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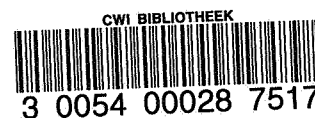
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Well-posedness of physiologically structured population models for Daphnia magna

Well-Posedness of Physiologically Structured Population

Models for Daphnia Magna

(How biological concepts can benefit by abstract mathematical analysis)

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In this paper we heuristically discuss the well-posedness of three variants of the Kooijman/Metz model. Shortcomings concerning the uniqueness and continuous dependence on data of the solutions to one of the variants are traced back to an inconsistency in the biological concept of energy allocation in this model version. The conceptional consequences are discussed and an open question concerning energy allocation is pin-pointed. A rigorous mathematical treatment will be presented in a forthcoming publication.

Acknowledgement

Introduction

Kooijman and Metz [7] (see also [2]) recently presented
a mathematical model for the development of waterflea
(Daphnia magna) populations which takes the observation
seriously that the mortality of Daphnia magna widely
depends on the age, the fertility, however, on the size
of the individual. In particular, the length of the
juvenile period (the period before reproduction starts)
is essentially affected by the amount of food the water-
fleas are supplied with and thus represents a regulatory
mechanism for the population density, which is neglected
in conventional mathematical models.

The Kooijman/Metz model belongs to the class of physio-
logically structured population models (see [3] for a
survey and a bunch of references) which associate the
development of the individual with the dynamics of the

population by means of a population structure which is
generated by one or several relevant physiological traits
of the individual (age, size, energy reserves etc.). In
this way physiologically structured population models
translate physiological impacts on the individual into
impacts on the population development and vice versa.
So the Kooijman/Metz model can possibly be used to iden-
tify the toxic effects of chemicals on the various physio-
logical functions of Daphnia magna (which are difficult
to observe directly) via the impact of the chemical onto
the development of population size and distribution [7].
The applicability of the Kooijman/Metz model (all rates
are given explicitly with a limited number of parameters
all of which can be estimated or at least be guessed
from experimental observation) is achieved by a number
of idealizations which neglect biological details for
which sufficient information is not available in practice
or even in principle. These idealizations, however, which
simplify the model, create unusual (at least for mathe-
matical models in population dynamics) mathematical
difficulties in proving the well-posedness of the model
equations (nonlinear partial functional-differential
equations of first order or, alternatively, nonlinear
integral equations), i.e. in showing that solutions
exist and are uniquely determined by and continuously
depend on the model data. The latter point is of particular
interest for the modelling itself because it decides upon
whether the idealizations are actually justified and the
solutions of the idealized model (which is a limiting
model) are not too far away from the solution of a pre-
sumably more realistic model.

It must be expected that similar problems will arise in
many physiologically structured population models which
are not only tailored for theory but for practice, so
that the analysis of the Kooijman/Metz model as a proto-

type of such models will also be a step towards a
general mathematical theory which, up to now, is still
in its infancy. In this paper we only give a heuristic
analysis of the Kooijman/Metz model; in a forthcoming
paper [8] we will give a rigorous analysis of a much
more general model in order to leave the theory open
for other physiologically structured population models,
e.g. for a Daphnia model incorporating energy reserves
(see Kooijman's model in [5]).

Though the original Kooijman/Metz model is well-posed
for many initial data (in particular if they are close
to the equilibrium), one can construct initial conditions
under which uniqueness of solutions (and so their con-
tinuous dependence on data) fails. So we introduce two
other variants of the Kooijman/Metz model: one which
incorporates some of the ideas of another group of
Daphnia modellers (Gurney, McCauley, Murdoch, Nisbet)
and a second one which modifies the original Kooijman/
Metz model according to the lessons taught by the mathe-
matical analysis of this paper. (See section 1 for the
general ideas behind the Kooijman/Metz model and its
variants, and section 2 for the specific features of
the three versions.) We compare the three versions for
uniqueness of solutions and for continuous dependence
of solutions on the data of the model. In order to study
the latter point properly we have to extend the Kooijman/
Metz model such that it admits solutions (representing
age-size-distributions of the population in dependence
on time) which are measures (see chapter 3 for this
extension, see also [4] for another model for physio-
logically structured populations which also involves
measure-valued solutions.). In the forthcoming paper [8]
we present and prove a fairly general result concerning
the existence of solutions for a large class of physio-
logically structured population models. Therein we also

study various conditions for the uniqueness of solutions
and show that uniqueness implies continuous dependence
on model data under very mild assumptions. Three of
those conditions are particularly suited for each of
the three variants of the Kooijman/Metz model respective-
ly. In section 4 we present the conditions in terms of
the Kooijman/Metz model and illustrate heuristically how
each of them implies uniqueness of solutions and how
uniqueness fails if none of them is satisfied. We discuss
the restrictions they impose on the three versions of the
Kooijman/Metz model. The phenomenon that certain initial
conditions do not induce a unique solution to the original
Kooijman/Metz model is traced back to the underlying con-
cept of energy allocation. We offer some speculations how
this concept can be modified and leave the question to
the biologists whether they can identify corresponding
physiological mechanisms.

1. ## Some general ideas about the Kooijman/Metz Daphnia model and its variants

In contrast to age-structured population models (see the
monograph by Webb [9] for a survey and a flood of referen-
ces) which are particularly suited for human populations,
the Kooijman/Metz model acknowledges the importance of
the size structure of the population for its future de-
velopment. For, according to the observations by Kooijman
and Metz, an individual waterflea does not become mature
(or adult, i.e. starts reproducing under favourable food
conditions) when reaching a certain age, but when its
body length passes a threshold length l_J (= 2,5 mm).

The assimilation energy which the individual wins from
food consumption is assumed to be proportional to its
surface area and to be partitioned between maintenance
of tissue and metabolism (with the energy costs being
proportional to the volume of the individual), growth,
and maturation/reproduction. The Kooijman/Metz model
supposes that juveniles and adults channel the same
proportion of assimilation energy into growth and so
implicitly supposes that the energy which adults use for
reproduction is used for maturation (whatever that
means) by juveniles. This view is not shared by another
group of Daphnia modellers (Gurney, McCauley, Murdoch,
Nisbet), who do not separate maturation from growth
but assume that juveniles channel all the assimilation
energy into maintenance and growth, whereas adults also
use energy for reproduction. This assumption, however,
(at least if the assimilation energy is not smoothly
diverted, but abruptly switched from growth to repro-
duction) does not lead to the van Bertalanffy individual
growth curves which follow from the Kooijman/Metz model
and seem to fit quite well the data Kooijman and Metz
work with (see [6], [7]). If one distinguishes between
growth and maturation in juveniles as is implicitly done
in the Kooijman/Metz model one has to acknowledge the
apparently perfect synchronization between maturation
and growth, namely that even under different food regimes
maturity is always reached at the same length l_J. This
involves that, by some unknown mechanism, maturation
stops when growth stops and vice versa. Since it is the
same portion of energy which juveniles channel into
maturation and adults channel into reproduction, an in-
dividual whose growth stops when reaching the threshold
size l_J should not be able to reproduce. But this relation
is not satisfied by the reproduction law of the Kooijman/
Metz model. So we introduce a third version (the second
incorporates the ideas of Gurney, McCauley, Murdoch and
Nisbet) in which the reproduction law is modified such

that individuals with length l_J can only reproduce if
they grow. The feature of the Kooijman/Metz model that
non-growing individuals which are larger than l_J can
reproduce under certain food conditions (as it is
actually observed in the laboratory) is preserved. Un-
fortunately there are several mathematical possibilities
to modify the Kooijman/Metz reproduction law, but there
is no evidence from biological observation or theory
which helps to choose the appropriate one. (In chapter
5 we will offer some speculation which tries to explain
the synchronization of maturation and growth and in-
volves a definite reproduction law satisfying our postu-
lates.)

The subsequent analysis of these three versions (which
is done heuristically in this paper and will be made
rigorous in [8]) scrutinizes whether they are mathe-
matically well-posed, i.e. whether the model equations
allow the existence and induce the uniqueness of solu-
tions and whether the solutions depend continuously
(in an appropriate sense) on the data of the model
(e.g. on the per capita growth and reproduction rate).
The last point is of particular importance, for all
three versions are idealizations in at least two aspects:

i) The rapid, but presumably continuous increase of
reproduction as growth passes the threshold size is
idealized by a jump.

ii) The high concentration of the birth size distribution
at one particular size is idealized by assuming that
all individuals are born with exactly the same length l_B.

These idealizations are necessary because the application
of the idealized more realistic set-up requires detailed
biological information which cannot be obtained in practice
or even in principle. The continuous dependence of the

solutions on the model data decides upon whether the
idealizations (which are actually limits) are justified.
If it does not hold or only holds under restrictions,
then there are good reasons to reconsider the under-
lying biological concept of the model and to identify
and modify the hypotheses which are responsible.

2. The submodels for development, reproduction and mortality of individual Daphnia in the three versions of the Kooijman/Metz model

Physiologically structured population models draw their
appeal from allowing the modeller first to establish
submodels for the relevant processes on the level of
the individual and then, only in a second step of
modelling, to combine these submodels into an overall
model for the dynamics of the populations. In this
chapter we present the submodels for the processes
affecting the individual Daphnia, namely development,
reproduction and mortality. The Kooijman/Metz model
assumes that the way in which an average waterflea is
subject to these processes depends on its developmental
state x which can be described by two variables $(a,l) = x$,
namely by its age a and its length l. (The Kooijman/Metz
model neglects energy reserves. These are taken into
account in the Kooijman model [5] which is not considered
here.) The submodels for reproduction and mortality define
the average per capita birth and death rates $ß(E,x)$ and
$\mu(E,x)$ in terms of the state x of the individual and on
the environmental conditions E. According to the observa-
tions by Kooijman and Metz the reproduction only depends
on the length and the mortality (apart from starvation) on
the age of the individual. The development of the individual

is described by a two-dimensional system of ODEs for the developmental state, namely

$$(2.1) \qquad \dot{x} = \begin{pmatrix} \dot{a} \\ \dot{l} \end{pmatrix} = \begin{pmatrix} g_1(E,x) \\ g_2(E,x) \end{pmatrix} = g(E,x)$$

Here $\dot{x}$ denotes the time derivative $\frac{d}{dt} x(t)$ of the state $x(t)$ at time t, $E = E(t)$ the environmental conditions at time t. g_1 and g_2 denote the rates of aging and growth in dependence on the environment and the state of the individual. It is reasonable to assume that the rate of aging g_1 does not depend on age a and length l. As a rule of thumb, however, aging speeds up with temperature (i.e. the life span is shorter at higher temperatures) so that g_1 certainly depends on the environment. If the temperature (and maybe other environmental factors) are kept constant, one can assume that $g_1 = 1$.

As we explained the general ideas of the Kooijman/Metz model in the previous chapter and as we can refer to the specific explanations in [2], [7], we only outline the submodels for development, reproduction and mortality in the three versions of the Kooijman/Metz model.

2.1. The original Kooijman/Metz model (version 1)

A waterflea wins assimilation energy $\tilde{E} = f(E)$ (per unit area of body surface) by digesting food which is partitioned into maintenance of tissue and metabolism, maturation/reproduction and growth. $\tilde{E}$ may not only depend on the food density, but also on other environmental conditions, e.g. on temperature, the increase of which speeds up the digestion rate. The length growth rate g_2 is given by

$$(2.2) \qquad g_2(E,a,l) = [k \tilde{E} - l]_+ \quad ,$$

the per capita birth rate by

$$\text{ß}(E,a,l) = 0 \quad , \text{ if } l < l_J$$

(2.3)

$$\text{ß}(E,a,l) = \text{ß}_0(E,l), \text{ if } l > l_J$$

with

(2.4) $$\text{ß}_0(E,l) = wl^2\{[\tilde{E} - 1]_+ - [\kappa\tilde{E} - 1]_+\} .$$

Here l does not denote actual length, but some scaled length. $[\tilde{E} - 1]_+ l^2$ is the energy which is available after having covered the energy costs of maintenance. k is the fraction of energy channelled into growth. Reproduction takes priority over growth because the energy needed for maintenance is subtracted from the energy put into growth as long as the outcome is positive.
For

$$\text{ß}_0(E,l) = wl^2(1 - \kappa) \tilde{E}$$

if $\kappa\tilde{E} > 1$. w is the factor converting assimilation energy into offspring. l_J indicates the threshold length which separates juvenile from adult (reproductive) individuals. Note that the fraction of energy channelled into growth is the same for both stages. The energy which adults use for reproduction is used for maturation by juveniles.

2.2. Version 2 of the Kooijman/Metz model

Another group of Daphnia modellers (Gurney, McCauley, Murdoch and Nisbet) integrate maturation into growth and assume that juveniles channel all the energy which is not needed for maintenance into growth. We modify the Kooijman/Metz model accordingly by supposing that

energy is switched from growth to reproduction as soon
as the individual passes the threshold length l_J.

$$(2.5) \quad \begin{aligned} g_2(E,a,l) &= [\tilde{E} - 1]_+ \quad , \text{ if } l < l_J \\ g_2(E,a,l) &= [\kappa\tilde{E} - 1]_+ \quad , \text{ if } l > l_J \end{aligned}$$

The reproduction rate is not affected by this modification
and is given by (2.3), (2.4).

2.3 Version 3 of the Kooijman/Metz model

We have pointed out in section 1 that separating, but
synchronizing growth and maturation has the conceptual
consequence that individuals which have just passed the
threshold length l_J only reproduce if they grow. Incor-
porating this idea in the Kooijman/Metz model does not
affect the rate of length growth g_2 in (2.2), but re-
quires modifying β_o in (2.3), (2.4) such that

$$(2.6) \quad \beta_o(E,l_J) = 0 \quad \text{ iff } \quad g_2(E,a,l_J) = 0 \; .$$

This can be done in replacing β_o in (2.4) by

$$(2.7) \quad \beta_o(E,l) = w \left\{ [\tilde{E}l^2 - l^3 - (\frac{1}{\kappa} - 1) \, l_J^\alpha \, l^{3-\alpha} \,]_+ \right.$$
$$\left. - [\kappa\tilde{E}l^2 - l^3 \,]_+ \right\}$$

with some $0 < \alpha \leq 3$. Note that

$$\beta_o(E,l_J) = (\frac{1}{\kappa} - 1) \, w \, g_2(E,a,l_J) \, l_J^2$$

so that (2.6) is satisfied. Moreover we keep the property
that individuals of length $l > l_J$ can reproduce without
growing under certain environmental conditions. Unfortuna-
tely there is no stringent indication how α should be

chosen. In section 4.6 we offer some speculation which supports the choice $\alpha = 3$.

We do not specify the per capita mortality rates here because there is no difference between the three versions. Kooijman and Metz originally assume (see [2]) that a waterflea dies as soon as the assimilation energy won from the food does not cover the maintenance needs. Although this idea has some conceptional appeal, it appears to me unrealistic (even as an idealization) and mathematically difficult to be handled. Actually this point is one of the drawbacks of neglecting energy re-serves. Incidentally the Kooijman/Metz model neglects certain aspects of starvation from the very beginning, because it does not include that Daphnia magna may switch from parthenogenetic to sexual reproduction under sudden food shortage. In order to keep the theory open for a better understanding of starvation (e.g. for adding energy reserves as a further state variable) we develop the model for the dynamics of the population more broadly than it is actually needed for the three versions of the Kooijman/Metz model, in particular we admit rather general mortality rates which depend on the environment and on the individual's state in a sufficiently smooth way.

3. Model for the dynamics of the population

Imagine that, starting at time t = 0, we rear a population of Daphnia magna in a spatially homogeneous environment such that, at any time t ≥ 0, all individuals experience identical environmental conditions.(Here environment means the totality of exterior components affecting the animal like temperature, salinity, pH-value, food density etc..) Laboratory experiments [6,7] have shown that a model which wants to draw a not too unrealistic picture of the development of the population has to include the processes of aging and growth of individuals. For, apart

from environmental impacts, the mortality of Daphnia
magna seems to depend on the age of the individual, whereas
reproduction is strongly related to its size. In ecto-
thermic animals like Daphnia, however, age does not
necessarily mean chronological age (i.e. the time since
birth). So, more precisely, the probability of surviving
for a period of length τ (starting from birth) is a
function of τ provided that temperature (and other environ-
mental impacts perhaps) are kept constant. As a rule of
thumb ectothermic animals die the earlier the higher the
temperature (death from frost excepted) [6].

3.1. The general submodel for individual development

More generally than before we assume that the state of
an individual is indicated by a vector $x \in [0, \infty)^m$ of
m traits (like age, size, energy reserves etc.). The
development of an average individual is described by the
change of its state. Let $X(t,s,y)$ denote the state of
the individual at time t if it has the state y at time
s. Then X is supposed to satisfy the following ODE:

$$X(s,s,y) = y$$
(3.1)
$$\partial_t X(t,s,y) = g(E(t), X(t,s,y))$$

with $g(E,x)$ indicating the developmental rate of an
individual with state x under environmental conditions E.
Setting $x(t) = X(t,s,y)$, (3.1) corresponds to (2.1) in
the Kooijman/Metz model with initial conditions $x(s) = y$.

3.2. The general submodel for individual survival

In general it is reasonable to assume that the per capita
mortality rate $\mu(E,x)$ depends both on the environmental
conditions E and on the individual's state x. We want
to derive a formula for the probability $K(t,s,x)$ at which

14

an individual survives from time s to time $t \geq s$ if x is
the individual's state at time s. It is obvious from the
interpretation of K that

$$K(s,s,x) = 1$$

(3.2)

$$K(t+h, s,x) = K(t+h,t,X(t,s,x)) K(t,s,x)$$

for $t \geq s$, $h > 0$. If h is sufficiently small

(3.3) $$K(t+h,t,y) = 1 - \mu(E(t),y) \cdot h + o(h)$$

with $o(h)/h \longrightarrow 0$ for $h \searrow 0$. So we obtain the
following differential equation for K:

(3.4) $$\partial_t K(t,s,x) = -\mu(E(t), X(t,s,x)) K(t,s,x)$$

As $K(s,s,x) = 1$, integration of (3.4) yields

(3.5) $$K(t,s,x) = \exp\left(-\int_s^t \mu(E(r), X(r,s,x)) \, dr\right)$$

The model for the dynamics of the population associates
individual development and mortality (as they are des-
cribed in section 3.1 and 3.2) with the dynamics of the
population. For the ease of the reader we first discuss
the case that all individuals are born equal.

3.3. The case of identical birth state

In the Kooijman/Metz model all waterfleas are born with
age $a = 0$ and length l_B (= 0,8 mm). More generally we
consider the case that all neonates have the same state
x_B. This implies that all individuals which have been born
at some time $s > 0$ have the same state $X(t,s,x_B)$ at time
$t \geq s$ provided they did not die before. The probability

to survive from time s to time t is given by $K(t,s,x_B)$.
Further individuals from the initial population that
had the same state y at time $s = 0$, have the same
state $X(t,0,y)$ at time $t \geq 0$, if they are still alive.
The probability of survival is given by $K(t,0,y)$ in
this case.

Let now the continuous (or more generally Borel measurable)
function $\Phi(x)$ denote some action (e.g. reproduction,
food consumption) of an individual in state x. We want
to describe the corresponding action of the whole popula-
tion at time t in terms of the population birth rate B(s),
$0 \leq s \leq t$, and the initial state distribution $N_0(y)$,
$y \in [0, \infty)^m$. We first note that an individual acting at
time t was either born at some instant s, $0 < s < t$, or
was already present at time 0 with a state y. If the in-
dividual was born at time s, its action at time $t \geq s$ is
given by

$$\Phi(X(t,s,x_B)) \, K(t,s,x_B)$$

If it was already present at time 0 with state y, its
action at time $t \geq 0$ is given by

$$\Phi(X(t,0,y)) \, K(t,0,y)$$

Then the corresponding action $A_\Phi(t)$ of the whole
population at time t is given by

$$
(3.6) \quad
\begin{aligned}
A_\Phi(t) \\
&= \int_0^t \Phi(X(t,s,x_B)) \, K(t,s,x_B) \, B(s) \, ds \\
&\quad + \int_{[0,\infty)^m} \Phi(X(t,0,y)) \, K(t,0,y) \, N_0(y) \, dy
\end{aligned}
$$

In order to write down the formula for the population
birth rate we introduce the per capita birth rate $ß(E,x)$
which depends on the state x of the individual and the
environmental conditions E. Then, by the preceding con-
siderations with $\bigoplus(x) = ß(E(t),x)$ and (3.6),

$$B(t) = \int_o^t ß(E(t), X(t,s,x_B))\, K(t,s,x_B)\, B(s)ds$$

(3.7)
$$+ \int_{[0,\infty)^m} ß(E(t), X(t,0,y))\, K(t,0,y)N_o(y)dy\ .$$

Similarly we can describe the dynamics of the environment:

$$\frac{d}{dt}E(t) = q(E(t))$$

(3.8)
$$- \int_o^t f(E(t), X(t,s,x_B))\, K(t,s,x_B)\, B(s)ds$$

$$- \int_{[0,\infty)^m} f(E(t),X(t,0,y))\, K(t,0,y)N_o(y)dy$$

The ODE

$$\frac{d}{dt}E(t) = q(E(t))$$

describes the dynamics of the environment in absence of
Daphnia, $f(E,x)$ indicates the negative feed back of an
individual in state x onto the environment E. The equations
(3.1), (3.5), (3.7), (3.8) form a closed model. After
having solved the model equations (3.1), (3.5), (3.7), (3.8)
we can obtain the state distribution of the population
from formula (3.6). In general the state distribution
cannot be described by a Lebesque density, i.e.

$$A_{\bigoplus}(t) = \int_{[0,\infty)^m} \bigoplus(x)\, \tilde{N}(t,x)dx$$

for all continuous bounded ϕ. This raises the question
whether it is reasonable to restrict to initial distribu-
tions $N_o(y)$ which are Lebesque densities. Anyhow it should
be possible to include initial populations in which all
individuals have the same state. This amounts to re-
placing the integration $N_o(y)dy$ by $N_o(dy)$ in (3.7)
and (3.8) with N_o being now a Borel measure on $[0, \infty)^m$.

This formulation of the Kooijman/Metz model corresponds
to the formulation (2.10) in [2] after integration and
reduction to the population birth rate B. In our
derivation we have replaced chronological age by the
time of birth in order to avoid confusion because, in
this approach, age is a state variable incorporated in
the state x already. This has the advantage that
temperature-dependent aging is included and that, in a
further step of generalization, we can consider initial
populations in which all individuals have the same age.

3.4 The general model

If we want to study the continuous dependence of solutions
on the model data properly we must abandon the formulation
in section 3.3 which relies on the assumption that all
individuals are born in the same state. The assumption
of the Kooijman/Metz model that all neonates have exactly
the same length $l_B = 0.8$ mm is certainly the idealization
of a highly concentrated but dispersed birth length. This
requires that the model must be formulated from the very
beginning in terms of state distributions which are repre-
sented by measures. The following derivation might appear
a bit exotic to those who are used to work with densities,
but this approach seems unavoidable and quite natural.
Those who are only interested in the results may proceed
to section 4 immediately. We now start from the state

distribution $N(t,L)$ of individuals at time t with state x in a Borel set L (e.g. an open or a closed set) in $[0, \infty)^m$. $N(t,L)$ is assumed to be a Borel measure on the Borel sets L of $[0, \infty)^m$. If $\Phi(x)$ again denotes some action of an individual in state x, the corresponding action $A_\Phi(t)$ of the whole population at time t is given by

$$(3.9) \qquad A_\Phi(t) = \int_{[0, \infty)^m} \Phi(x) \, N(t,dx)$$

As the state at birth is not fixed any more, we similarly introduce the state distribution $B(t,L)$ of the population birth rate at time t. If an individual is born in state y at time $s \in (0,t)$, its action at time t is

$$\Phi(X(t,s,y)) \, K(t,s,y)$$

with $X(t,s,y)$ giving its state at time t and $K(t,s,y)$ giving the probability of having survived to time t. So the action of the whole population at time t is given by

$$A_\Phi(t) = \int_{[0, \infty)^m} \Phi(x) \, N(t,dx)$$

$$(3.10) \qquad = \int_0^t \int_{[0, \infty)^m} \Phi(X(t,s,y)) \, K(t,s,y) \, B(t,dy) \, ds$$

$$+ \int_{[0, \infty)^m} \Phi(t,0,y) \, K(t,0,y) \, N_0(dy)$$

with N_0 denoting the initial state distribution of the population. The second term on the right hand side of (3.10) gives the action of the individuals which were already present at the beginning and is essentially the same as in (3.6). Let now $\beta(L; E,x)$ describe the rate

of neonates with state y in the set L produced by an average individual in state x under the environmental conditions E. Then the population birth rate B is given by (3.9) with $\Phi = \beta(L; E, \cdot)$, i.e.

$$(3.11) \qquad B(t,L) = \int_{[0,\infty)^m} \beta(L; E(t),y)\, N(t,dy).$$

From (3.10) we obtain

$$(3.12) \qquad \begin{aligned} B(t,L) &= \int_0^t \int_{[0,\infty)^m} \beta(L; E(t),X(t,s,y))K(t,s,y)\, B(s,dy)ds \\ &+ \int_{[0,\infty)^m} \beta(L; E(t),X(t,0,y))K(t,0,y)\, N_0(dy). \end{aligned}$$

In a similar way (3.8) is generalized to

$$(3.13) \qquad \begin{aligned} \frac{d}{dt}E(t) &= q(E(t)) - \int_0^t \int_{[0,\infty)^m} f(E(t),X(t,s,y))K(t,s,y)\, B(s,dy)ds \\ &- \int_{[0,\infty)^m} f(E(t),X(t,0,y))K(t,0,y)N_0(dy). \end{aligned}$$

The equations (3.12) and (3.13) in combination with (3.1) and (3.5) form a closed model for the dynamics of Daphnia magna populations. The special case of identical birth state which has been discussed in section 3.3 can be embedded into this model via

$$\beta(L;E,x) = \beta(E,x)\,\mathbb{1}_L(x_B)$$

$$B(t,L) = B(t)\,\mathbb{1}_L(x_B)$$

with x_B denoting the identical birth state and $\pi_L(x_B) = 1$ if $x_B \in L$, $\pi_L(x_B) = 0$ if $x_B \notin L$.

We conclude this section with some remarks.

<u>Remark 3.1</u> a) Let Φ be any bounded continuously differentiable non-negative function on $[0, \infty)^m$. Then we find from (3.10), (3.1), (3.4), and (3.11) that

$$\frac{d}{dt} \int_{[0, \infty)^m} \Phi(x) \, N(t,dx)$$

$$= \int_{[0, \infty)^m} (\nabla \Phi(x)) \cdot g(E(t),x) \, N(t,dx)$$

(3.14)

$$- \int_{[0, \infty)^m} \Phi(x) \, \mu(E(t),x) \, N(t,dx)$$

$$+ \int_{[0, \infty)^{2m}} \Phi(x) \, \beta(dx; E(t),y) \, N(t,dy)$$

In other words N is a distributional solution of the partial differential equation

$$\partial_t N(t,dx) + \nabla_x \cdot g(E(t),x) \, N(t,dx)$$

(3.15)

$$+ \mu(E(t),x) \, N(t,dx) = \int_{[0, \infty)^m} \beta(dx; E(t),y) \, N(t,dy)$$

Together with

$$(3.16) \quad \frac{d}{dt} E(t) = q(E(t)) - \int_{[0, \infty)^m} f(E(t),x) \, N(t,dx)$$

and appropriate initial conditions this is also a closed model for Daphnia magna population dynamics. Compare

(3.15) and (3.16) with the formulas in [2], p. 89, above. Whereas the formulation of the model in terms of B seems to be more useful for studying the existence, uniqueness and continuous dependence on data of solutions, the formulation in terms of N seems to be more appropriate for studying the qualitative behaviour. Namely, for fixed E, N induces a linear evolutionary system on the Banach space Z^K of regular Borel measures on $[0, \infty)^m$. Z^* is the dual space of continuous function on $[0, \infty)^m$ vanishing at infinity. N and E together induce a (nonlinear) dynamical system (semiflow) on $Z^* \times [0, \infty)^n$. A first step towards a general theory of such dynamical systems is done in [1].

b) In order to write (3.15) in a more familiar way let us assume that the state of the individual is characterized by one trait alone, i.e. $x \in [0, \infty)$, that all individuals are born in the same state x_B and that the state distribution of the population can be represented by a suffiently smooth Lebesque density. Then (3.15) takes the form

$$\partial_t N(t,x) + \nabla_x \cdot (g(E(t),x) N(t,x))$$

$$+ \mu(E(t),x) N(t,x) = 0 \; ; \; x \neq x_B$$

(3.17)

$$g(E(t),x_B +) N(t,x_B +) - g(E(t),x_B -) N(t,x_B -)$$

$$= \int_0^\infty ß(\{x_B\} ,E(t),y) N(t,y)dy$$

Here $x_B +$ and $x_B -$ denote the limits at x_B from the right and from the left. This can be seen from the distributional formulation by first choosing $\bigoplus$ such that $\bigoplus(x_B) = 1$, $\bigoplus(x) = 0$ if $|x - x_B| \geq 1/n$ and the graph of $\bigoplus$ for $|x - x_B| \leq 1/n$ is formed by the straight lines connecting the points $(x_B - 1/n,0)$, $(x_B,1)$, $(x_B + 1/n,0)$ and by then taking the limit $n \longrightarrow \infty$.

4. Heuristic outline of results

Differently from most other mathematical models in population dynamics the Kooijman/Metz model is mathematically challenging even as far as the most elementary mathematical question a mathematical model can raise is concerned: namely whether the model is mathematically correctly posed, i.e. whether the model equations allow the existence and induce the uniqueness of solutions and whether the solutions depend continuously on the data of the model. The last point is of paramount importance for the modelling itself: for the jump in the birth rate at the threshold length l_J is the idealization of a drastic increase of births as well as the fixed birth length l_B is the idealization of a highly concentrated birth size distribution.

In this paper we explain heuristically why well-posedness is a problem for the Kooijman/Metz model and to what extent it can be solved. The precise statement and the proof of much more general results can be found in a forthcoming paper [8].

4.1 The mathematical crux of the Kooijman/Metz model

Actually the idealizations (jump of the birth rate, fixed birth size) which simplify the model biologically are responsible for making well-posedness a nontrivial problem. Note that in all three versions of the Kooijman/Metz model we left the birth rate undefined for $l = l_J$ namely

$$(4.1) \qquad ß(E,a,l) = \begin{cases} 0 & ; \; l < l_J \\ \\ ß_0(E,l) & ; \; l > l_J \end{cases}$$

with $ß_0(E,l)$ being a continuous function of $E, l \geq 0$ and

$B_0(E,l_J) > 0$ being not excluded for appropriate values
of E (See (2.3), (2.4), (2.7)). We did this because there
is no biological indication from observations or from
inherent logic (version 2 excepted) how the birth rate
should be defined at l_J. Actually there are solutions
for both of the extreme cases

$$(4.2) \qquad \tilde{B}(E,a,l) = \begin{cases} 0 & ; \ l < l_J \\ \\ B_0(E,l); & l \geq l_J \end{cases}$$

$$(4.3) \qquad \underset{\sim}{B}(E,a,l) = \begin{cases} 0 & ; \ l \leq l_J \\ \\ B_0(E,l); & l > l_J \end{cases}$$

which are called upper and lower solutions (see [8]).
The ambiguity of the birth rate makes no problem as long
as no length cohort of individuals stops their length
growth at $l = l_J$. (A length cohort is a part of the
population which only contains individuals of identical
length and has non-zero measure.) In other words a length
cohort is a Dirac delta peak of the length distribution
of the population.) Once a length cohort had been formed,
one cannot exclude that it stops at $l = l_J$ because the
growth rate g_2 in all versions of the Kooijman/Metz model
can be zero under appropriate conditions. If this happens,
upper and lower solutions will be different, unless
$B_0(E(t),l_J) = 0$. But the situation is even worse: It is
not clear whether the upper and the lower solutions
are determined uniquely because one cannot (in general)
derive a Lipschitz condition or other conditions which
usually imply uniqueness. Without such conditions unique-
ness fails for ODEs $\dot{y}' = \eta(\dot{y})$ with continuous η
already.

4.2 Continuous dependence of solutions on model data

For the Kooijman/Metz model the continuous dependence
of solutions on the model data is closely linked with
their uniqueness. For we show in [8] that a sequence of
approximating models (i.e. the data of the models
approximate the data of the model under consideration
in an appropriate sense) contains a subsequence of
models the solutions of which (provided that they exist)
converge towards a solution of the approximated model.
(While the solutions of (3.1) and (3.13) converge
strongly, the measures which solve (3.12) only con-
verge in a weak$^{\varkappa}$ sense, i.e. when they integrate con-
tinuous functions with compact support in $[0, \infty)^2$.)If
the approximated model admits only one solution, not
only the solutions of a subsequence of models, but of
the whole sequence must converge towards the solution
of the approximated model.

One might not understand immediately why we bother
about the justification of a troublesome idealizing
model if the idealized model (with a sharply increasing,
but sufficiently smooth birth rate) is much better
behaved mathematically. The point is that, for any
practical application (e.g. for computing solutions
numerically) it is on principle not possible to describe
the 'real' birth rate in sufficient detail. The question
how sensitively the solution depends on the choice of
an approximate birth rate brings us immediately back
to the problem whether the solution of the idealizing
model is the limit of the solutions of approximating
models whose smooth birth rates approximate the jump
in an appropriate sense. Actually this is the way in
which we prove the existence of upper and lower solutions
in [8]: namely we approximate the upper and lower per
capita birth rates $\tilde{\beta}$ and $\underset{\sim}{\beta}$ in (4.2) and (4.3) by smooth
birth rates from above and below respectively. Then we
solve the approximating problems the solutions of which

(after the choice of a subsequence) converge towards
a solution of the approximated problem. The approxi-
mating problems can be solved by a standard application
of Banach's fixed point principle.

4.3 Uniqueness of solutions

So uniqueness of solutions remains as the crucial
problem and, as we have already seen, might not hold
in general. We remember that the trouble comes from
the fact that the birth rate jumps and is not defined
at $l = l_J$ and that it cannot be excluded a priori
that a length cohort of individuals stops at length l_J.
Finding conditions which induce uniqueness of solutions
now amounts to discovering relations between the birth
and the growth rate, which have one of the following
two effects:

i)   They actually exclude that length cohorts are
       formed.

ii)   The ambiguity of the birth rate β at $l = l_J$
       is at least removed under environmental conditions
       E which arrest length growth at $l = l_J$.

Each version of the Kooijman/Metz model requires a
specific approach.

Version 3   We have already pointed out in section 2.3
that β_0 is defined in such a way that

(4.4) $\beta_0(E, l_J) = 0$ iff $g_2(E, l_J) = 0$.

This involves that individuals that have just passed l_J
only reproduce if they continue to grow. So, if a length
cohort stops at $l = l_J$, the jump and the ambiguity in
the birth rate (4.1) are removed. So it is heuristically
plausible and will be proved rigorously in [8] that the
third version of the Kooijman/Metz model has a unique
solution.

<u>Version 2</u>   At a first glance this version gives a lot
of freedom to an individual of length l_J in allocating
its assimilation energy between growth and reproduction.
The individual only has to satisfy the constraints that
the portion going into growth lies between $[\kappa\hat{E} - l_J]_+ l_J^2$
and $[\tilde{E} - l_J]_+ l_J^2$ and both portions sum to $[\tilde{E} - l_J]_+ l_J^2$.
But there is some inherent logic how the allocation
should be done.

<u>Case 1</u>: $\tilde{E} \leq l_J$

Then no energy is available both for reproduction and
growth, so

$$ß(E,a,l_J) = 0 = ß_0(E,l_J)$$

$$g_2(E,a,l_J) = 0 .$$

<u>Case 2</u>: $\tilde{E} > l_J$, $\kappa\tilde{E} \leq l_J$

In this situation the individual could decide to put
energy into growth, but there is no use in doing so,
because, for any $l > l_J$, $g_2(E,a,l) = 0$ such that
growth beyond l_J is impossible; so it will channel all
the energy which is left after covering the maintenance
costs into reproduction, thus

$$ß(E,a,l_J) = \tilde{E} - l_J = ß_0(E,l_J)$$

$$g_2(E,a,l_J) = 0 .$$

<u>Case 3</u>: $\kappa\tilde{E} > l_J$

In this situation the individual continues to grow in-
evitably and immediately is larger than l_J such that it
does not matter how g_2 and $ß$ are defined in this case.

Note that in all three cases $\beta = \widetilde{\beta}$ with $\widetilde{\beta}$ from (4.2) (i.e. the upper per capita birth rate) is the reasonable choice. So upper solutions appear to be the relevant ones. Actually we prove in [8] that there is a unique upper solution to version 2. Continuous dependence of solutions on data, however, only holds in a restricted sense, but the restriction appears to be quite natural: Version 2 differs from the other versions by the following allocation law:

$$(4.5) \qquad wl^2 g_2(E,a,l) + \beta(E,a,l) = wl^2 [\widetilde{E} - l]_+$$

for $l \neq l_J$.

If the per capita growth and reproduction rate are approximated by continuous ones, then the approximating rates should satisfy the same allocation law in order to make biological sense. Under this restriction (actually it can be weakened) the solutions of the approximating models converge towards the upper solution of the approximated model. See [8].

<u>Version 1</u> First we observe that neither (4.4) nor (4.5) hold. In particular we realize that, under appropriate environmental conditions, individuals may reach the threshold length l_J with the growth rate g_2 slowing down to zero, but $\beta_0(E,l_J) > 0$. So the only option which is left to induce uniqueness consists in excluding length cohorts. As the growth rate g_2 is a Lipschitz function of length in version 2, two individuals which have a different length at time s will have a different length at all later times. So length cohorts which might stop at $l = l_J$ originate from two sources:

i)   There is already a length cohort of individuals with some length $l \leq l_J$ at the beginning.

ii) Individuals accumulate at the birth length l_B.

The second happens if individuals are born which cannot immediately start growing. This is excluded by assuming

$$\beta_0(E,l) = 0 \quad \text{for all} \quad l \geq l_J$$

(4.6)

$$\text{if} \quad g_2(E,0,l_B) = 0 .$$

Looking closely to the definitions of β_0 and g_2 in (2.2) and (2.4) we find that (4.6) is satisfied if and only if

(4.7) $\quad \kappa l_J \geq l_B .$

This relation seems to hold for Daphnia magna because Kooijman and Metz [7] estimated $\kappa = 1/3$, $l_J = 2.5$ mm, $l_B = 0.8$ mm. But the (obviously necessary) assumption (i) that the population contains no length cohorts with some length $l \leq l_J$ at time 0 is a severe restriction. If a length cohort is present at time $t = 0$ the original version of the Kooijman/Metz model is only a proper idealization after the cohort has died out.

Remark   Actually length cohorts only matter if length growth stops when the cohort reaches l_J. If you have complete control over the environment, you can easily regulate it in such a way that this really happens. This already causes enough concern because version 1 should also be mathematically well-posed if the population does not couple back to the environment via equation (3.13). But even with the feed back one can readily adjust the initial values and the parameters in such a way that starting with a length cohort growth stops for a while when the cohort reaches length l_J. Note that in version 1 and 3 of the Kooijman/Metz model length growth (once it has started) never really stops again, if the environmental conditions are constant. A stop of length growth is possible, however, if the environmental conditions deteriorate.

5. Comparison of the three versions of the Kooijman/Metz model

Mathematical models in population dynamics are inevitably gross oversimplifications of reality with many idealizations and even conceptual inconsistencies. A mathematical study like this cannot decide, of course, whether a model is biologically appropriate, but it can help to identify inconsistencies which should be taken seriously (by revealing the mathematical pathologies they generate) and may give some advice for possible modifications and pinpoint open biological questions.

As for conceptional simplicity and consistency version 2 is superior to the other two versions. As we have seen heuristically in the previous section and will prove rigorously in [8], version 2 is mathematically well-posed. The length growth curves which Kooijman and Metz observed for Daphnia magna [6,7], however, seem to agree more with the assumptions of version 1 and 3 that juveniles and adults channel the same portion of energy into growth than with the assumption of version 2 that energy is switched from growth to reproduction, if the individual becomes mature. But maybe the last word has not yet been said in this matter. In version 1 (the original Kooijman/ Metz model) uniqueness of solutions may fail, if initial populations are admitted which contain length cohorts (i.e. have a Dirac delta peak in the length distribution). In this case version 1 can only be considered a well-founded idealization after the initial population has died out. Version 3 modifies the reproduction law of version 1 such that the model is well-founded. We now offer some speculation concerning the apparent synchronization between growth and maturation which explains the inconsistency of version 1 and supports the modification (2.7) with $\alpha = 3$.

Some speculation about the energy allocation of Daphnia magna

The original Kooijman/Metz model (i.e. version 1) leaves the question open what juveniles do with the assimilation energy that adults put into reproduction. As a waste of energy makes no biological sense, Kooijman (personal communication) has the idea that juveniles put this energy into maturation with interpreting maturation as an increase of the complexity of the tissue, while growth is a simple enlargement of already existing body structure. But energy is not only needed for increasing size and complexity of the tissue, but already for maintaining the status quo, so that further progress can only be made, if the maintenance needs have been covered. In view of this interpretation version 1 implicitly assumes that the maintenance costs of energy only depend on the size and not on the complexity of the body and are sub-tracted only from the energy allocated to growth as long as this is sufficient. (See the growth rate g_2 in (2.2) and the per capita reproduction law β_0 in (2.4).) The observation that under all food conditions maturity is achieved at the fixed length $l_J = 2.5$ mm suggests, however, that growth and maturation are perfectly syn-chronized in juveniles, i.e. growth stops if and only if . maturation stops. This seems only to be possible if maintenance costs are not only subtracted from the energy determined for growth, but also from the energy determined for maturation. This does not contradict the observation that adults can reproduce without growing, if we assume that maturation stops when the individual passes the threshold length l_J. Let us make this idea more pre-cise and calculate the maintenance costs of an individual of length $l < l_J$ under the assumption that the length growth rate is given by (2.2), namely $g_2(E,a,l) = [k\tilde{E} - l]_+$, and the assimilation energy available is $\tilde{E}l^2$. Then growth and, simultaneously, maturation stop, if $k\tilde{E} = l$,

i.e. $\tilde{E}l^2 = \frac{1}{k}l^3$. Since at that moment the available energy just covers the maintenance costs, we conclude that the maintenance costs of an individual of length $l < l_J$ amount to $\frac{1}{k}l^3$. From the growth rate g_2 we derive that maintenance costs l^3 are subtracted from the energy allocated to growth. Hence the remaining maintenance costs $(\frac{1}{k} - 1)l^3$ are subtracted from the energy allocated to maturation. It is suggestive to associate the maintenance costs l^3 with the size and the maintenance costs $(\frac{1}{k} - 1)l^3$ with the maturity of the individual.
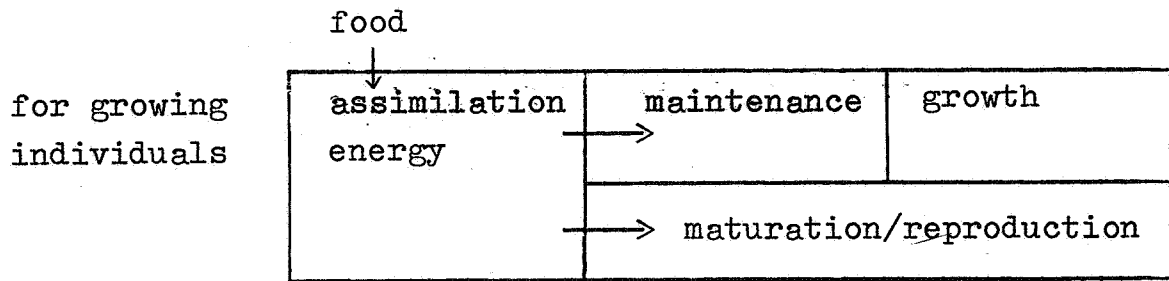
If this relation holds for any length $l < l_J$, it should extend to $l = l_J$ such that an individual of length l_J has maintenance costs $(\frac{1}{k} - 1)l_J^3$ which are associated with its maturity. Assuming that the maturity of mature individuals, i.e. of length $l > l_J$, does not increase we conclude that the maintenance costs associated with complexity still amount to $(\frac{1}{k} - 1)l_J^3$. So the assimilation energy which is available after all the maintenance costs have been covered amounts to

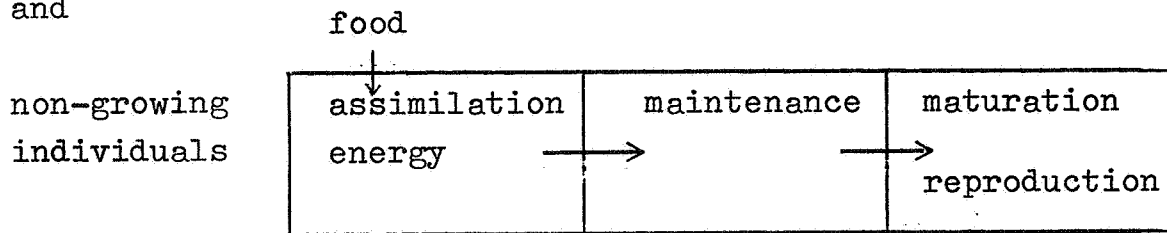$$[\tilde{E}l^2 - l^3 - (\frac{1}{k} - 1)\, l_J^3\,]_+ .$$

Subtracting the energy put into growth we obtain the energy put into reproduction, namely

$$(5.1) \qquad B_0(\tilde{E},l) = [\tilde{E}l^2 - l^3 - (\frac{1}{k} - 1)l_J^3\,]_+$$

$$- [k\tilde{E} - l^3]_+ .$$

With these new ideas about the energy allocation of Daphnia magna the allocation diagrams of the original Kooijman/Metz model

food

for growing individuals

| assimilation energy | maintenance ⟶ | growth |
| ⟶ maturation/reproduction |||

and

food

non-growing individuals

| assimilation energy ⟶ | maintenance ⟶ | maturation ⟶ reproduction |

can be unified by the diagram

food

| assimilation energy ⟶ | maintenance costs associated with size ⟶ | growth ⟶ |
| | maintenance costs associated with complexity ⟶ | maturation/ reproduction ⟶ |
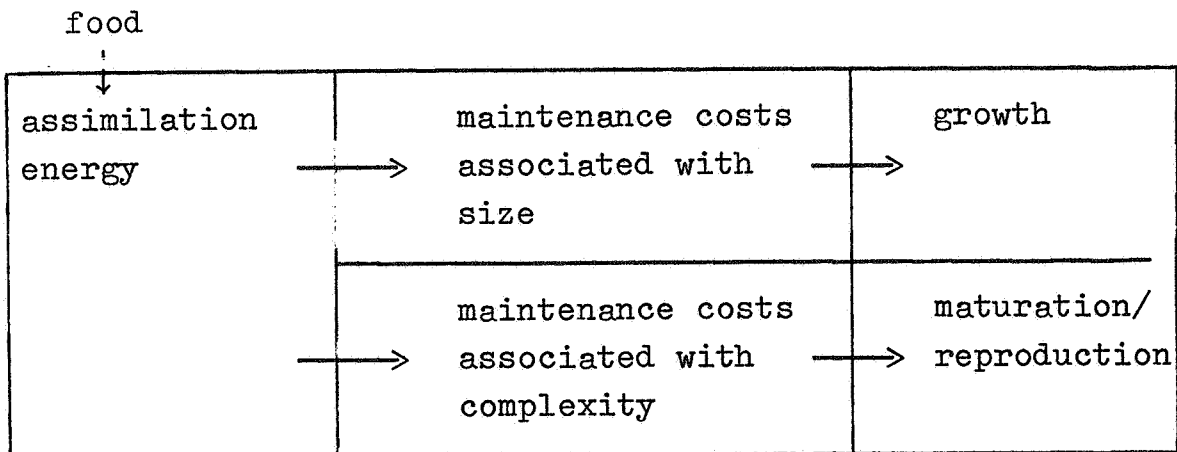
The switch from the first to the second diagram in the Kooijman/Metz model is replaced by the assumption that the maintenance costs due to maturity stagnate after the individual has become mature (i.e. has passed the threshold size), while the maintenance costs associated with size still increase with further growth.

It remains mysterious, however, how Daphnia magna should manage to cover the maintenance costs due to size just from the energy allocated to growth and to cover the costs due to maturity just from the energy allocated to maturation/reproduction. Here a deeper understanding would be helpful by which biological mechanisms the

assimilation energy is allocated to the different
physiological functions. It might appear even more
mysterious in which way the perfect synchronization
of growth and maturation is achieved in juveniles,
if the assimilation energy is partitioned from the
very beginning (i.e. before the maintenance costs
have been covered). The synchronization would not be
astonishing, if the individual covers the maintenance
costs first (wherever they come from) and does the
allocation to growth and maturation/reproduction
afterwards. But such a hypothesis involves that adults
only reproduce if they grow, in contrast to the obser-
vations. There is an easy mathematical explanation for
this mystery, however. We recall that, in versions 1
and 3 of the Kooijman/Metz model the length growth of
an individual waterflea is described by

$$(5.2) \qquad \overset{\bullet}{l} = [k\tilde{E} - l]_{+}$$

Here E is the assimilation energy which an individual
wins from its food per unit area of body surface l^2.
Then

$$(5.3) \qquad (l^3)^{\bullet} = 3 \, [k\tilde{E}l^2 - l^3]_{+}$$

and $\tilde{E}l^2$ is the assimilation energy the individual has
available. As before k is the fraction of energy which
is channelled into growth. In this scaling l^3 are the
maintenance costs which are due to the size l^3. We
assume that maturation is described by a similar law:

$$(5.4) \qquad \overset{\bullet}{m} = [(1 - k) \, \tilde{E}l^2 - \delta m]_{+} \, .$$

Here m is some measure for the maturity of the individual.
δm are the maintenance costs due to the maturity of the
individual. We easily find that the set $\delta_{km} = (1 - k)l^3$
is invariant under the flow generated by (5.3), (5.4),

if $\tilde{\delta} = 3$. The condition $\tilde{\delta} = 3$ has a biological meaning:
For 3 is the relation between the energy needed to in-
crease the volume for one volume unit (in the right
scaling) and the energy needed to increase the maturity
for one maturity unit. $\tilde{\delta}$ is the relation between the
energy cost of maintaining one volume unit and the energy
cost of maintaining one maturity unit. $\tilde{\delta} = 3$ means that
these relations are just the same.

Let us assume that

$$(5.5) \qquad \tilde{\delta} = 3 \quad \text{and} \quad 3km_B = (1 - k)l_B^3$$

with m_B and l_B denoting maturity and length at birth.
Then

$$(5.6) \qquad 3km(t) = (1 - k)(l(t))^3$$

as long as $l(t) \leq l_J$. Fitting (5.6) into (5.3) and
(5.4) we obtain

$$(5.7) \qquad (l^3)^\bullet = 3k[\tilde{E}l^2 - l^3 - 3m]_+$$

$$(5.8) \qquad \overset{\bullet}{m} = (1 - k)[\tilde{E}l^2 - l^3 - 3m]_+ .$$

So, if (5.5) is satisfied, (5.3) and (5.4) induce a
perfect synchronization of maturation and growth. If
growth and maturation are discriminated, it goes without
saying that an individual becomes mature by passing a
fixed threshold maturity m_J and not some threshold size.
But due to the synchronization of both processes this
amounts to the same and so an individual becomes mature
just when it passes the threshold length l_J satisfying
$3km_J = (1-k)l_J^3$. Although the assimilation energy is
partitioned first and the maintenance costs due to size
are covered from the energy allocated to growth and the
maintenance costs due to maturity are covered from the
energy allocated to maturation, growth and maturation

behave as if the total maintenance costs were covered
from the total energy available and the energy were
allocated between growth and maturation only afterwards.
It is just a question of finding the appropriate relation
between the size and the maturity of a neonate.

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