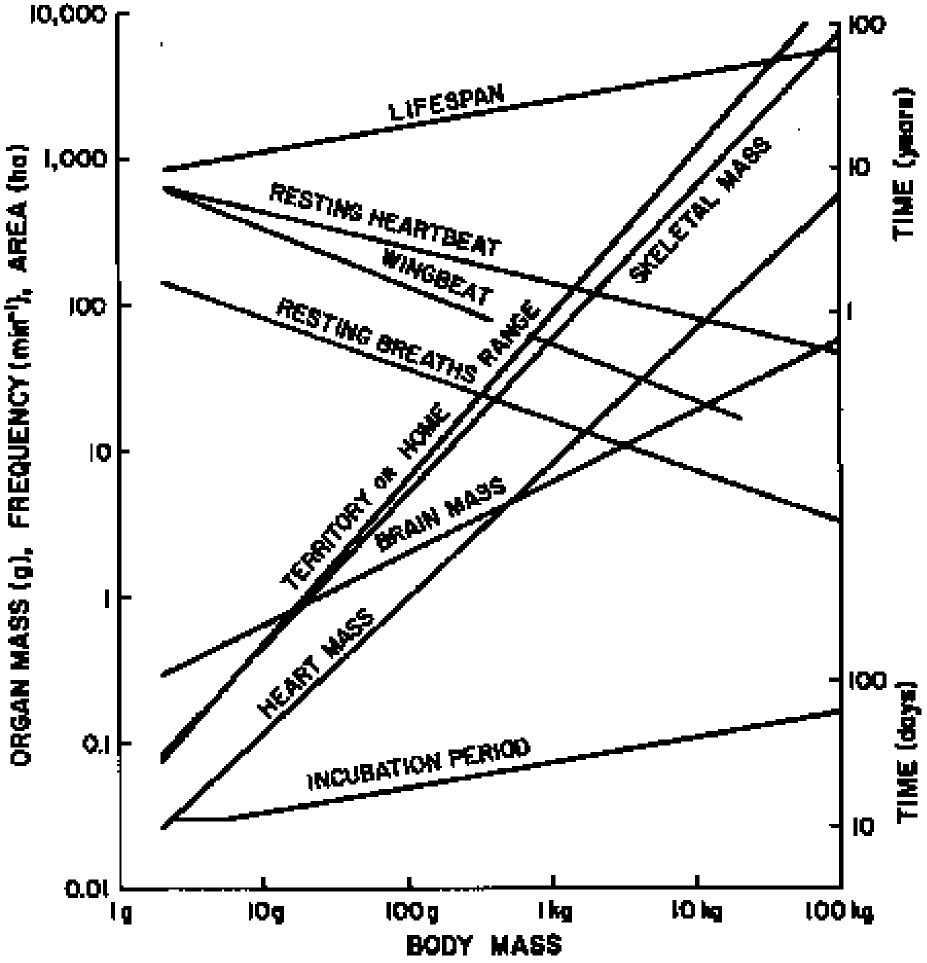
$$P = P_{max} \tanh (a \phi I / P_{max}), \ P_{max} = kV^{3/4}$$





Finkel *et al.*, in press

Other essential features of organisms change even more rapidly (or slowly) with increasing size than the ratio of surface to volume



Advantages of being small

- High resource acquisition efficiency
- High biomass-specific metabolic rates
- Low minimum resource requirements
- Higher population sizes
- More genetic diversity
- Therefore less likely to be susceptible to chance extinction events

Problems with Small Size

Loss of heat

Loss of water

- Why small organisms such as small mammals are not found in the far reaches of the north
- Why insects have a chitinous exoskeleton with a wax secretion

A limit to complexity

Disadvantages of large size
Why don't large animals fly?

Pr = Muscle power required for flight

$Pr \sim W^{1.17}$

If an organism is 2X another then the power needed is 2.25X's as much

Pa=Power available $Pa \sim W^{0.67}$

Only 1.59X as much power available - so power available increases less rapidly than power required

Advantages of being large

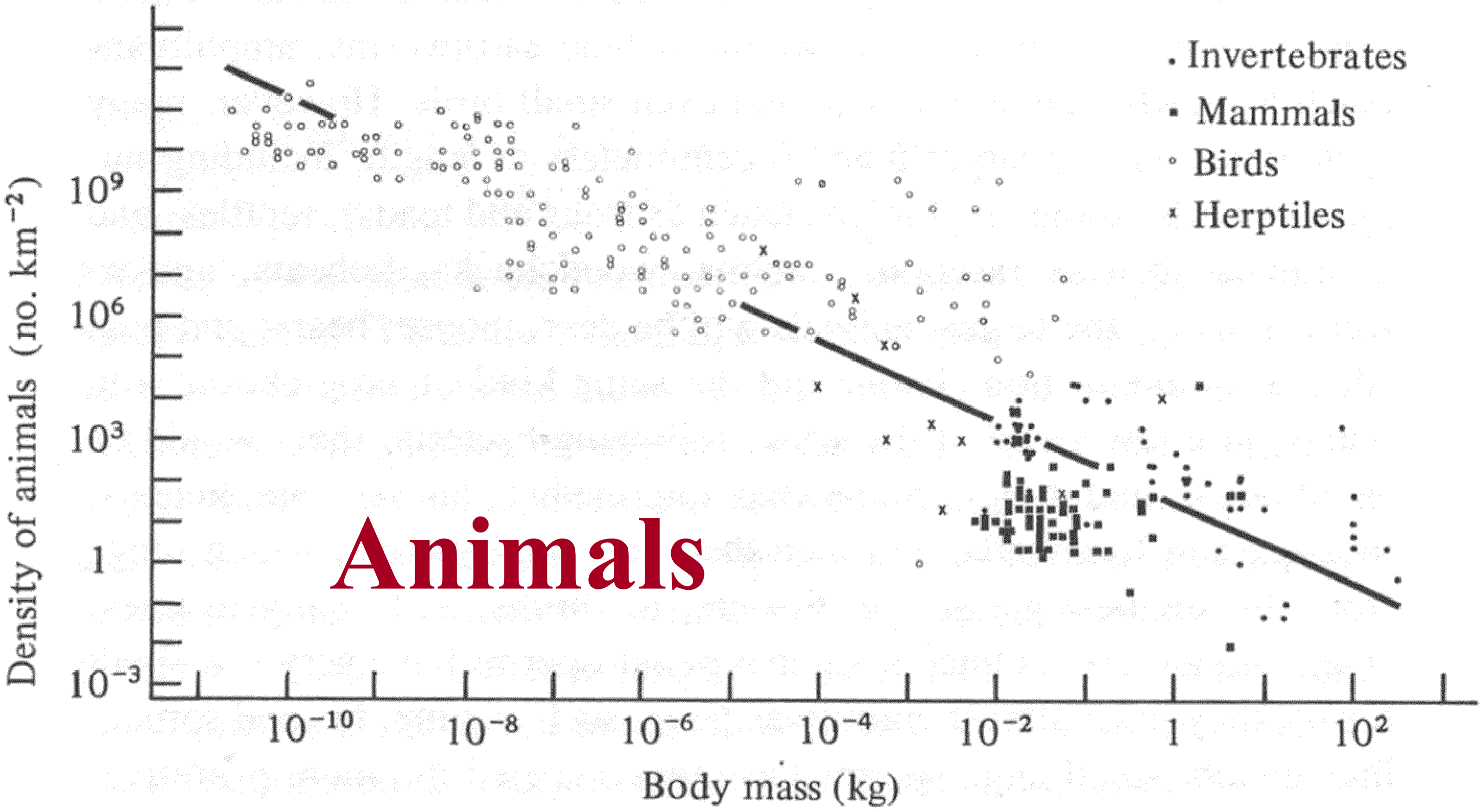
- COMPLEXITY
- Changes in size, and the adaptations associated with these changes, often define the differences between higher taxonomic groupings (Gould 1966). These changes in size has environmental consequences.
- Example: development of internal organs associated with multicellularity

4. Ecological consequences of size-dependent physiology

- Body size has an impact on ecological patterns

Population size is highly correlated with body size

population size related to probability of extinction

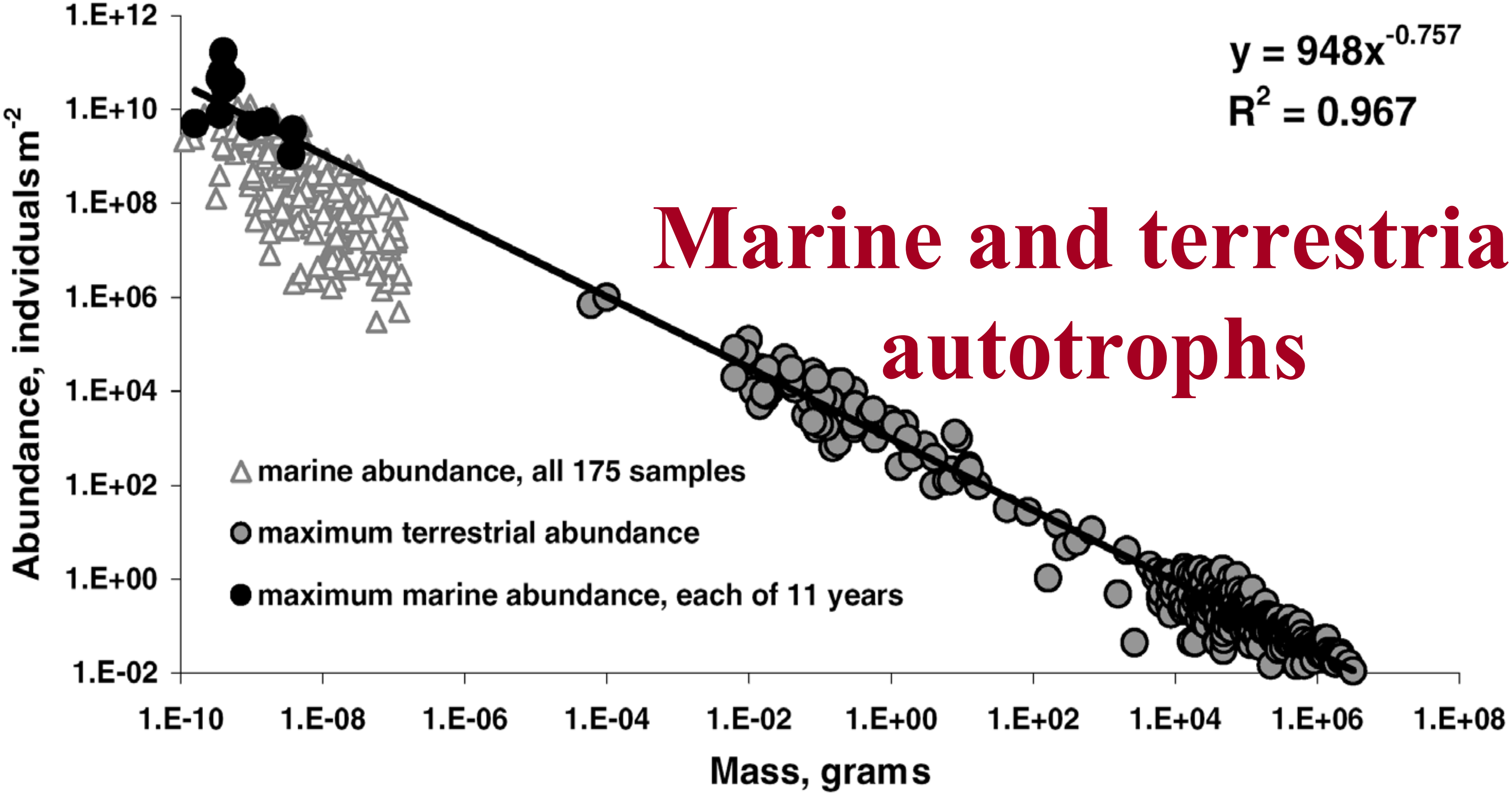


Animals

Fig. 16. The general relationship between the body size of different animals

(Bonner, 1988)

What controls the size distribution of communities?



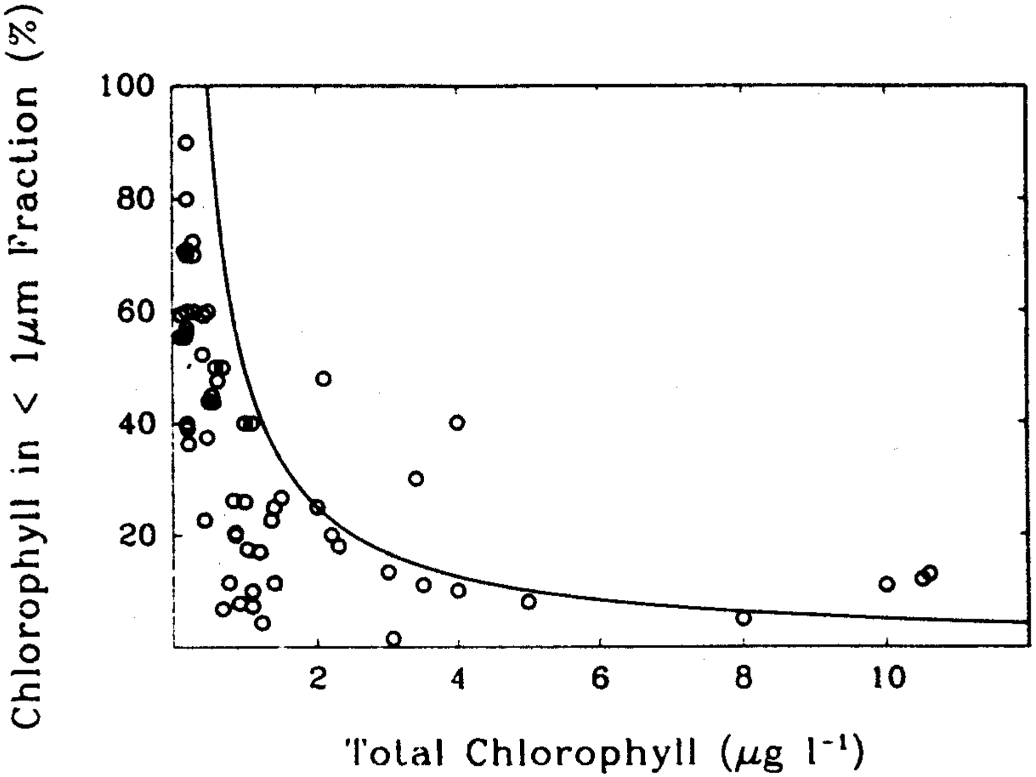
Marine and terrestrial autotrophs

Belgrano *et al*., Ecology Letters (2002) 5:611-613.

There is characteristic size structure in different habitats

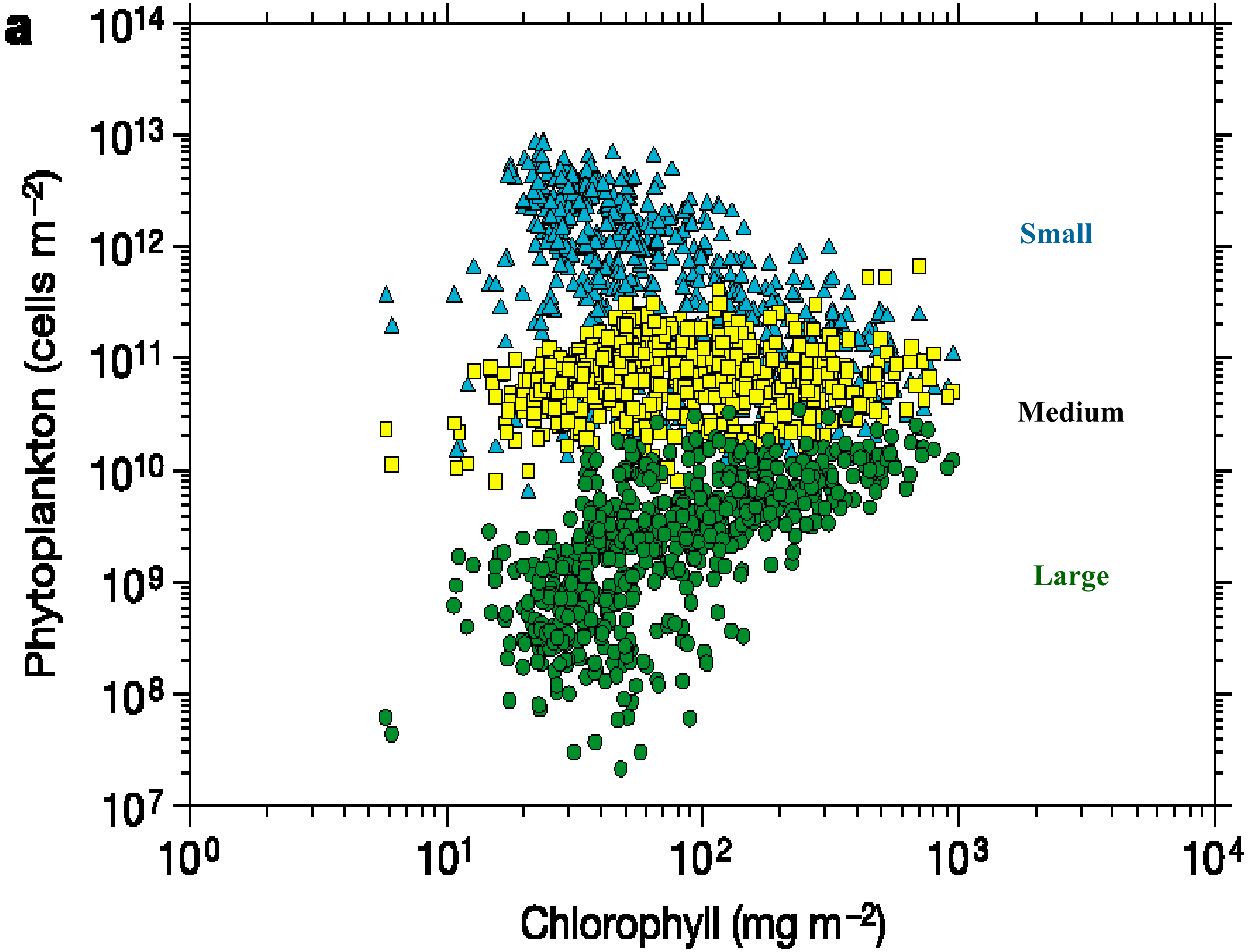
- Large organisms have higher resource requirements
- Larger organisms require more habitat to maintain viable population sizes to prevent genetic isolation, genetic bottlenecks, and chance extinction
- Example: Small phytoplankton dominate communities in the open ocean, while large phytoplankton dominate in coastal areas

Characteristic size structure of phytoplankton communities



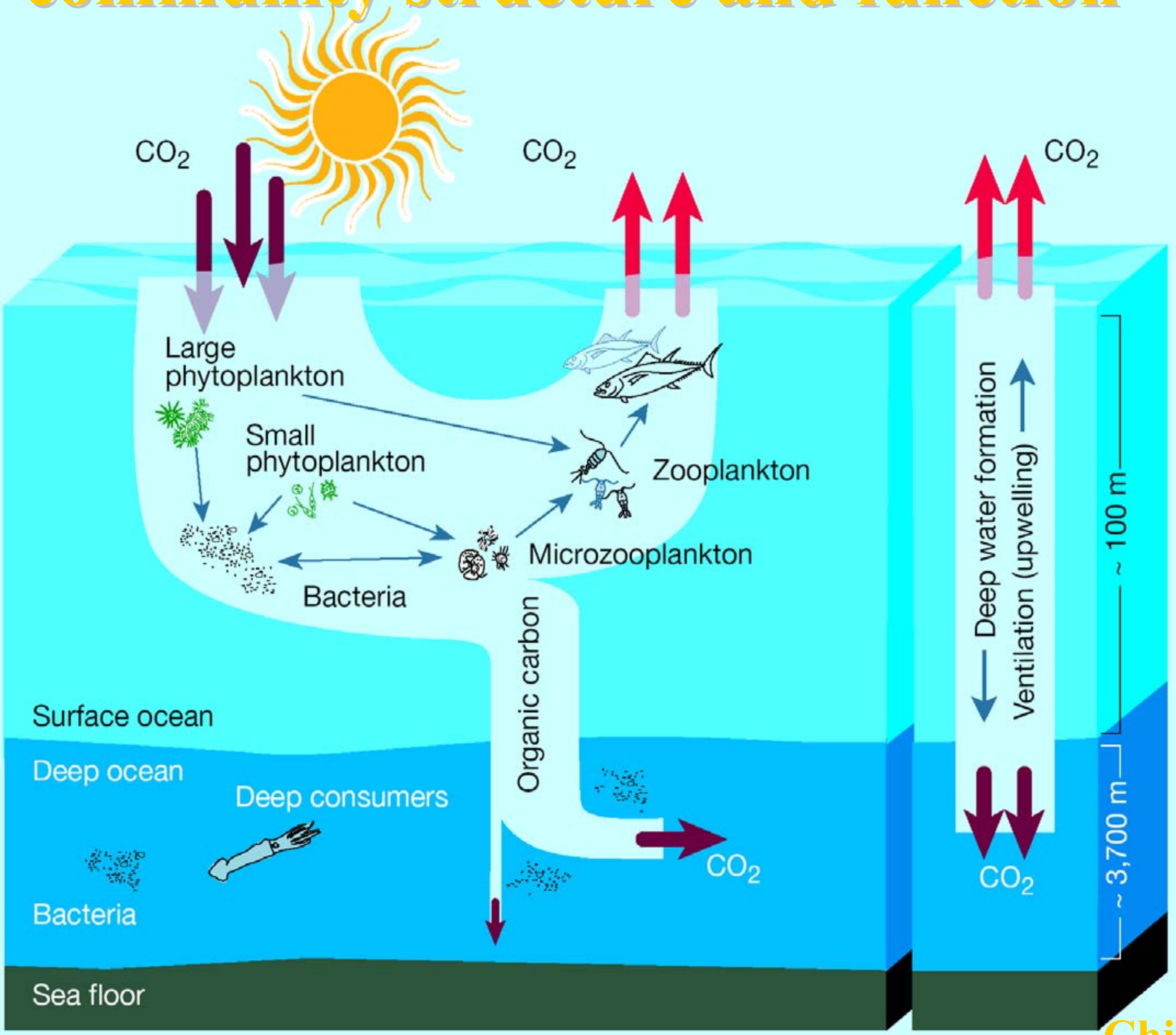
Chisholm, 1992

Resource availability causes variation in the size scaling of maximum abundance



Li, W.K.W. Nature, 2002. 419: p. 154 - 157.

Phytoplankton cell size, climate change and community structure and function



Chisholm, 2000

Temporal change in size structure

- A change in environmental conditions is associated with changes in the size structure of communities
- Long term environmental change can drive changes in phytoplankton size structure
- Potential for a climatic feedback

5. Size-dependent selection: evolutionary patterns in body size

- Body size is correlated with species longevity in the fossil record

- Maximum size (range) is correlated to evolutionary time (Cope’s rule)

Size and species longevity

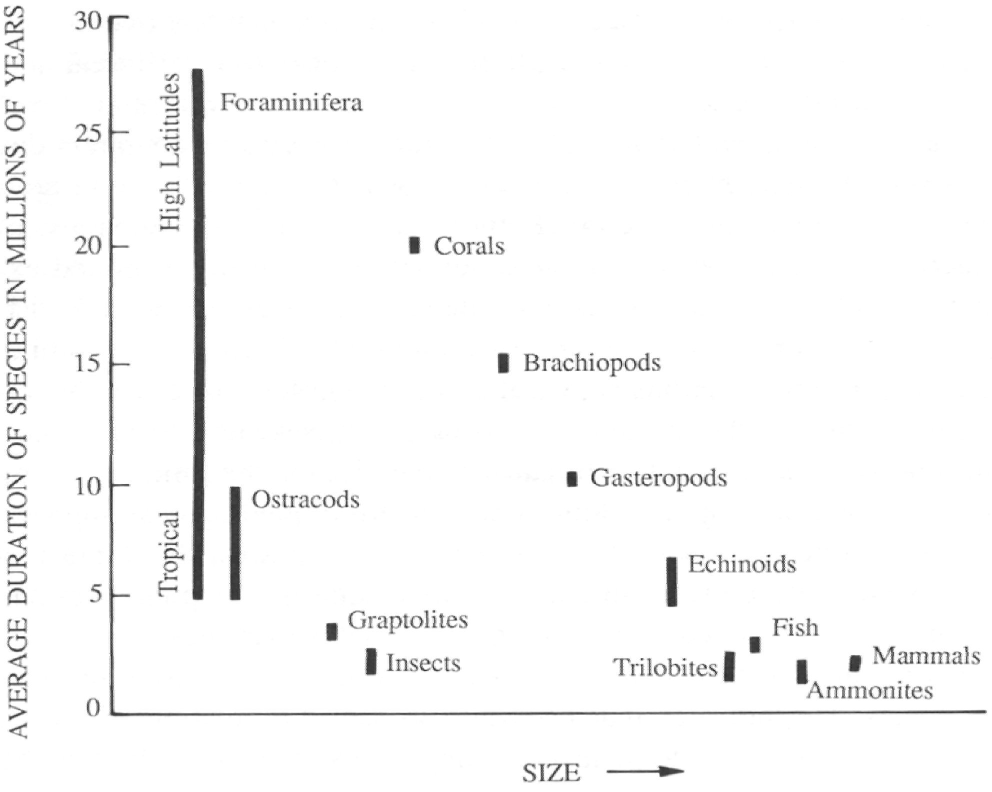


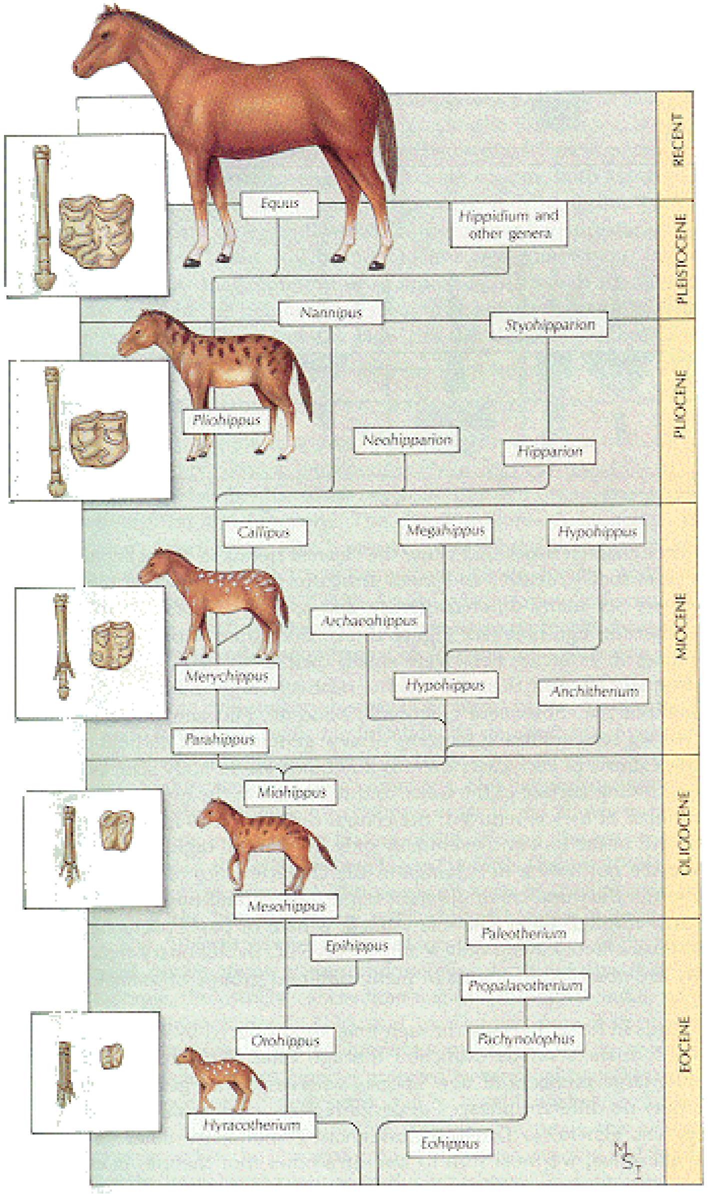
Fig. 14. The average duration of species for different groups of animals

Cope's Rule in Equidae

Cope's rule states that the body sizes of species in a lineage of organisms tends to get **bigger** through time

Successive taxa in the lineage from *Hyracotherium* to *Equus* have increased steadily in size over time.

Cope’s rule has been documented in a large variety of organisms including: foraminifera, brachiopods, gastropods, and mammals



A general increase in body size over geological time.

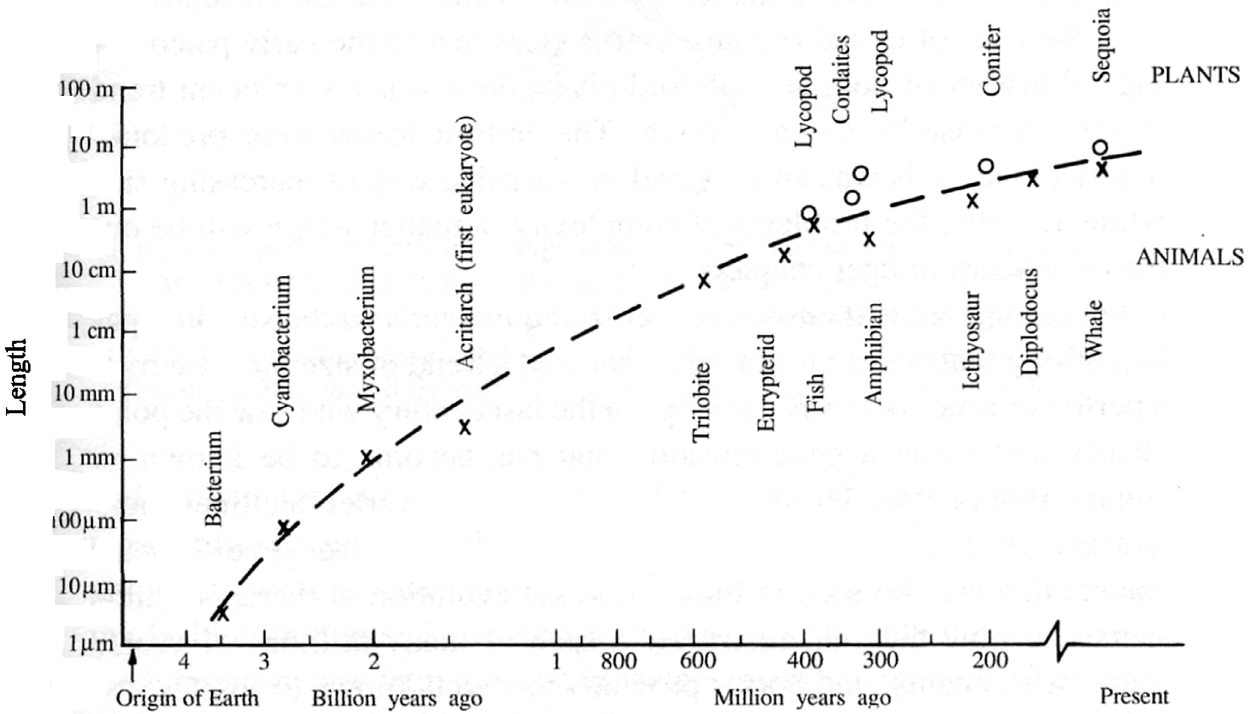


Fig. 5. A graph showing a rough estimate of the maximum sizes of organisms at different periods of life on earth.

(Bonner, 1988)

Origin of Cope’s Rule

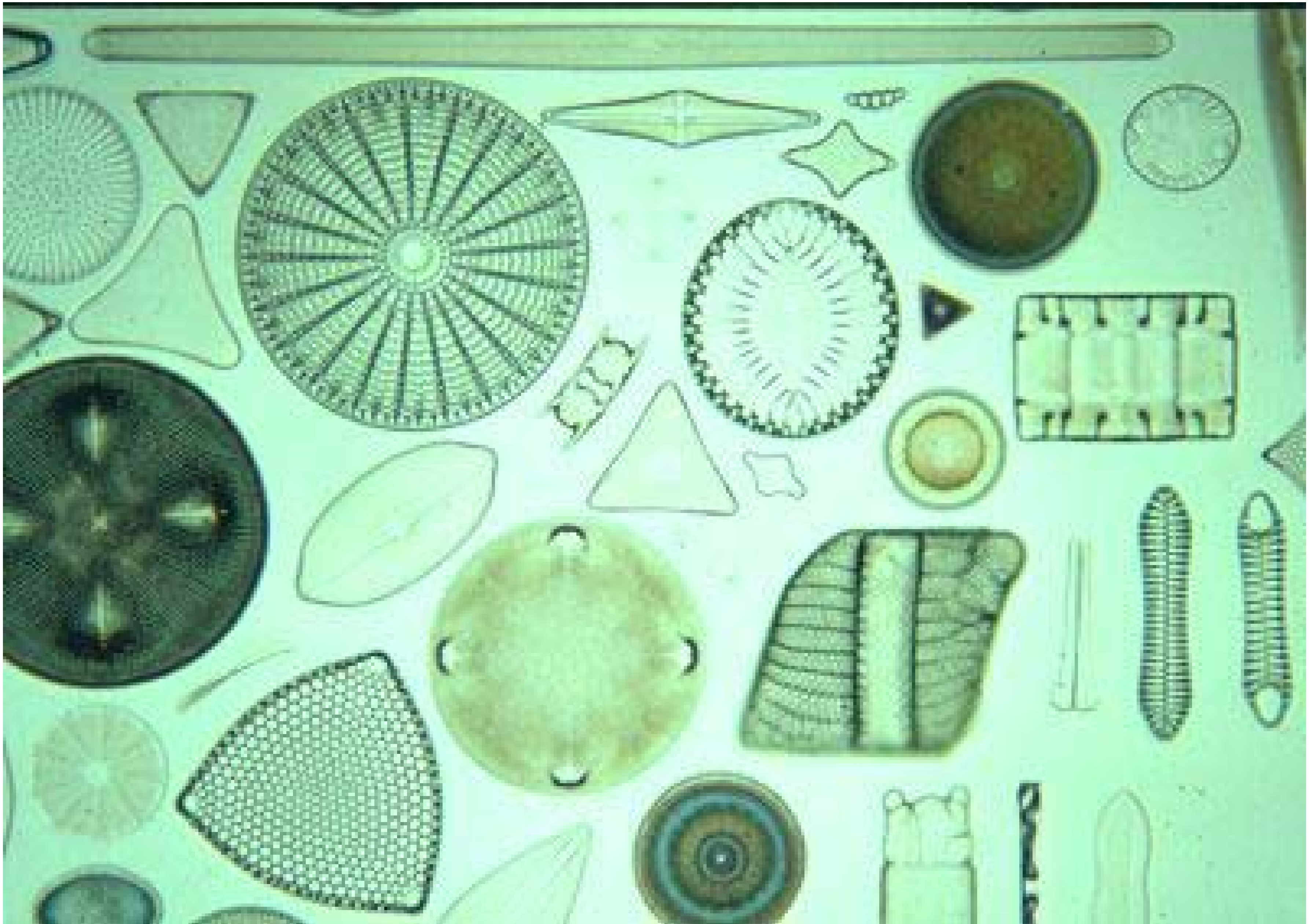
- Why do lineages tend to get bigger? Is this trend robust?

- Optimal body size for a given strategy under a given set of conditions

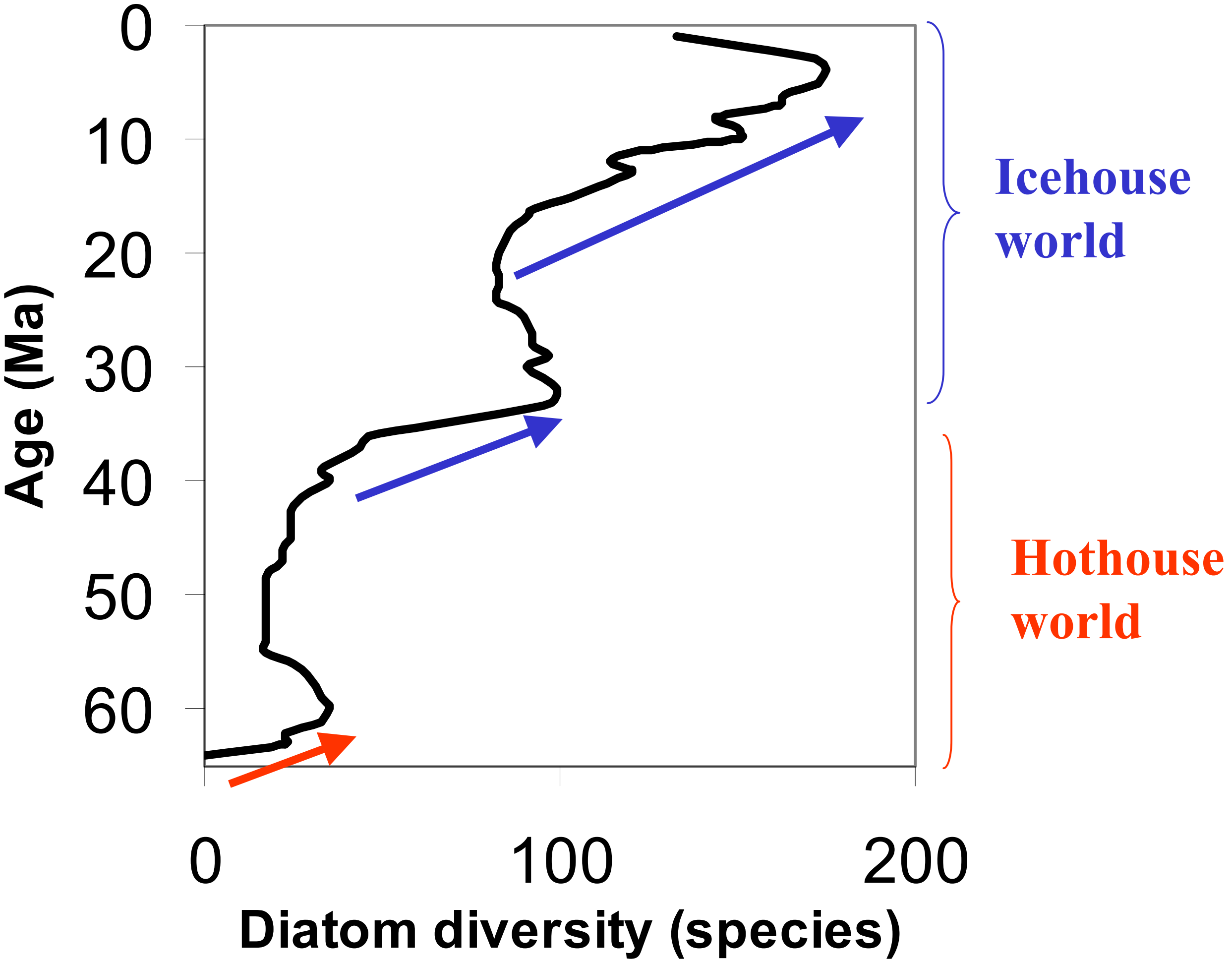
6. Environmental consequences of changes in the body size of organisms.

- Remember that export of photosynthetically produced carbon by phytoplankton is size-dependent.
- Environmental change that alters the size of the phytoplankton community may alter export production
- Evolutionary changes in the size of organisms, specifically phytoplankton will alter export of C out of surface ocean into the deep

Diatoms



Rapid radiation of diatom taxa in contrasting climatic conditions



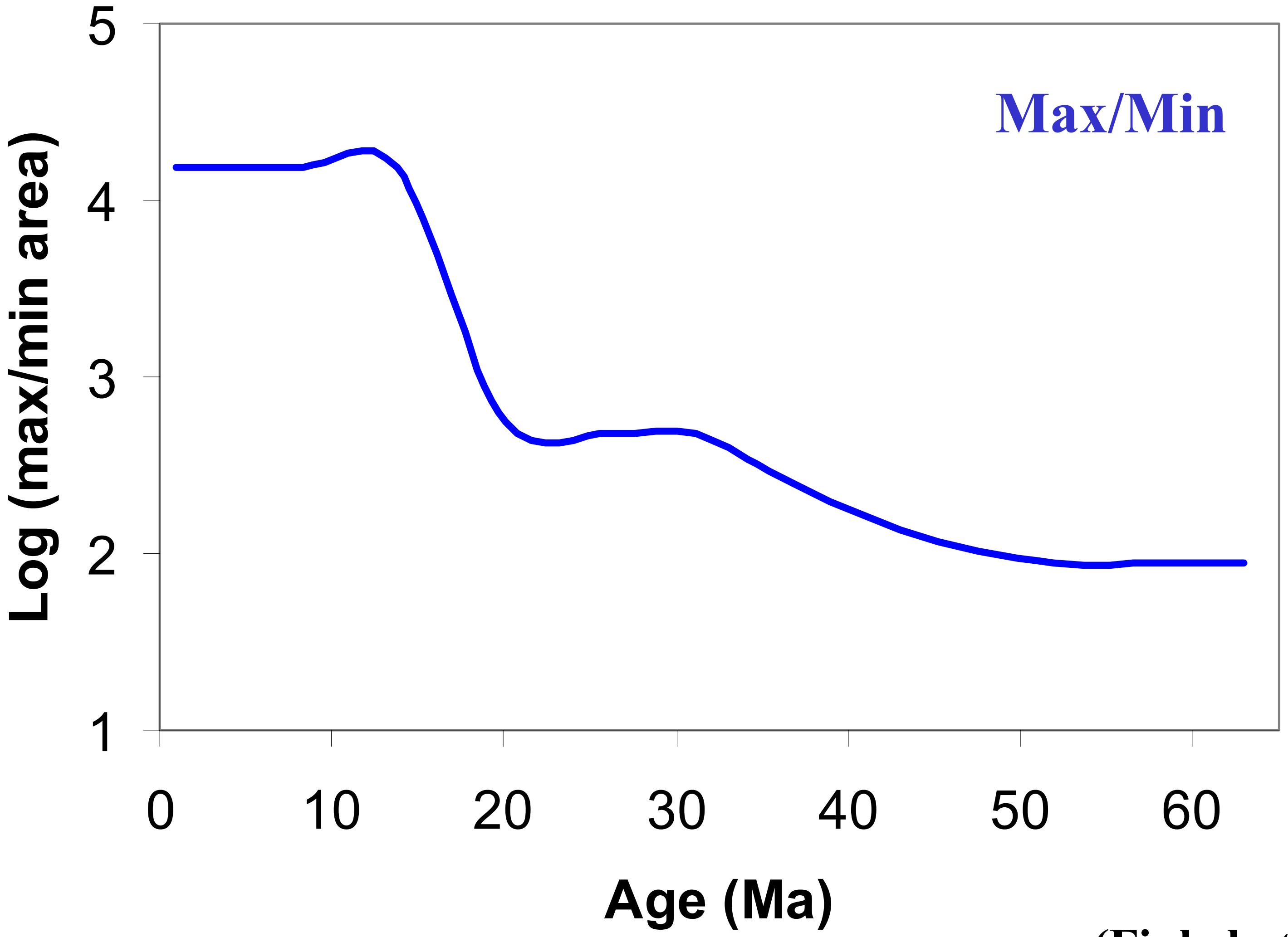
Diatom diversity data from Spencer-Cervato, NEPTUNE database

A Comparison of Diverse Features of the Icehouse and Hothouse Worlds

	'ICEHOUSE' WORLD	'HOTHOUSE' WORLD
Example	Late Cenozoic	Mesozoic-Early Cenozoic
Tectonic Style	Collision, Telescoping	Stretching, Rifting
Sea Floor Spreading	Slow	Rapid
Volcanism	Low	High
Sea-level	Narrow Shelves	Broad Epeiric Seas
Ocean Basins	Cold, Oxygenated	Warm, often Anoxic
Weathering, Erosion	Fast, Mechanical	Slow, Chemical

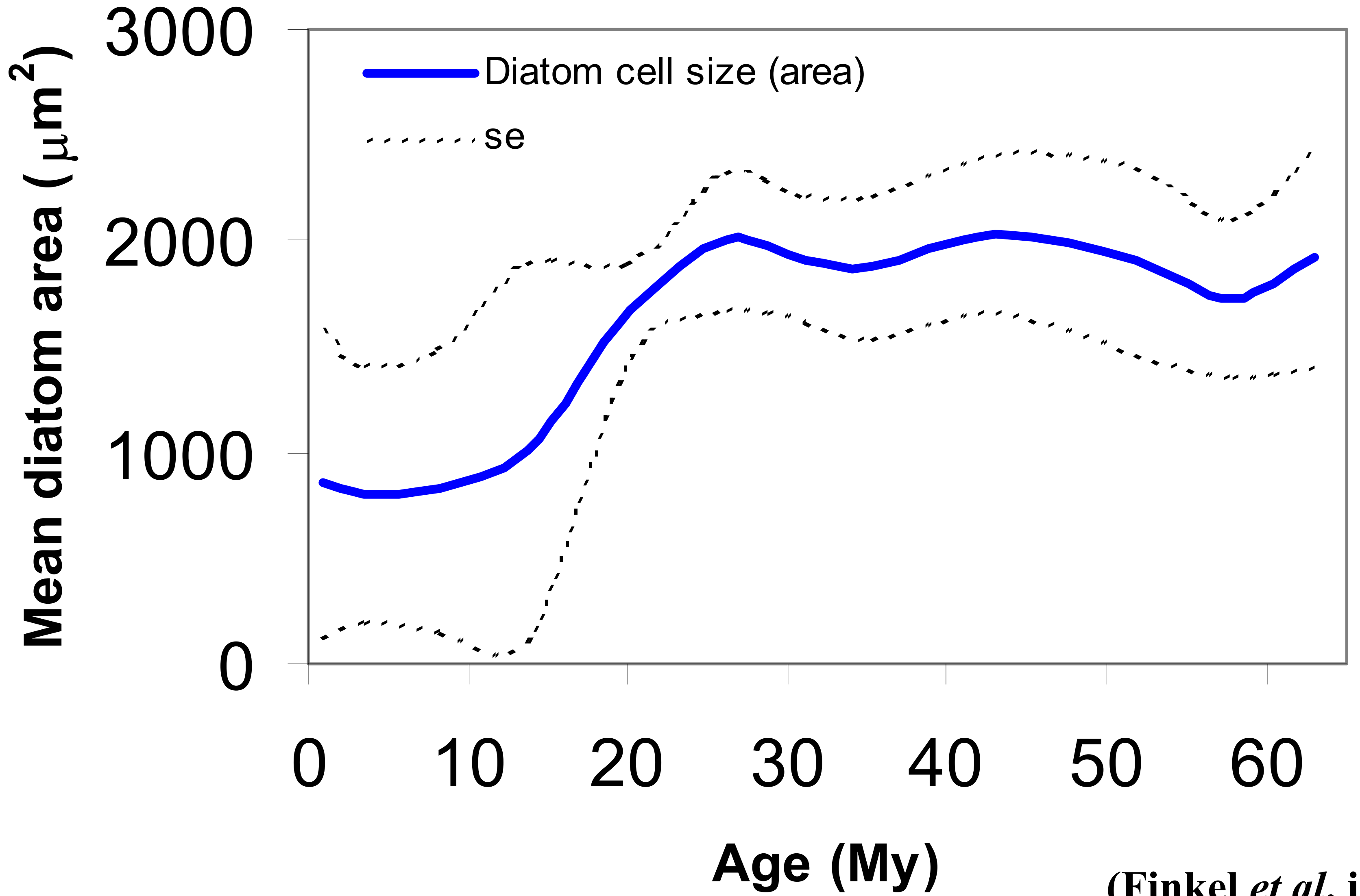
This table was modified from © 2001 The Paleogeographic Atlas Project. All rights reserved.

Maximum range in diatom cell size over geological time



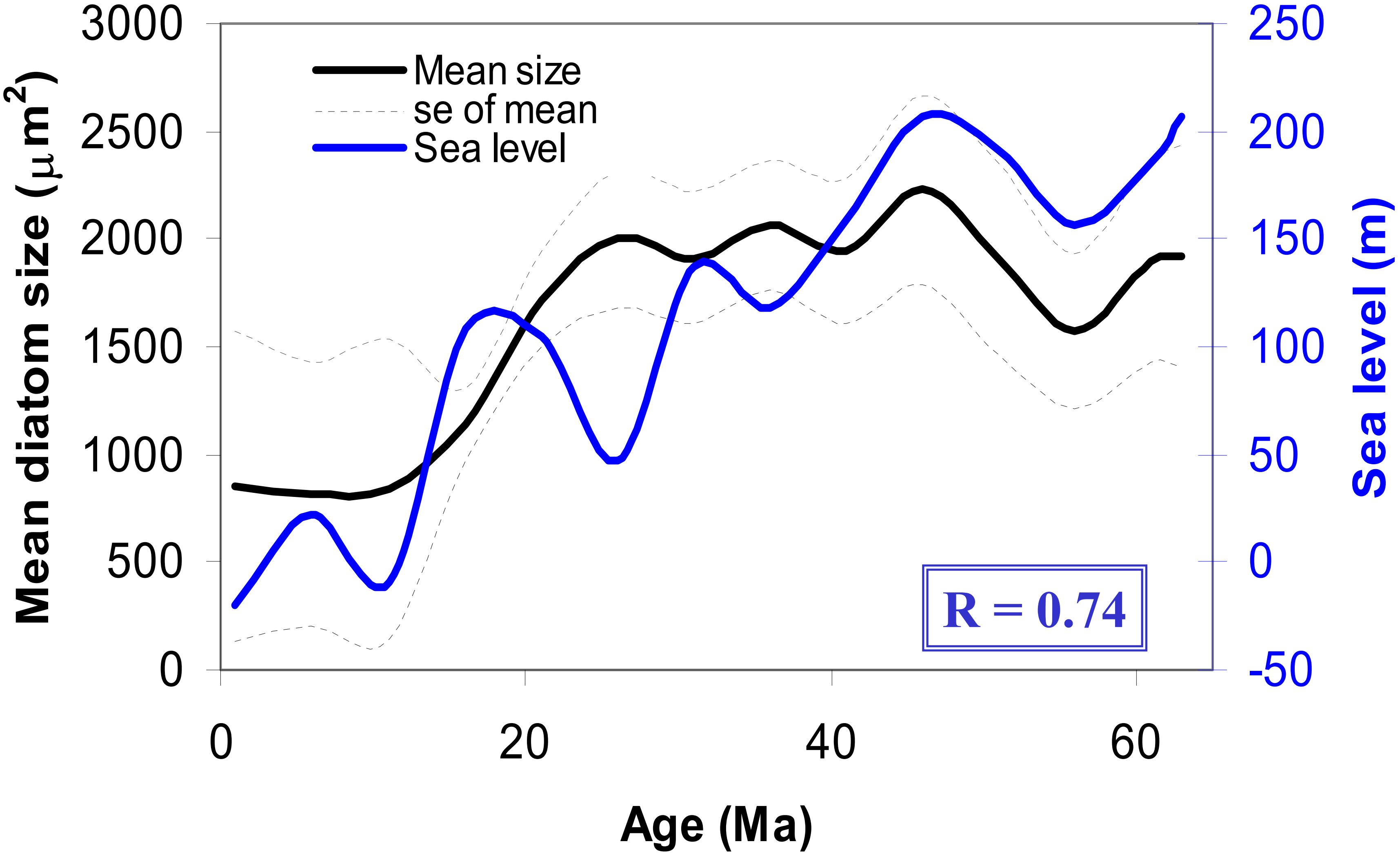
(Finkel *et al*. in prep)

Mean size of diatom community

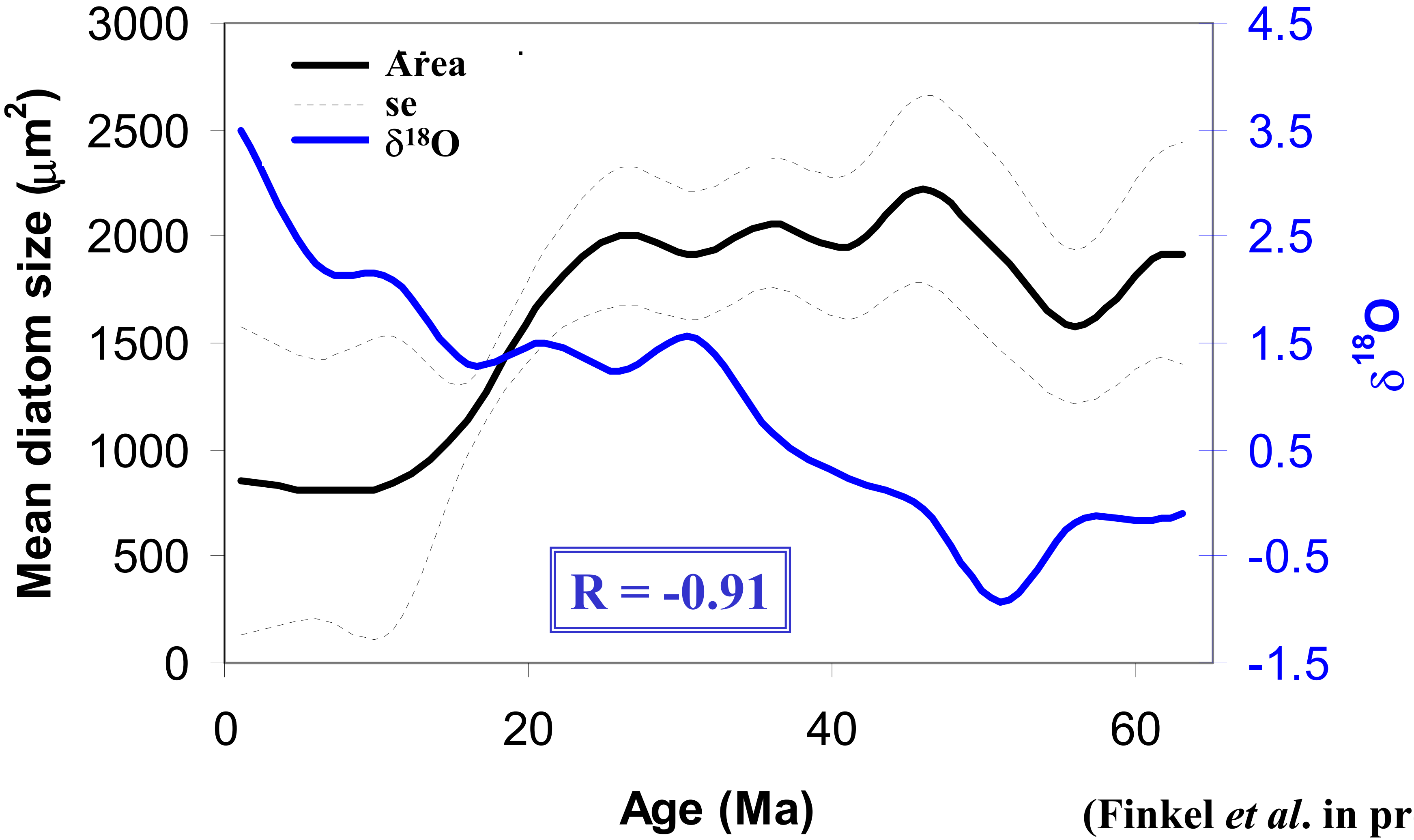


(Finkel *et al*. in prep)

Sea level and the size of diatoms

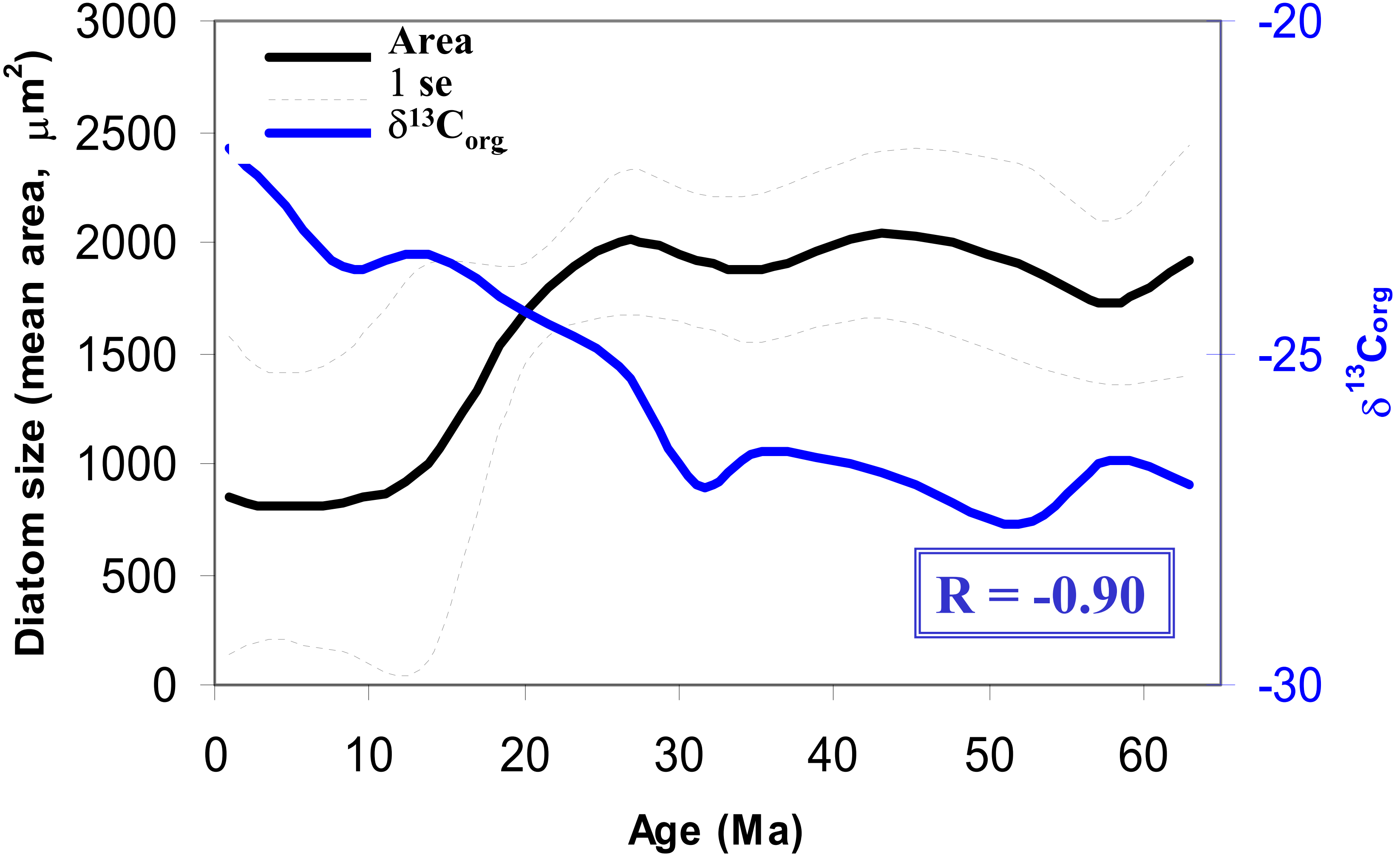


$\delta^{18}O$ (deep water) and the size of diatoms over the Cenozoic



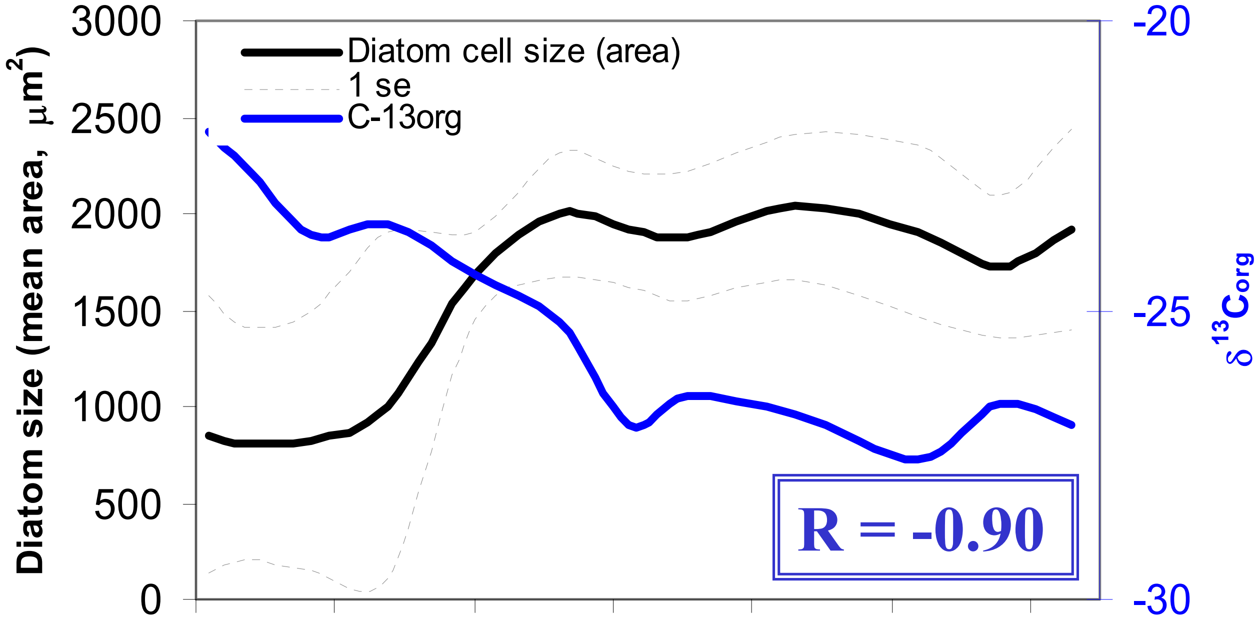
(Finkel *et al*. in prep)

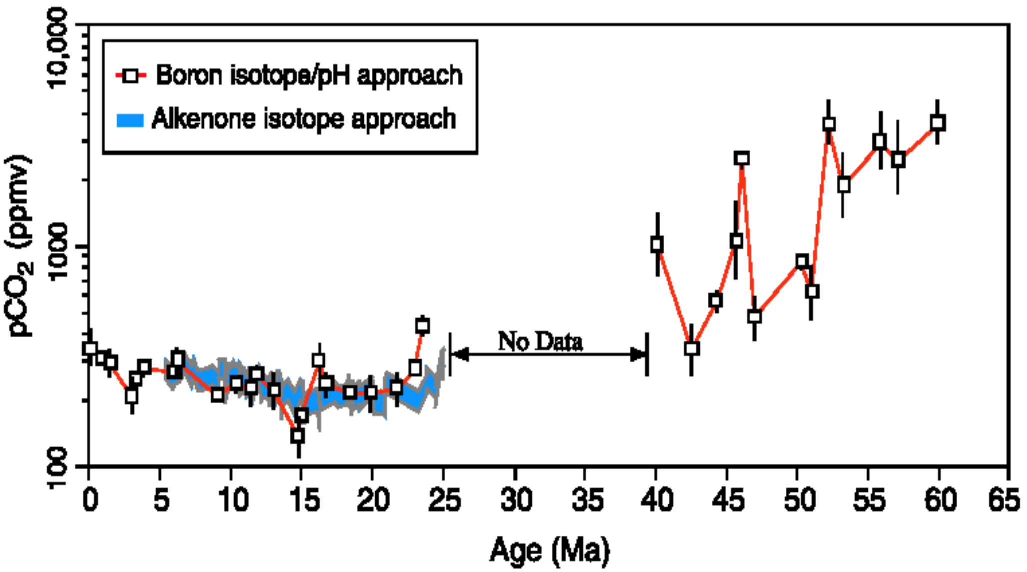
$\delta^{13}C_{org}$ and the size of diatoms



(Finkel *et al*. in prep)

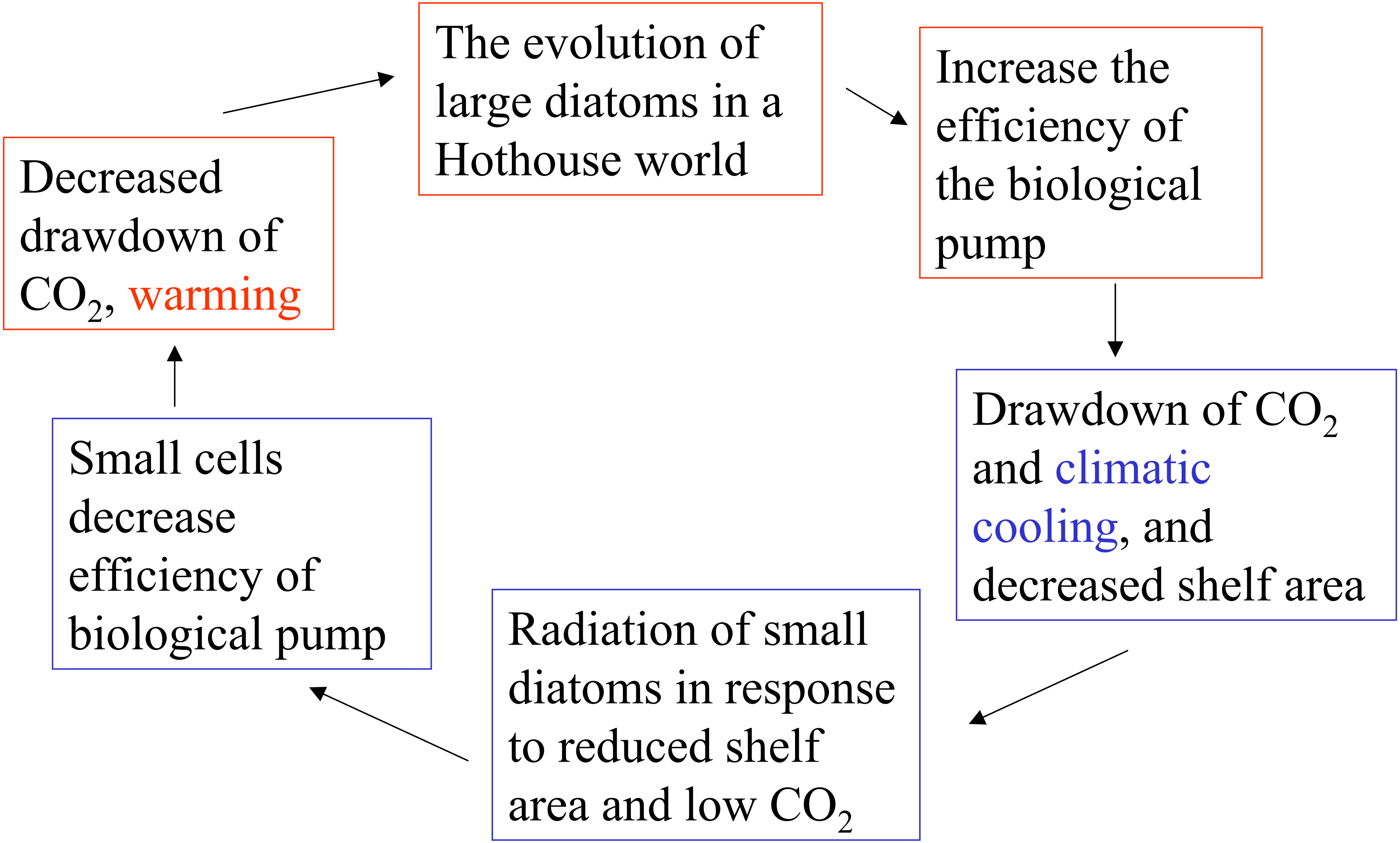
pCO_2, $\delta^{13}C_{org}$ & cell size





Zachos *et al.*, 2001

A potential climatic feedback:



The evolution of large diatoms in a Hothouse world

Increase the efficiency of the biological pump

Drawdown of CO_2 and climatic cooling, and decreased shelf area

Radiation of small diatoms in response to reduced shelf area and low CO_2

Small cells decrease efficiency of biological pump

Decreased drawdown of CO_2, warming

(Finkel *et al*. in prep)