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INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS
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SMR.780 - 8

FOURTH AUTUMN COURSE ON MATHEMATICAL ECOLOGY

(24 October - 11 November 1994)

"Models with Dimensional Problems"

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These are preliminary lecture notes, intended only for distribution to participants.

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Models with dimensional problems

Allometric model: $y = \alpha W^\beta$

y	some quantity	W	body weight
α	proportionality constant	β	allometric parameter $\in (\frac{2}{3}, 1)$

Usual form: $\ln y = \ln \alpha + \beta \ln W$
Alternative form: $y = y_0(W/W_0)^\beta$ with $y_0 \equiv \alpha W_0^\beta$
Alternative model: $y = \alpha L^2 + \beta L^3$, where $L \propto W^{1/3}$ is a length measure

Freundlich's model: $C = kc^{1/n}$

C	density of compound in soil	c	concentration in liquid
k	proportionality constant	n	parameter $\in (1.4, 5)$

Alternative form: $C = C_0(c/c_0)^{1/n}$ with $C_0 \equiv kc_0^{1/n}$
Alternative model: $C = 2C_0c(c_0 + c)^{-1}$ (Langmuir's model)

Problem in these models: no natural reference values W_0, c_0
The values of y_0, C_0 depend on the arbitrary choice

No problem in Arrhenius model: $\ln \dot{k} = \alpha - T_0/T$

$\dot{k}$	some rate	T	absolute temperature
α	parameter	T_0	Arrhenius temperature

Alternative form: $\dot{k} = \dot{k}_0 \exp\{1 - T_0/T\}$, with $\dot{k}_0 \equiv \exp\{\alpha - 1\}$

Difference with other two models:
no reference value required to solve dimensional problems

Message:
Use *never* transcendental functions of arguments that have dimensions

Biodegradation of compounds

X	concentration of compound	X_0	value for X at $t = 0$
t	time	$\dot{k}$	degradation rate
n	order	K	saturation constant

n-th order degradation

$$
\begin{aligned}
\frac{d}{dt}X &= -\dot{k}X^n \\
X(t) &= \left(X_0^{1-n} - (1-n)\dot{k}t\right)^{(1-n)^{-1}} \\
X(t) &\overset{n=0}{=} X_0 - \dot{k}t \quad \text{for } t < X_0/\dot{k} \\
X(t) &\overset{n=1}{=} X_0 \exp\{-\dot{k}t\} \\
t(\alpha X_0) &= X_0^{1-n}\dot{k}^{-1}\frac{1-\alpha^{1-n}}{1-n}
\end{aligned}
$$

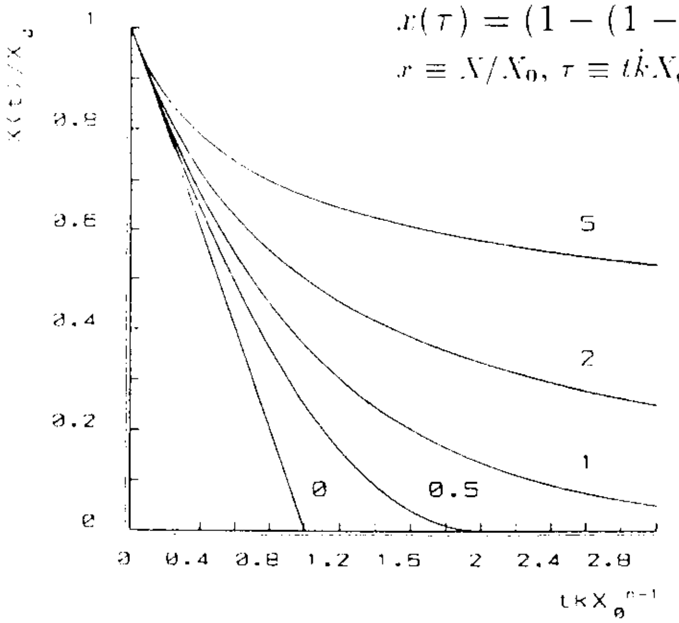
Monod degradation

$$
\begin{aligned}
\frac{d}{dt}X &= -\dot{k}\frac{X}{K+X} \\
0 &= X(t) - X_0 + K\ln\{X(t)/X_0\} + \dot{k}t \\
X(t) &\overset{K \ll X_0}{=} X_0 - \dot{k}t \quad \text{for } t < X_0/\dot{k} \\
X(t) &\overset{K \gg X_0}{=} X_0 \exp\{-\dot{k}t/K\} \\
t(\alpha X_0) &= X_0\dot{k}^{-1}(\alpha - 1) - K\dot{k}^{-1}\ln\alpha
\end{aligned}
$$

n-th order degradation

$$x(\tau) = (1-(1-n)\tau)^{(1-n)^{-1}}$$

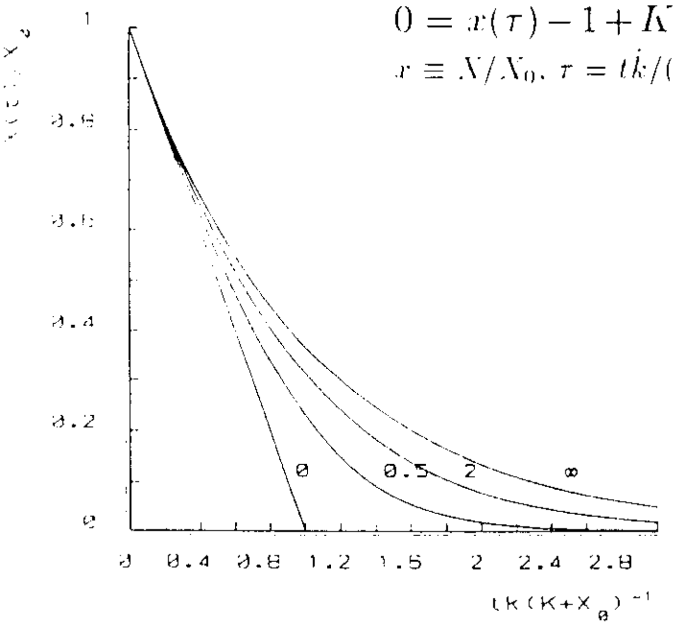
$x \equiv X/X_0$, $\tau \equiv tkX_0^{n-1}$



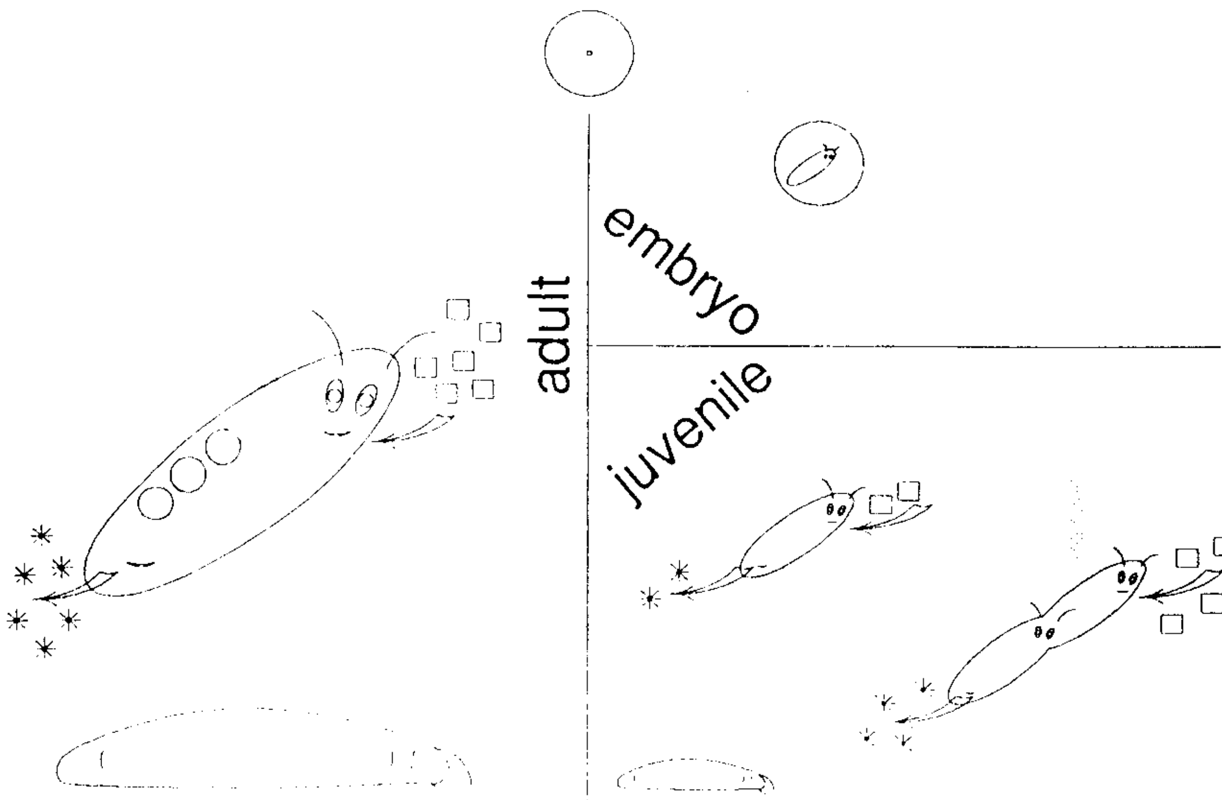
Monod degradation

$$0 = x(\tau) - 1 + K^* \ln x(\tau) + (K^*+1)\tau$$

$x \equiv X/X_0$, $\tau = tk/(K+X_0)$, $K^* = K/X_0$



Dynamic Energy Budget theory



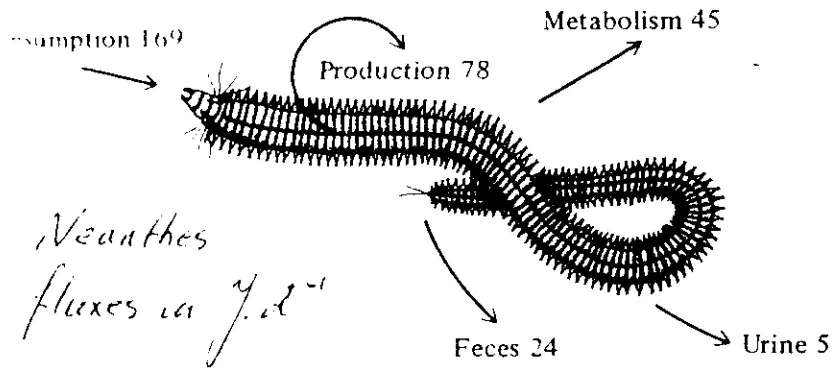
The theory quantifies
the energetics of heterotrophs
as it changes during life history

The key processes are

feeding	storage	growth	reproduction
digestion	maintenance	development	aging

DEB-strategy

- energy, no compounds
  - general
  - simple
  - hidden variable (entropy)
- all heterotrophic systems
  - general
  - comparison between species, life histories
- focus on individuals
  - mass/energy balances (input/output relationships)
  - consequences for populations, ecosystems
  - context for modelling suborganismal levels
- choice for homeostasis
  - simplicity
  - difinition of body size
- state variables
  - reserve energy (contributes to weight)
  - volume (links up with surface area ⇔ feeding)
  - cumulated damage (aging)



Scheme for the allocation of energy consumption into its components, and equations for various efficiency terms.

Energy Partitioning

Gross energy consumption (*C*)
- —— Fecal energy (*F*)

Apparent assimilated energy ($A = C - F$)
- —— Urinary energy (*U*)

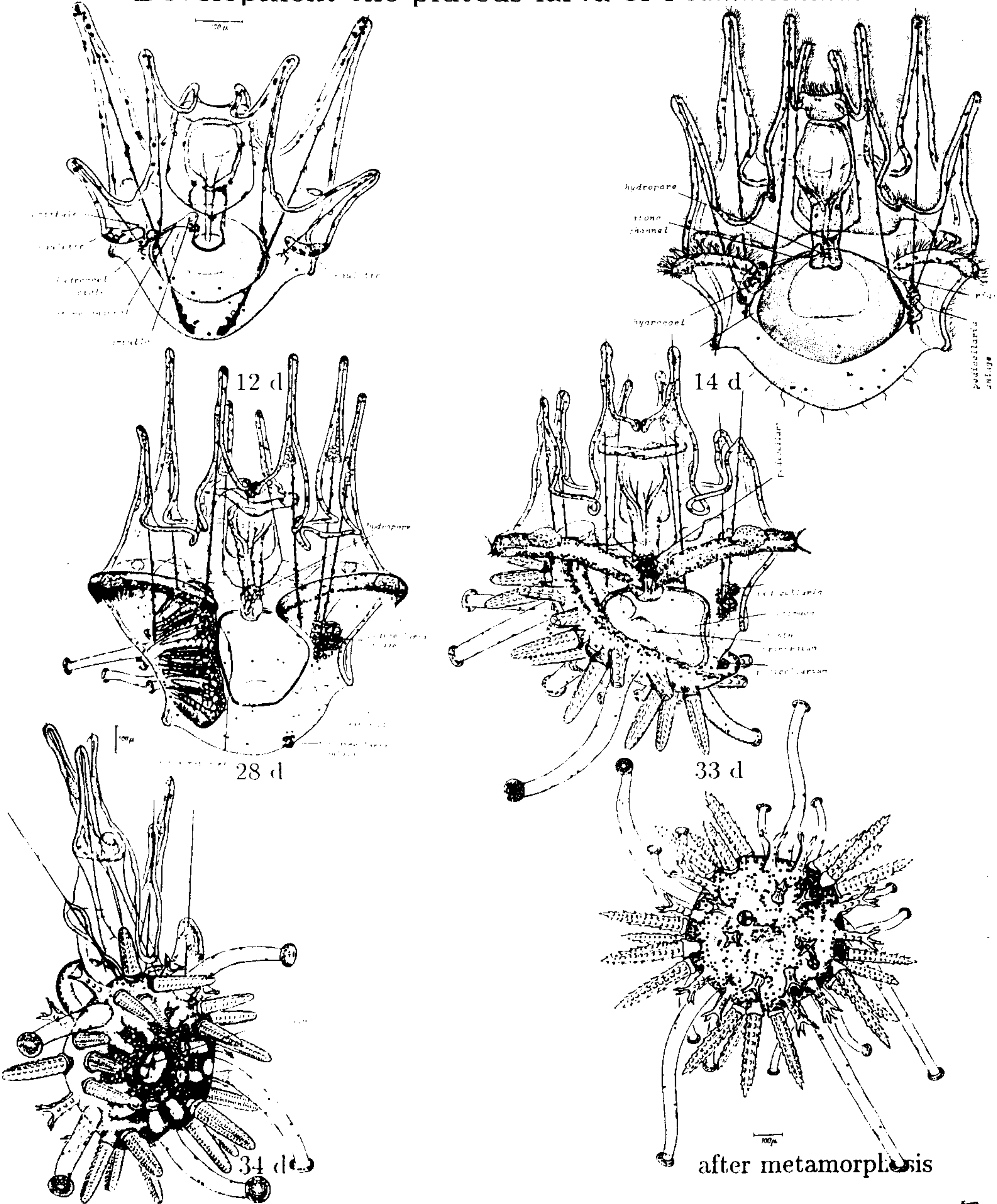
Metabolizable energy ($M = C - F - U$)
- —— Heat increment of feeding (SDE)
- —— Heat increment of fermentation (*HF*)

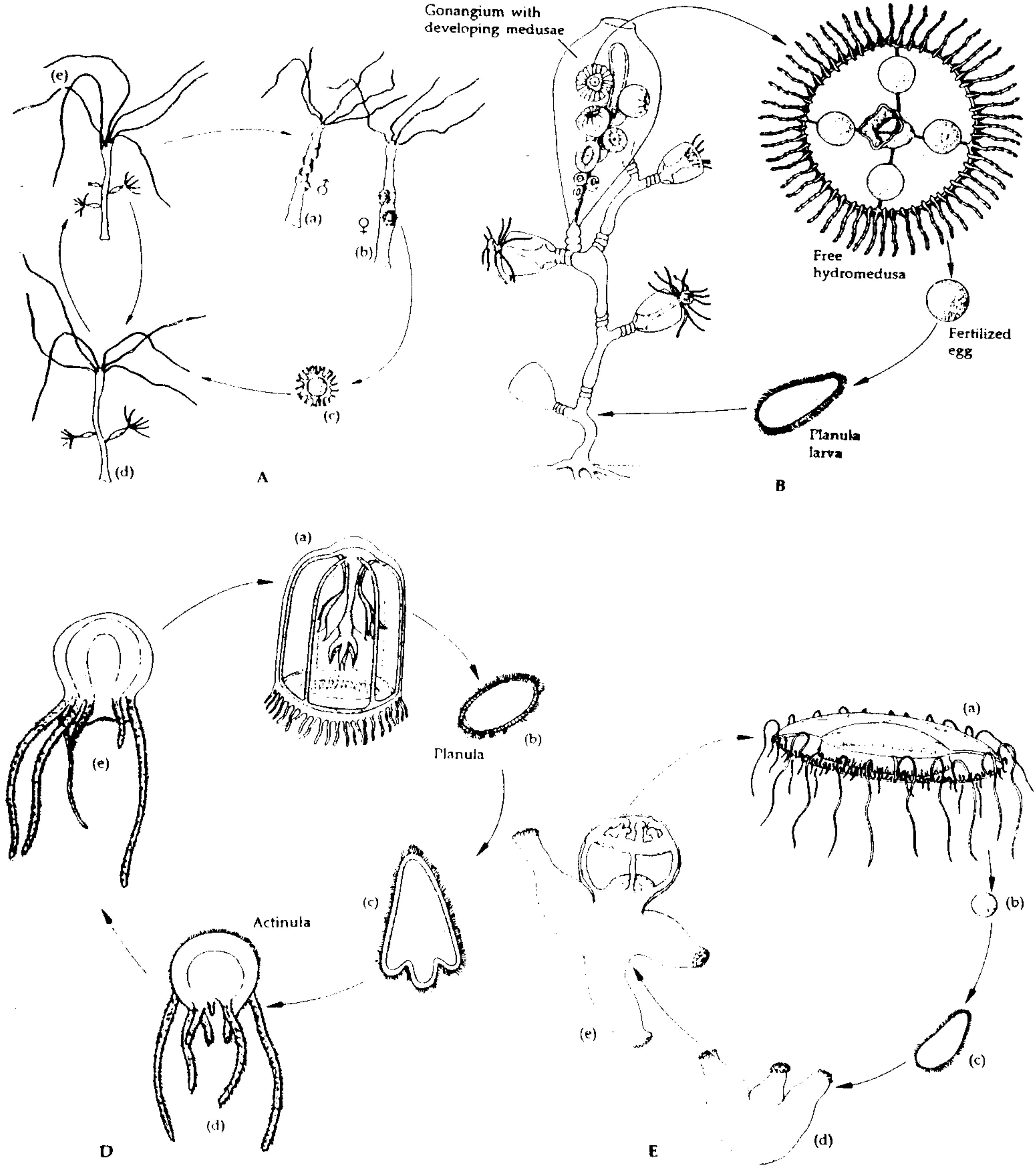
Net energy ($N = C - F - U$ - SDE $- HF$)
- —— Maintenance metabolism
  - —— Basic/Standard metabolism (*BMR*, *SMR*)
  - —— Thermoregulatory
  - —— Activity
- —— Production (*P*)
  - —— Energy storage (growth)
  - —— Hair, feathers, cuticle
  - —— Reproduction (eggs, semen, milk)
- —— Work (*W*)

Efficiency Terms

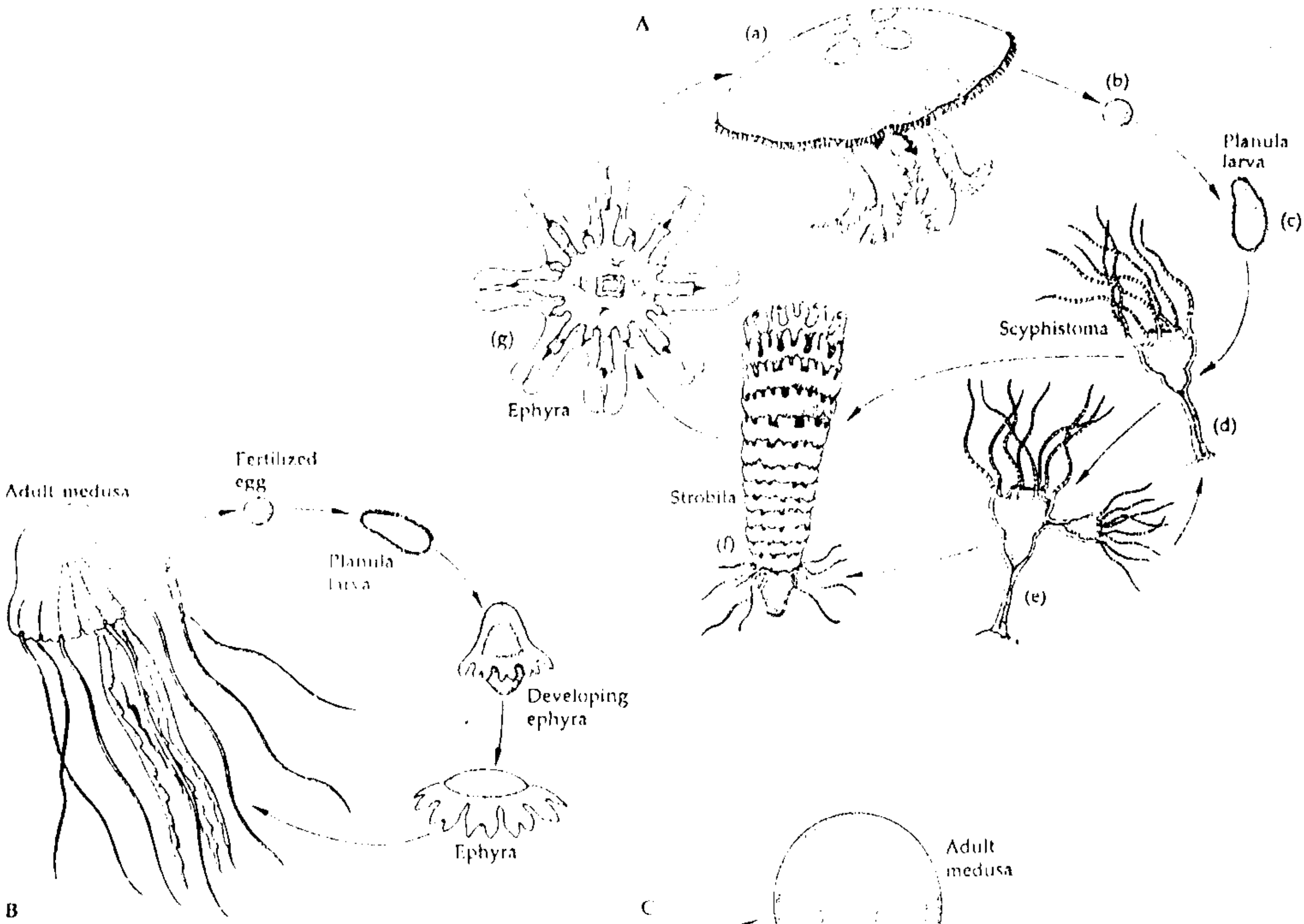
Apparent assimilation efficiency	100 *A*/*C*
Gross production	100 *P*/*C*
Net production	100 *P*/*A*
Gross work	100 *W*/*C*
Net work	100 *W*/*A*

Development the pluteus larva of *Psammechinus*





(e)
(a)
♂
♀
(b)
(c)
(d)
A
Gonangium with developing medusae
Free hydromedusa
Fertilized egg
Planula larva
B
(a)
(b)
Planula
(c)
Actinula
(d)
(e)
D
(a)
(b)
(c)
(d)
(e)
E



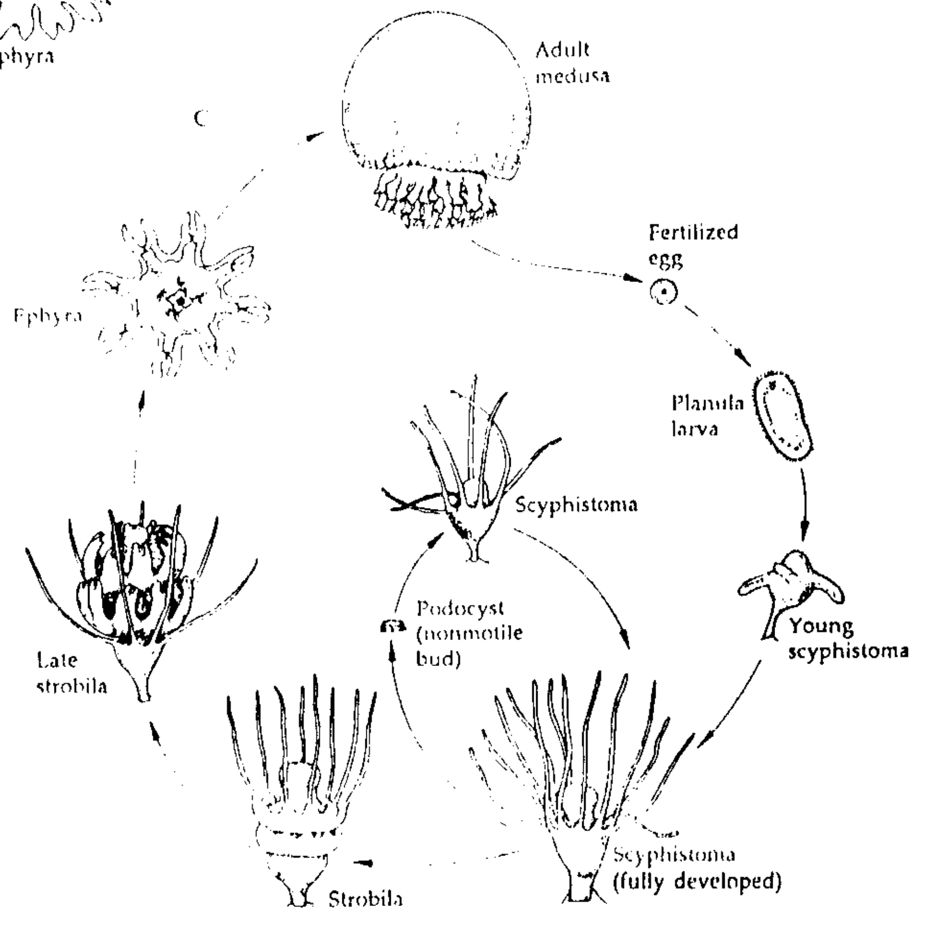
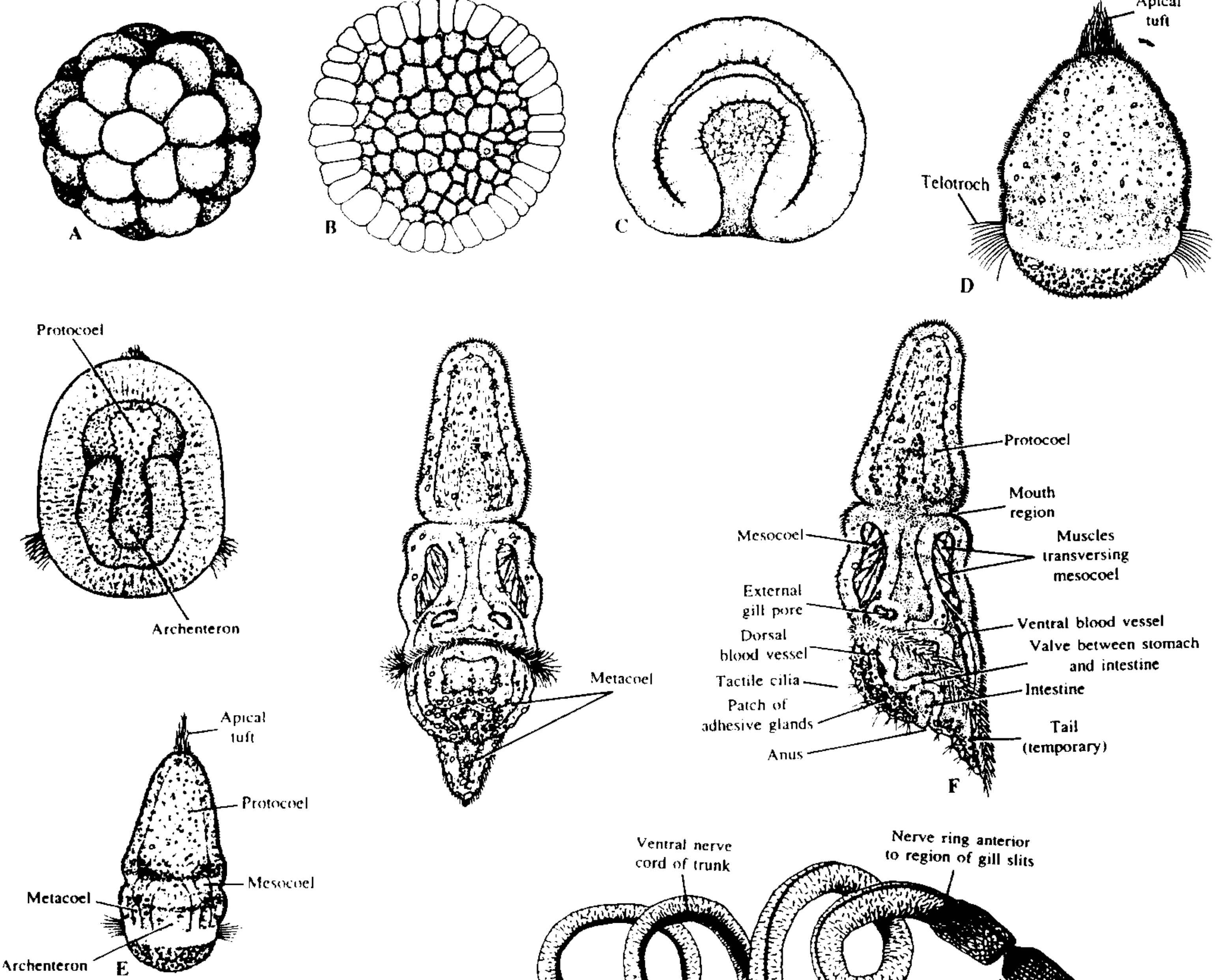
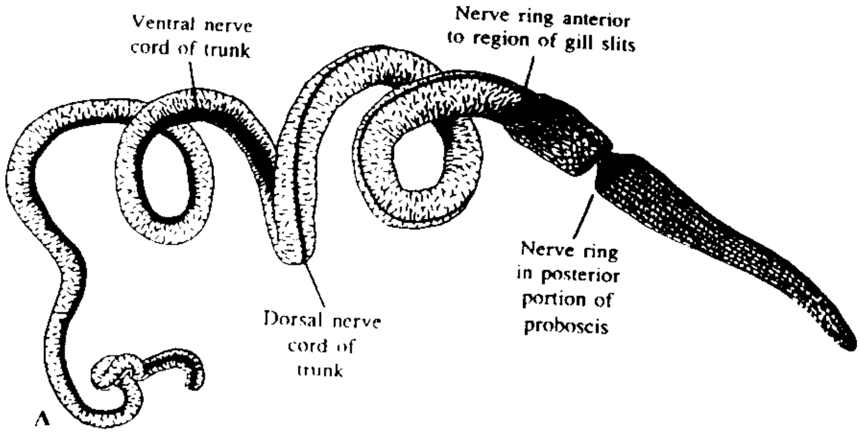
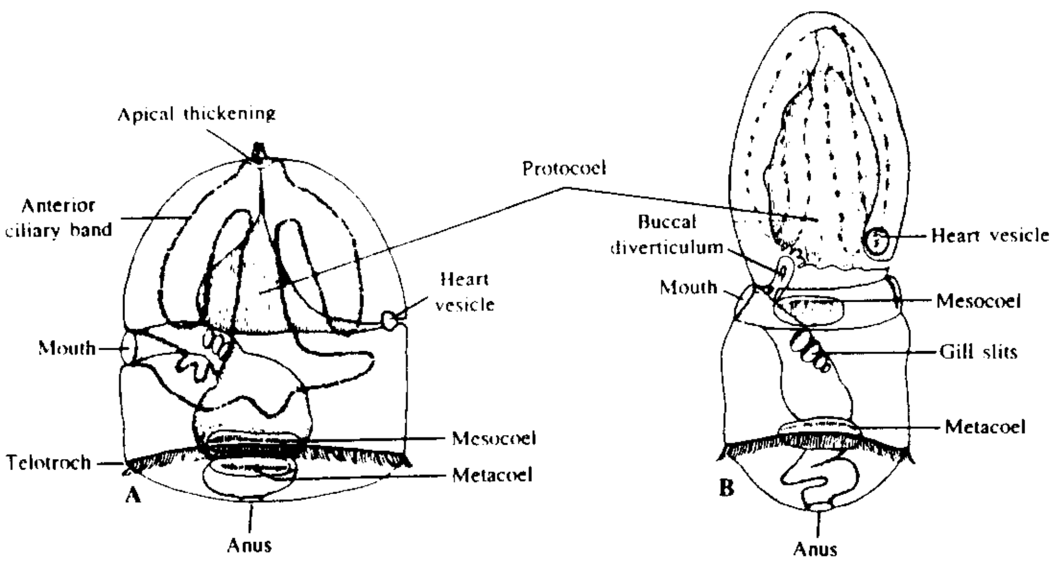


Figure 11

Scyphozoan life cycles. A, Life cycle of *Aurelia*. The fertilized egg (b) is released to develop into a planula larva (c), which settles to grow into a polyp, the scyphistoma (d). The scyphistoma either buds off new polyps (e) or produces ephyrae by strobilation (f); the ephyra (g) grows into an adult medusa (a). B, Life cycle of *Pelagia*, a scyphomedusa lacking the polypoid stage. C, Life cycle of the "cannonball jellyfish," *Stomolophus meleagris*. (A, B from Bayer and Owre 1968; C after Calder 1982)


Apical tuft
Telotroch
A
B
C
D
Protocoel
Archenteron
Metacoel
Apical tuft
Protocoel
Mesocoel
Metacoel
Archenteron
E
Protocoel
Mouth region
Mesocoel
Muscles transversing mesocoel
External gill pore
Dorsal blood vessel
Ventral blood vessel
Valve between stomach and intestine
Tactile cilia
Intestine
Patch of adhesive glands
Tail (temporary)
Anus
F


Ventral nerve cord of trunk
Nerve ring anterior to region of gill slits
Nerve ring in posterior portion of proboscis
Dorsal nerve cord of trunk
A

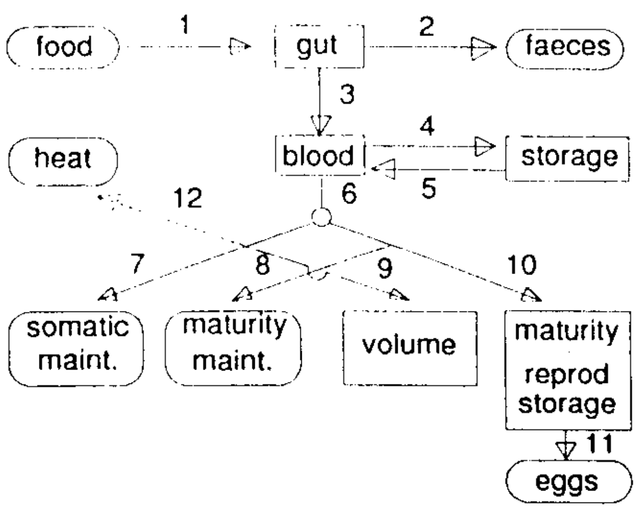

Apical thickening
Protocoel
Anterior ciliary band
Heart vesicle
Mouth
Telotroch
Mesocoel
Metacoel
A
Anus
Buccal diverticulum
Heart vesicle
Mouth
Mesocoel
Gill slits
Metacoel
B
Anus

Energy fluxes through a heterotroph

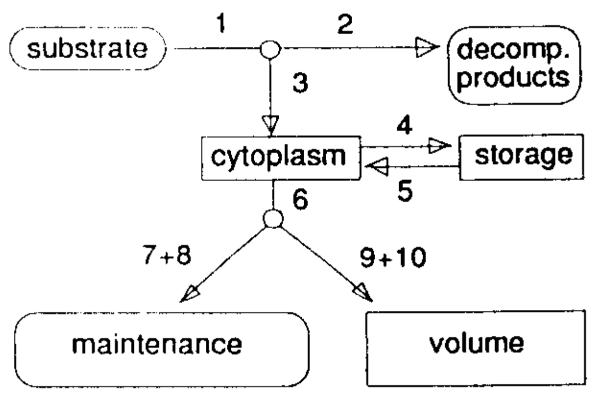
1 ingestion (uptake)	2 defecation	3 assimilation	4 demobilization
5 mobilization	6 utilization	7 maintenance	8 maturation maintenance
9 growth investment	10 maturation	11 reproduction	12 heating (endotherms only)

The rounded boxes indicate sources or sinks. Rates 3, 7, 8, 9 and 10 contribute to a bit to heating, this is not indicated to simplify the scheme.

multicellular



unicellular



Key assumptions of the DEB model

- Homeostasis of structural biomass and reserves

- Life stages: embryo, juvenile, adult (size defined)
  initial structural biomass: negligibly small
  reserve density at hatching equals that of mother

- Food uptake $\propto$ surface area; type II functional response

- Reserve density dynamics: first order

- Allocation to maintenance+growth: fixed fraction of catabolic power

- Constant
  food-energy conversion
  volume specific maintenance costs
  volume specific growth costs

- Hazard rate $\propto$ accumulated damage
  damage production $\propto$ changed DNA
  DNA change $\propto$ catabolic rate

1 Body volume, stored energy and accumulated damage are the state variables

2 Three life stages exist: embryo's, which do not feed, juveniles, which do not reproduce, and adults. The transition between stages depends on the accumulated energy invested into maturation. Unicellulars are mostly confined to the juvenile stage

3 The feeding rate is proportional to surface area and depends hyperbolically on food density

4 Food is converted to energy with a fixed efficiency

5 The dynamics of the energy density in reserve is a first order process, while the maximum capacity is independent of volume

6 A fixed fraction of energy utilized from the reserves is spent on somatic maintenance plus growth, the rest on maturity maintenance plus maturation or reproduction

7 Somatic as well as maturity maintenance are proportional to body volume

7a the heating costs for endotherms are proportional to surface area

8 The costs for growth are proportional to volume increase

9 The energy reserve density of the hatchling equals that of the mother at egg formation, which begins at an infinitesimally small size

9a foetuses develop like embryo's in eggs, but at a rate unrestricted by energy reserves

9b unicellulars divide after a fixed time interval after exceeding a certain volume. At division bacteria must synthesize extra cell wall material, which takes some time

10 Under starvation conditions individuals always give priority to somatic maintenance and follow one of two possible strategies:

10a they do not change the reserve dynamics (so continue to reproduce)

10b they cease energy investment in reproduction and maturity maintenance (so change reserves dynamics)

10c most unicellulars and some animals shrink during starvation

11 Damage accumulates proportionally to the concentration of damage inducing compounds, which accumulate proportionally to the volume-specific metabolic rate. For unicellulars, damage is lethal, so it does not accumulate

12 The hazard rate is proportional to the accumulated damage, but death strikes for sure if somatic maintenance costs can no longer be paid

Powers as specified by the DEB model

l	scaled length	e	scaled reserve density
l_b	l at birth	$[E_m]$	max reserve density
l_p	l at puberty	f	scaled functional response
$V_m^{1/3}$	max length: $\frac{\kappa}{mg}$	κ	frac. catabol. to maint+growth
$[G]$	vol.-spec. growth costs	$[\dot{M}]$	vol.-spec. maintenance costs
$\dot{m}$	maint. rate coef.: $[\dot{M}]/[G]$	$\{\dot{A}_m\}$	sur.-spec. max assim. rate
g	investment ratio: $[G]/\kappa[E_m]$		

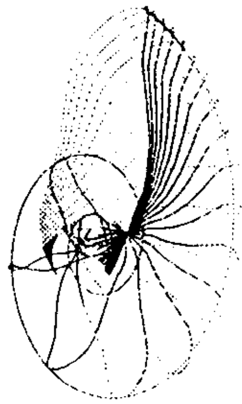
$\frac{\text{power}}{[E_m]V_m\dot{m}g}$	embryo $0 < l \leq l_b$	juvenile $l_b < l \leq l_p$	adult $l_p < l < 1$
assimilation	0	$l^2 f$	$l^2 f$
catabolic	$el^2\frac{l+g}{e+g}$	$el^2\frac{l+g}{e+g}$	$el^2\frac{l+g}{e+g}$
somatic maint.	κl^3	κl^3	κl^3
maturity maint.	$(1-\kappa)l^3$	$(1-\kappa)l^3$	$(1-\kappa)l_p^3$
endoth.heat	0	$\kappa l^2 l_h$	$\kappa l^2 l_h$
somatic growth	$\kappa l^2 g\frac{e-l}{e+g}$	$\kappa l^2\left(g\frac{e-l}{e+g} - l_h\right)$	$\kappa l^2\left(g\frac{e-l}{e+g} - l_h\right)$
maturaty growth	$(1-\kappa)l^2 g\frac{e-l}{e+g}$	$(1-\kappa)l^2 g\frac{e-l}{e+g}$	0
reproduction	0	0	$(1-\kappa)(l^2 g\frac{e-l}{e+g} + l^3 - l_p^3)$

Mass fluxes: ingestion $\{\dot{I}_m\}V_m^{-2/3}l^2 f$, defecation $\{\dot{F}_m\}V_m^{-2/3}l^2 f$

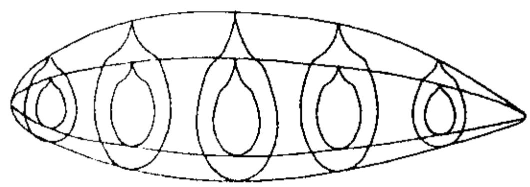
Shape correction function:

$$\mathcal{M}(V) = \frac{\text{real surface area at volume } V}{\text{isomorphic surface area at volume } V}$$

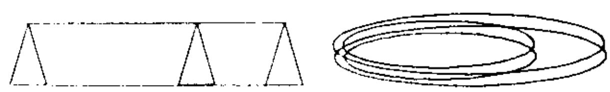
3D-isomorph: $\mathcal{M}(V) = (V/V_d)^0$



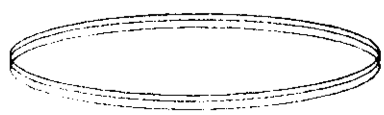
2D-isomorph: $\mathcal{M}(V) = (V/V_d)^{-1/6}$



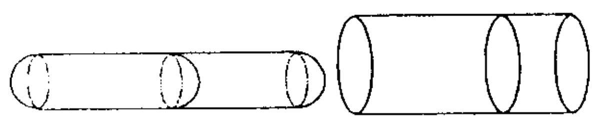
1D-isomorph: $\mathcal{M}(V) = (V/V_d)^{1/3}$



0D-isomorph: $\mathcal{M}(V) = (V/V_d)^{-2/3}$

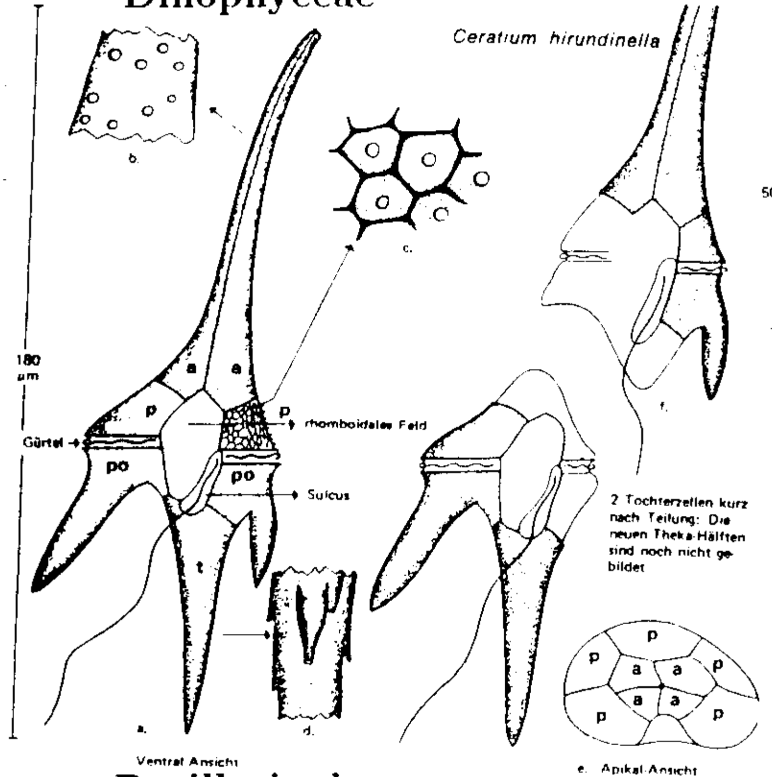


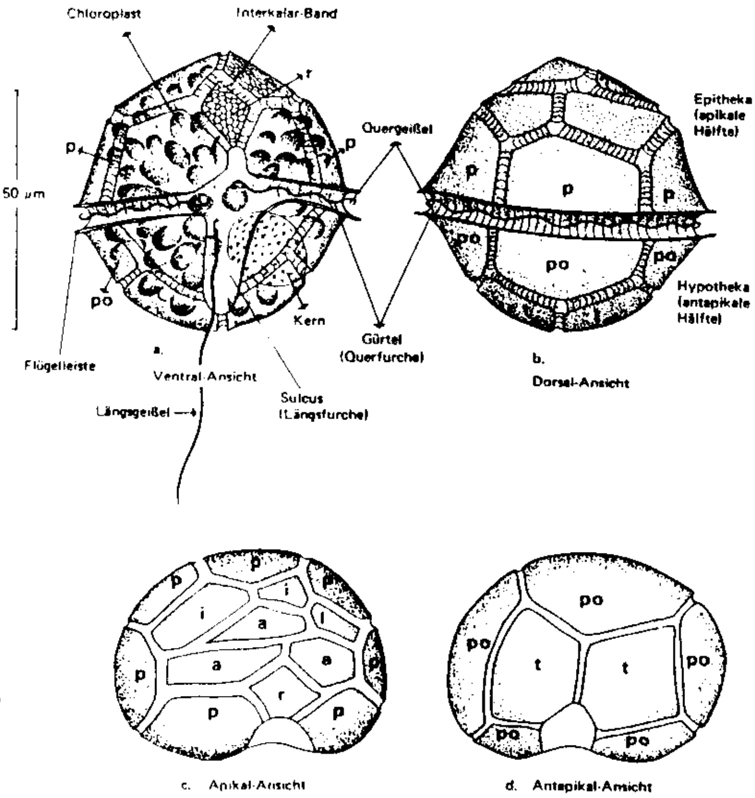
0D/1D static mixtures:
$\mathcal{M}(V) = w(V/V_d)^{-2/3} + (1-w)(V/V_d)^{1/3}$



Examples of 0D-isomorphs

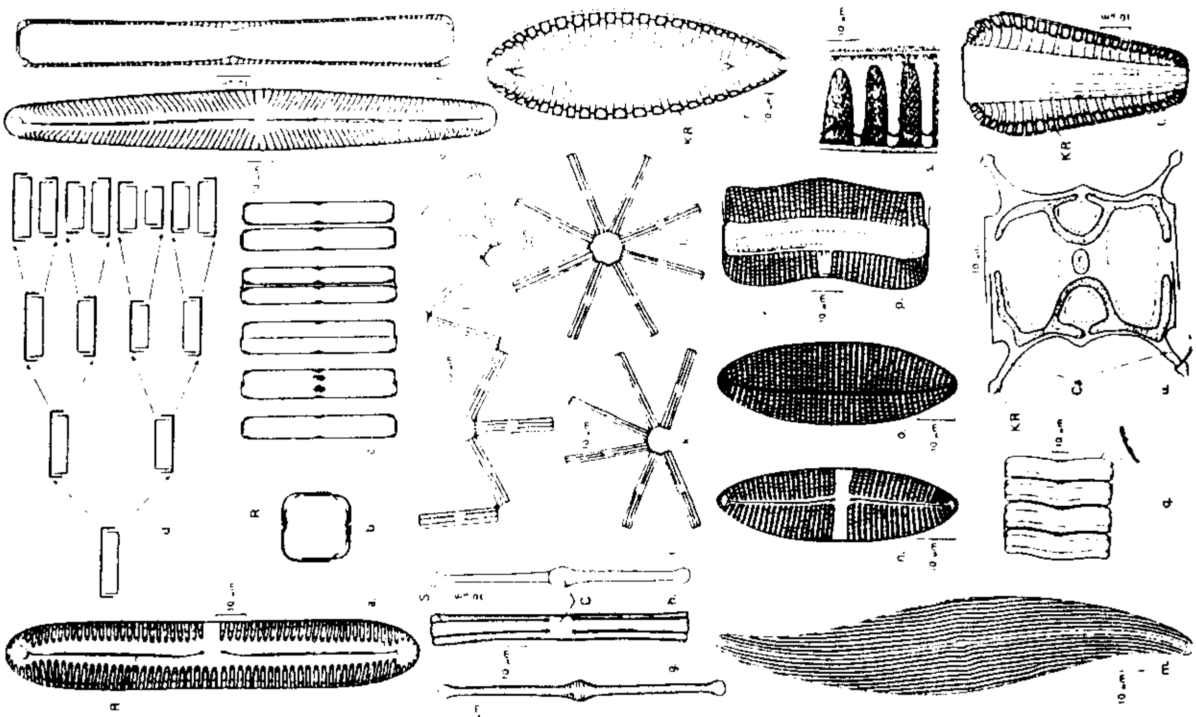
Dinophyceae

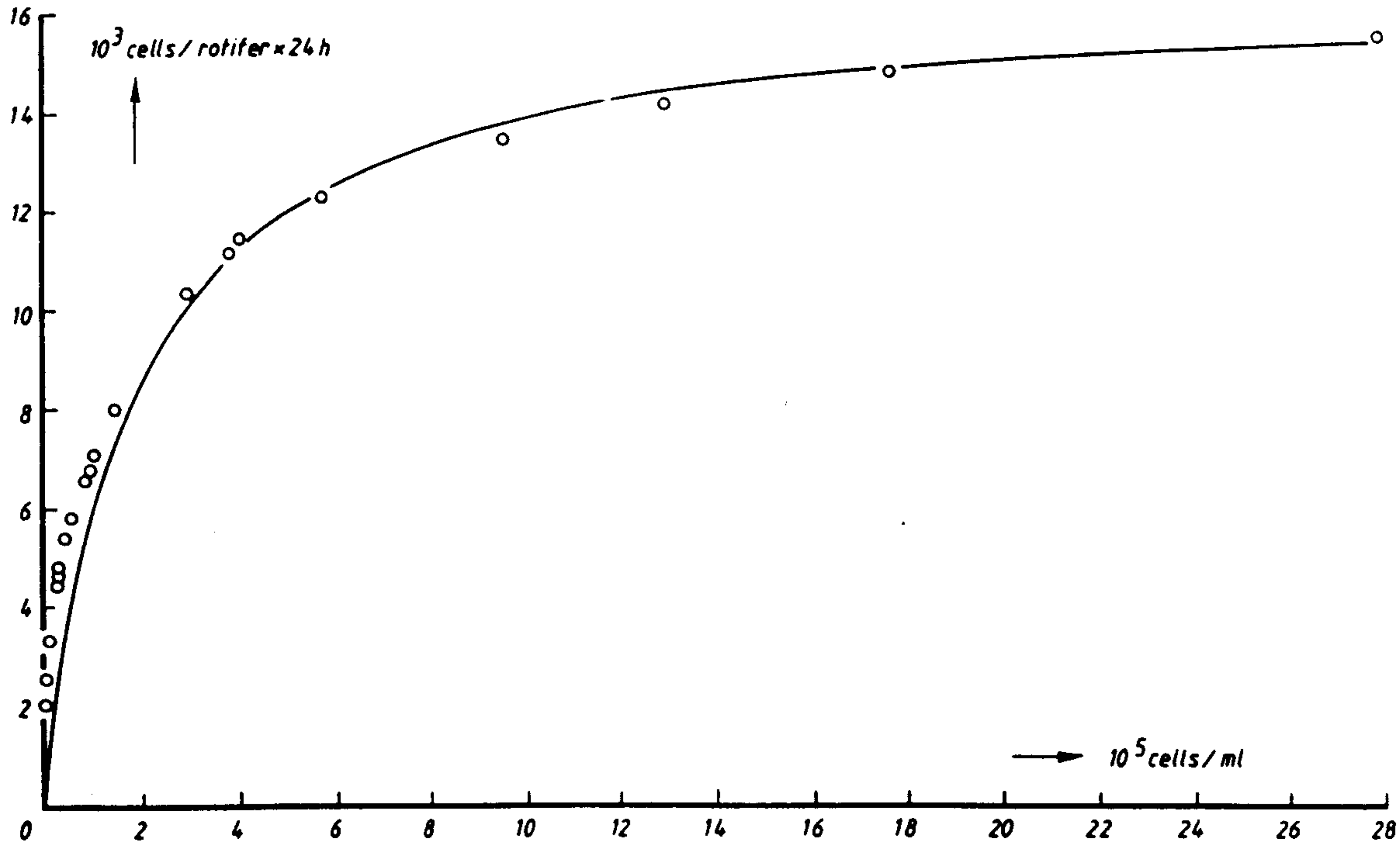




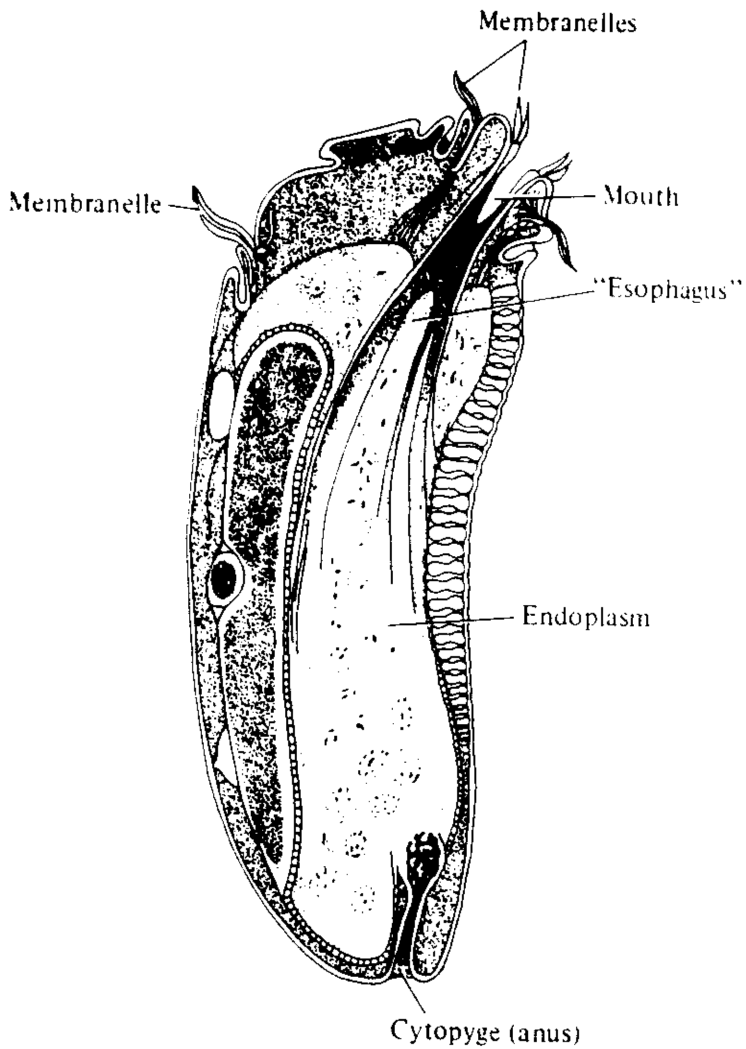
Peridinium cinctum (a – apikale Platten, i – interkalare Platten, p – Präzingularplatten, po – Postzingularplatten, r – rhomboidales Feld, Schloß-platte, t – antapikale Platten)

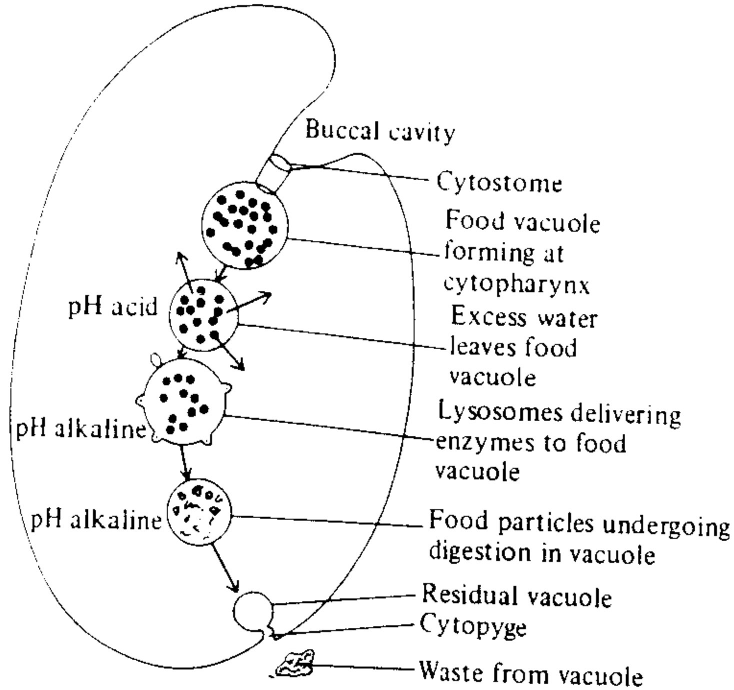
Bacillariophyceae





10^3 cells / rotifer × 24 h
10^5 cells / ml
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28





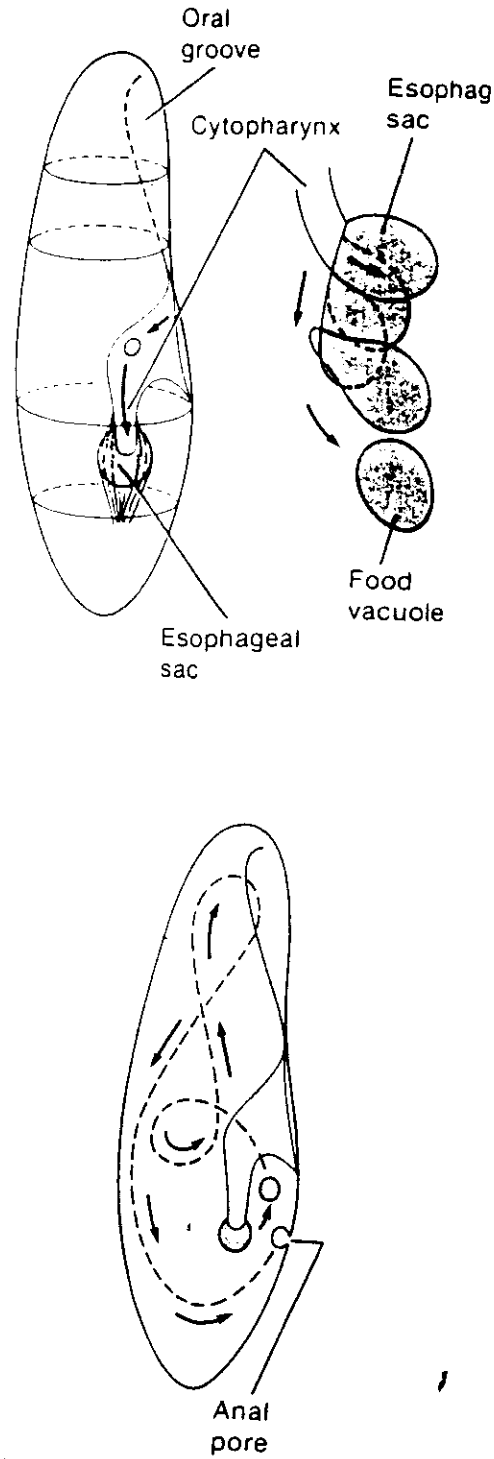
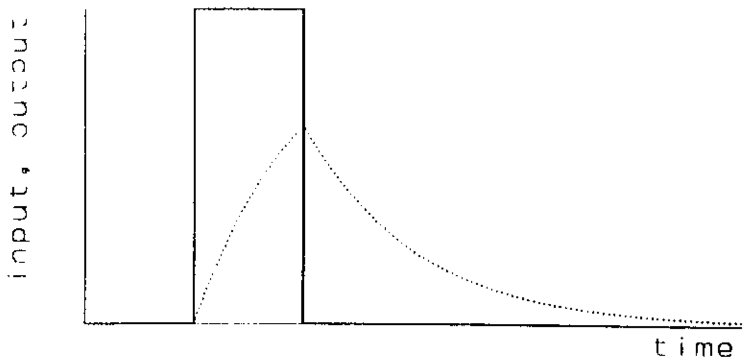


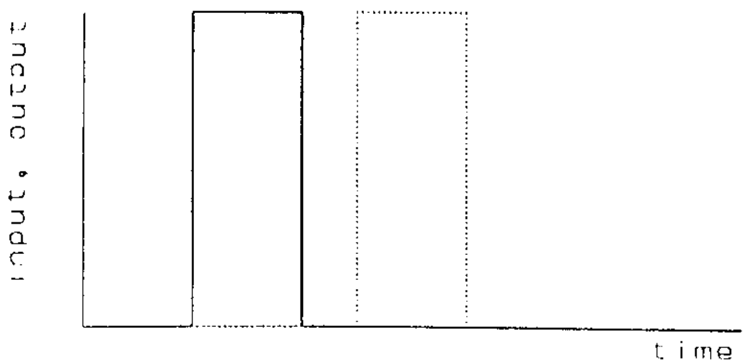
FIGURE 18–26 Representation of digestion in a ciliated protozoan (right). Food directed by ciliary membranelles towards the cytostome, or "mouth," enters the cytopharynx where food vacuoles form and detach from the cytopharynx. The detached food vacuoles undergo acidic and then alkaline digestion, and the waste laden vacuole migrates to the cytopyge, the "anus," for excretion. A typical example of such a ciliate protozoan is the entodiniomorph ciliate *Diplodinium*, which is a symbiont in the rumen of cattle (left). *(From Barnes 1987.)*

Ingestion and defecation

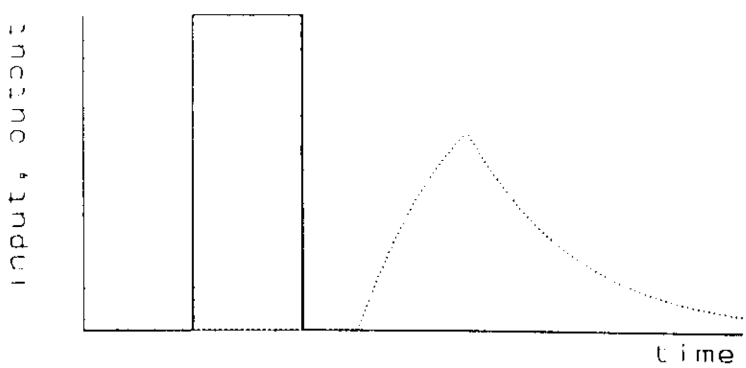
completely stirred reactor



plug flow reactor

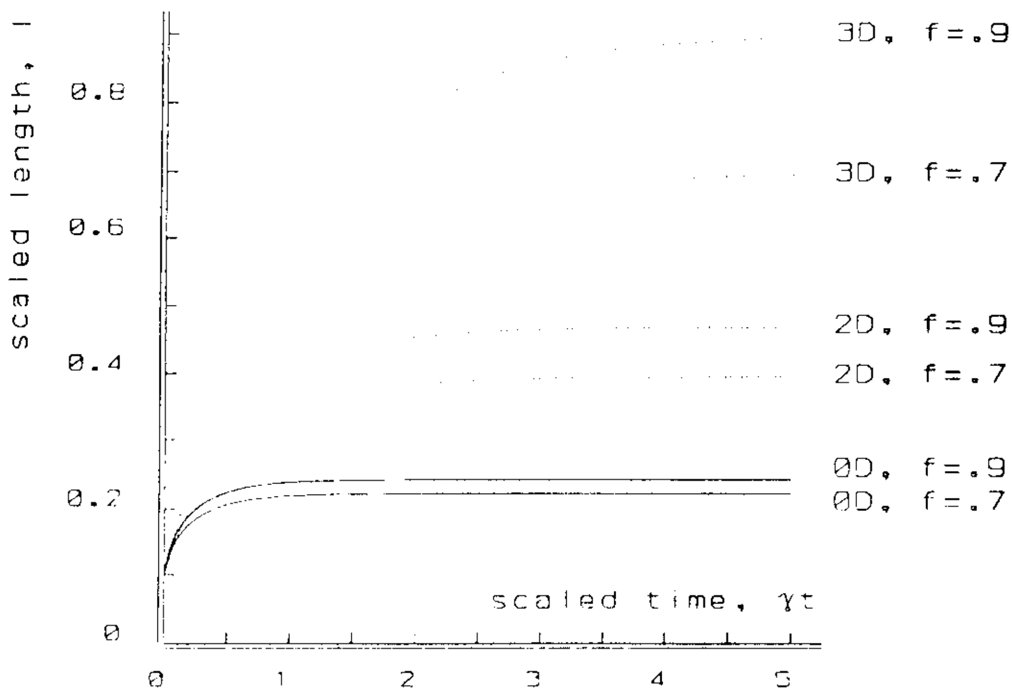


both reactors in series



Growth of 0, 2 and 3 dim. isomorphs

$l_b = 0.1, \; l_d = l_b 2^{1/3}$

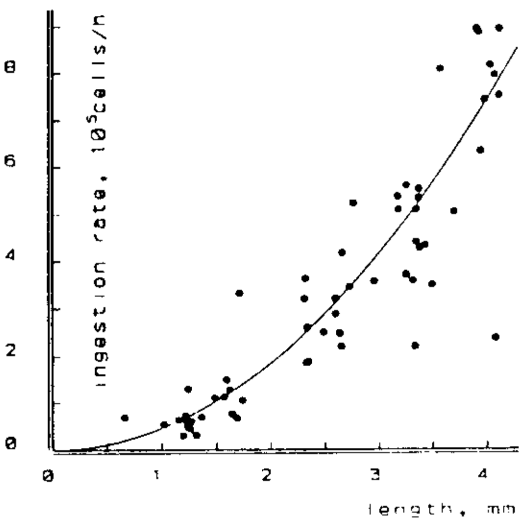


$$
\begin{aligned}
3D : l(t) &= f - (f - l_b)\exp\{-\dot{\gamma} t\} \\
2D : l(t) &= \left(f\sqrt{l_d} - \left(f\sqrt{l_d} - l_b^{3/2}\right)\exp\{-t\dot{\gamma}3/2\}\right)^{2/3} \\
1D : l(t) &= l_b \exp\{t\dot{\gamma}(f/l_d - 1)\} \\
0D : l(t) &= \left(f l_d^2 - (f l_d^2 - l_b^3)\exp\{-t\dot{\gamma}3\}\right)^{1/3}
\end{aligned}
$$

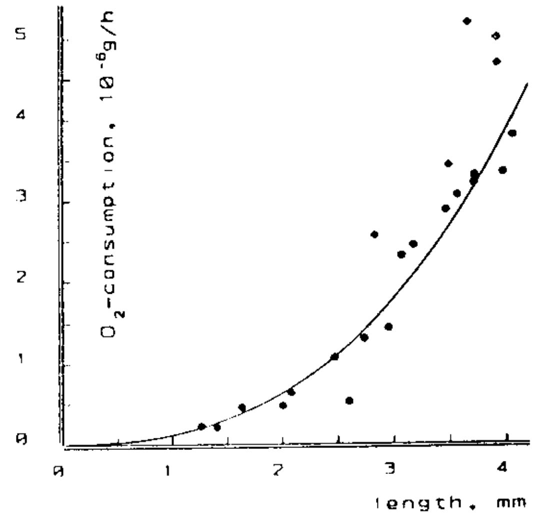
κ-rule for allocation

Daphnia magna starts to reproduce upon exceeding 2.5 mm.
Reproduction takes about 80% of the budget
Where does this energy come from?

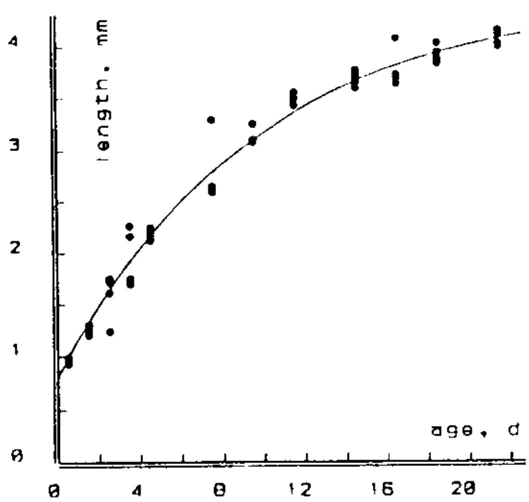
ingestion $\propto V^{2/3}$



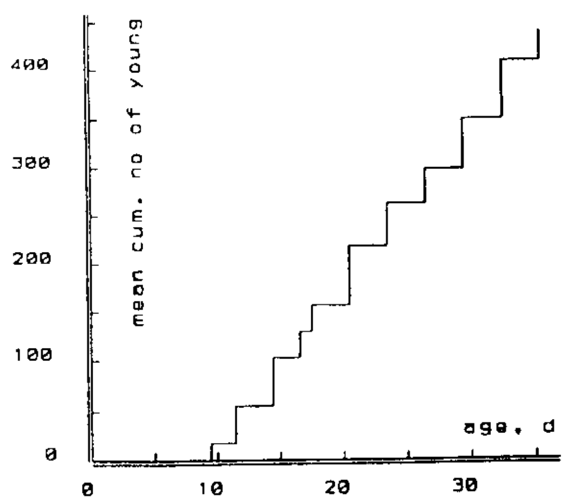
respiration $\propto V^{2/3} + V\dot{m}/\dot{v}$

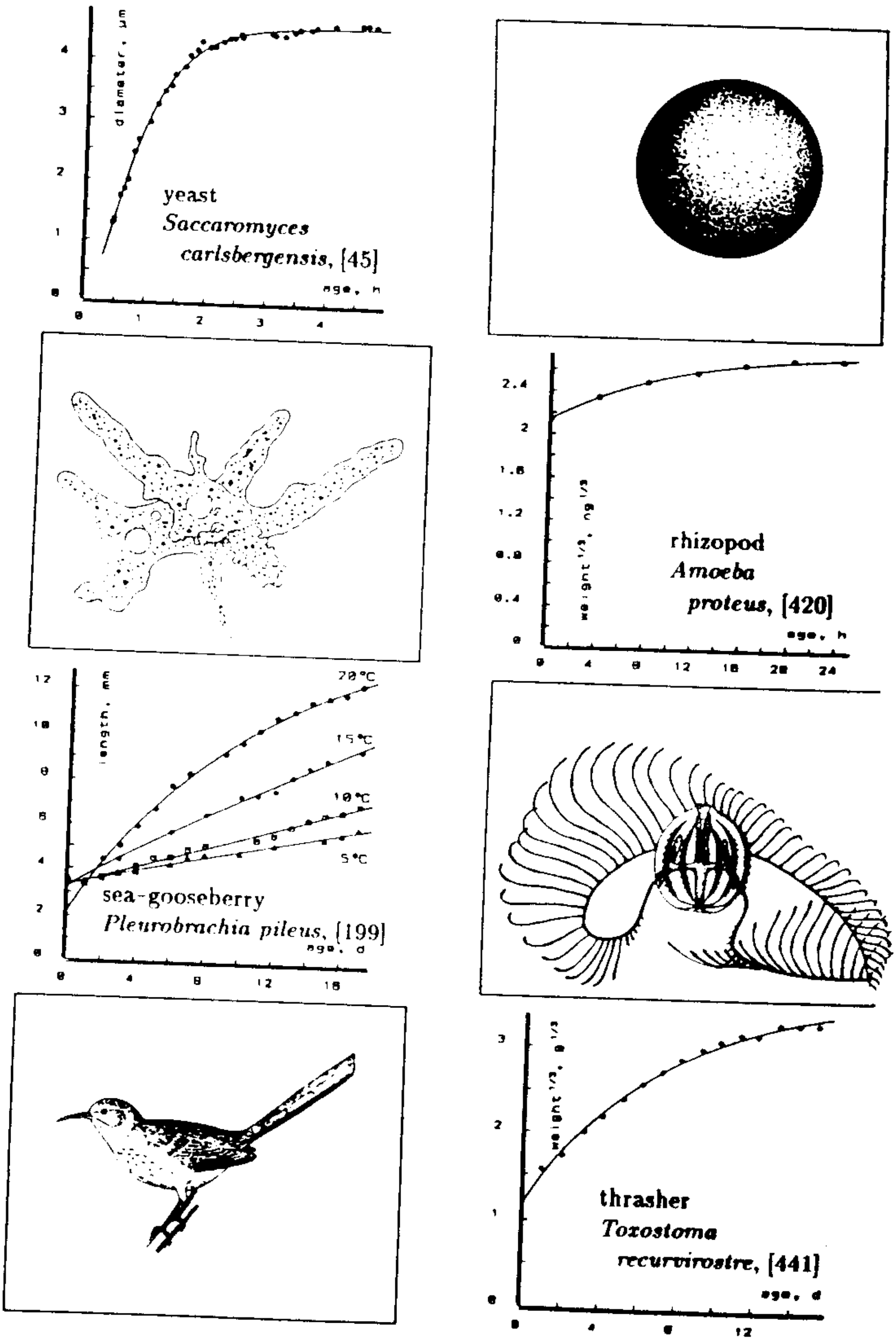


growth: $L_\infty - (L_\infty - L_b)\exp\{-\dot{\gamma}a\}$

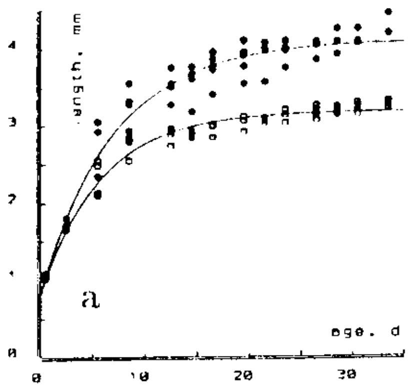


reproduction

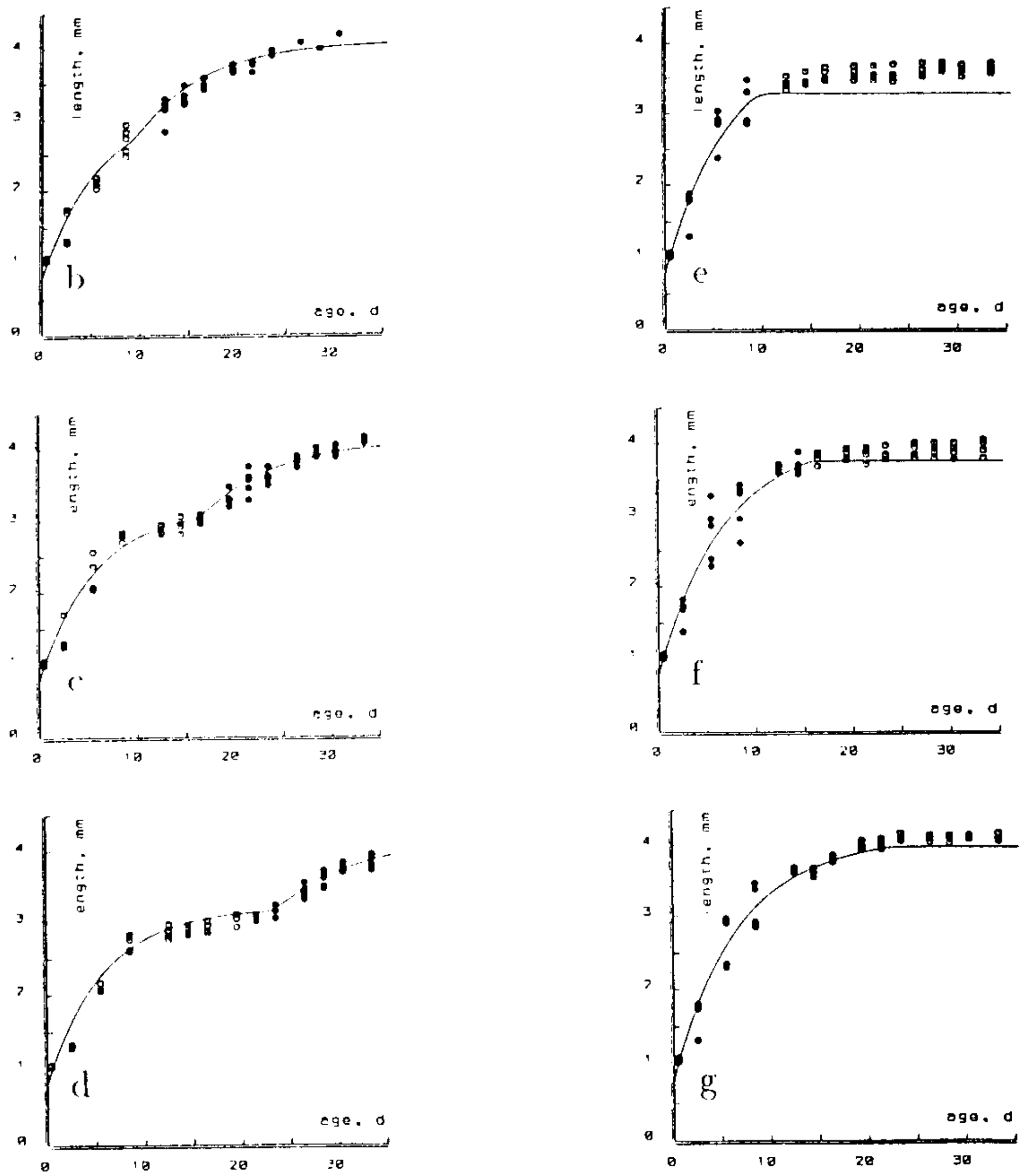



diameter, µm
age, h
yeast
Saccaromyces
carlsbergensis, [45]
weight 1/3, ng 1/3
age, h
rhizopod
Amoeba
proteus, [420]
length, mm
20°C
15°C
10°C
5°C
age, d
sea-gooseberry
Pleurobrachia pileus, [199]
weight 1/3, g 1/3
age, d
thrasher
Toxostoma
recurvirostre, [441]

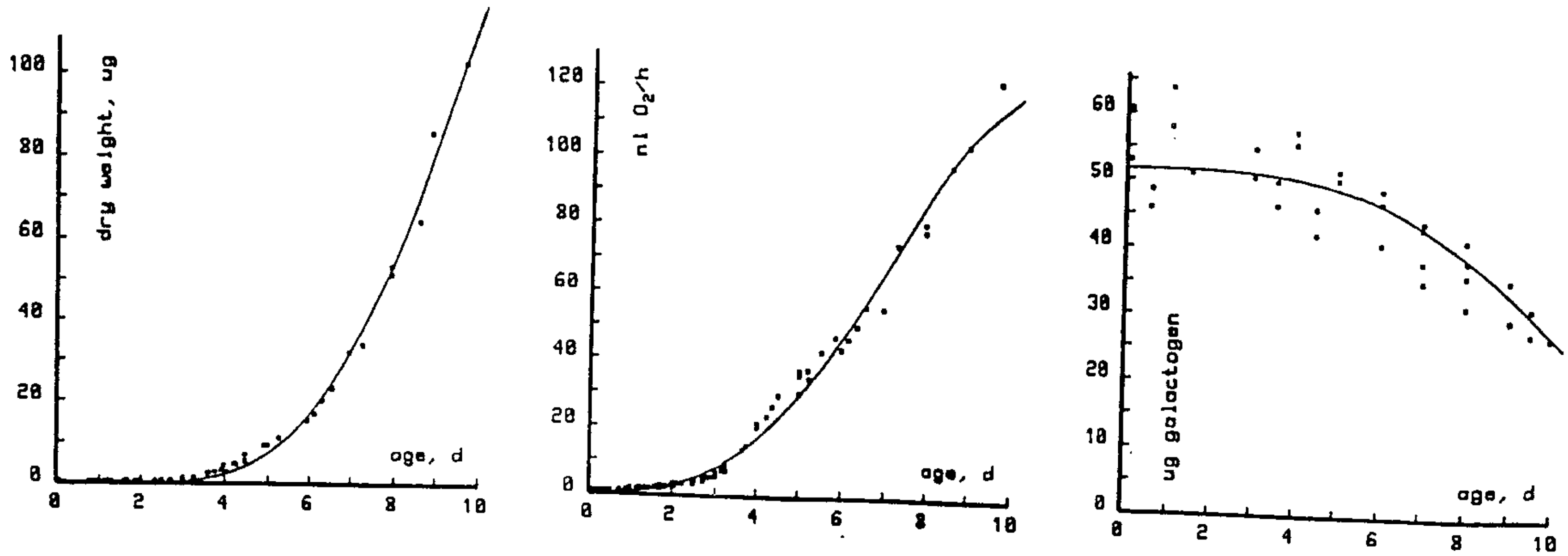
Change in feeding conditions

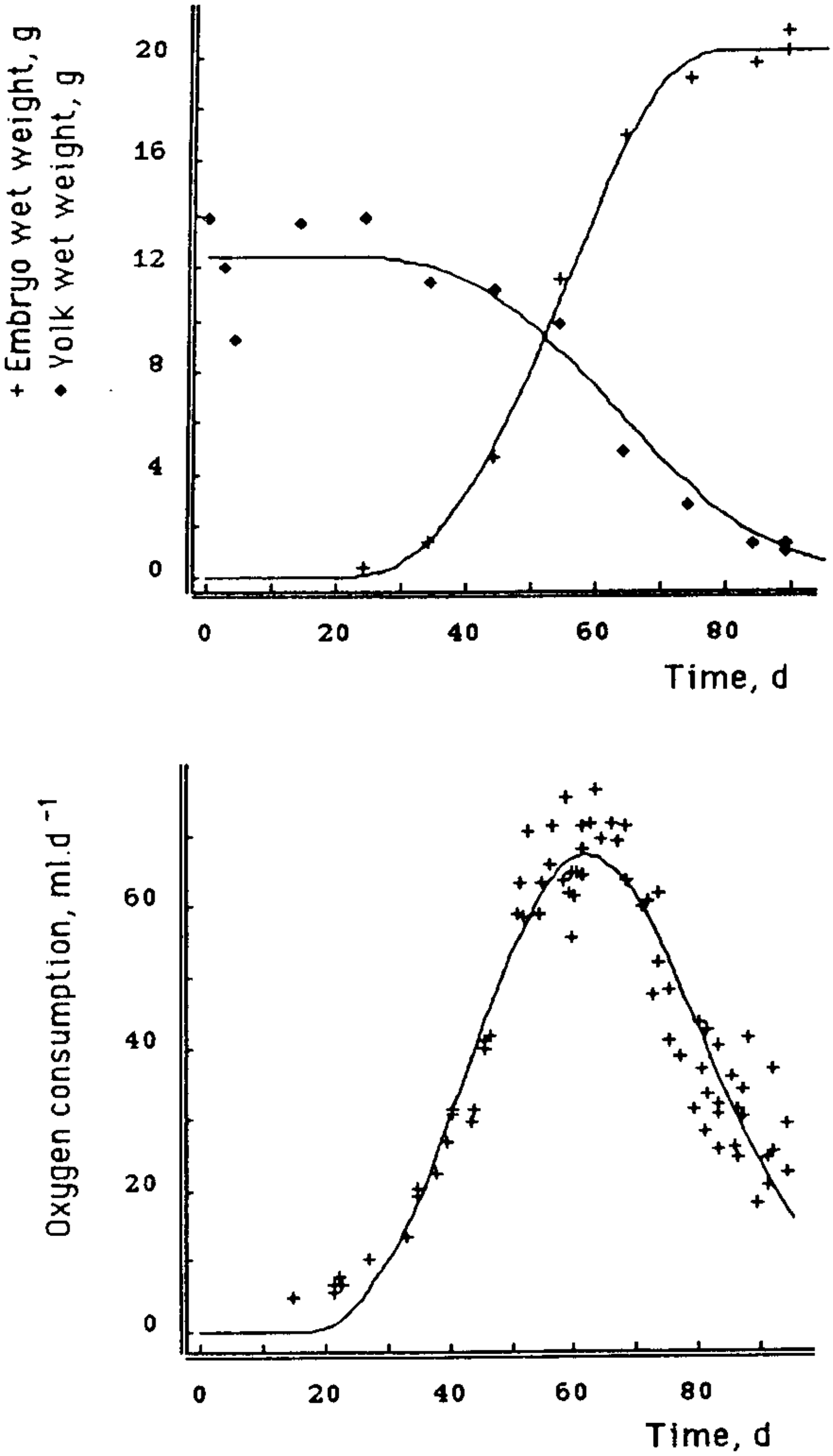


Length-at-age for *D. magna* high (•) and low (o) constant density (a), with a single interchange of these two densities at 1 (b,e), 2 (c,f) or 3 (d,g) weeks. The curves are completely based on the 5 parameters obtained from a.



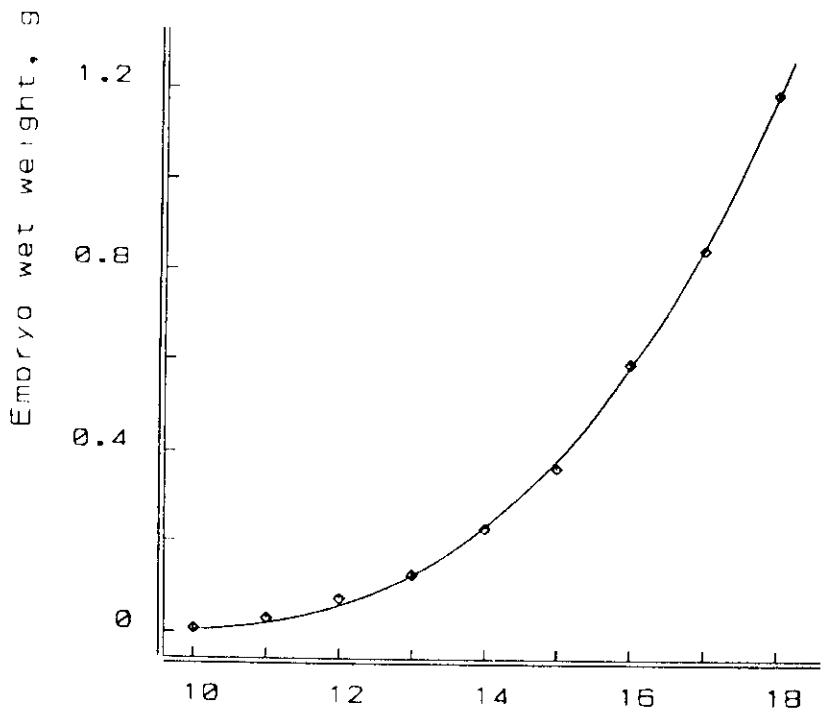
Growth of embryo of
Lymnaea stagnalis at 23°C
data from Horstman (1958)



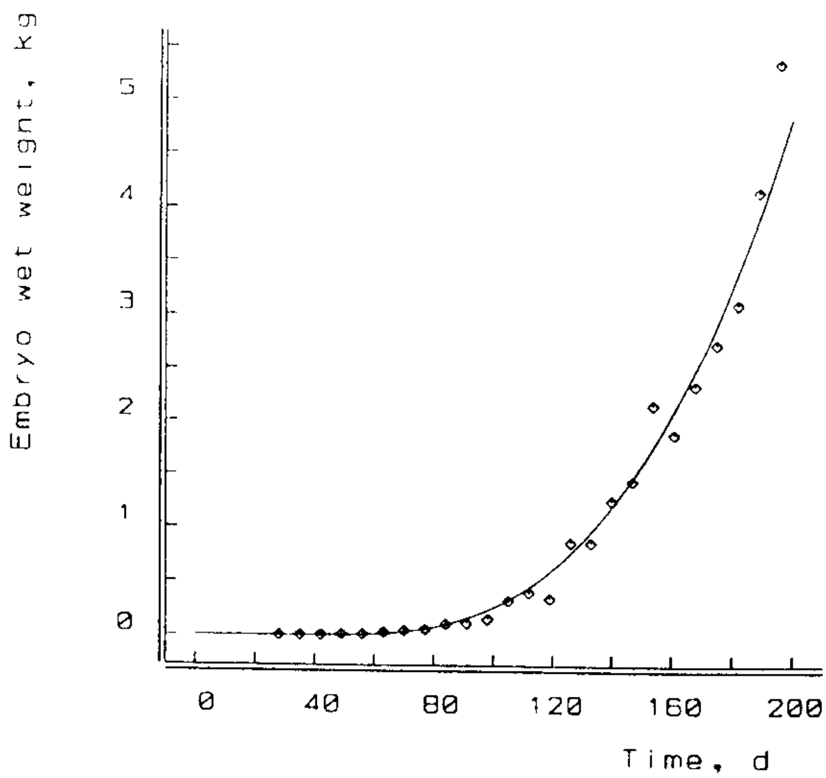


Egg development of *Carettochelys insculpta* at 30 °C

house mouse, *Mus musculus*



impala, *Aepyceros melampus*



Pupa

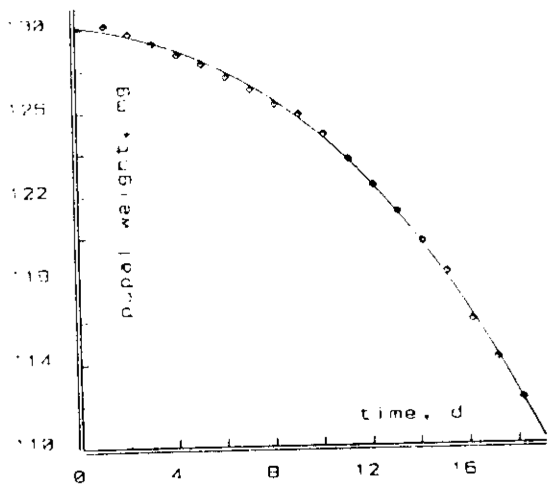
V	structural body volume	t	time
E	energy reserve	W_w	wet weight
$[G]$	vol.-spec. growth costs	$[\dot M]$	vol.-spec. maintenance costs
$[E_m]$	max adult reserve density	g	investment ratio $\frac{[G]}{\kappa[E_m]}$
κ	allocation fraction	$\dot v$	energy conductance

E_0 large $\rightarrow \frac{d}{dt}V = \dot v V^{2/3}$ so $V^{1/3}(t) = V_0^{1/3} + \dot v t$

$$\begin{aligned} E(t) &= E_0 - \frac{[G]}{\kappa}V(t) - \frac{[\dot M]}{\kappa}\int_0^t V(t_1)\,dt_1 \\ &= E_0 - \frac{[G]}{\kappa}(V_0^{1/3} + \dot v t)^3 - \frac{[\dot M]}{4\kappa\dot v}(V_0^{1/3} + \dot v t)^4 + \frac{[\dot M]}{4\kappa\dot v}V_0^{4/3} \end{aligned}$$

Since $W_w = [d_{wv}]V + [d_{we}]E/[E_m]$:

$$W_w(t) = \frac{[d_{we}]E_0}{[E_m]} - (g[d_{we}] - [d_{wv}])(V_0^{1/3} + \dot v t)^3 - \frac{[d_{we}]}{4V_m^{1/3}}\left(\left(V_0^{1/3} + \dot v t\right)^4 - V_0^{4/3}\right)$$



Pupa of the green-veined white butterfly *Pieris napi* until eclosion
Data from Forsberg and Wiklund, 1988
Curve: $W_w(t) = 130.56 - (\frac{7.16+t}{0.104})^3$, with weight in mg and time in days

$\dot{h}(t)$	hazard rate
$t_\dagger$	age at death

$$
\begin{aligned}
\frac{d}{dt}\text{Prob}\{\underline{t}_\dagger > t\} &= -\text{Prob}\{\underline{t}_\dagger > t\}\dot{h}(t) \\
\dot{h}(t) &= -\frac{d}{dt}\ln\ \text{Prob}\{\underline{t}_\dagger > t\} \\
\text{Prob}\{\underline{t}_\dagger > t\} &= \exp\{-\int_0^t \dot{h}(s)ds\}
\end{aligned}
$$

mean life span

$$
\begin{aligned}
\mathcal{E}\underline{t}_\dagger &= \int_0^\infty \text{Prob}\{\underline{t}_\dagger > t\}dt \\
&= \int_0^\infty \exp\{-\int_0^t \dot{h}(s)ds\}dt
\end{aligned}
$$

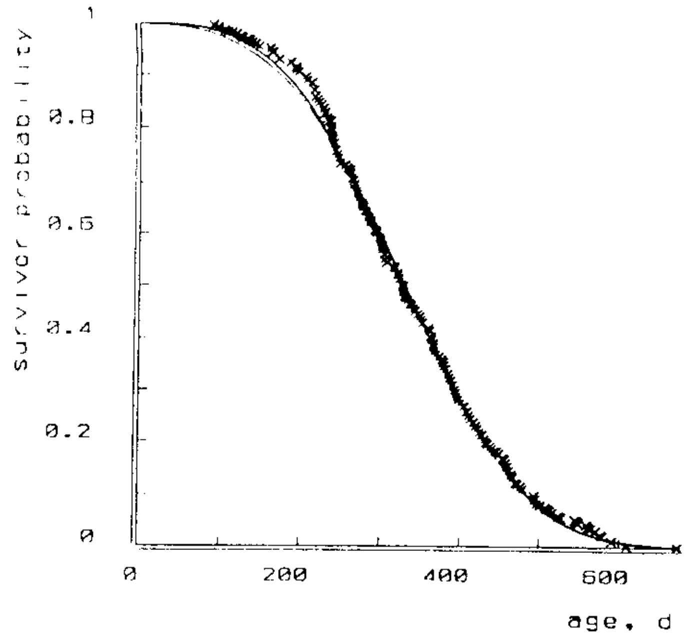
model	$\dot{h}(t)$	$\text{Prob}\{\underline{t}_\dagger > t\}$
exponential	$\dot{\lambda}$	$\exp\{-\dot{\lambda}t\}$
Weibull	$\beta\dot{\lambda}(\dot{\lambda}t)^{\beta-1}$	$\exp\{-(\dot{\lambda}t)^\beta\}$
Gompertz	$\beta\dot{\lambda}\exp\{\dot{\lambda}t\}$	$\exp\{-\beta\exp\{\dot{\lambda}t\}\}$

Aging

V	body volume
t	time
$[\dot{C}] \equiv \dot{C}/V$	volume–specific catabolic rate
$[\dot{M}]$	volume–specific maintenance costs
$[G]$	volume–specific costs for tissue synthesis
$\dot{m} \equiv [\dot{M}]/[G]$	maintenance rate coefficient
κ	partition coefficient for catabolic energy
$[Q]$	concentration of damage inducing compounds

$$
\begin{aligned}
\frac{d}{dt}Q &= d_Q \dot{C} \\
\frac{d}{dt}[Q] &= d_Q[\dot{C}] - [Q]\frac{d}{dt}\ln V \\
\kappa \dot{C} &= [G]\frac{d}{dt}V + [\dot{M}]V \\
\frac{d}{dt}[Q] &= \frac{d_Q}{\kappa}[G]\frac{d}{dt}\ln V + \frac{d_Q}{\kappa}[\dot{M}] - [Q]\frac{d}{dt}\ln V \\
[Q](t) &= \frac{d_Q}{\kappa}[G]\left(1 - \frac{V(0)}{V(t)}\right) + \frac{d_Q}{\kappa}\frac{[\dot{M}]}{V(t)}\int_0^t V(t_1)\,dt_1 \\
\dot{h}(t) &\propto V(t)^{-1}\int_0^t Q(t_1)\,dt_1 \\
&= \ddot{p}_a V(t)^{-1}\int_0^t \left(V(t_1) - V(0) + \dot{m}\int_0^{t_1} V(t_2)\,dt_2\right) dt_1
\end{aligned}
$$

$$
\begin{aligned}
\text{growth period} &\ll \text{life span} \\
\dot{h}(t) &= \frac{1}{2}\ddot{p}_a \dot{m} t^2
\end{aligned}
$$



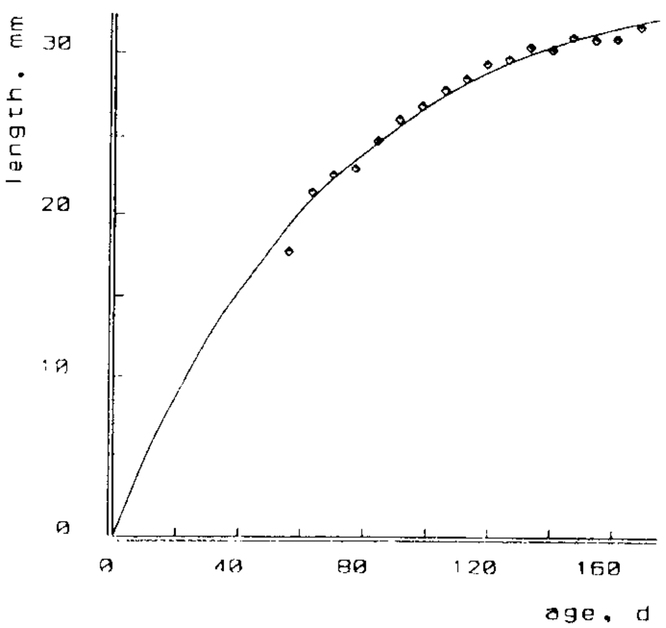


Figure 1: The survival probability and the growth curve of the pond snail *Lymnaea stagnalis* at 20°C. Data from Slob & Janse 1988, Zonneveld & Kooijman 1989. The fitted growth curve is the von Bertalanffy one, giving an ultimate length of 35 mm and a von Bertalanffy growth rate of $\dot{\gamma} = 0.015$ d^{-1}. The survival curve was used to estimate both the maintenance rate constant, $\dot{m} = 0.073$ d^{-1} and the aging acceleration $\ddot{p}_a = 2.563$ 10^{-6} d^{-2}. On top of the DEB-model based survival curve, the Weibull one is plotted to show that both curves are hard to distinguish in practice.

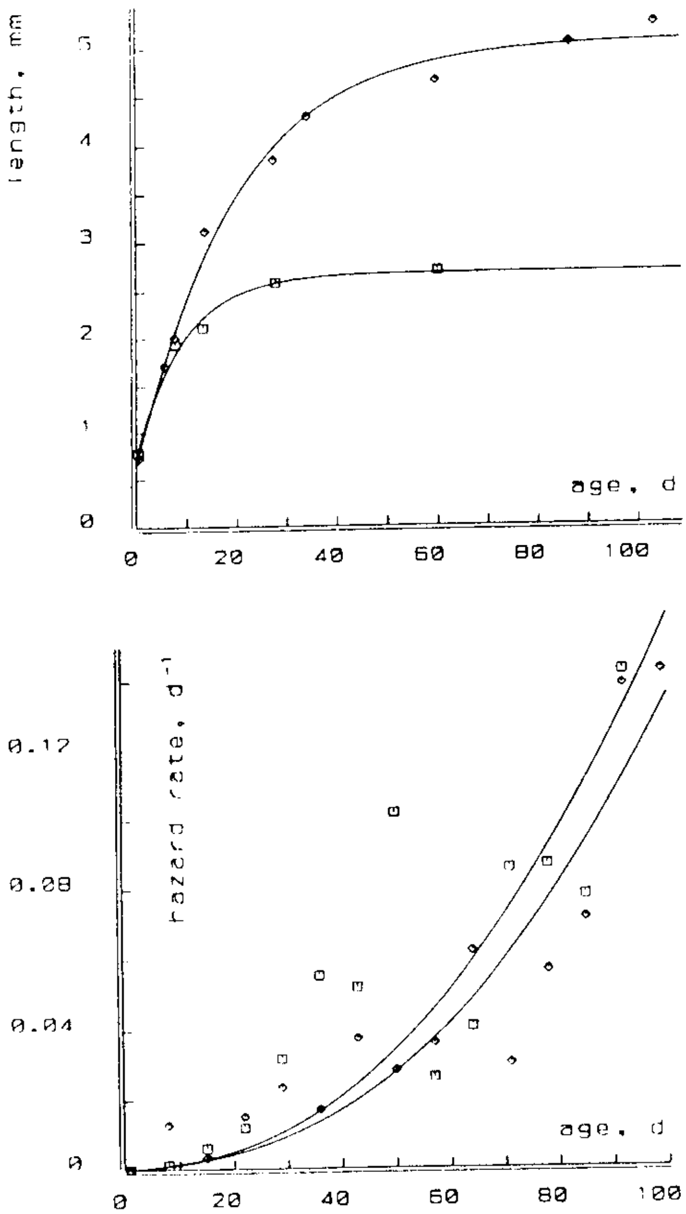


Figure 2: The growth curves of female and male daphnid *Daphnia magna* at 18°C and the observed hazard rates. Data from MacArthur & Bailey 1929. The growth curves are of the von Bertalanffy type with common length at birth. The hazard rates are fitted on the basis of the damage genesis discussed in the text, with a common aging acceleration of 2.587 10^{-5} d^{-2}. The difference in the hazard rates are due to difference in ultimate lengths.

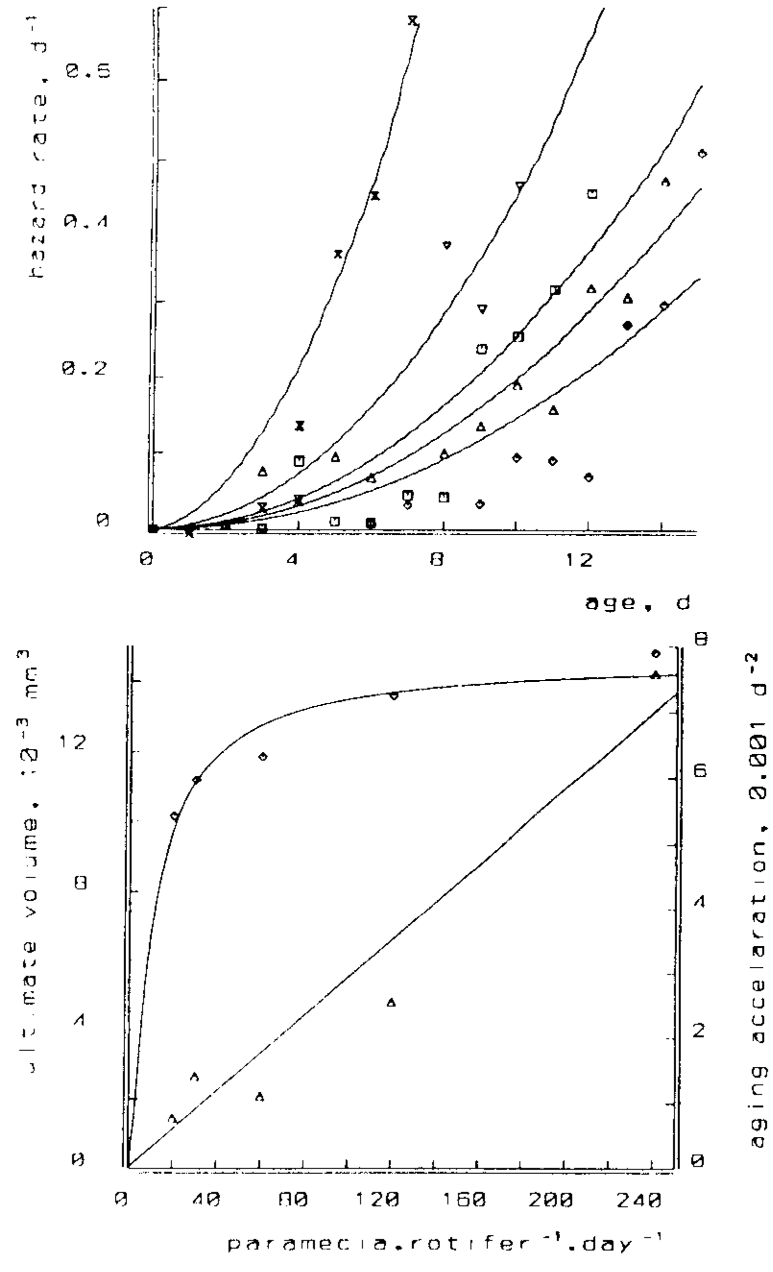
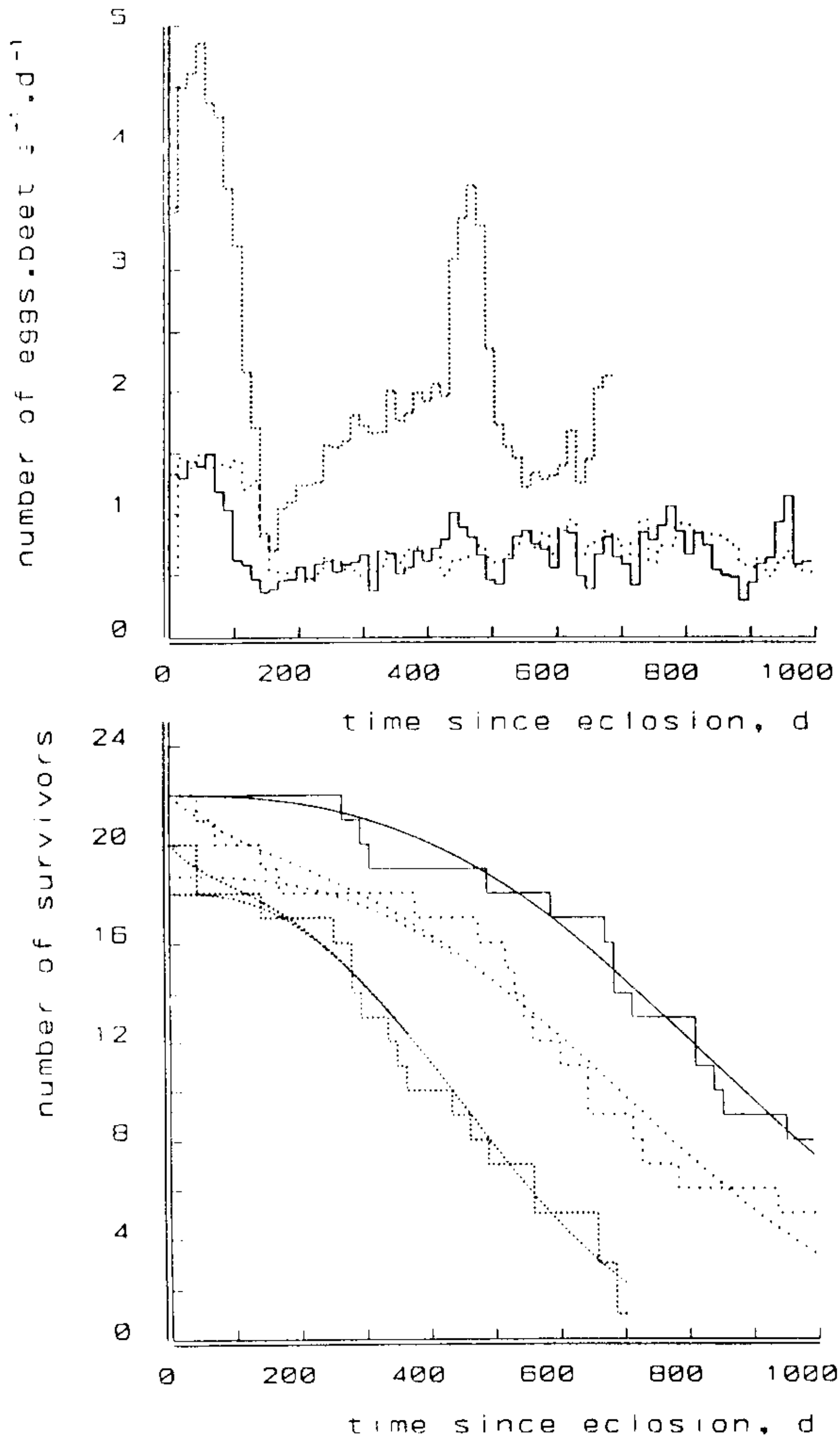
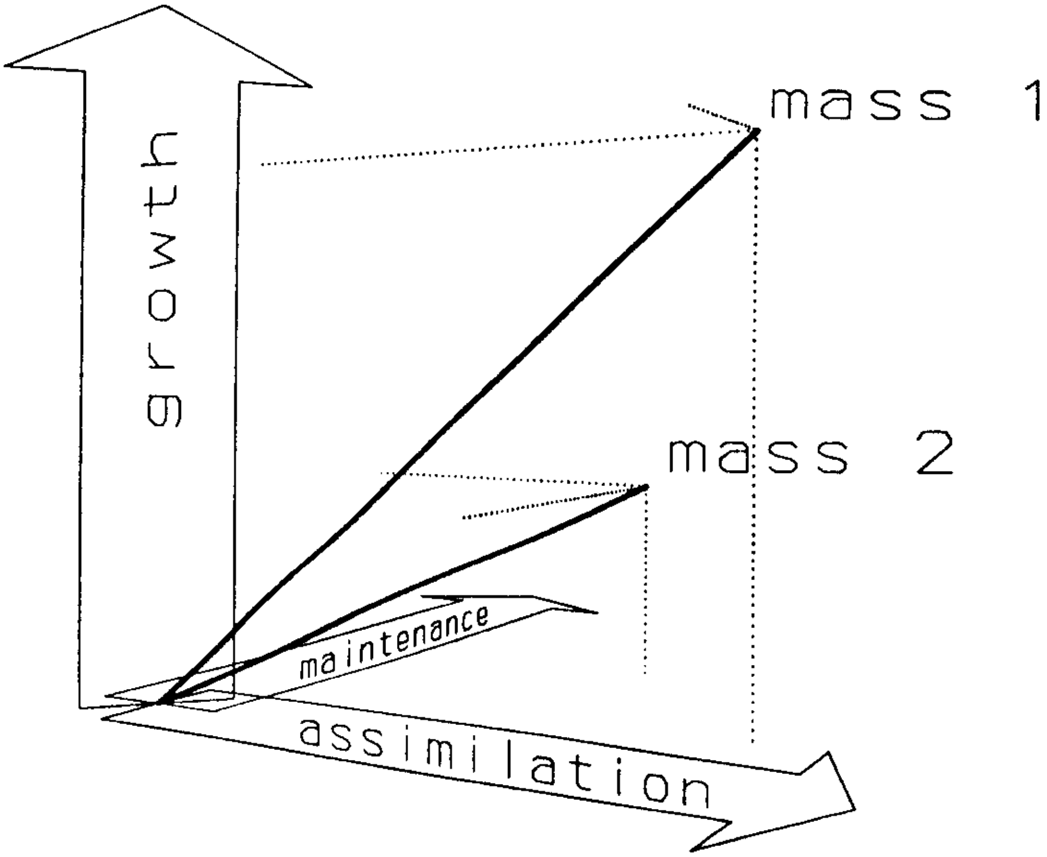


Figure 4: The hazard rates for the rotifer *Asplanchna girodi* for different food levels: 20 30 60 120 and 240 paramecia.rotifer^{-1}.day^{-1} at 20°C. Data from Robertson & Salt 1981. The hazard curves were based on the scaled food densities as estimated from the ultimate volumes (right), which gave f= 0.877, 0.915, 0.955, 0.977, 0.988. As described in the text, the aging accelerations proved to depend linearly on food density, with an intercept that is consistent with the aging acceleration found for daphnids



Reproduction and survival of *Nothiophilus biguttatus*.
Data from Ger Ernsting. High food (stippled graphs) at high (densely stippled) and low (sparsely stippled) temperature and low food (drawn) at high temperature.

Mass-energy coupling



Powers of assimilation, maintenance and growth may vary in time, but each mass flux can be written as a weighted sum of these powers with **fixed** weight coefficients. This also holds for dissipating heat. Mass fluxes include O_2 and CO_2, for instance.

Macro-chemical reaction equation

$$
\begin{aligned}
0 = {}& {}_mY_{EE}\ \underset{\text{reserves, } E}{CH_{n_{HE}}O_{n_{OE}}N_{n_{NE}}} + {}_mY_{VE}\ \underset{\text{struc.biovolume, } V}{CH_{n_{HV}}O_{n_{OV}}N_{n_{NV}}} + {}_mY_{AE}\ \underset{\text{water, } A}{H_2O} + \\
& {}_mY_{OE}\ \underset{\text{oxygen, } O}{O_2} + {}_mY_{CE}\ \underset{\text{C-dioxide, } C}{CO_2} + {}_mY_{NE}\ \underset{\text{N-waste, } N}{C_{n_{CN}}H_{n_{HN}}O_{n_{ON}}N_{n_{NN}}} + \\
& \left({}_mY_{XE}\ \underset{\text{food, } X}{CH_{n_{HX}}O_{n_{OX}}N_{n_{NX}}} + {}_mY_{FE}\ \underset{\text{feaces, } F}{CH_{n_{HF}}O_{n_{OF}}N_{n_{NF}}} + \left({}_mY_{RE}\ \underset{\text{eggs, } R}{CH_{n_{HE}}O_{n_{OE}}N_{n_{NE}}} \right) \right)
\end{aligned}
$$

Mass balance

$$
\begin{pmatrix} 1 & 0 & 0 & n_{CN} \\ 0 & 2 & 0 & n_{HN} \\ 2 & 1 & 2 & n_{ON} \\ 0 & 0 & 0 & n_{NN} \end{pmatrix}
\begin{pmatrix} {}_mY_{CE} \\ {}_mY_{AE} \\ {}_mY_{OE} \\ {}_mY_{NE} \end{pmatrix}
= -
\begin{pmatrix} 1 & 1 & 1 & 1 \\ n_{HX} & n_{HV} & n_{HE} & n_{HF} \\ n_{OX} & n_{OV} & n_{OE} & n_{OF} \\ n_{NX} & n_{NV} & n_{NE} & n_{NF} \end{pmatrix}
\begin{pmatrix} {}_mY_{XE} \\ {}_mY_{VE} \\ {}_mY_{RE} - 1 \\ {}_mY_{FE} \end{pmatrix}
$$

$$
\begin{pmatrix} {}_mY_{CE} \\ {}_mY_{AE} \\ {}_mY_{OE} \\ {}_mY_{NE} \end{pmatrix}
= -
\begin{pmatrix} 1 & 0 & 0 & -\frac{n_{CN}}{n_{NN}} \\ 0 & 2^{-1} & 0 & -\frac{n_{HN}}{2n_{NN}} \\ -1 & -4^{-1} & 2^{-1} & \frac{n}{4n_{NN}} \\ 0 & 0 & 0 & \frac{1}{n_{NN}} \end{pmatrix}
\begin{pmatrix} 1 & 1 & 1 & 1 \\ n_{HX} & n_{HV} & n_{HE} & n_{HF} \\ n_{OX} & n_{OV} & n_{OE} & n_{OF} \\ n_{NX} & n_{NV} & n_{NE} & n_{NF} \end{pmatrix}
\begin{pmatrix} {}_mY_{XE} \\ {}_mY_{VE} \\ {}_mY_{RE} - 1 \\ {}_mY_{FE} \end{pmatrix}
$$

with $n \equiv 4n_{CN} + n_{HN} - 2n_{ON}$

Mass flux

$$
\dot{\mathbf{k}}_D =
\begin{pmatrix} \dot{k}_X \\ \dot{k}_V \\ \dot{k}_E + \dot{k}_R \\ \dot{k}_F \end{pmatrix}
= \tilde{\mu}_E^{-1}
\begin{pmatrix} -\frac{d_{mx}}{[d_{me}]}\frac{\{\dot{I}_m\}}{\dot{v}} & 0 & 0 \\ 0 & 0 & \frac{[d_{mv}]}{[E_m]}\frac{1}{\kappa g} \\ 1 & -1 & -1 \\ \frac{d_{mf}}{[d_{me}]}\frac{\{\dot{F}_m\}}{\dot{v}} & 0 & 0 \end{pmatrix}
\begin{pmatrix} \dot{A} \\ \dot{M} + \dot{G}_m \\ \dot{G}_s \end{pmatrix}
$$

$$
\mathbf{Y}_M = -\mathbf{unY}_D \quad \dot{\mathbf{k}}_M = -\mathbf{un}\dot{\mathbf{k}}_D \quad {}_mY_{*_1*_2} = \dot{k}_{*_1}/\dot{k}_{*_2}
$$

Indirect calorimetry

$\dot{k}_H$	dissipation heat	$\dot{A}$	assimilation power
$\dot{\mathbf{k}}_M$	mineral fluxes	$\dot{D}$	dissipating power
$\dot{\mathbf{k}}_D$	organic fluxes	$\dot{G}_s$	somatic growth
$\tilde{\boldsymbol{\mu}}_M$	chemical pot. of minerals	$\mathbf{J}$	matrix of loadings
$\tilde{\boldsymbol{\mu}}_D$	chemical pot. of organics	$\mathbf{h}$	weight coeff.
$\tilde{\mu}_E$	chemical pot. of reserves	$\mathbf{Y}_{M,D}$	stoichiometric coeff.
$\mathbf{un}$	matrix of chemical coeff.		

Empirical energy-respiration coupling: Heat loss in J equals

$$11.16 \text{ mg } O_2 + 2.62 \text{ mg } CO_2 - \begin{cases} 9.41 \text{ mg } NH_3 & \text{aquatic animals} \\ 1.20 \text{ mg N} & \text{birds} \\ 5.93 \text{ mg N} + 3.39 \text{ mg } CH_4 & \text{mammals} \end{cases}$$

In symbolic form:

$$\dot{k}_H = \mathbf{h}^T \dot{\mathbf{k}}_M \quad \text{with}$$
$$\mathbf{h}^T \equiv \begin{pmatrix} h_C & h_A & h_O & h_N \end{pmatrix}$$

From conservation law for energy:

$$\begin{aligned} 0 &= \dot{k}_H + \dot{k}\tilde{\boldsymbol{\mu}}_M^T \mathbf{Y}_M + \dot{k}\tilde{\boldsymbol{\mu}}_D^T \mathbf{Y}_D \\ &= \dot{k}_H + (\tilde{\boldsymbol{\mu}}_D^T - \tilde{\boldsymbol{\mu}}_M^T \mathbf{un})\dot{\mathbf{k}}_D \\ &= \dot{k}_H + \tilde{\mu}_E^{-1}(\tilde{\boldsymbol{\mu}}_D^T - \tilde{\boldsymbol{\mu}}_M^T \mathbf{un})\mathbf{J} \begin{pmatrix} \dot{A} \\ \dot{D} \\ \dot{G}_s \end{pmatrix} \end{aligned}$$

Chemical potentials of organic components (combustion reference):

$$\tilde{\boldsymbol{\mu}}_D^T = \mathbf{h}^T \mathbf{un}$$

Respiration coefficient

Embryo's and starving juveniles and adults for $n \equiv 4n_{CN} + n_{HN} - 2n_{ON}$:

$$-_mY_{CO} = -_mY_{CE}/_mY_{OE} = \dot{k}_C/\dot{k}_O$$
$$= \frac{1 - n_{NE}\frac{n_{CN}}{n_{NN}} - (1 - n_{NV}\frac{n_{CN}}{n_{NN}})\,_mY_{VE}}{1 + \frac{n_{HE}}{4} - \frac{n_{OE}}{2} - \frac{n}{4}\frac{n_{NE}}{n_{NN}} - (1 + \frac{n_{HV}}{4} - \frac{n_{OV}}{2} - \frac{n}{4}\frac{n_{NV}}{n_{NN}})\,_mY_{VE}}$$

The respiration quotient is independent of l and e if

$$\frac{1 + \frac{n_{HE}}{4} - \frac{n_{OE}}{2} - \frac{n}{4}\frac{n_{NE}}{n_{NN}}}{1 + \frac{n_{HV}}{4} - \frac{n_{OV}}{2} - \frac{n}{4}\frac{n_{NV}}{n_{NN}}} = \frac{1 - \frac{n_{NE}}{n_{NN}}}{1 - \frac{n_{NV}}{n_{NN}}}$$

in which case respiration $\propto$ catabolic power, and

$$-_mY_{CO} = \frac{1 - n_{NE}\frac{n_{CN}}{n_{NN}}}{1 + \frac{n_{HE}}{4} - \frac{n_{OE}}{2} - \frac{n}{4}\frac{n_{NE}}{n_{NN}}} = \frac{1 - n_{NV}\frac{n_{CN}}{n_{NN}}}{1 + \frac{n_{HV}}{4} - \frac{n_{OV}}{2} - \frac{n}{4}\frac{n_{NV}}{n_{NN}}}$$

The condition on N-waste composition that is of special interest

$$\begin{pmatrix} n_{NE} & -2n_{NE} & -n_{HE} + 2n_{OE} \\ n_{NV} & -2n_{NV} & -n_{HV} + 2n_{OV} \end{pmatrix} \begin{pmatrix} n_{HN} \\ n_{ON} \\ n_{NN} \end{pmatrix} = \mathbf{0}$$

Specific dynamic action per C-mole of food is

$$\frac{\dot{k}_{OA}}{d_{mx}\dot{I}} = \mathbf{u}_{O*}\mathbf{n} \begin{pmatrix} 1 \\ 0 \\ -\frac{[d_{me}]}{d_{mx}}\frac{\dot{v}}{\{\dot{I}_m\}} \\ -\frac{d_{mf}}{d_{mx}}\frac{\{\dot{F}_m\}}{\{\dot{I}_m\}} \end{pmatrix}$$

Water balance

- Water flux $\dot{k}_A$: follows from DEB model and mass conservation
- Evaporation has two main routes (in land animals)
  respiration $\propto$ oxygen consumption $\dot{k}_O$
  transpiration $\propto$ surface area $V^{2/3}$
- Drinking rate $\dot{k}_{A_d}$: follows from water balance

Assuming that the water content of the N-waste is fixed, we have

$$\dot{k}_{A_d} = \dot{k}_A + d_{AO}\dot{k}_O + \{\dot{k}_{A_t}\}V^{2/3}$$

Coupling with energy budget via

$$\begin{aligned}\dot{k}_A &= -\mathbf{u}_{A*}\mathbf{n}\dot{\mathbf{k}}_D \\ \dot{k}_O &= -\mathbf{u}_{O*}\mathbf{n}\dot{\mathbf{k}}_D\end{aligned}$$

where the DEB model specifies $\dot{\mathbf{k}}_D$

In aquatic animals we have that $\dot{k}_{A_d} = \dot{k}_A$

Scaling

K	saturation const	V_b	vol at birth	V_p	vol at puberty
$\{\dot{I}_m\}$	max spec ingestion	$\{\dot{A}_m\}$	max spec assim	$[E_m]$	max spec reserve dens
$[\dot{M}]$	spec maint costs	$[G]$	spec growth costs	κ	allocation par
$\{\dot{H}\}$	spec heating costs	$\ddot{p}_a$	aging acceleration	q	1-overhead frac for reprod

invariance property

Individuals number 1 and 2 have identical DEB's for constant food density and arbitrary zoom factor z if

$$
\begin{array}{lllllll}
K_2 = K_1 z + X(z-1) & \{\dot{I}_m\}_2 = \{\dot{I}_m\}_1 z & [\dot{M}]_2 = [\dot{M}]_1 & \{\dot{H}\}_2 = \{\dot{H}\}_1 \\
V_{b,2}^{-1/3} = V_{b,1}^{-1/3} & \{\dot{A}_m\}_2 = \{\dot{A}_m\}_1 z & [G]_2 = [G]_1 & \ddot{p}_{a,2} = \ddot{p}_{a,1} \\
V_{p,2}^{-1/3} = V_{p,1}^{-1/3} & [E_m]_2 = [E_m]_1 z & \kappa_2 = \kappa_1 & q_2 = q_1
\end{array}
$$

primary scaling relationships

The DEB parameters of species number 1 and 2 tend to relate as

$$
\begin{array}{llll}
K_2 = K_1 z & \{\dot{I}_m\}_2 = \{\dot{I}_m\}_1 z & [\dot{M}]_2 = [\dot{M}]_1 & \{\dot{H}\}_2 = \{\dot{H}\}_1 \\
V_{b,2}^{-1/3} = V_{b,1}^{-1/3} z & \{\dot{A}_m\}_2 = \{\dot{A}_m\}_1 z & [G]_2 = [G]_1 & \ddot{p}_{a,2} = \ddot{p}_{a,1} \\
V_{p,2}^{-1/3} = V_{p,1}^{-1/3} z & [E_m]_2 = [E_m]_1 z & \kappa_2 = \kappa_1 & q_2 = q_1
\end{array}
$$

The maximum volumetric length of an individual equals $V_m^{1/3} = \kappa\{\dot{A}_m\}/[\dot{M}]$, so zoom factor z equals the ratio of the maximum volumetric lengths of the two species.

Secondary scaling relationships

$g = [G]/\kappa[E_m]$	investment ratio	$V_h = (\{\dot{H}\}/[\dot{M}])^3$	heating volume
$\dot{m} = [\dot{M}]/[G]$	maint rate coeff	$\dot{v} = \{\dot{A}_m\}/[E_m]$	energy conductance

Example: respiration $\propto$ catabolic rate

$$\dot{C} = \frac{g[E]}{g + [E]/[E_m]} \left(\dot{v}V^{2/3} + \dot{m}V_h^{1/3}V^{2/3} + \dot{m}V \right)$$

Step 1:
Write variable of interest as function of primary parameters while $V = V_m$ and $[E] = [E_m]$

$$\dot{C}_m = \frac{[G]/\kappa}{[G]/\kappa[E_m] + 1} \left(\left(\frac{\{\dot{A}_m\}}{[E_m]} + \frac{[\dot{M}]}{[G]} V_h^{1/3} \right) \left(\frac{\{\dot{A}_m\}}{[\dot{M}]/\kappa} \right)^2 + \frac{[\dot{M}]}{[G]} \left(\frac{\{\dot{A}_m\}}{[\dot{M}]/\kappa} \right)^3 \right)$$

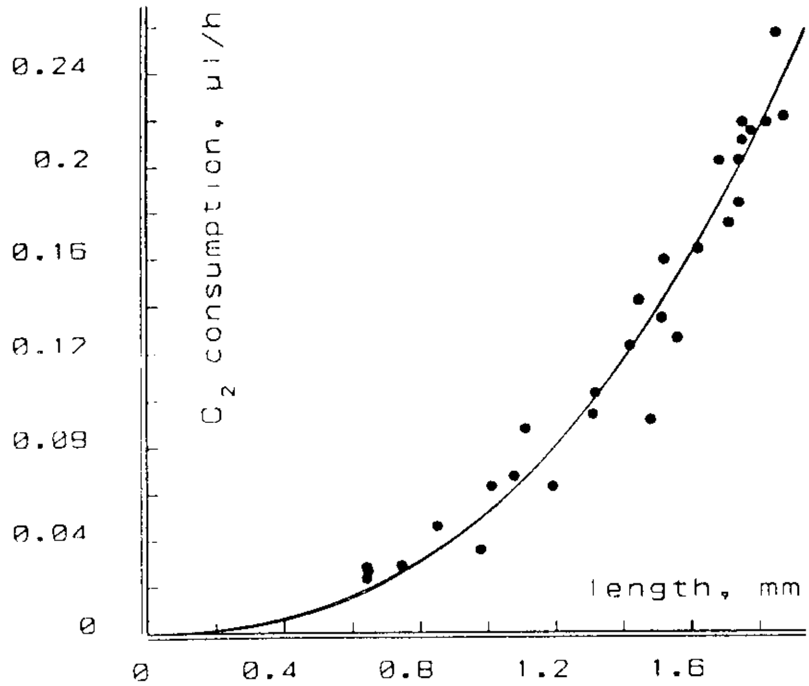
Step 2:
Multiply the physical design parameters by the zoom factor z

$$\begin{aligned} \dot{C}_{m,z} &= \frac{[G]_1/\kappa_1}{[G]_1/\kappa_1[E_m]_1 z + 1} \left(\left(\frac{\{\dot{A}_m\}_1 z}{[E_m]_1 z} + \frac{[\dot{M}]_1}{[G]_1} V_{h,1}^{1/3} \right) \left(\frac{\{\dot{A}_m\}_1 z}{[\dot{M}]_1/\kappa_1} \right)^2 + \frac{[\dot{M}]_1}{[G]_1} \left(\frac{\{\dot{A}_m\}_1 z}{[\dot{M}]_1/\kappa_1} \right)^3 \right) \\ &= \frac{[\dot{M}]_1}{\kappa_1} \frac{(\dot{v}_1/\dot{m}_1 + V_{h,1}^{1/3}) z^2 V_{m,1}^{2/3} + z^3 V_{m,1}}{g_1/z + 1} \end{aligned}$$

Step 3:
Substitute $z = (\mathcal{V}/V_{m,1})^{1/3}$, where $\mathcal{V}$ is the compound parameter for max body volume

$$\dot{C}_{m,\mathcal{V}} = \frac{[\dot{M}]_1}{\kappa_1} \frac{(\dot{v}_1/\dot{m}_1 + V_{h,1}^{1/3})\mathcal{V}^{2/3} + \mathcal{V}}{\mathcal{V}^{-1/3}\dot{v}_1/\dot{m}_1 + 1}$$

The respiration rate of *Daphnia pulex* with few eggs at 20°C as a function of length. Data from Richman 1958. The DEB model based curve $0.0336L^2 + 0.01845L^3$ as well as the standard allometric curve $0.0516L^{2.437}$ have been plotted on top of each other.



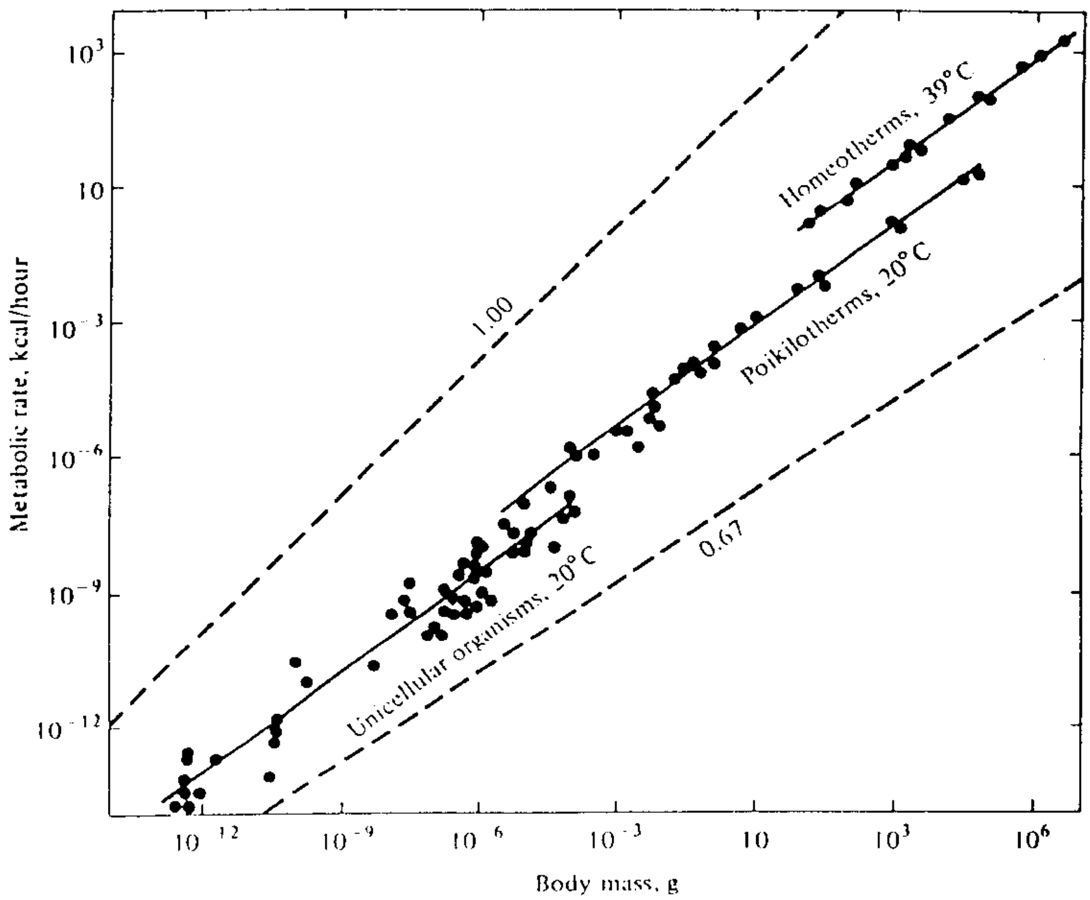
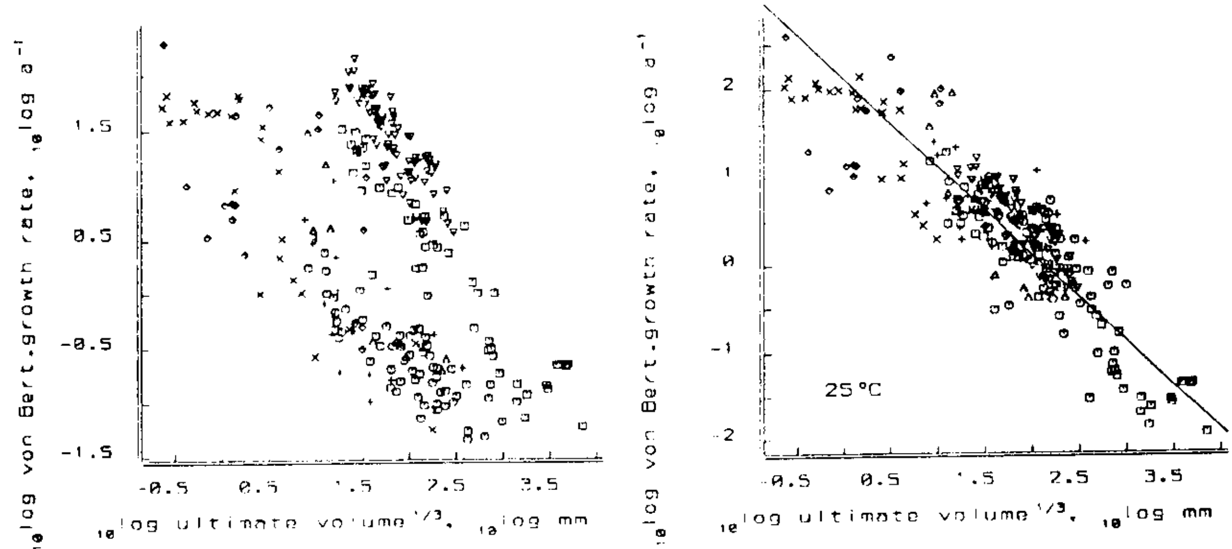


Figure 4.3 Metabolic rates of a variety of organisms of different sizes (log-log plot). Total oxygen consumption increases with increasing body size. [From Schmidt-Nielsen (1975).]

von Bertalanffy growth rate



von Bertalanffy growth rate

$$\dot{\gamma}_{\mathcal{V}} = (3/\dot{m}_1 + 3\mathcal{V}^{1/3}/\dot{v}_1)^{-1}$$

where

$\dot{m}$	maintenance rate coefficient
$\dot{v}$	energy conductance
$\mathcal{V}$	maximum body volume

markers

▽	birds
□	mammals
△	reptiles, amphibians
○	fishes
×	crustaceans
+	molluscs
◇	others

The line has slope −1

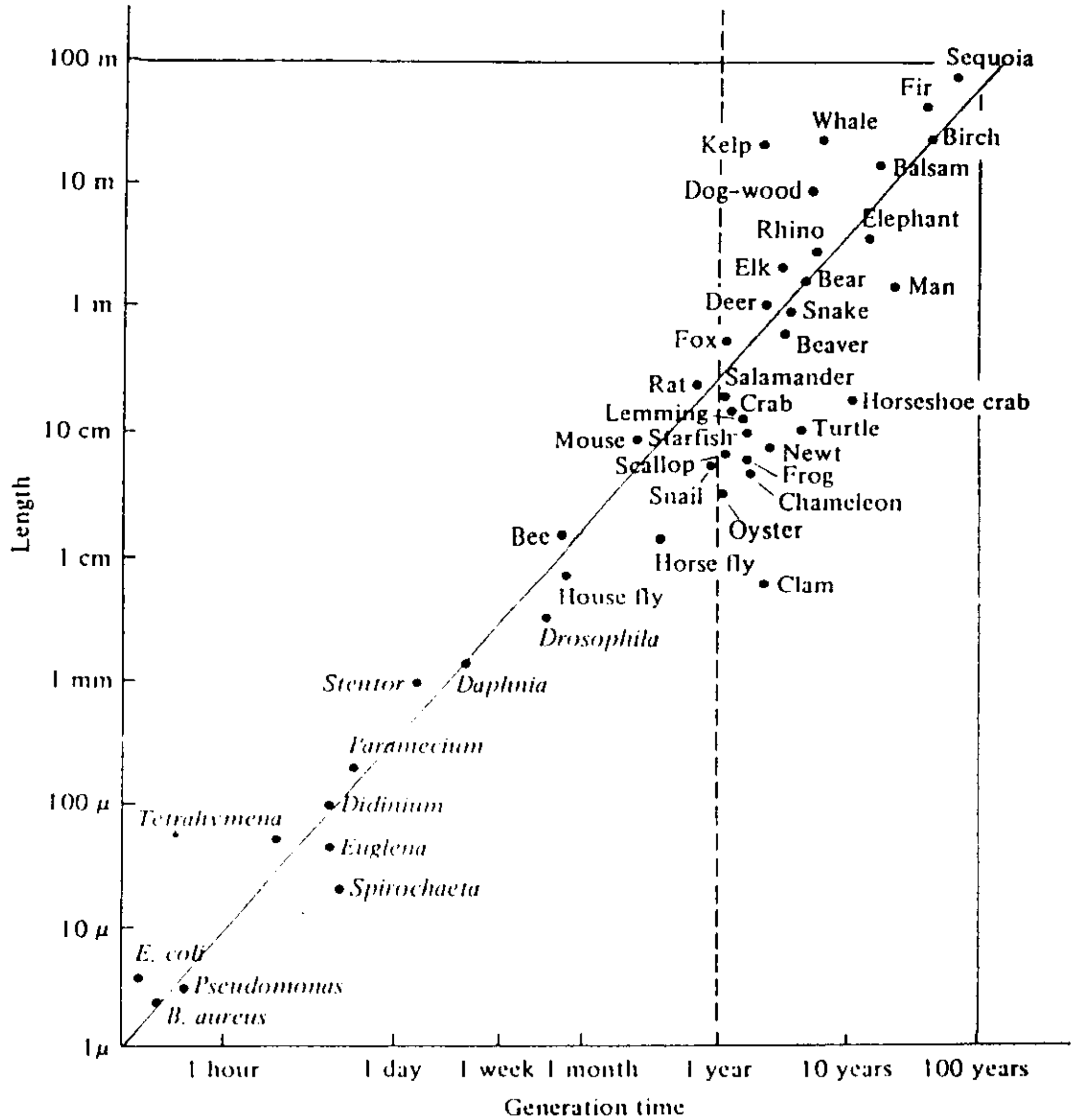
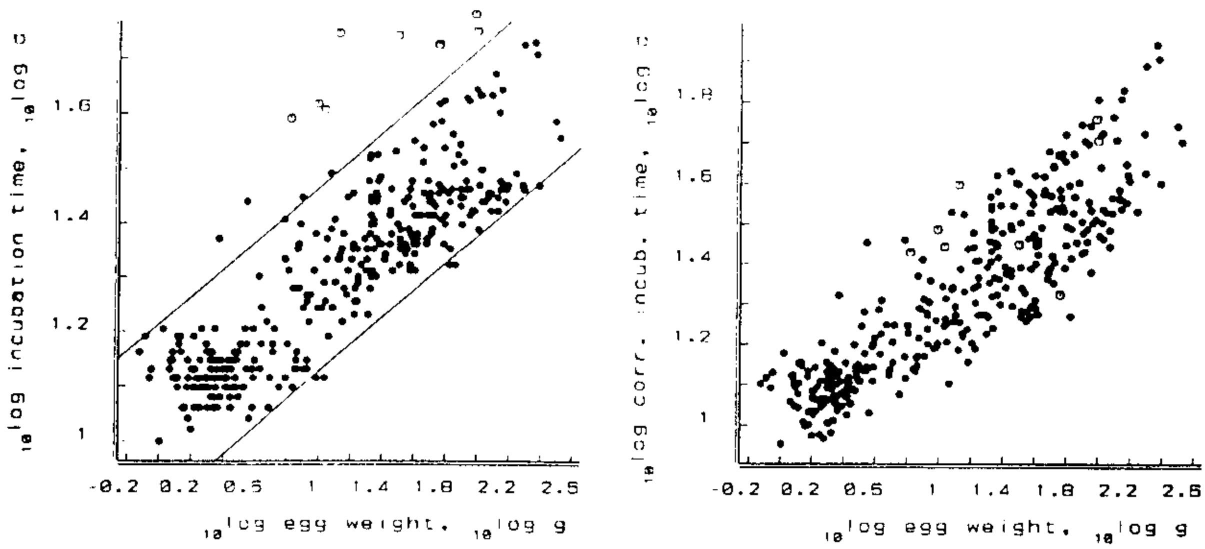


Figure 5.28 Log-log plot of organism length against generation time for a wide variety of organisms. [From John Tyler Bonner, *Size and Cycle: An Essay on the Structure of Biology* (Copyright © 1965 by Princeton University Press), Fig. 1, p. 17. Reprinted by permission of Princeton University Press.]

Incubation time



Incubation time for european breeding birds

$$a_b \simeq \alpha + \beta/g \propto \mathcal{V}^{1/3} \quad \text{and} \quad E_0 \propto \mathcal{V}^{4/3} \quad \text{so} \quad a_b \propto E_0^{1/4}$$

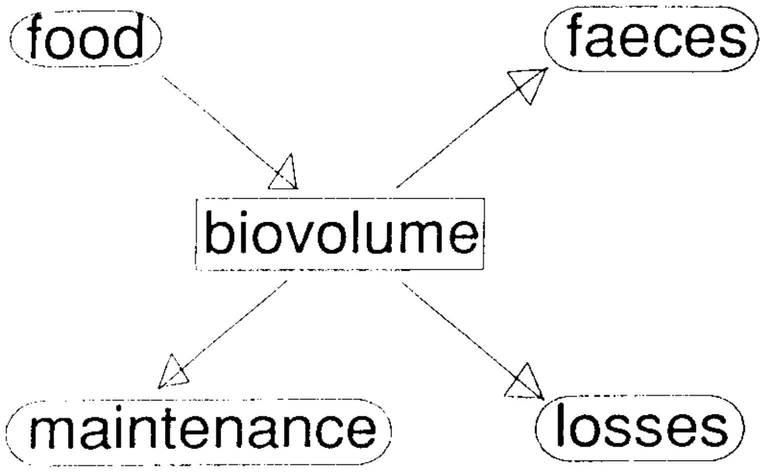
where $g \equiv [G]/\kappa[E_m]$ is the investment ratio

Data from Harrison 1975.

The lines have slope of 1/4

The tube noses (o) sport long incubation times If corrected for a common relative volume at birth, this difference largely disappears.

Population as an entity



The population, quantified as the sum of the volumes of the individuals, converts food into faeces, while extracting energy.

Part of this energy becomes lost in maintenance processes and part of it is deposited in losses, i.e. the cumulated harvest.

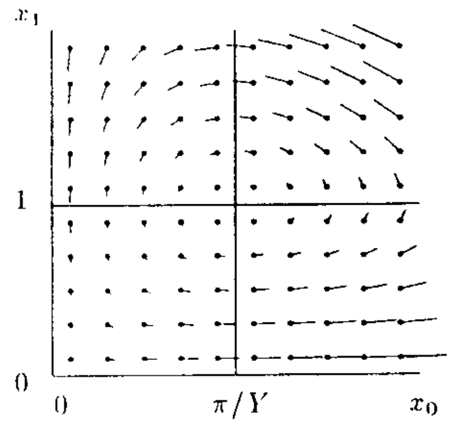
The harvesting effort determines the allocation rules and sets the population size and so its impact on resources.

Lotka–Volterra tradition in population dynamics

t	time	$\dot{p}$	spec. death rate
τ	scaled time: $\dot{\mu}t$	π	death parameter: $\dot{p}K/[\dot{I}_m]$
X_0	prey density	X_1	predator density
x_0	scaled prey density: X_0/K	x_1	scaled pred. dens.: $X_1[\dot{I}_m]/K\dot{\mu}$
$[\dot{I}_m]/K$	spec. feeding rate	Y	yield coefficient
$X_{0,\infty}$	carrying capacity of prey	$\dot{\mu}$	pop. growth rate of prey
$x_{0,\infty}$	scaled carrying cap.: $X_{0,\infty}/K$		

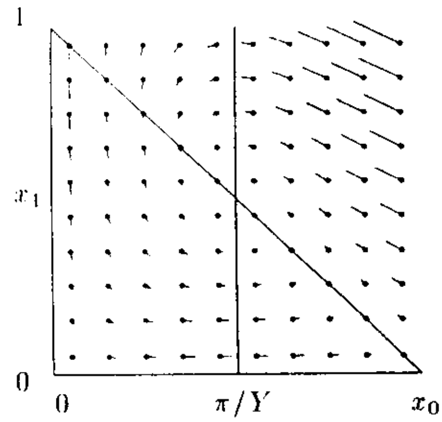
Exponential growth of prey population:

$$\frac{d}{dt}X_0 = \dot{\mu}X_0 - X_0X_1[\dot{I}_m]/K$$
$$\frac{d}{dt}X_1 = YX_0X_1[\dot{I}_m]/K - \dot{p}X_1$$
$$\frac{d}{d\tau}x_0 = x_0 - x_0x_1$$
$$\frac{d}{d\tau}x_1 = Yx_0x_1 - \pi x_1$$



Logistic growth of prey population:

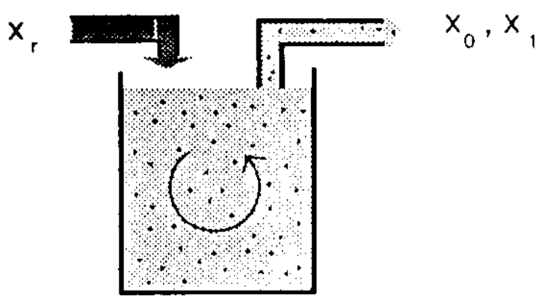
$$\frac{d}{dt}X_0 = \dot{\mu}X_0(1 - X_0/X_{0,\infty}) - X_0X_1[\dot{I}_m]/K$$
$$\frac{d}{dt}X_1 = YX_0X_1[\dot{I}_m]/K - \dot{p}X_1$$
$$\frac{d}{d\tau}x_0 = x_0(1 - x_0/x_{0,\infty}) - x_0x_1$$
$$\frac{d}{d\tau}x_1 = Yx_0x_1 - \pi x_1$$



$Y = 3/4$, $\pi = 0.5$, $x_{0,\infty} = 4/3$

chemostat dynamics

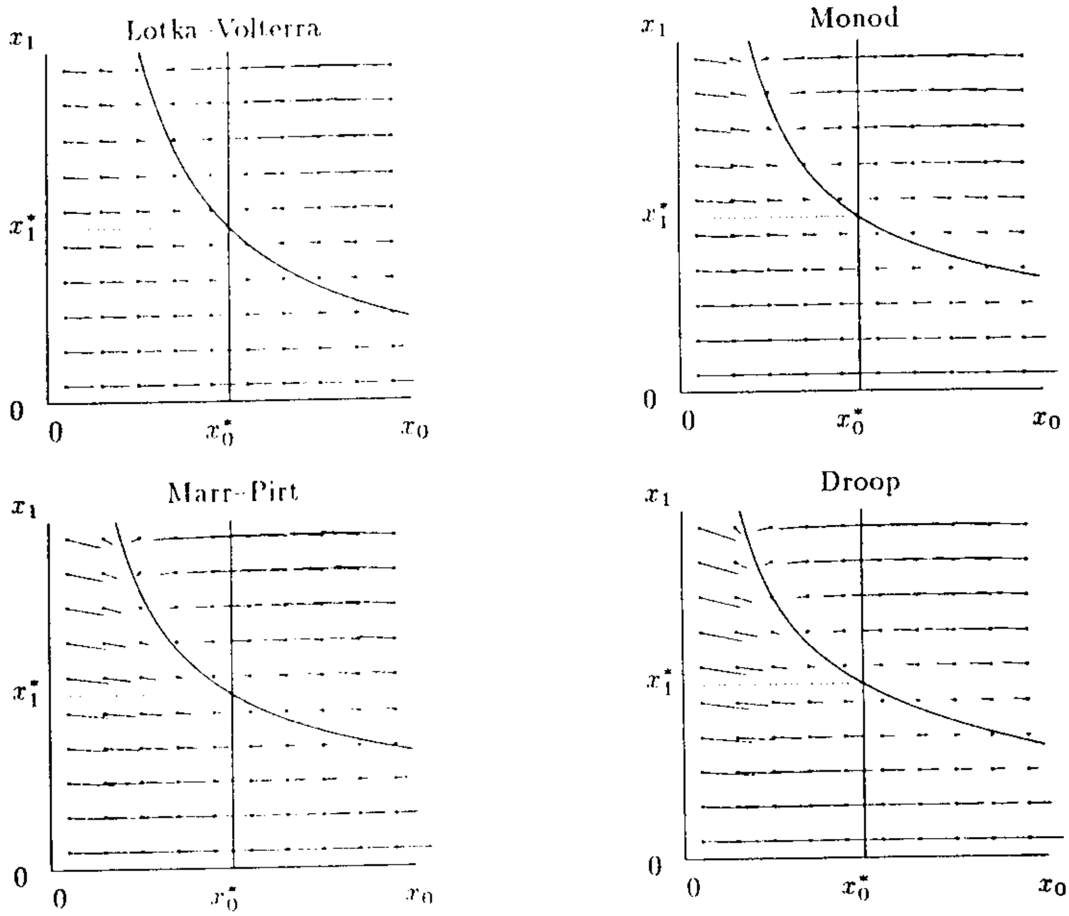
τ	time × throughput rate	Y	yield coefficient: $\frac{x_r - x_0}{x_1}$
x_r	substrate in feed/sat. coef.	Y_g	Monod's yield coef.: $\frac{\kappa[\dot{A}_m]}{[G][\dot{I}_m]}$
x_0	substrate/saturation coef.	f	scaled functional response: $\frac{x_0}{1+x_0}$
x_1	biovolume	κ	$\frac{\text{energy to growth + maintenance}}{\text{energy to development}}$
$[\dot{I}_m]$	max ingestion rate	l_d	scaled length at division: $\frac{[\dot{M}]}{\kappa[\dot{A}_m]}$
$[\dot{A}_m]$	max vol.-spec. assim. rate	g	investment ratio: $\frac{[G]}{\kappa[E_m]}$
$[E_m]$	max energy density	$[\dot{M}]$	vol.-spec. maintenance costs
$[G]$	vol.-spec. growth costs		

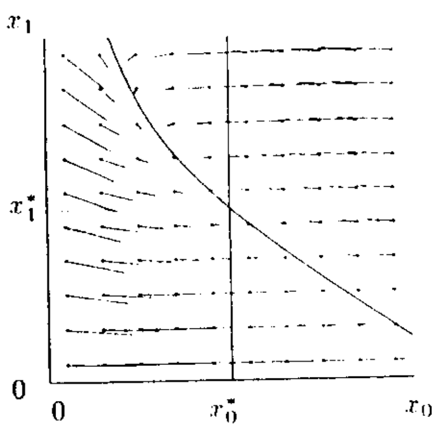


$$\frac{d}{d\tau}x_0 = x_r - [\dot{I}_m]fx_1 - x_0$$
$$\frac{d}{d\tau}x_1 = Y[\dot{I}_m]fx_1 - x_1$$

$[E_m]$ \ $[\dot{M}]$	0	$\neq 0$
0	Monod Y_g	Marr-Pirt $Y_g \frac{f-l_d}{f}$
$\neq 0$	Droop $Y_g \frac{g}{f+g}$	DEB for fil. $Y_g \frac{g}{f} \frac{f-l_d}{f+g}$

Lotka-Volterra as Monod but $f = x_0$

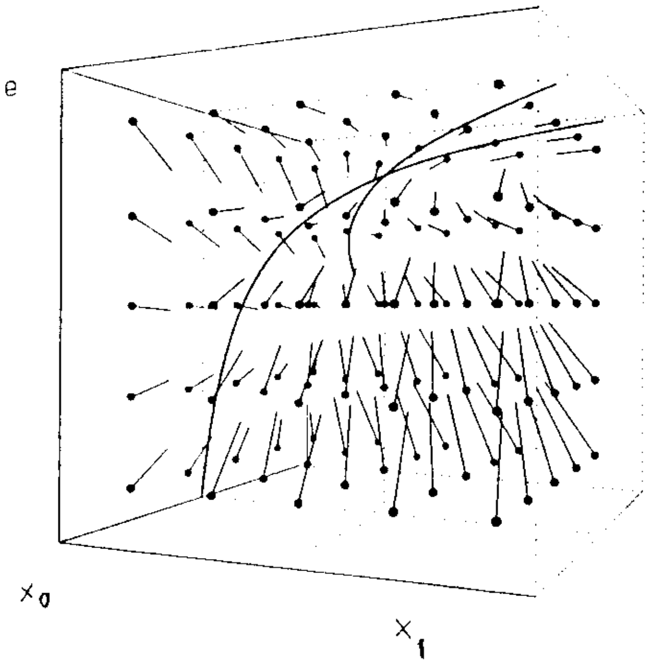




Equilibrium values for x_0 and x_1 and parameters

model	x_0^*	x_1^*	x_r	Y_g	$[I_m]$	g	l_d
Lotka	0.39	8.17	10	0.85	3	-	-
Monod	0.65	7.95	10	0.85	3	-	-
Marr	0.97	6.12	10	0.85	3	-	0.1
Droop	1.82	4.23	10	0.85	3	1	-
DEB	4.25	2.37	10	0.85	3	1	0.1

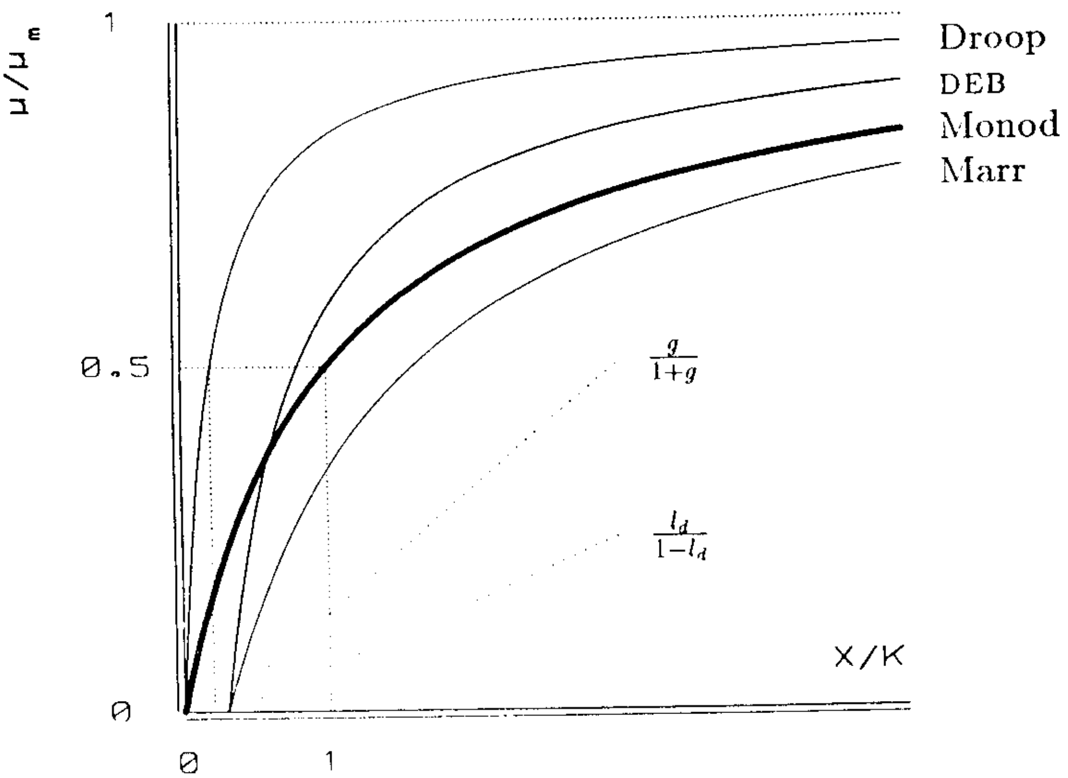
The direction fields and isoclines for the DEB model for filaments in a chemostat with reserves at equilibrium, and the various simplifications of this model. The lengths and directions of the line segments indicate the change in scaled food density x_0 and scaled biovolume x_1. The isoclines represent x_0, x_1-values where $\frac{d}{d\tau}x_0 = 0$ or $\frac{d}{d\tau}x_1 = 0$.



The direction field and isoclines for
the DEB model for filaments in a chemostat:

$$\begin{aligned}
\frac{d}{d\tau}x_0 &= x_r - [I_m]fx_1 - x_0 \\
\frac{d}{d\tau}e &= Y_g[I_m]g(f - e) \\
\frac{d}{d\tau}x_1 &= Y_g[I_m]g\frac{e - l_d}{e + g}x_1 - x_1
\end{aligned}$$

Population growth as a function of substrate level



In all models, Monod, Marr–Pirt, Droop and DEB, uptake as a fraction of its maximum depends hyperbolically on substrate density X as a fraction of the saturation coefficient K, as indicated by the thick curve. In the Monod model $\dot{\mu} \propto \frac{x}{x+1}$, this curve coincides with the population growth rate $\dot{\mu}$ as a fraction of its maximum $\dot{\mu}_m$. The Marr–Pirt model $\dot{\mu} \propto \frac{x-l_d/(1-l_d)}{x+1}$, which includes maintenance, has a translation to the right. The Droop model $\dot{\mu} \propto \frac{x}{x+g/(1+g)}$, which includes storage, has a smaller saturation coefficient, whereas the DEB model for filaments $\dot{\mu} \propto \frac{x-l_d/(1-l_d)}{x+g/(1+g)}$ has both. All four curves are hyperboles with horizontal asymptote 1.

Macro-chemical reaction equation and mass balance

$$\begin{aligned} 0 \;=\; & -\overset{\text{E-substrate},X_0}{\mathrm{CH}_{n_{HX_0}}\mathrm{O}_{n_{OX_0}}\mathrm{N}^{n_{+X_0}}_{n_{NX_0}}} + {}_mY_{X_1}\overset{\text{biomass},X_1}{\mathrm{CH}_{n_{HX_1}}\mathrm{O}_{n_{OX_1}}\mathrm{N}_{n_{NX_1}}} + {}_mY_E\overset{\text{reserves},E}{\mathrm{CH}_{n_{HE}}\mathrm{O}_{n_{OE}}\mathrm{N}_{n_{NE}}} + \\ & {}_mY_P\overset{\text{product},P}{\mathrm{CH}_{n_{HP}}\mathrm{O}_{n_{OP}}\mathrm{N}^{n_{+P}}_{n_{NP}}} + {}_mY_C\overset{\text{carbonate},C}{\mathrm{CHO}_3^{-1}} + {}_mY_H\overset{\text{water},A}{\mathrm{H_2O}} + {}_mY_O\overset{\text{oxygen},O}{\mathrm{O_2}} + \\ & {}_mY_N\overset{\text{N-substrate},N}{\mathrm{H}_{n_{HN}}\mathrm{O}_{n_{ON}}\mathrm{N}^{n_{+N}}_{n_{NN}}} + {}_mY_+\overset{\text{protons},+}{\mathrm{H}^{+1}} \end{aligned}$$

$$\begin{pmatrix} 1 & 0 & 0 & 0 & 0 \\ 1 & 2 & 0 & n_{HN} & 1 \\ 3 & 1 & 2 & n_{ON} & 0 \\ 0 & 0 & 0 & n_{NN} & 0 \\ -1 & 0 & 0 & n_{+N} & 1 \end{pmatrix} \begin{pmatrix} {}_mY_C \\ {}_mY_A \\ {}_mY_O \\ {}_mY_N \\ {}_mY_+ \end{pmatrix} = - \begin{pmatrix} 1 & 1 & 1 & 1 & 1 & \cdots \\ n_{HX_0} & n_{HX_1} & n_{HE} & n_{HP_1} & n_{HP_2} & \cdots \\ n_{OX_0} & n_{OX_1} & n_{OE} & n_{OP_1} & n_{OP_2} & \cdots \\ n_{NX_0} & n_{NX_1} & n_{NE} & n_{NP_1} & n_{NP_2} & \cdots \\ n_{+X_0} & 0 & 0 & n_{+P_1} & n_{+P_2} & \cdots \end{pmatrix} \begin{pmatrix} {}_mY_{X_0} \\ {}_mY_{X_1} \\ {}_mY_E \\ {}_mY_{P_1} \\ {}_mY_{P_2} \\ \vdots \end{pmatrix}$$

$$\begin{aligned} \mathbf{Y}_M &= -\mathbf{unY}_D \\ \mathbf{Y}_M^T &\equiv \begin{pmatrix} {}_mY_C & {}_mY_A & {}_mY_O & {}_mY_N & {}_mY_+ \end{pmatrix} \\ \mathbf{Y}_D^T &\equiv \begin{pmatrix} -1 & {}_mY_{X_1} & {}_mY_E & {}_mY_{P_1} & {}_mY_{P_2} & \cdots \end{pmatrix} \end{aligned}$$

$$\mathbf{u} \equiv \begin{pmatrix} 1 & 0 & 0 & 0 & 0 \\ 1 & 2 & 0 & n_{HN} & 1 \\ 3 & 1 & 2 & n_{ON} & 0 \\ 0 & 0 & 0 & n_{NN} & 0 \\ -1 & 0 & 0 & n_{+N} & 1 \end{pmatrix}^{-1} \qquad \mathbf{n} \equiv \begin{pmatrix} 1 & 1 & 1 & 1 & 1 & \cdots \\ n_{HX_0} & n_{HX_1} & n_{HE} & n_{HP_1} & n_{HP_2} & \cdots \\ n_{OX_0} & n_{OX_1} & n_{OE} & n_{OP_1} & n_{OP_2} & \cdots \\ n_{NX_0} & n_{NX_1} & n_{NE} & n_{NP_1} & n_{NP_2} & \cdots \\ n_{+X_0} & 0 & 0 & n_{+P_1} & n_{+P_2} & \cdots \end{pmatrix}$$

$$\begin{aligned} {}_mY_E &= t_E\dot{\mu} & \qquad {}_mY_{X_1} &= t_{X_1}\frac{\dot{\mu}}{g}\frac{\dot{\nu}-\dot{\mu}}{\dot{m}+\dot{\mu}} \\ {}_mY_{W_1} &= {}_mY_E + {}_mY_{X_1} & \qquad {}_mY_P &= t_{PA}\dot{\nu} + (t_{PM}\dot{m} + t_{PG}\dot{\mu})\frac{\dot{\nu}-\dot{\mu}}{\dot{m}+\dot{\mu}} \end{aligned}$$

$$\begin{pmatrix} t_{X_1} & t_E & t_{PA} & t_{PM} & t_{PG} \end{pmatrix} \equiv (d_{mx}[\dot{I}_m])^{-1}\begin{pmatrix} [d_{mv}] & [d_{me}] & [d_{PA}] & [d_{PM}] & [d_{PG}] \end{pmatrix}$$

Coupling between mass flux and power

Volume-specific power to
assimilation $[E_m]\dot{\nu}f$, maintenance $[E_m]\dot{m}g$ and growth $[E_m]g\frac{\dot{\nu}e-\dot{m}g}{e+g}$

Example: oxygen uptake

$$(d_{mx}[\dot{I}_m]X_1)^{-1}\frac{d}{dt}O = t_{OA}\dot{\nu}f + t_{OM}\dot{m}g + t_{OG}g\frac{\dot{\nu}e - \dot{m}g}{e+g}$$

In equilibrium, where $e = f$ and $\dot{\mu} = \frac{\dot{\nu}f-\dot{m}g}{f+g}$ or $f = g\frac{\dot{\mu}+\dot{m}}{\dot{\nu}-\dot{m}}$

$$(d_{mx}f[\dot{I}_m]X_1)^{-1}\frac{d}{dt}O = t_{OA}\dot{\nu} + (t_{OM}\dot{m} + t_{OG}\dot{\mu})\frac{\dot{\nu}-\dot{\mu}}{\dot{m}+\dot{\mu}} = {}_mY_O$$

In general:

$$\mathbf{t}_M\begin{pmatrix}\dot{\nu}\\ \dot{m}\frac{\dot{\nu}-\dot{\mu}}{\dot{m}+\dot{\mu}}\\ \dot{\mu}\frac{\dot{\nu}-\dot{\mu}}{\dot{m}+\dot{\mu}}\end{pmatrix} = \mathbf{Y}_M \quad \text{and} \quad \mathbf{t}_D\begin{pmatrix}\dot{\nu}\\ \dot{m}\frac{\dot{\nu}-\dot{\mu}}{\dot{m}+\dot{\mu}}\\ \dot{\mu}\frac{\dot{\nu}-\dot{\mu}}{\dot{m}+\dot{\mu}}\end{pmatrix} = \mathbf{Y}_D \quad \text{with}$$

$$\mathbf{t}_M \equiv \begin{pmatrix} t_{CA} & t_{CM} & t_{CG}\\ t_{HA} & t_{HM} & t_{HG}\\ t_{OA} & t_{OM} & t_{OG}\\ t_{NA} & t_{NM} & t_{NG}\\ t_{+A} & t_{+M} & t_{+G}\end{pmatrix} \quad \text{and} \quad \mathbf{t}_D \equiv \begin{pmatrix} t_{X_0A} & t_{X_0M} & t_{X_0G}\\ t_{X_1A} & t_{X_1M} & t_{X_1G}\\ t_{EA} & t_{EM} & t_{EG}\\ t_{P_1A} & t_{P_1M} & t_{P_1G}\\ t_{P_2A} & t_{P_2M} & t_{P_2G}\\ \vdots & \vdots & \vdots\end{pmatrix} = \begin{pmatrix} -\dot{\nu}^{-1} & 0 & 0\\ 0 & 0 & t_{X_1}/g\\ t_E & -t_E & -t_E\\ t_{P_1A} & t_{P_1M} & t_{P_1G}\\ t_{P_2A} & t_{P_2M} & t_{P_2G}\\ \vdots & \vdots & \vdots\end{pmatrix}$$

So $\mathbf{t}_M = -\mathbf{u}\mathbf{n}\,\mathbf{t}_D$

Heat dissipation

Define the chemical potentials

$$\tilde{\boldsymbol{\mu}}_M^T \equiv (\ \tilde{\mu}_C \ \ \tilde{\mu}_A \ \ \tilde{\mu}_O \ \ \tilde{\mu}_N \ \ \tilde{\mu}_+\ )$$
$$\tilde{\boldsymbol{\mu}}_D^T \equiv (\ \tilde{\mu}_{X_0} \ \ \tilde{\mu}_{X_1} \ \ \tilde{\mu}_E \ \ \tilde{\mu}_{P_1} \ \ \tilde{\mu}_{P_2} \ \ \cdots\ )$$

Energy balance $0 = \Delta H + \tilde{\boldsymbol{\mu}}_D^T \mathbf{Y}_D + \tilde{\boldsymbol{\mu}}_M^T \mathbf{Y}_M = \Delta H + (\tilde{\boldsymbol{\mu}}_D^T - \tilde{\boldsymbol{\mu}}_M^T \mathbf{un})\mathbf{Y}_D$
Coupling of dissipating heat to power:

$$\begin{aligned}
\Delta H &= \kappa_{HA}\tilde{\mu}_{X_0} + \frac{\kappa_{HM}[\dot{M}]X_1}{d_{mx}[\dot{I}_m]fX_1} + \frac{\kappa_{HG}[G]\frac{d}{dt}X_1}{d_{mx}[\dot{I}_m]fX_1} \\
&= \kappa_{HA}\tilde{\mu}_{X_0} + \frac{\kappa_{HM}[\dot{M}]}{d_{mx}[\dot{I}_m]f} + \frac{\kappa_{HG}[G]}{d_{mx}[\dot{I}_m]f}\,\frac{\dot{\nu}e - \dot{m}g}{e+g} \\
\Delta H/\tilde{\mu}_E &= t_{HA}\dot{\nu} + t_{HM}\frac{\dot{m}g}{f} + t_{HG}\frac{g}{f}\,\frac{\dot{\nu}e - \dot{m}g}{e+g} \\
&= t_{HA}\dot{\nu} + (t_{HM}\dot{m} + t_{HG}\dot{\mu})\frac{\dot{\nu} - \dot{\mu}}{\dot{m} + \dot{\mu}} \quad \text{in equilibrium}
\end{aligned}$$

$\tilde{\mu}_E = [E_m]/[d_{me}]$: the chemical potential of the reserves
$(\ t_{HA} \ \ t_{HM} \ \ t_{HG}\ ) \equiv t_E(\ \kappa_{HA}/\kappa_{EA} \ \ \kappa_{HM} \ \ \kappa_{HG}\ )$: time parameters
$\kappa_{EA} \equiv [\dot{A}_m](d_{mx}[\dot{I}_m]\tilde{\mu}_{X_0})^{-1}$: fraction of energy that has been taken up as substrate that arrives in the reserves as assimilation energy.

$$\tilde{\mu}_E(\ t_{HA} \ \ t_{HM} \ \ t_{HG}\ ) = (\tilde{\boldsymbol{\mu}}_M^T\mathbf{un} - \tilde{\boldsymbol{\mu}}_D^T)\mathbf{t}_D$$

Consider t_{HA}, t_{HM}, t_{HG}, $\tilde{\mu}_{X_1}$ and $\tilde{\mu}_E$ all as free parameters in the regression of measured ΔH as a function of $\dot{\mu}$, with three contraints provided by the energy balance equation.

Obtain the entropy S from measured values of the enthalpy H and the free energy G via Gibb's relationship $H = G - TS$.

Partitionning of power of uptake A, maintenance M and growth G

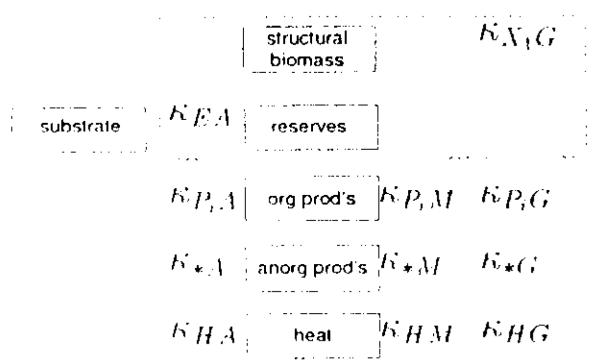
X_0	substrate	X_1	structural biomass
E	energy reserves	P_i	(organic) product i
H	heat	$\tilde{\mu}_*$	chemical potential of $*$
$t_{*_1,*_2}$	time parameter for compound $*_1$ in power $*_2$		

The size of the fluxes depends on substrate density, body size and amount of reserves, but the partitionning κ is fixed

The κ's in vertical direction add to 1

The stippled box indicates the organism

$*$ stands for C, A (aqua), O, N or $+$ (electrical charge)



$$\kappa_{EA} = -\frac{\tilde{\mu}_E t_{EA}}{\tilde{\mu}_{X_0} t_{X_0A}} \qquad \kappa_{X_1G} = -\frac{\tilde{\mu}_{X_1} t_{X_1G}}{\tilde{\mu}_E t_{EG}}$$

$$\kappa_{P_iA} = -\frac{\tilde{\mu}_{P_i} t_{P_iA}}{\tilde{\mu}_{X_0} t_{X_0A}} \qquad \kappa_{P_iM} = -\frac{\tilde{\mu}_{P_i} t_{P_iM}}{\tilde{\mu}_E t_{EM}} \qquad \kappa_{P_iG} = -\frac{\tilde{\mu}_{P_i} t_{P_iG}}{\tilde{\mu}_E t_{EG}}$$

$$\kappa_{*A} = -\frac{\tilde{\mu}_* t_{*A}}{\tilde{\mu}_{X_0} t_{X_0A}} \qquad \kappa_{*M} = -\frac{\tilde{\mu}_* t_{*M}}{\tilde{\mu}_E t_{EM}} \qquad \kappa_{*G} = -\frac{\tilde{\mu}_* t_{*G}}{\tilde{\mu}_E t_{EG}}$$

$$\kappa_{HA} = -\frac{\tilde{\mu}_E t_{HA}}{\tilde{\mu}_{X_0} t_{X_0A}} \qquad \kappa_{HM} = -\frac{\tilde{\mu}_E t_{HM}}{\tilde{\mu}_E t_{EM}} \qquad \kappa_{HG} = -\frac{\tilde{\mu}_E t_{HG}}{\tilde{\mu}_E t_{EG}}$$

Disentangling reserves from structural biomass

$$ {}_mY_{W_1}CH_{n_{HW_1}}O_{n_{OW_1}}N_{n_{NW_1}} = {}_mY_{X_1}CH_{n_{HX_1}}O_{n_{OX_1}}N_{n_{NX_1}} + {}_mY_ECH_{n_{HE}}O_{n_{OE}}N_{n_{NE}} $$

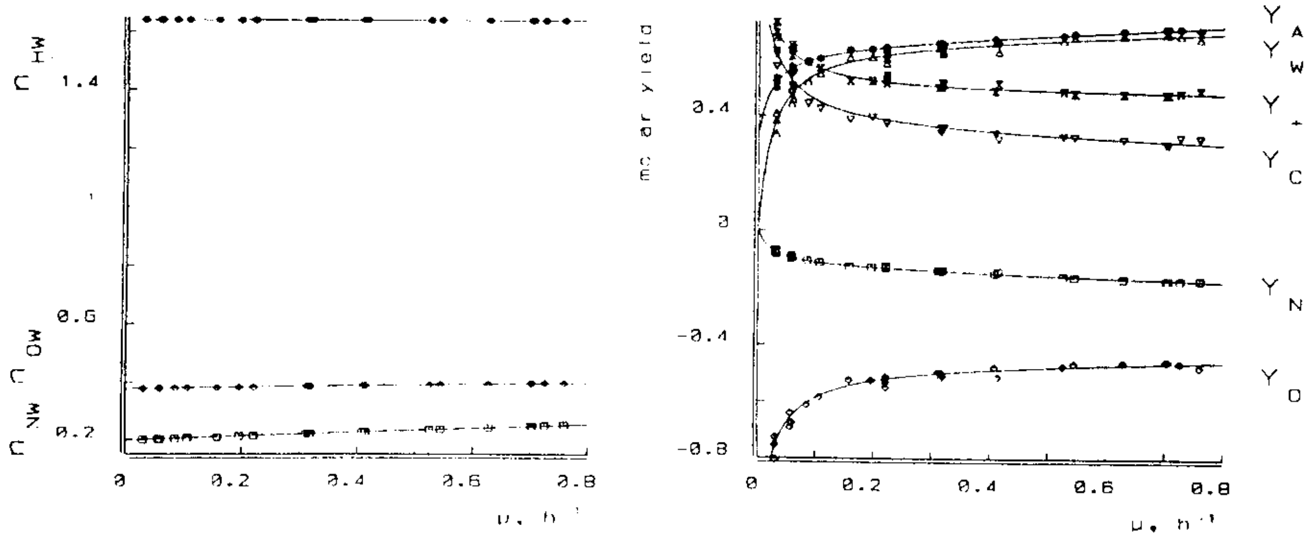
$$ {}_mY_{W_1} = {}_mY_{X_1} + {}_mY_E \quad \text{and} \quad n_{*W_1} = {}_mY_{W_1}^{-1}({}_mY_{X_1}n_{*X_1} + {}_mY_En_{*E}) $$

$*$ stands for H, O, N or $+$

$$ {}_mY_{W_1} = t_{W_1A}\dot{\nu} + (t_{W_1M}\dot{m} + t_{W_1G}\dot{\mu})\frac{\dot{\nu} - \dot{\mu}}{\dot{m} + \dot{\mu}} $$

$$ \text{with } \left(t_{W_1A} \;\; t_{W_1M} \;\; t_{W_1G} \right) = \left(t_{X_1A} \;\; t_{X_1M} \;\; t_{X_1G} \right) + \left(t_{EA} \;\; t_{EM} \;\; t_{EG} \right) $$

So instead of measured ${}_mY_{X_1}$ and ${}_mY_E$ and known n_{*X_1} and n_{*E}
we now have measured ${}_mY_{W_1}$ and n_{*W_1} with n_{*X_1} and n_{*E} to be estimated
The way how n_{*W_1} depends on $\dot{\nu}$ allows decomposition into n_{*X_1} and n_{*E}



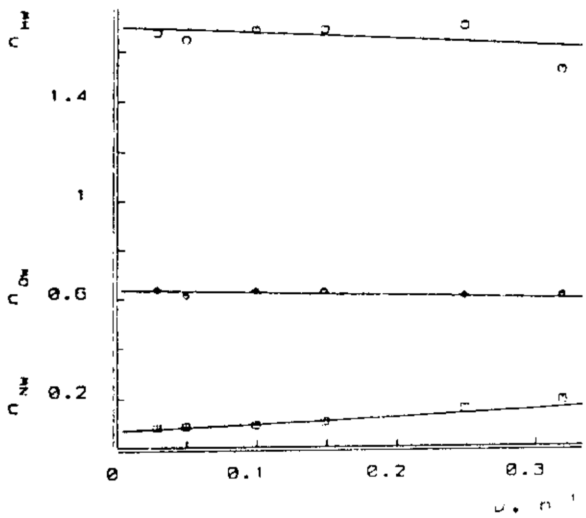
Klebsiella aerogenes growing on glycerol at 35 °C
Data from Esener *et al.* 1983
Given $\dot{\mu}_m = 1.2$ h^{-1} and $f_0 = 0.01$, the estimated parameters are

$\dot{\nu}$ = 2.7 (3.7) h^{-1}	g = 1.2 (3.1)	$\dot{m}$ =0.022 (0.00064) h^{-1}
t_{X_1} = 0.29 (0.34) h	t_E = 0.31 (0.34) h	
n_{HX_1}= 1.641 (0.0038)	n_{OX_1}= 0.38 (0.0038)	n_{NX_1}= 0.195 (0.0026)
n_{HE} = 1.646 (0.008)	n_{OE} = 0.43 (0.63)	n_{NE} = 0.36(0.17)

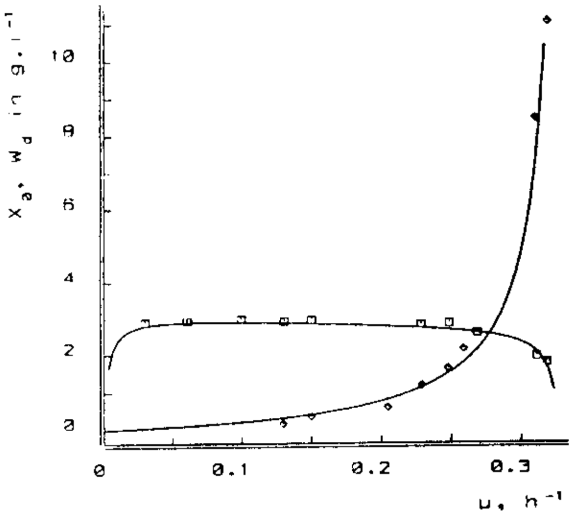
Fermentation

$_mY_O = 0$ for all μ or $\mathbf{0}^T = (\ t_{OA}\ \ t_{OM}\ \ t_{OG}\ )$

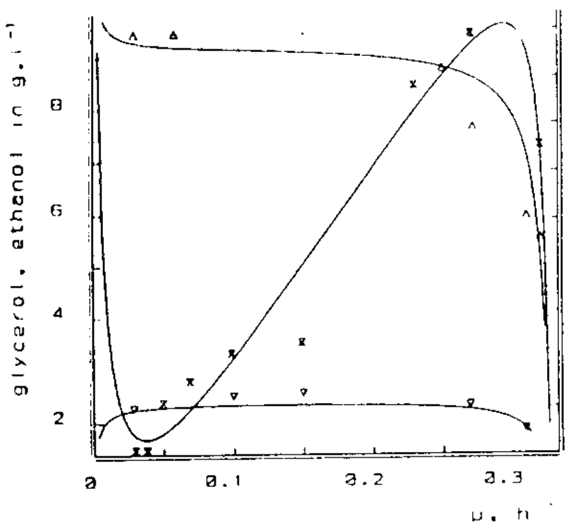
Relative abundances of the elements H (o), O (◇) and N (□) in the biomass.



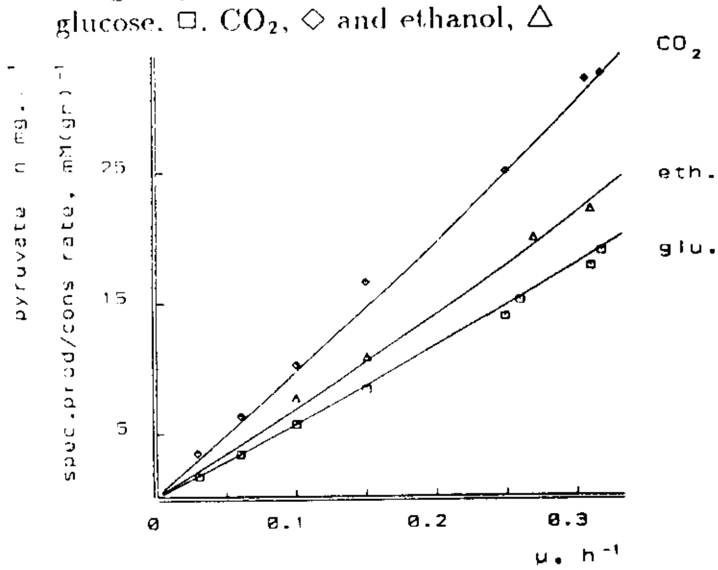
Densities of substrate (glucose, ◇) and biomass (dry weight, □)



Densities of products ethanol, △, glycerol, ▽, pyruvate, ⊠



Weight-specific consumption/prod. rates of glucose, □, CO_2, ◇ and ethanol, △



Saccharomyces cerevisiae growing anaerobically on glucose ($X_r = 30$ g l^{-1}) at 30 °C
Maximum throughput rate is 0.31 h^{-1}. Data from Schatzmann 1975.

ν = 0.461 (0.008) h^{-1}	g = 0.385 (0.022)	m = 0.0030 (0.0007) h^{-1}
t_{X_1} = 0.098 (0.001) h	t_E = 0.211 (0.006) h	K = 1.79 g l^{-1}
n_{HX_1} = 1.70 (0.011)	n_{OX_1} = 0.637 (0.011)	n_{NX_1} = 0.071 (0.011)
n_{HE} = 1.55 (0.022)	n_{OE} = 0.572 (0.020)	n_{NE} = 0.205 (0.021)
ethanol	glycerol	pyruvate
t_{P_1A} = 1.698 (0.011) h	t_{P_2A} = 1.561 (0.022) h	t_{P_3A} = 0.0066 (0.00004) h
t_{P_1M} = 0.637 (0.011) h	t_{P_2M} = 0.572 (0.020) h	t_{P_3M} = 0.0013 (0.0018) h
t_{P_1G} = 0.071 (0.011) h	t_{P_2G} = 0.205 (0.021) h	t_{P_3G} = −0.0077 (0.00006) h

Isomorphs in chemostats

t	time	e	scaled reserves
$n(t, e, l) de\, dl$	frequency	l	scaled length
$N\mathcal{E}\underline{l}^2$	total surface area	$\{\dot{I}_m\}V_m^{2/3}$	max ingestion rate
$\dot{p}$	throughput rate	$\dot{h}$	hazard rate
X_0	resource level	X_r	resource level in the feed
$\dot{R}$	reproduction rate	a_b	embryonic period

Change in resources with $N\mathcal{E}\underline{l}^2(t) = \int_0^1 \int_0^1 l^2 n(t, e, l)\, dl\, de$

$$\frac{d}{dt}X_0 = \dot{p}(X_r - X_0) - \{\dot{I}_m\}V_m^{2/3}\frac{X_0}{K + X_0}N\mathcal{E}\underline{l}^2$$

Change in frequency (von Foerster)

$$\frac{\partial}{\partial t}n(t, e, l) = -\frac{\partial}{\partial l}\left(n(t, e, l)\frac{d}{dt}l\right) - \frac{\partial}{\partial e}\left(n(t, e, l)\frac{d}{dt}e\right) - (\dot{p} + \dot{h}(e, l))n(t, e, l)$$

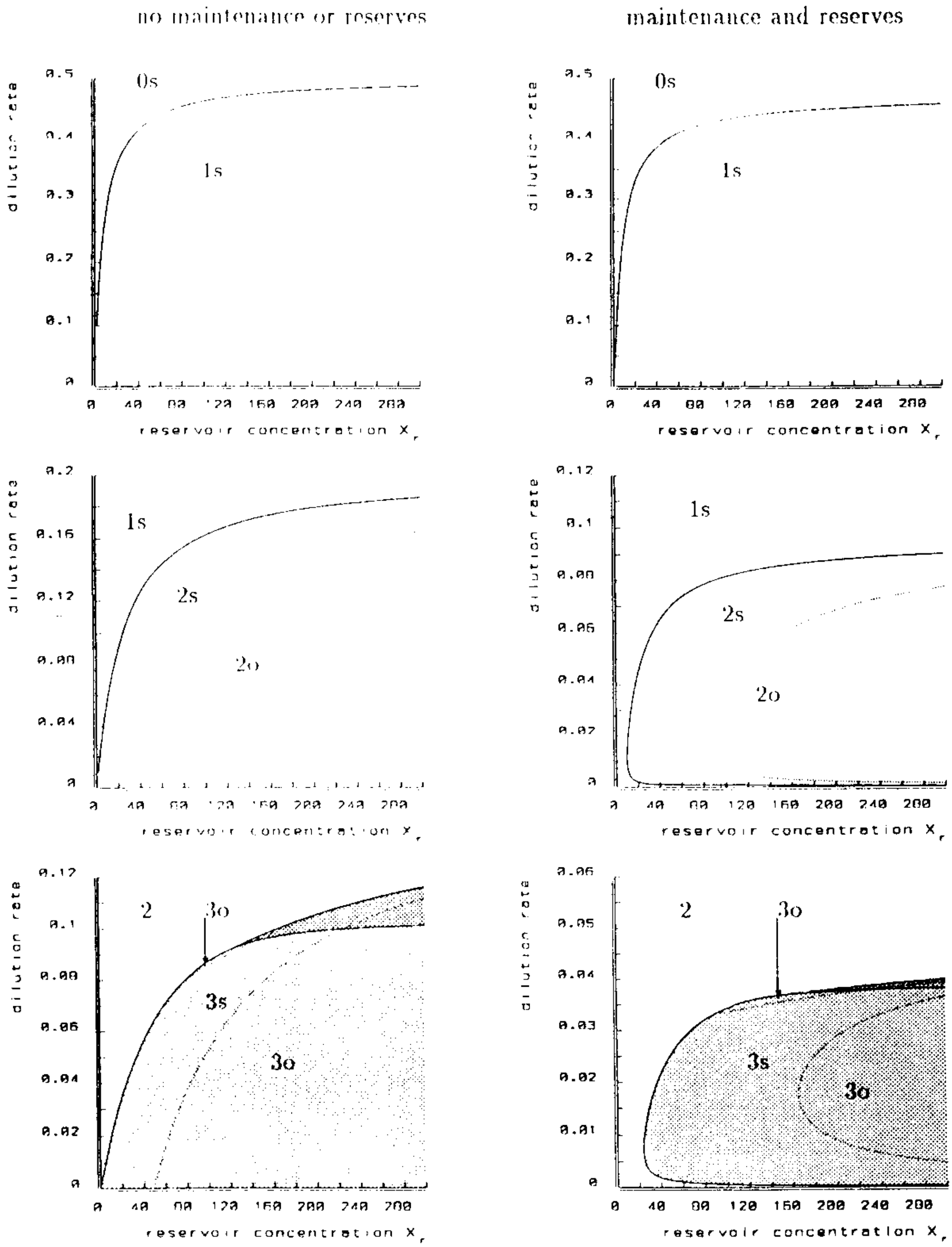
Boundary condition for **dividers** $\quad l_b = l_d 2^{-1/3}$

$$n(t, e, l_b)\left.\frac{d}{dt}l\right|_{l=l_b} = 2n(t, e, l_d)\left.\frac{d}{dt}l\right|_{l=l_d}$$

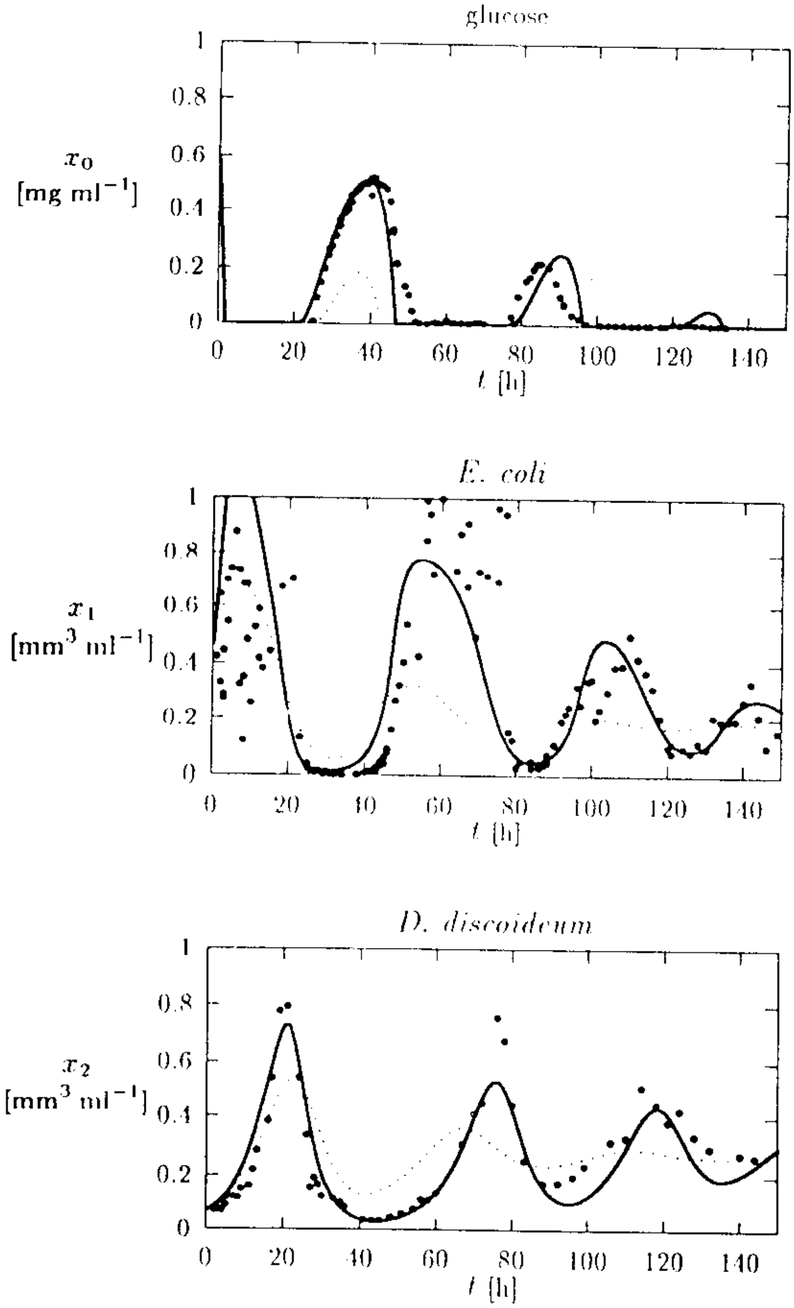
Boundary condition for **reproducers**

$$n(t, e, l_b)\left.\frac{d}{dt}l\right|_{l=l_b} = \int_l \dot{R}(e, l)n(t - a_b, e, l)\, dl$$

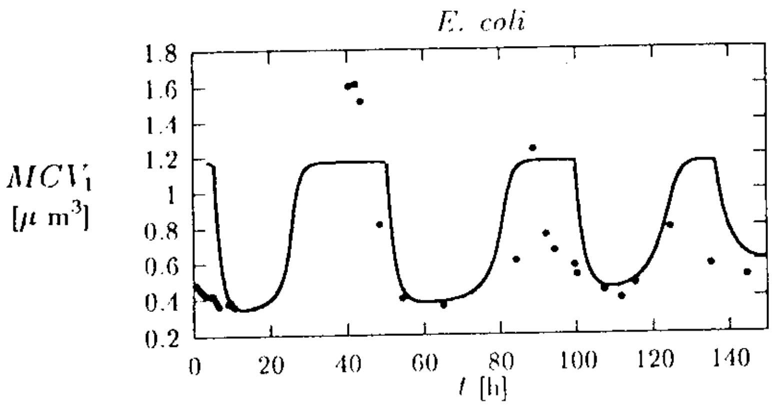
stability in chemostats with food chains of length 2, 3, 4

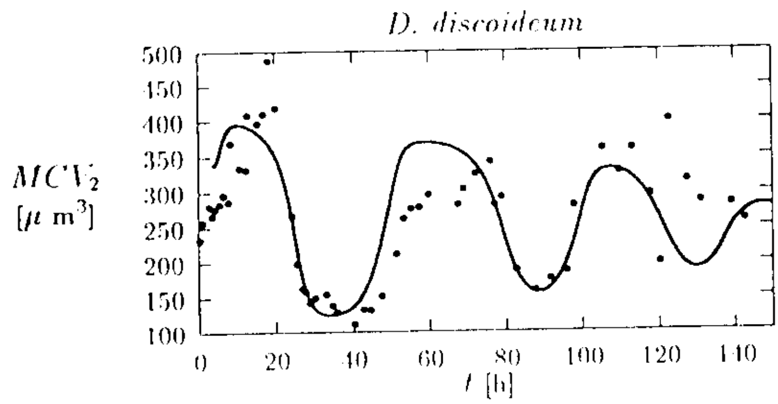


DEBf


glucose
x_0 [mg ml^{-1}]
t [h]
E. coli
x_1 [mm^3 ml^{-1}]
t [h]
D. discoideum
x_2 [mm^3 ml^{-1}]
t [h]

Mean cell size





mass and energy cycle in a community