CENT'ANNI DI BIOMATEMATICA

un percorso lungo il sentiero
tracciato da Volterra e Lotka

Mimmo Iannelli
Università di Trento

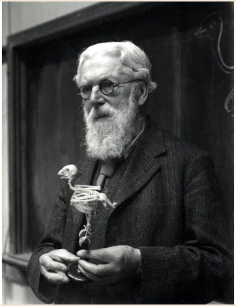
Milano, 21 ottobre, 2024

Qualche anno fa, la ESMTB (European Society for Mathematical and Theoretical Biology), ha celebrato il 2018 come centenario della nascita della Biomatematica. Allora, infatti, si decise che la nascita della disciplina potesse essere identificata con la pubblicazione, nel 1917, della monografia "On Growth and Form" da parte di D'Arcy Thompson.

Cent'anni di Biomatematica

One hundred years ago, in 1917, D'Arcy Thompson published his classic *"On Growth and Form"*. Explaining biological morphology based on physical analogy and mathematical transformations, he was among the first to argue that mathematical theory should have a prominent role in biological explanation. In D'Arcy Thompson's opinion, mathematics described and explained biological morphology more elegantly and efficiently than *"mere words"*.

From: The letter from the president of



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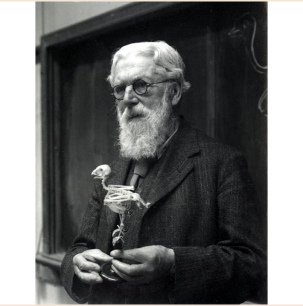

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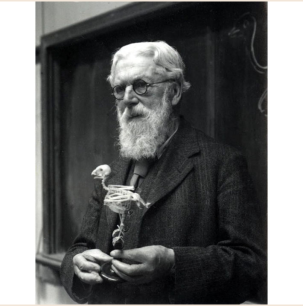

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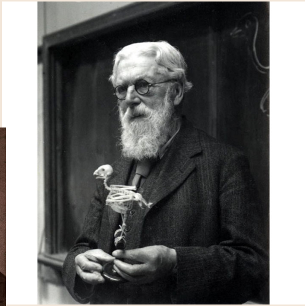

EULERO

BERNOULLI

1202 1760 1917

Cent'anni di Biomatematica

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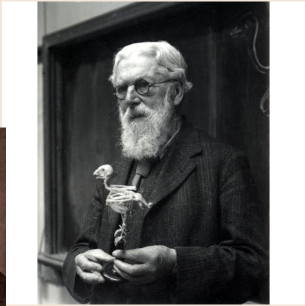

FIBONACCI EULERO BERNOULLI

1202 1760 1917

Cent'anni di Biomatematica

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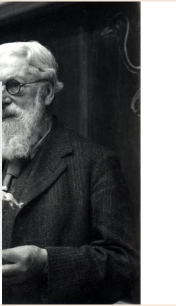
MALTHUS

VERHULST



1202 — 1760 — 1798 — 1838 — 1917

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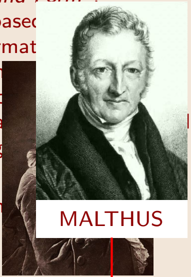

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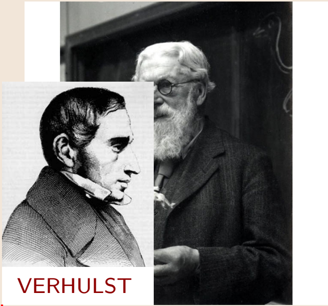


VERHULST

1202 1760 1798 1838 1917 1927

THE GOLDEN AGE

THE GOLDEN AGE

Alfred Lotka

Vito Volterra

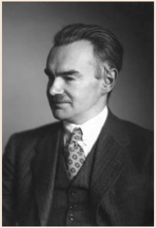
Lotka, A.J. Elements of Mathematical Biology. Dover Publication, New York (1924).

Volterra, V. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi, Mem. della R. Accademia dei Lincei, ser. VI, vol II, 31-113 (1926)

THE GOLDEN AGE

Alfred Lotka

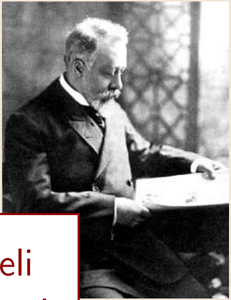
Vito Volterra



W. O. Kermack
A.G. McKendrick

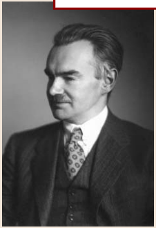
THE GOLDEN AGE

Alfred L



Volterra

due percorsi paralleli
destinati ad incrociarsi



W. O. Kermack
A.G. McKendrick

THE GOLDEN AGE

Vito Volterra
1927

Mi permetto presentare alcuni studi sulla coabitazione di specie in un medesimo ambiente .... Per poter trattare la questione matematicamente conviene partire da ipotesi che, pure allontanandosi dalla realtà, ne diano un'immagine approssimata .... Ecco come può impostarsi la questione: cerchiamo di esprimere con parole come procede all'ingrosso il fenomeno; quindi traduciamo queste parole in linguaggio matematico. Questa traduzione conduce ad equazioni differenziali. Se allora ci lasciamo guidare dai metodi dell'analisi siamo condotti molto più lontani di quanto potrebbero portarci il linguaggio ed il ragionamento ordinario e possiamo formulare delle leggi precise matematiche

THE GOLDEN AGE

Two basic equations (models) for the growth of a single population

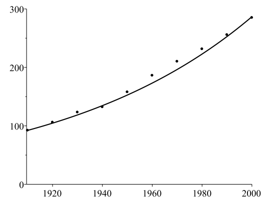
Malthus: $N'(t) = rN(t)$

Verhulst: $N'(t) = r\left(1 - \frac{N(t)}{K}\right) N(t)$

- growth rate: $r = \beta - \mu$
- carrying capacity: K

THE GOLDEN AGE

Two basic equations (models) for the growt



on

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THE GOLDEN AGE

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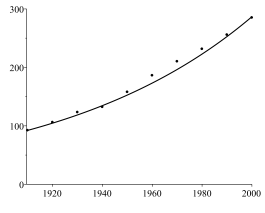


Malthus: $N'(t) = rN(t)$

Verhulst: $N'(t) = r\left(1 - \frac{N(t)}{K}\right) N(t)$

- gro
- car

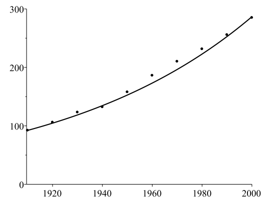
Cette équation étant intégrée donne, en observant que $t=0$ répond à $p=b$,

$$t = \frac{1}{m} \log. \left[\frac{p(m-nb)}{b(m-np)}\right] \quad \ldots\ldots\ldots \quad (4)$$

Nous donnerons le nom de *logistique* à la courbe (*voyez la figure*)

THE GOLDEN AGE

Two basic equations (models) for the growt… on



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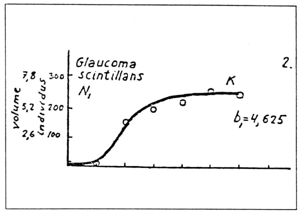


$-\mu$

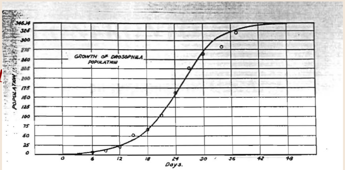


Fig. 5. Growth of a Population of Drosophila (Fruit Flies) under Controlled Experimental Conditions, According to Pearl and Parker

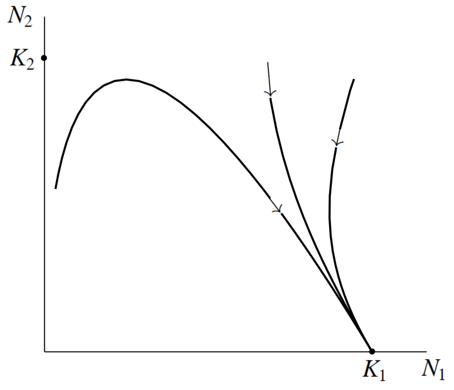
Two prototypes for Ecology

competition
$$\begin{cases} N_1'(t) = r_1\left(1 - \gamma_1(h_1 N_1(t) + h_2 N_2(t))\right) N_1(t) \\ N_2'(t) = r_2\left(1 - \gamma_2(h_1 N_1(t) + h_2 N_2(t))\right) N_2(t) \end{cases}$$

predator-prey
$$\begin{cases} H'(t) = rH(t) - \gamma H(t)P(t) \\ P'(t) = -\mu P(t) + \omega H(t)P(t) \end{cases}$$

Two prototypes for Ecology

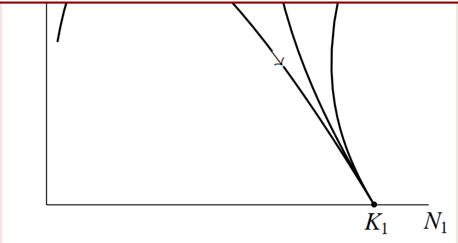
competition: the principle of exclusion



Two prototypes for Ecology

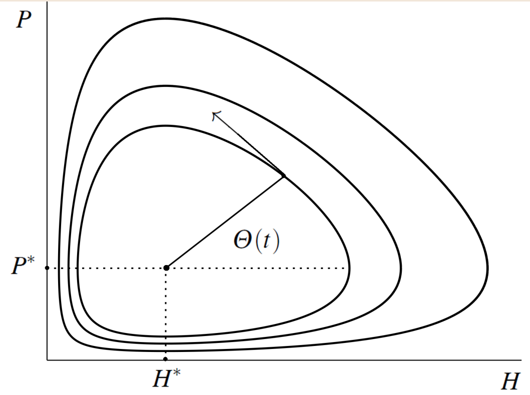
competition: the principle of exclusion

two different species cannot indefinitely occupy the same ecological niche, but one of the two necessarily goes extinct, while the other saturates the niche



Two prototypes for Ecology

predator-prey: periodic fluctuation



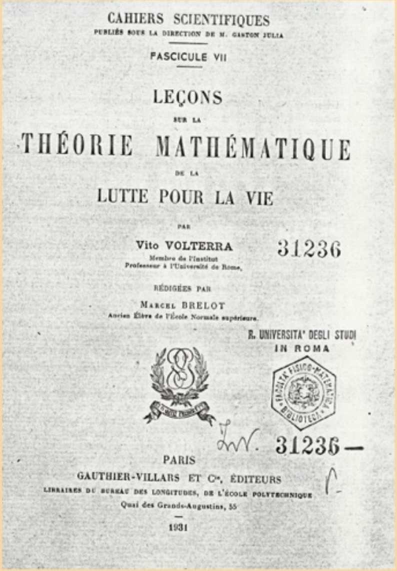
Two prototypes for Ecology

predator-prey: Volterra basic laws

- Law of periodic cycle: the fluctuations of the two species are periodic;
- Law of conservation of averages: the averages of the numbers of the individuals of the two species over a period of time are constant and do not depend upon initial values;
- Law of perturbation of averages: if the two species are uniformly destroyed proportionally to the number of their individuals, the average of the number of individuals of the devoured species increases and the average of the number of individuals of the devouring species decreases.

THE GOLDEN AGE

1931



CAHIERS SCIENTIFIQUES
PUBLIÉS SOUS LA DIRECTION DE M. GASTON JULIA

FASCICULE VII

LEÇONS
SUR LA
THÉORIE MATHÉMATIQUE
DE LA
LUTTE POUR LA VIE

PAR
Vito VOLTERRA
Membre de l'Institut
Professeur à l'Université de Rome.

31236

RÉDIGÉES PAR
MARCEL BRELOT
Ancien Élève de l'École Normale supérieure.

R. UNIVERSITA' DEGLI STUDI
IN ROMA

31236 —

PARIS
GAUTHIER-VILLARS ET C^ie, ÉDITEURS
LIBRAIRES DU BUREAU DES LONGITUDES, DE L'ÉCOLE POLYTECHNIQUE
Quai des Grands-Augustins, 55

1931

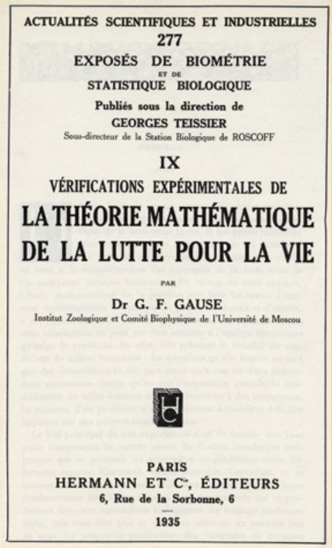
THE GOLDEN AGE

1931

We will present only the researches relative to what we can call the rational phase of the study of the biological associations. Those who will work on the experimental verifications of the theoretical results and will enter into the applied phase will be concerned with a careful discussion of the assumptions and of the biological validity of the arguments, mainly based on experiments, observations and statistics.

THE GOLDEN AGE

G. F. Gause
1935



ACTUALITÉS SCIENTIFIQUES ET INDUSTRIELLES
277
EXPOSÉS DE BIOMÉTRIE
ET DE
STATISTIQUE BIOLOGIQUE
Publiés sous la direction de
GEORGES TEISSIER
Sous-directeur de la Station Biologique de ROSCOFF

IX

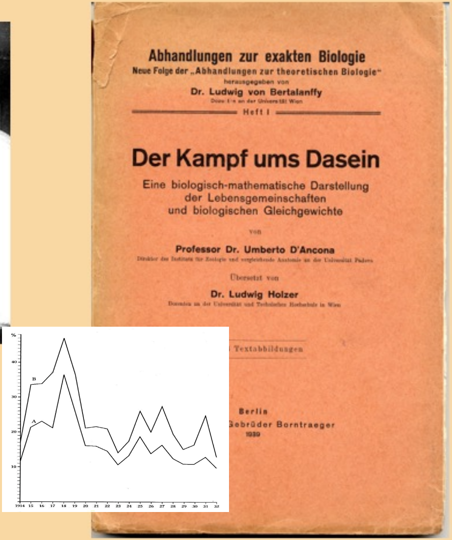
VÉRIFICATIONS EXPÉRIMENTALES DE
LA THÉORIE MATHÉMATIQUE
DE LA LUTTE POUR LA VIE

PAR
Dr G. F. GAUSE
Institut Zoologique et Comité Biophysique de l'Université de Moscou

PARIS
HERMANN ET Cie, ÉDITEURS
6, Rue de la Sorbonne, 6
—
1935

THE GOLDEN AGE

Umberto D'Ancona
1939



THE GOLDEN AGE

1939

[Reprinted from Human Biology, May Issue, Vol. 11, No. 2]

HUMAN BIOLOGY
a record of research

MAY, 1939

VOL. 11 **No. 2**

CALCULUS OF VARIATIONS AND THE LOGISTIC CURVE

BY VITO VOLTERRA

Rome

I HAVE been able to show that the equations of the struggle for existence depend on a question of Calculus of Variations, or more precisely on a problem of minimum.

In order to obtain this result, I have replaced the notion of *population* by that of *quantity of life*.[1] In this manner I have also obtained some results by which dynamics is brought into relation to problems of the struggle for existence.

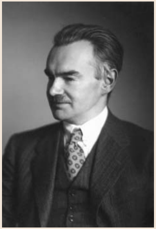
2. The quantity of life X and the population N of a species are connected by the relations

$$X = \int_{t_0}^{t} N dt \quad , \quad N = \frac{dX}{dt}$$

where N is to be considered as a function of the time. All depends on a theorem of Calculus of Variations that I have already used in my memoir above cited. I shall now give the enunciation, the demonstration, and some applications of this theorem.

[1] Principes de Biologie Mathématique: Ière Partie. §1 N. 2. *Acta Biotheoretica*, Vol. 3, Pars 1, 1937.

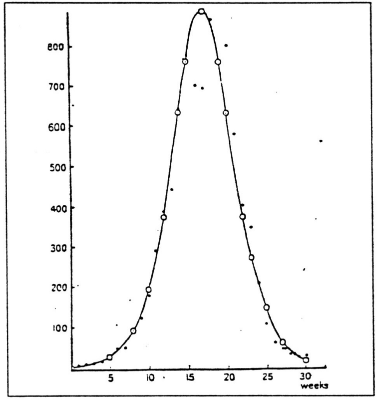
The mathematical approach to epidemics (1927)

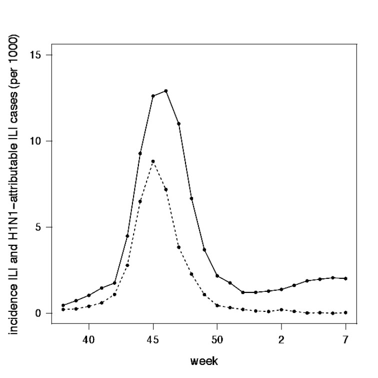


A.G. McKendrick
W. O. Kermack

A look to data

(the single epidemic outbreak)

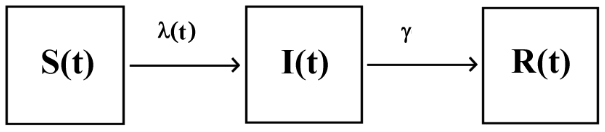




The Kermack-McKendrick model

(the single epidemic outbreak)

$$\begin{cases} S'(t) = -\lambda(t)S(t), & S(0) = S_0 \\ I'(t) = \lambda(t)S(t) - \gamma I(t), & I(0) = I_0 \\ R'(t) = \gamma I(t), & R(0) = R_0 \end{cases}$$



THE GOLDEN AGE

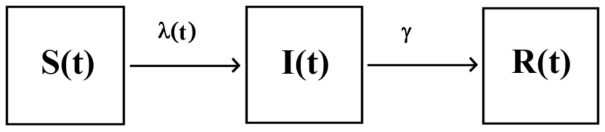
The Kermack-McKendrick model

(the single epidemic outbreak)

$$\begin{cases} S'(t) = -\lambda(t)S(t), \\ I'(t) = \lambda(t)S(t) - \gamma I(t), \\ R'(t) = \gamma I(t), \end{cases}$$

- $\tau = \frac{1}{\gamma}$ = durata dell'infezione
- $\lambda(t) = \frac{c\chi}{N} I(t)$ = forza di infezione

  c = contatti nell'unità di tempo
  χ = infettività di un contatto
  N = popolazione totale



The Kermack-McKendrick model

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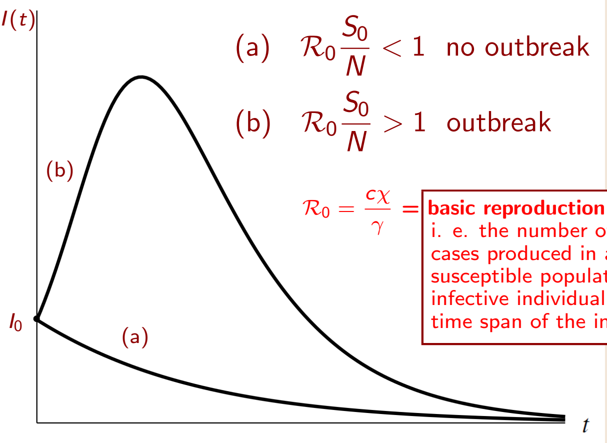


$\mathcal{R}_0 = \frac{c\chi}{\gamma} =$ **basic reproduction number**
i. e. the number of secondary cases produced in a totally susceptible population by a single infective individual during the time span of the infection

The importance of $\mathcal{R}_0$

- Herd immunity : $\dfrac{R_0}{N} > 1 - \dfrac{1}{\mathcal{R}_0}$
- Quarantine : $\rho < \dfrac{1}{\mathcal{R}_0}$
- Critical vaccination ratio : $V_c = 1 - \dfrac{1}{\mathcal{R}_0}$

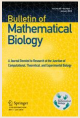
QUIESCENZA 1940-1970 ...

Quando Vito Volterra muore la Biomatematica sembra scomparire. I matematici dimenticano le equazioni di Lotka-Volterra e le applicazioni ai fenomeni biologici. D'altra parte Volterra stesso viene dimenticato, dopo essere stato messo da parte a seguito della sua vicenda personale e politica. La guerra fa il resto, coinvolgendo la scienza in questioni molto differenti dai problemi ecologici, mentre il dopoguerra si concentra sulla ricostruzione e sulla crescita economica industriale. Così, gli anni che vanno dal 1940 al 1970 sono una pagina bianca per la Biomatematica.

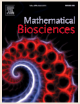
GLI ANNI SETTANTA (formidabili quegli anni ...)

- 1974, Journal of Mathematical Biology

- 1973, Bulletin of Mathematical Biology



- 1967, Mathematical Bioscences



- 1961, Journal of Theoretical Biology

GLI ANNI SETTANTA (formidabili quegli anni ...)

- 1974, Journal of Mathematical Biology

Editorial

Experimental Results Motivated by a Theory

Theoretical Work Disciplined by Biological Facts

Developing a better theoretical understanding of biology is a continuing challenge. Physics and the engineering sciences, which are inconceivable without interaction with mathematics, are the example and the envy of mathematical biology. The example can be misleading. Biological phenomena are physical-chemical phenomena of higher complexity than those usually studied in physics and chemistry. Mathematical methods have limitations. Stating laws of nature is just the beginning. Consequences must be derived by logical-analytical deductions or through computations or through a combination of both. The same as a microscope has a limit of resolution so deductive inference and computation have limits of resolution. These limits may not be very important for some questions in the physical sciences, they are always important in the life sciences.

Because of the limited resolving power the standard method of mathematical biology is to consider simplified descriptions of the biological reality, that is mathematical models. A model should be as realistic as possible yet simple enough so that inferences can be drawn from it. These two requirements often conflict with each other. Also sometimes very simple models give a

GLI ANNI SETTANTA (formidabili quegli anni ...)

C.I.M.E.
CENTRO INTERNAZIONALE MATEMATICO ESTIVO
(INTERNATIONAL MATHEMATICAL SUMMER CENTRE)

II ciclo 1979
Palazzone della Scuola Normale Superiore
Cortona - Arezzo

Mathematics of Biology

Coordinatore: Prof. Mimmo Iannelli

Liguori editore

C O N T E N T S

Metodi Matematici per la Biologia

- Analisi qualitativa di O.D.E.
  - equilibri, stabilità, coesistenza, esclusione, persistenza, endemicità, oscillazioni, chaos, ...
- Equazioni con ritardo (concentrato o distribuito)
  - effetti ereditari, struttura di età, gestazione, tempi di maturazione, incubazione di malattie ...
- PDE
  - struttura spaziale, movimento di popolazioni, propagazione di epidemie, habitat eterogeneo, crescita dei tessuti, struttura di età ...
- Matematica discreta e algebra lineare
  - modelli a tempo discreto ...
- Individual-based modeling (IBM)
  - simulazione di sistemi complessi, descrizione dettagliata individuale, learning ....
- Equazioni stocastiche

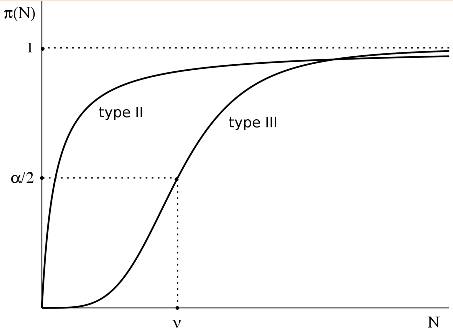
Qualche Esempio Significativo

- Predatore generalista
- Struttura di età
- COVID-19 e controllo ottimale

Predatore Generalista

$$N'(t) = r\left(1 - \frac{N(t)}{K}\right) N(t) - \alpha \frac{N^2(t)}{\nu^2 + N^2(t)}$$

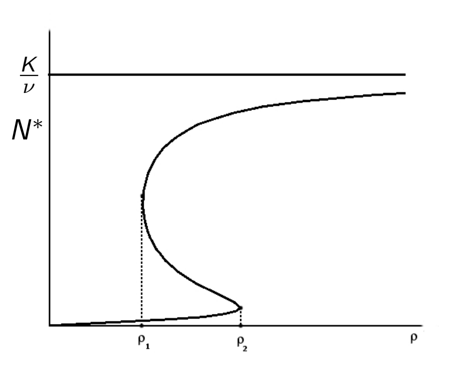
Holling type III
functional response



Predatore Generalista

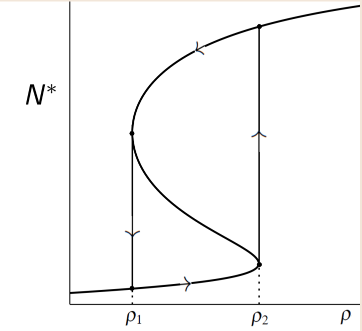
$$0 = r\left(1 - \frac{N^*}{K}\right) N^* - \alpha \frac{N^{*2}}{\nu^2 + N^{*2}}$$

Stati stazionari
in funzione
del parametro
$\rho = \frac{r\nu}{\alpha}$



Predatore Generalista

$$0 = r\left(1 - \frac{N^*}{K}\right)N^* - \alpha\frac{N^{*2}}{\nu^2 + N^{*2}}$$



Struttura di età

the elements of a description

- age $a \in [0, \alpha_\dagger]$ ($a_\dagger$ is the maximum age, usually $a_\dagger < +\infty$)
- density of the population with respect to age, at time t.

$$p(t, a), \qquad t \geq 0, \qquad a \in [0, \alpha_\dagger] \qquad \left(N(t) = \int_0^{a_\dagger} p(t, a) da \right)$$

- birth rate $B(t)$: the number of newborn in a time unit at time t

$$B(t) = \int_0^{a_\dagger} \beta(a) p(t, a) da$$

  where $\beta(a)$ is the age-specific fertility.
- survival probability $\Pi(a)$: the probability for a newborn to survive to age a

$$\Pi(a) = e^{-\int_0^a \mu(a) da}$$

  where $\mu(a)$ is the age-specific mortality

Struttura di età

two equivalent approaches

- Lotka an equation for the birth rate

$$B(t) = \int_0^t \beta(a)\Pi(a)B(t-a)da + F(t) \qquad \left(F(t) = \int_{-\infty}^0 \beta(t-a)\Pi(t-a)\phi(a)da\right)$$

- McKendrick an hyperbolic PDE with a non-local boundary condition

$$\begin{cases} p_t + p_a + \mu(a)p(t,a) = 0 \\ p(0,t) = \int_0^{a_\dagger} \beta(a)p(t,a)da \\ p(0,a) = p_0(a) \end{cases}$$

connected by

$$p(t,a) = B(t-a)\Pi(a) \qquad t \geq 0, \quad a \in [0, a_\dagger]$$

Struttura di età

the demographer's deligth: the stable distribution
(Sharpe-lotka theorem)

The population eventually forgets
its initial age distribution $p_0(a)$,
to attain the stable population profile

$$\omega^*(a) = \frac{e^{-\alpha^* a}\Pi(a)}{\int_0^{a_\dagger} e^{-\alpha^* a}\Pi(a)}$$

where α^* is the (unique) real solution of the characteristic equation

$$\int_0^{a_\dagger} \beta(a)\Pi(a)e^{-\lambda a}da = 1$$

indeed

$$B(t) = b_0 e^{\alpha^* t}(1 + \Omega(t)) \quad \text{with} \quad \lim_{t\to+\infty} \Omega(t) = 0$$

Struttura di età

the demographer's deligth: the stable distribution
(Sharpe-lotka theorem)

The population eventually forgets
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to attain the stable population profile → $\frac{p(t,a)}{N(t)}$

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Struttura di età

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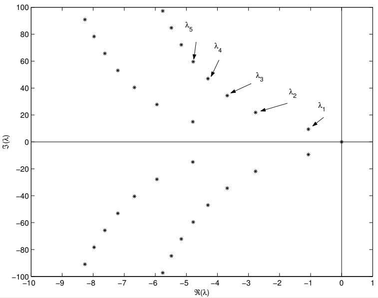

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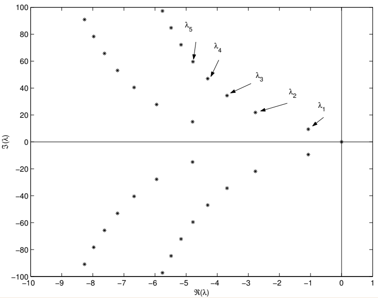
the demographer's deligth: the stable distribution

$$\mathcal{R}_0 = \int_0^{a_\dagger} \beta(a)\Pi(a)da$$

$\alpha^* > 0$ if and only if $\mathcal{R}_0 > 1$



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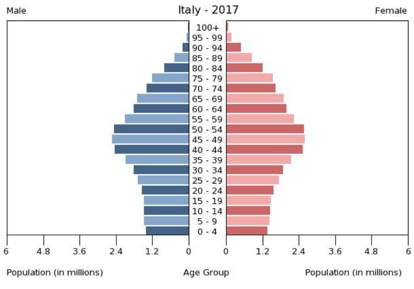

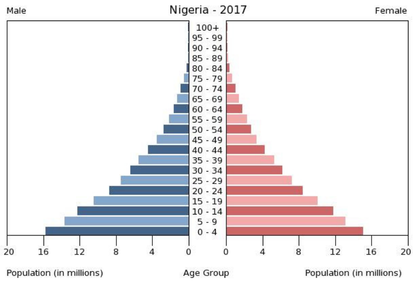

Yet another approach: semigroups

$$\begin{cases} p_t + p_a + \mu(a)p(t,a) = 0 \\ p(0,t) = \int_0^{a_\dagger} \beta(a)p(t,a)da \\ p(0,a) = p_0(a) \end{cases} \longrightarrow \begin{cases} u'(t) = \mathcal{A}\ u(t) \\ u(0) = u_0 \end{cases}$$

$$u(t) := p(\cdot,t), \quad u_0 := p_0(\cdot), \qquad \text{in} \quad E = L^1(0,a_\dagger)$$

$$\mathcal{A} := \begin{cases} D_{\mathcal{A}} := \Big\{ f(\cdot) \in E \ \mid \ f'(\cdot) + \mu(\cdot)f(\cdot) \in E, \\ \qquad\qquad f(0) = \int_0^{a_\dagger} \beta(a)f(a)da \Big\} \\ \mathcal{A}f(\cdot) := -f'(\cdot) - \mu(\cdot)f(\cdot) \end{cases}$$

COVID-19 e controllo ottimale

Determining optimal strategies for controlling the disease

State system ($t \in [0, T]$)

$$\begin{cases} i) \quad \left(\frac{\partial}{\partial t} + \frac{\partial}{\partial x}\right) Y(x,t) = -\gamma(x) Y(x,t), \\ ii) \quad Y(0,t) = c(t) \int_0^{x_+} \chi(x) Y(x,t) dx, \end{cases}$$

Cost function to be minimized

$$\mathcal{C}_{total}(c) = \chi\, \mathcal{C}_E(c) + (1-\chi)\, \mathcal{C}_w(c)$$

Determ… …disease

State system (…

Direct health costs of the epidemic:
all cases of serious disease following infection
i.e., yielding to hospitalizations and deaths.
These cases arise from the total incidence:

$$c_E \int_0^T c(t) \int_0^\infty \chi(x) Y(t,x) dx dt$$

c_E is the average cost generated by one infected individual per unit of time over period $[0, T]$

Cost function to be minimized

$$\mathcal{C}_{total}(c) = \chi\, \mathcal{C}_E(c) + (1-\chi)\, \mathcal{C}_w(c)$$

COVID-19 e controllo ottimale

Determ… …disease

State system (…

Overall indirect cost, arising from a prescribed *social distancing policy* $c(t)$ through $[0, T]$.

$$C_w \int_0^T Q(c(t))dt$$

$Q(x)$ is a loss function, it is decreasing and

$$Q(c_-) = 1 \quad , \quad Q(c_0) = 0$$

C_w is the maximum cost occurring at $c = c_-$
(a fraction of the total welfare per unit time)

Cost function to be minimized

$$\mathcal{C}_{total}(c) = \chi\, \mathcal{C}_E(c) + (1-\chi)\, \mathcal{C}_w(c)$$

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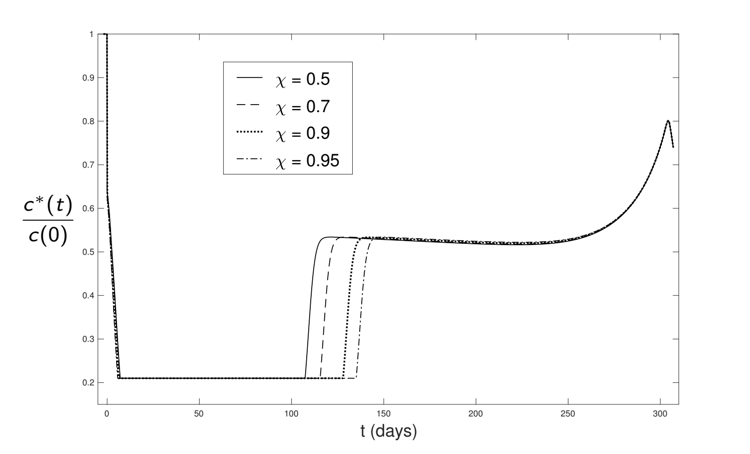
The relative weight of the epidemics cost against economic cost. It reflects the governmental preference for indirect costs

Cost function to be minimized

$$\mathcal{C}_{total}(c) = \chi\, \mathcal{C}_E(c) + (1-\chi)\, \mathcal{C}_w(c)$$

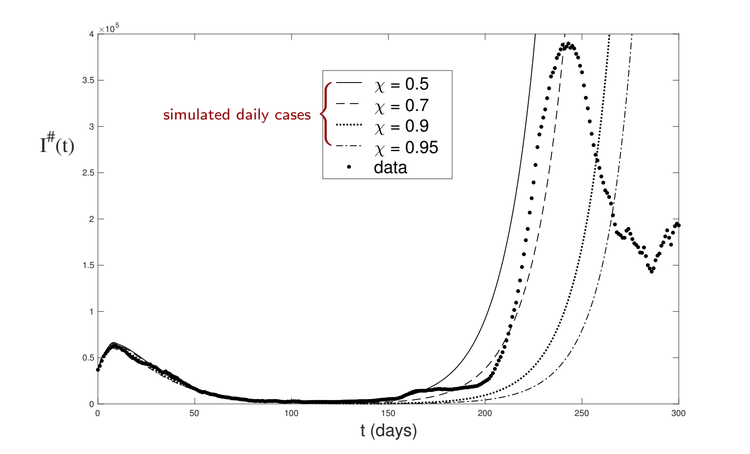
COVID-19 e controllo ottimale

Optimal lock-down (parameters from COVID-19)



COVID-19 e controllo ottimale

Optimal lock-down (parameters from COVID-19)



Daniel Bernoulli 1760

A proposito della inoculazione contro il vaiolo

" … io spero solo che su una questione che riguarda così da vicino il bene dell'umanità, non si decida nulla se non con quella cognizione di causa che un po' di analisi e di calcolo possono fornire …"

La costruzione d'un modello era dunque per lui un miracolo d'equilibrio tra i principi (lasciati nell'ombra) e l'esperienza (inafferrabile), ma il risultato doveva avere una consistenza molto più solida degli uni e dell'altra.

Italo Calvino
da "Il modello dei modelli" in "Palomar", 1983

GRAZIE PER L'ATTENZIONE