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COURSE ON "MEDITERRANEAN SEA(S) CIRCULATION & ECOSYSTEM FUNCTIONING"

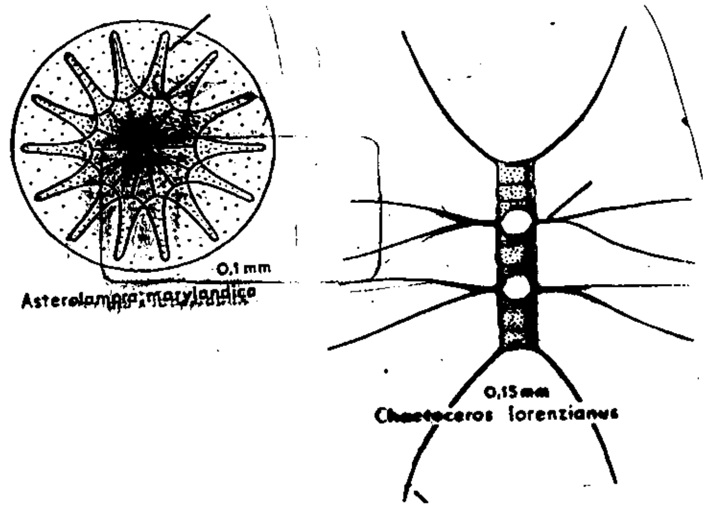
2 - 20 November 1998

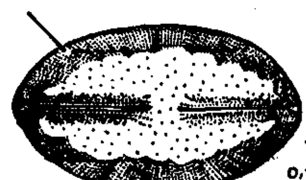
Trieste, Italy

"Secondary Production"

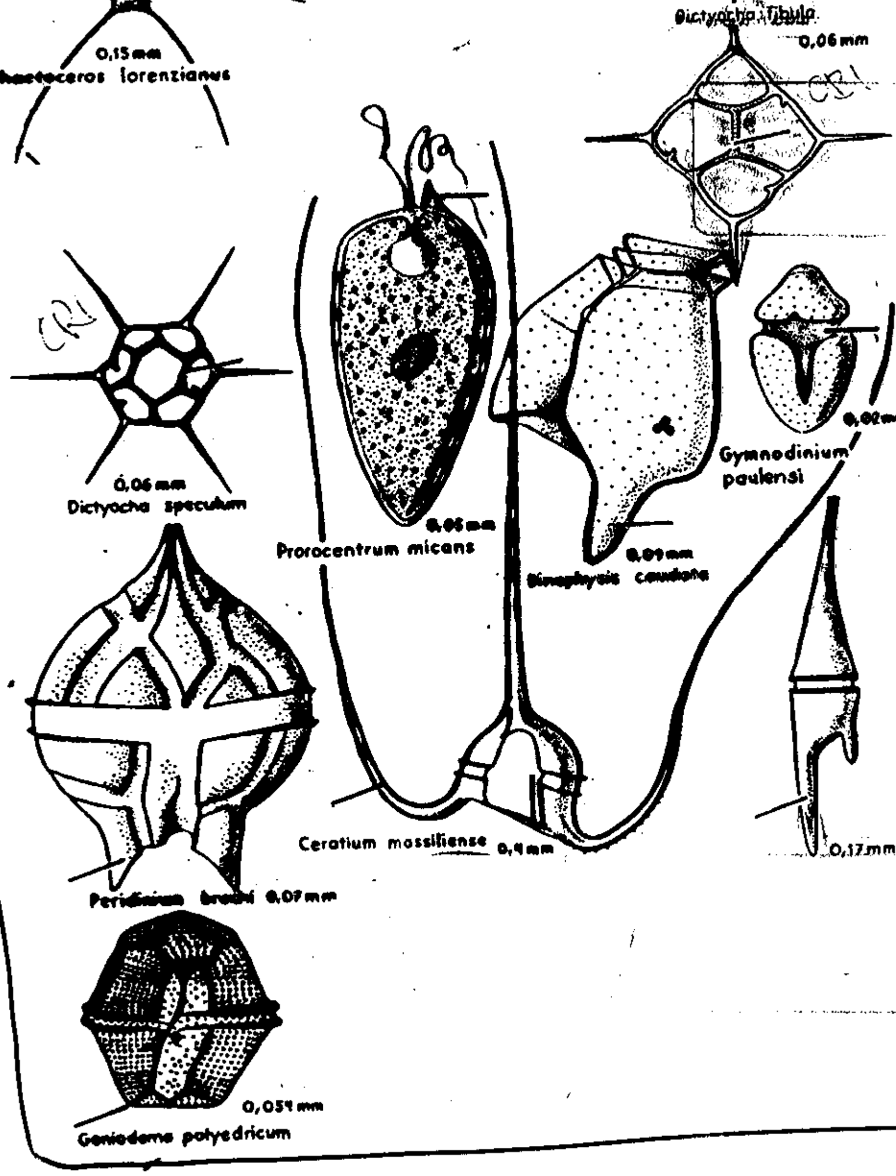
G. BENDORICCHIO
University of Padua
Italy

DIATOMEE (FITOP.)

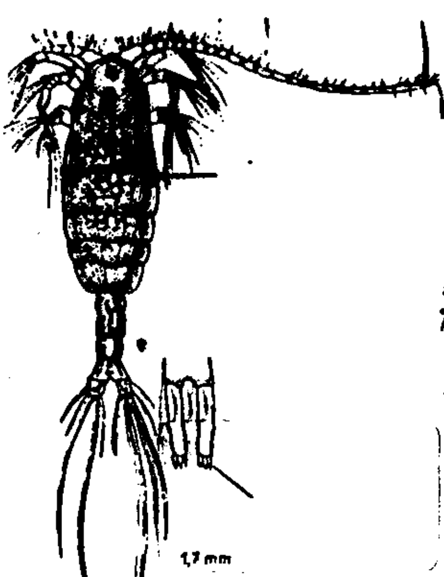


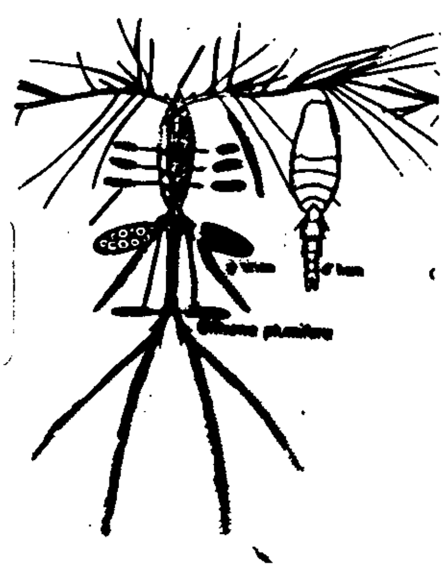


DINOFICEE (FITOP.)

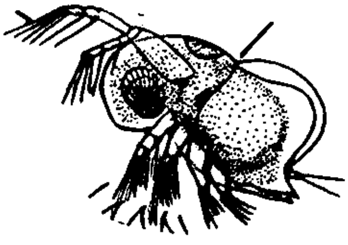


COPEPODI (ZOOP.)





CLADOCERI (ZOOP.



ZOOPLANKTON

$$
\begin{tikzcd}
 & \boxed{\text{Nut}} \arrow[dl, "\text{uptake}"'] & \\
\boxed{\text{Plank}} \arrow[rr, "\text{grazing}"'] & & \boxed{\text{Zoopl}} \arrow[ul, "\text{excretion}"']
\end{tikzcd}
$$

Interrelationships important for long-term simulations in lakes and estuaries

Zoop. Models

* simple constituent (Tot. zoop biomass)

* functional groups
    - feeding types
      herbivores, carnivores, omnivores, selective & non selective filter feeders.
    - Taxonomic groups
      cladocerans, copepods, rotifers.

ZOOPLANKTON DYNAMICS

$$\frac{dZ}{dt} = (g_z - r_z - m_z)Z - G_z \qquad (1)$$

Z zoop. biomass or equivalent nutrient mass

g_z gross growth rate (1/t)

r_z respiration + excretion rate (1/t)

m_z non predatory mortality rate

G_z ~~loss rate~~ due to predation (mass/t)

(settling is not important because zoop. is mobile)

(1) is for population as biomass pool
but some models use a partition
in age classes

Temperature is accounted, as for phytoplankton
usually ~~with~~ an optimum curve and
on a max and min lethal limits.

TABLE 7-1. GENERAL COMPARISON OF ZOOPLANKTON MODELS

Model (Author)	Number of Groups			Zooplankton Processes Computed Separately in Model				Zooplankton Units			Reference
	Zoo-plankton	Phyto-plankton	Fish	Growth	Respiration	Nonpredatory Mortality	Predatory Mortality	Dry Wt. Biomass	Carbon	Other Nutrient	
AQUA-IV	1	1		X	X	X			X		Baca & Arnett (1976)
CE-QUAL-R1	1	2	3	X	X	X	X	X			WES (EWQOS) (1982)
CLEAN	3	2	3	X	X	X	X	X			Bloomfield et al. (1973)
CLEANER	3	3	3	X	X	X	X	X			Scavia & Park (1976)
MS.CLEANER	5	4	8	X	X	X	X	X			Park et al. (1980)
EAM	3	4	20	X	X	X	X	X			Tetra Tech (1979, 1980)
ESTECO	1	2	3	X	X	X	X	X			Brandes & Masch (1977)
EXPLORE-1	1	1		X	X	X			X		Baca et al. (1973)
HSPF	1	1		X	X	X		X			Johanson et al. (1980)
LAKECO	1	2	3	X	X	X	X	X			Chen & Orlob (1975)
MIT Network	1	1		X	X	X				N	Harleman et al. (1977)
WASP	2	2		X	X	X	X		X		Di Toro et al. (1981)
WQRRS	1	2	3	X	X	X	X	X			Smith (1978)
Bierman	2	5		X	X	X		X			Bierman et al. (1980)
Canale	9	4		X	X	X	X		X		Canale et al. (1975, 1976)
Jorgensen	1	1	1	X	X	X	X	X			Jorgensen (1976)
Scavia	6	5		X	X	X	X		X		Scavia et al. (1976)

ZOOP GROWTH

Growth represents increases in the biomass due to reproduction and growth of individuals

Growth depends on the amount of food ingested and assimilated.

Ingestion rate & assimilation efficiencies vary according to:

* Zoop factors: species, age, size, feeding type, sex, reproductive state, physiological or nutritional state

* Food concentration, type, particle size, quality, desirability

* Temperature

ZOOP. MOD

SIMPLE MOD

$$g_z = C_g \, E$$

C_g ingestion (or grazing) rate (mass food/mass zoop time)

For filter feeders

$$C_g = C_f \, F_T$$

C_f filtration rate (water vol/mass zoop time)

F_T total food concentration (mass/vol)

E assimilation efficiency (adim)

SOPHISTICATED MOD

$$g_z = C_{g\,max}(T_{ref}) \; E_{max}(T_{ref}) \; f(T) \; f_g(F_1, \dots, F_n)$$

for filter feeders $C_{f\,max}(T_{ref}) \, F_T$ $\qquad$ $f_f(F_1, \dots, F_n)$

in some models

$C_{g\,max}$ & E_{max} are combined in g_{max}

GROWTH LIMITATION

predators

At low food conc. zoop ingestion rates increase in the food supply since less energy ~~expenditure~~ are required to find and capture prey ~~items~~ as the prey density increases

At abundant food the zoop ingestion rates become saturated

~~filters feeders~~

- ~~grazing rates~~ is directly proportional to the food concentration.
- regulate the ingestion rates at high food levels reducing the filtering rates

MODELS saturation response curve

$$f_g(F_1,\dots,F_n) = \begin{cases} \dfrac{F_T}{K_Z + F_T} & \text{(Michaelis Menten)} \\ 1 - e^{-KF_T} & \text{(Ivlev)} \end{cases}$$

at very low conc. zoop do not feed

F_T can be modified $F_T - F_0$

F_0 conc food below which feeding does not

GROWTH LIMITATION

For filtration form

In ~~con contrast~~ with the previous functions the limitation growth functions for filter feeders generally decrease with increases in the food concentration

$$f_f(F_1, \dots, F_n) = 1 - \frac{F_T}{F_T + K_F} = \frac{K_f}{F_T + K_f}$$

FOOD SUPPLY.

$$F_T = \sum_{K=1}^{n} F_K$$

F_K conc of potential food item K (mass/vol)

Zoop. has preference for some items

$$F_T = \sum_{K=1}^{n} p_K F_K$$

p_K food preference factor for food item K.

MAXIMUM RATES

Zoop. Group	INGESTION (1/day)	FILTRATION	GROTW (1/day)	ASSIMIL. effic.	M·M ½ SAT INGEST (mg/l)
TOTAL	0.3 – 0.8	0.1 – 1.0 1/mg C-day	0.1 – 0.3	0.6	0.5 – 2.0
OMNIVORES	0.4 – 1.4		–	0.6	0.3
HERBIVORES	–	0.7 – 1.4 1/mg C-day	–	0.6	0.01 – 0.015 mg(Chl a)/l
CARNIVORES	0.7 – 1.6	1.0 – 3.9 1/mg C-day	–	–	0.02 – 0.2
COPEPODS	1.7 – 1.8	0.1 – 6.0	0.5	–	1
ROTIFER	1.8 – 2.2	0.6 – 1.5	0.4 – 0.7	0.5	0.5
Mysidis	1.0 – 1.2		0.1	0.5	0.5
CLADOCERANS	1.6 – 19	0.2 – 16 ~~1/mg~~ DW-day	0.1 – 0.7	0.5	0.5 – 1.8

ASSIMILATION EFFICIENCY

The assimilation efficiency for different food types varies with the energy content, digestibility and quality of the food

MODELS

* can be incorporated in the food preference factors
* to define different maximum assimilation efficiencies for different food items

$$g_z = C_{gmax} \sum_{k=1}^{n} \left[E_{max\,k} \, f_{fk}(F_1, \ldots, F_n) \right]$$

or $$g_z \; C_{fmax} \, f_f(F_1, \ldots, F_n) \sum_{k=1}^{n} \left[E_{max\,k} \, p_k F_k \right]$$

Almost all models represent both respiration & non predatory mortality rates as

* constant coefficients
* simple functions of temperature

$$r_z = r_z(T_{ref})\, f_r(T)$$

$$m_z = m_z(T_{ref})\, f_m(T)$$

or

$$r_z + m_z = d_z(T_{ref})\, f_2(T)$$

Other more complicate models account for senescence, thermal mortality, toxic mortality, low dissolved oxigen

PREDATORY MORTALITY

- If zoop. is the highest trophic level

* G_2 = constant

* $G_2 = e_2 Z$ or $G_2\, e_z(T_{rof}) f_e(T) Z$

* non-predatory & predatory mortality are combined

$$m_{tot} = \left[m_2(T_{rof}) + e_2(T_{rof})\right] f_m(T)$$

If ~~higher~~ trophic levels are ~~present~~ simulated in the model

zoop. is divided in several functional groups

$$G_{z_i} = \sum_{j=1}^{n_p} \left[C_j X_j \frac{p_{ij} Z_i}{\sum_{k=1}^{n_f} p_{kj} f_{kj}} \right]$$

G_{z_i} total pred mort. rate for zoop. group i

n_p total number of zoop. consumers (higher Troph. lev)

C_j tot consp. rate by predator group j

X_j biomass or conc. of predator group j

p_{ij} food preference factor for pred group j feeding zoop

— — — (0.5.0)

FISH GROWTH

Fish growth depends on specimen and environment.

Growth is in relation to

- age
- Temperature
- ration
- body size

Earlier model have seen empirical

logistic Gompertz Johnson Richard	best fit without meaning of the parameters

FACTORS INFLUENCING THE G.

INTRINSIC
- Fish species
- Race
- Fish size
- Swimming activity
- Maturity
- Age

EXTRINSIC

ABIOTIC
- Photoperiod
- Temperature
- O_2 content of the water
- pH
- CO_2
- Toxic substances
- Salinity
- Light intensity

BIOTIC
- Diets
- Ration
- feeding frequency
- care
- diseases
- social hierarchy

METABOLIC MODEL

The basis for animal life and growth is the ~~fore~~ description of the food consumed the usual way to measure are energy units

FOOD CONSUMED (C)

→ FAECAL LOSS (F)

ASSIMILATED MATERIALS

→ Apparent Specific Dynamic Action
Absorption + digestion + Transportation + deposition of food + SDA (R_d)

→ Excretional loss (U)
urine + gills + skin

METABOLIZABLE MATERIALS

BASAL METABOLISM (R_s)

GROWTH (B)

ACTIVITY (R_a)

$$C = F + U + B + R$$

$$R = R_s + R_d + R_a$$

$$w(t+\Delta t) = w(t) + IN - OUT$$

w = weight

Δt = 1 day usually

matter measured in energy or matter

wet weight – dry weight – caloric content

$$IN = \Delta\xi(t) = \xi(t+\Delta t) - \xi(t)$$

$$\boxed{\xi = \text{food}}$$

$$OUT = \Delta w_{fasting} + (1-\beta)\Delta\xi + \alpha\beta\Delta\xi$$

Fasting catabolism (loss due to metabolic processes)

undigested food

energy costs to feed

$$\Delta w = \Delta\xi - (1-\beta)\Delta\xi - \alpha\beta\Delta\xi - \Delta w_{fasting}$$

$$\stackrel{!}{=} \beta(1-\alpha)\Delta\xi - \Delta w_{fasting}$$

$$\Delta w_{fasting} = K\, w(t)^{n}\, \Delta t$$

K coef. of fasting catabolism

n expon. of fasting catabolism.

FG 5

$$\Delta \xi = f\, h\, w(t)^m\, \Delta t$$

acceptable for short Δt

f = feeding level $0 < f < 1$

interaction with environment

m = exponent for food consumption

$$\Delta w = \beta(1-\alpha)\, f\, h\, w(t)^m\, \Delta t - K\, w(t)^n\, \Delta t$$

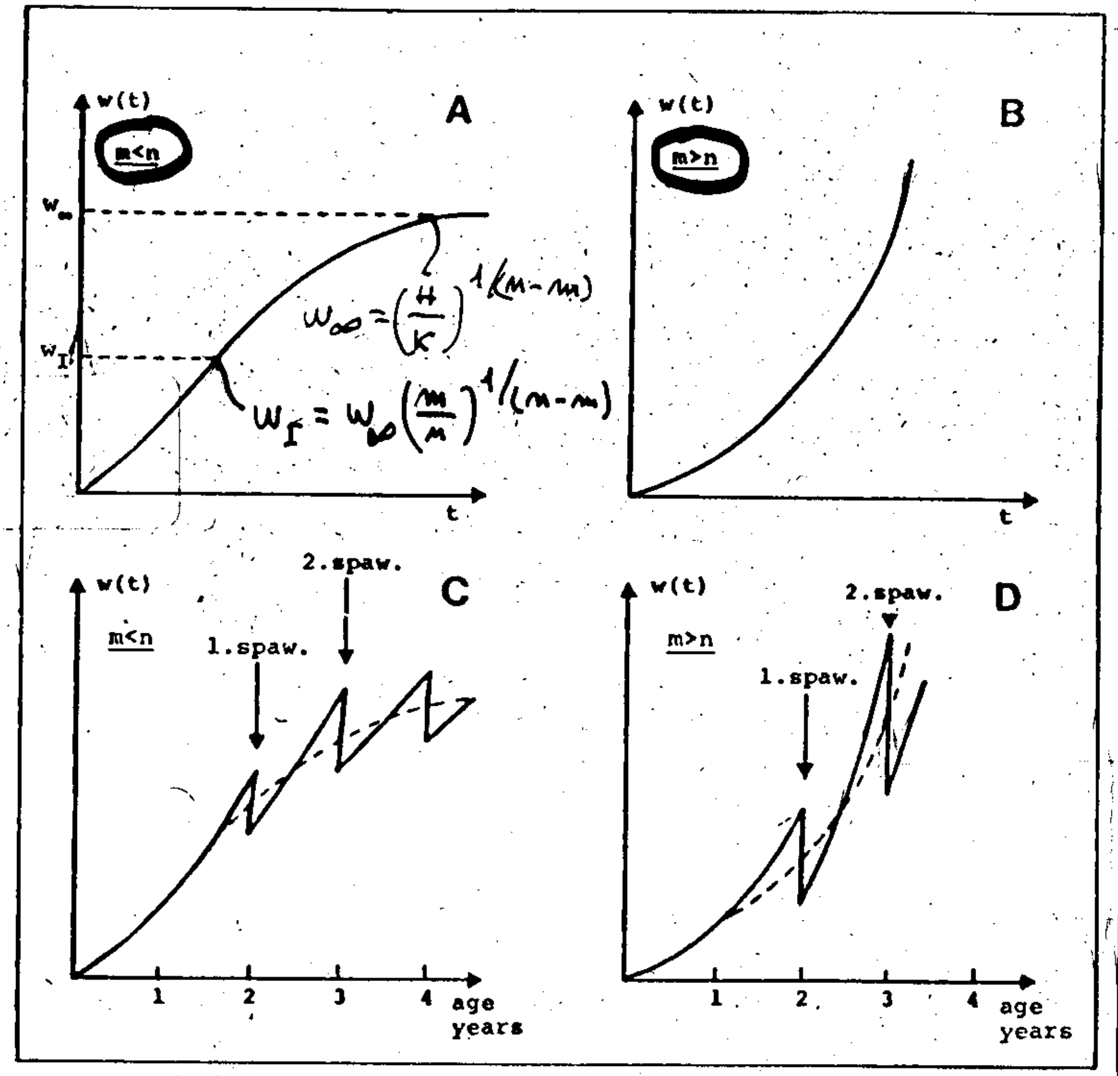
$$\frac{dw}{dt} = \beta(1-\alpha)\, f\, h\, w^m - K w^n$$

URSIN METABOLIC MODEL

If the parameter α, β, f, h, K are assumed to remain approximately constant

$$\frac{dw}{dt} = H w^m - K w^n$$

FG 6



B e D ~~et~~ only for species with
1 o 2 spawing in life

von BERTALANFFY Model

$$\boxed{\frac{dw}{dt} = H} w^{2/3} - K w$$

$m = 2/3$ area of the interface is proportional to $w^{2/3}$

$n = 1$ fasting is assumed proportional to the body weight

$$w(t) = w_\infty \left(1 - \exp\left(-\bar{K}(t - t_0)\right)\right)^3$$

$$w_\infty = \left(\frac{H}{K}\right)^3 , \quad \bar{K} = \frac{K}{3}$$

$$w(t) = q\, \ell(t)^3$$

q constant $\rightarrow$ condition factor $q = \boxed{0.01\ g/cm^3}$

$$\frac{d\ell}{dt} = \frac{H}{3q^{\frac{1}{3}}} - \frac{K}{3}\ell$$

$$\ell(t) = L_\infty \left(1 - \exp\left(-\bar{K}(t - t_0)\right)\right)$$

$$L_\infty = \frac{H}{Kq^{\frac{1}{3}}} \qquad \bar{K} = \frac{K}{3}$$

$t_0 = 0$

GROWTH MODELS

GOMPERTZ

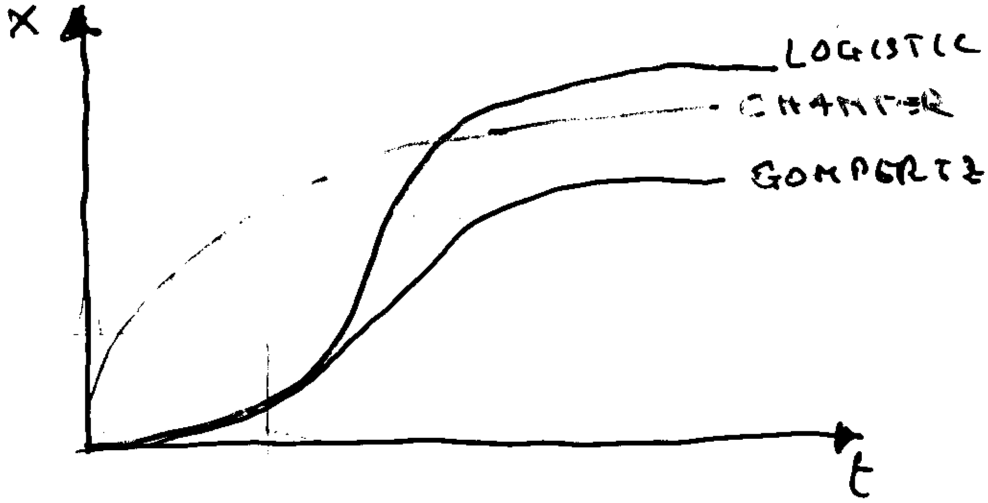
$$\begin{cases} \dfrac{dx}{dt} = r x \\[2ex] \dfrac{dr}{dt} = -D r \end{cases}$$

$$x = x_0 \, e^{\left(\frac{r_0}{D}\left(1 - e^{-Dt}\right)\right)}$$

CHANTER

$$\frac{dx}{dt} = r \cdot x \left(1 - \frac{x}{B}\right) e^{-Dt}$$

$$x = x_0 \, e^{-\left(\frac{r_0}{D}\left(1 - e^{-Dt}\right)\right)}$$



EXAMPLE 2.4.a

Logistic growth

the unlimited growth of a population Ex 2.2 $\alpha > 0$ is not always possible because of some limits the logistic (limited) growth is described by

$$\frac{dx}{dt} = r x \left(\frac{K - x}{K} \right) \qquad (1)$$

x is the number of individual
r is the grow rate (in unlimited conditions)
$\frac{K-x}{K}$ is the limitation term

K is the carrying capacity of the environment

when $x \simeq 0$ (1) is $\frac{dx}{dt} = rx$ exp growth

when $x = K$ (1) is $\frac{dx}{dt} = 0$ steady state sol (birth = death)

the max velocity of growth is when $x = \frac{K}{2}$

in fact: $\frac{d^2x}{dt^2} = \frac{d}{dt}\left(rx - \frac{r}{K} x^2 \right) = r - \frac{2r}{K} x$

$\frac{d^2x}{dt^2} = 0 \Rightarrow x = \frac{K}{2}$

EXAMPLE 2.4 :

(1) can be written as

$$\frac{1}{x\left(\frac{K-x}{K}\right)}\frac{dx}{dt} = r$$

$$\boxed{\begin{aligned}\frac{1}{x\,\frac{K-x}{K}} &= \frac{1}{x}\cdot\frac{K}{K-x} \\ &= \frac{K}{x(K-x)} = \frac{(K-x)+x}{x\,(K-x)} \\ &= \frac{1}{x} + \frac{1}{K-x}\end{aligned}}$$

ODE with separate variables

$$\int\left(\frac{1}{x}+\frac{1}{K-x}\right)dx = \int r\,dt$$

$$\ln|x| - \ln|K-x| = rt + c_1$$

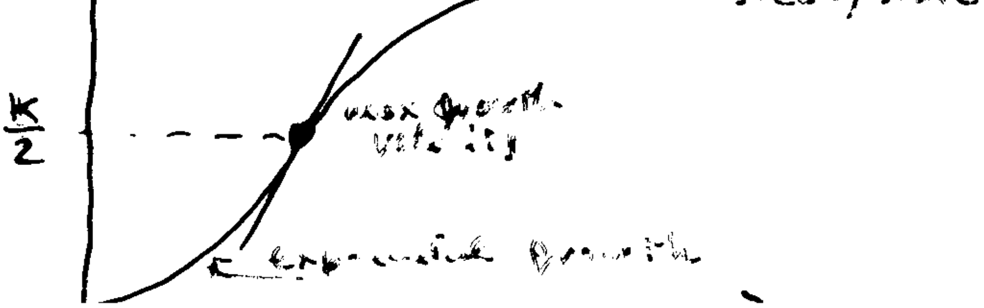
$$\ln\left|\frac{x}{K-x}\right| = rt + c_1$$

$$-\ln\left|\frac{K-x}{x}\right| = rt + c_1$$

$$\ln\left|\frac{K-x}{x}\right| = -rt - c_1$$

$$\frac{K}{x} - 1 = \frac{K-x}{x} = e^{-rt-c_1} = e^{-rt}\,e^{-c_1} = c\,e^{-rt}$$

$$x = \frac{K}{1+ce^{-rt}}$$



EXAMPLE 2.5

von Bertalanffy equation for the growth of fish species

If w is the weight of the fish
H, and K are constant
the von Bertalanffy eq. is written

$$\frac{dw}{dt} = \underbrace{H w^{\frac{2}{3}}}_{\text{anabolism}} - \underbrace{K w}_{\text{catabolism}}$$

the exponent $\frac{2}{3}$ ensures that area of the intestine is proportional to the surface area and thereby to weight to the power $\frac{2}{3}$

By substitution $w = x^3$ we get

$$3x^2 \frac{dx}{dt} = H x^2 - K x^3 \Rightarrow \frac{dx}{dt} = -\frac{K}{3} x + \frac{H}{3} = -\frac{K}{3}\left(x - \frac{H}{K}\right)$$

after Ex. 2.3.a
$$w = \left(\frac{H}{K} + c e^{-\frac{K}{3}t}\right)^3$$
$c<0$ because w increases

at steady state (final weight) $w_\infty = \left(\frac{H}{K}\right)^3$

if $w_0 = w(t_0) = 0$

$$w(t) = w_\infty \left(1 - e^{-\frac{K}{3}(t - t_0)}\right)^3$$