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POPULATION DYNAMICS ON BASIS OF BUDGETS

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SUMMARY

This paper describes a simple and general model for the feeding, storage, growth and reproduction of an ectotherm as functions of a possibly fluctuating food density at constant temperature. The model assumes a hyperbolic functional response, a fixed ratio between ingestion and assimilation rate, and a storage that is proportional to assimilation rate and weight when food supply has been constant for some time; it further assumes, a fixed ratio between energy spent on reproduction and growth plus maintenance at constant food density, a von Bertalanffy growth at constant food density, and a juvenile stage that ends as soon as the animal attains sufficient weight. In the present formulation, the storage dynamics is central. It describes the gradual increase in respiration when food density is suddenly increased, as well as the gradual decrease in respiration rate and time remaining until death when the animal is starved. The model is shown to fit quite well the available data on feeding, respiration, growth, reproduction of female Daphnia magna and their survival time when deprived of food. It explains the occurrence of males in this parthenogenetically reproducing species. The model can also be used to describe microbial dynamics, if it is assumed that division occurs as soon as a certain cell size has been attained. The relationship between the present model and existing descriptions on the substrate-limited growth of bacteria and the nutrient and light-limited growth of algae has been evaluated. They turn out to be special cases of the present model, which explains some observed deviations from existing theories.

INTRODUCTION

The purpose of this paper is to describe the growth and reproduction behaviour of individuals by a model that can serve as a basis for studies in population dynamics. The literature on this subject, although vast, largely falls into two categories. One concerns models that incorporate a great deal of biological detail, and so do not allow of studies in population dynamics other than through computer simulation. The other concerns simple models allowing of some mathematical analysis, but conflicting with known biological facts. The suitability of computer simulation as a research tool being limited, the first type of model can hardly be expected to be capable of tracking down general phenomena in population dynamics, and phenomena predicted by the second type of model may not be relevant.

More progress in the understanding of population dynamics is to be expected from relatively simple models involving just enough biology to fit the data in the literature on physiological ecology. In this paper an attempt has been made to formulate such a model on basis of a simple energy budget of an ectotherm. It extends the ideas given in Kooijman & Metz, 1984, to include storage considerations. Evidence from experiments with the water flea, Daphnia magna, will be adduced in support of the model, the formulation of which has nevertheless been kept as general as possible. However, no attempt has been made to cover all literature on the subject. The literature on marine poikilotherms has been reviewed by Conover, 1978, who cites some 1100 references, and more generally by Bradfield & Llewellyn, 1982. In the literature, several attempt have been made to model the growth process in Daphnia, but no description covers storage in addition to being explicit c.f. Wulff, 1980 and Paloheimo et al., 1982.

A further feature of the present model is that with minor adaptations it can also be used for unicellulars. The understanding of the substrate-limited growth of bacteria and the nutrient and light-limited growth of algae has recently made rapid progress. It will be shown how the proposed formulation relates to some of this work, and how it explains some experimental results deviating from existing theories on the dynamics of microbes. The successful concept of cell quota in the description of nutrient contents of algal cells (see Droop, 1983, for a review) is a special case of the wider concept of storage introduced here. The discussion will be restricted to the situation of constant temperature. A list of frequently used symbols is given in the appendix.

ENERGY BUDGETS OF ECTOTHERMS

This discussion is based on those two state variables of the organism which seem to be the most relevant viz. storage and 'weight'. The latter term is intended to be the measure of the size of the organism, e.g. volume, a cubic length measure, or wet weight; for small aquatic animals, wet weight is hard to measure directly, and most of the literature on these animals uses dry weight. The biomass of microbes is often indicated by their carbon content. These two weight measures are usually related to wet weight by power laws. Porter et al., 1983, state that the dry weight of daphnids is proportional to length to the power 2.39. Strathmann, 1966, state that the carbon content of diatoms is proportional to their volume to the power 0.758, and for other algae to the power 0.866. Energy storage materials usually consist of proteins, lipids and carbohydrates. When food is abundant, they contribute considerably to carbon content and to dry weight. Since the amount of storage materials depends on the availability of food, the abovementioned conversions to size do not make sense if they are not related to the feeding status of the organism. This problem is less relevant for the wet weight of aquatic animals, because storage materials usually replace water. For animals that do not change shape very much during their life, like daphnids, a cubic length measure seems to be the most appropriate measure of size, because it can be measured rapidly without harm to the animals. We shall assume, therefore, that energy and nutrient storage are related to the chemical composition of an individual, and weight to its size.

Figure 1 shows a diagram of the energy flow, in it simplest form, through an ectothermal individual. The pathways indicated by the numbered arrows will be discussed briefly in the sections numbered identically.

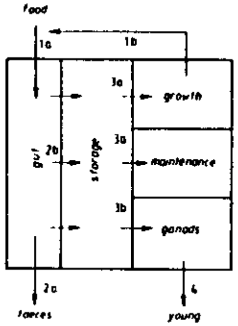

Fig. 1. The energy or nutrient flow through an individual

1. The ingestion rate, $\dot{i}$, tends to increase with the food density, X, and weight, W, of the animal. When starved animals are fed, they often ingest at a higher rate (see e.g. Watts & Young, 1980, for Daphnia feeding on algae), so ingestion rate may also depend on gut content. However, this fast process (,starved daphnids are able to fill their guts within 7.5 minutes, see Geller, 1975,) will not be incorporated in our model.

1a. For a fixed weight, the ingestion rate as a function of food density is known as the functional response, which frequently takes the form of a hyperbolic function. See Kooijman & Metz, 1984 for Daphnia. In symbols, we have $\dot{i} = X/(1/\dot{F}_m + X/\dot{i}_m)$, where X is the food density, $\dot{i}_m$ the maximum ingestion rate, and $\dot{F}_m$ the filtering or searching rate in the absence of food.

When offered different food items, individuals usually select for type and size. We shall briefly focus on the latter, because it provides an argument for the maximum ingestion being determined by the digestion rate; i.e. expressed as carbon content, the maximum ingestion rate is independent of the size of food items, provided that their chemical composition is similar. Frost, 1972, found this to be the case for copepods fed on species of diatoms of different cell sizes. On the other hand, Geller, 1975, found that, when the maximum ingestion rate is expressed in terms of ingested food volume instead of its carbon content, it is independent of the cell size of six widely different species of food algae. This may be a coincidence, merely due to one species of alga being less digestible than another. If X(V) denotes the density of food particles of volume V, and P(V) the ingestion probability of an item of volume V in the filtered water in the area searched, the ingestion rate $\dot{i}(V)$ of particles of volume V becomes $\dot{i}(V) = PX/[1/\dot{F}_m + \int_V PX/\dot{i}_m]$, where the maximum ingestion rate $\dot{i}_m$ is proportional to a weighted integral over the size distribution, of ingested particles, $\int_V PX/\int_V PXC$, where C(V) is the carbon content of a particle of volume V. An efficient filter feeder (e.g. Daphnia) feeding on a suitable algal or bacterial species will ingest all particles, so P(V)=1. For copepods, on the other hand, which capture their food particles more actively and tend to select the larger algae (Strickler, 1982), the results of Frost, 1972, can be interpreted to mean that the catching probability function increases with particle volume. If such is the case, it will probably also be a function of the size of the animal itself.

When the food contains several types of particles, the catch function may also depend on the (relative) abundances of the types, as has been found by DeMott, 1982, for Bosmina feeding on mixtures of algae and bacteria.

1b. Obviously, the ingestion rate increases with the size of organism. For daphnids, which do not change very much in shape during growth, it is about proportional to $W^{2/3}$ (Kooijman & Metz, 1984). This relation is plausible when we realize that the maximum filtering rate, i.e. $\dot{F}_m = (d\dot{I})/(dX)$ for $X = 0$, probably depends on the surface area of the filtering apparatus, and the maximum ingestion rate, $\dot{I}_m$, on the surface area of the gut. For microbes, $\dot{F}_m$ is related to the probability of a nutrient particle coming into contact with a free site on its surface, and $\dot{I}_m$ to the maximum number of binding sites; both magnitudes are related to surface area.

2a. The gut has the function of a buffer, frequently fortified by the presence of a stomach. The nutritional gains from the ingested food can be assumed to be about proportional to a moving average of the ingestion rate. For small-particle feeders like daphnids, the residence time of a food particle has been found to be between 28 and 54 minutes at 15°C, depending on the algal type (Geller, 1975). Because of these short residence times, we will neglect the buffer function of the gut, which is justified if food density does not change too rapidly. The energetic gain from the food, the so-called assimilation energy $\dot{A}$ will, for this type of animal, assumed to be proportional to ingestion rate, and we shall disregard the possibility of digestion being less efficient at high ingestion rates as has been postulated by Paloheimo et al., 1982.

2b. So $\dot{A} = [\dot{A}_m]\, W^{2/3} f$, where $f = X/(K+X)$, the shape parameter of the functional response curve, $K = \dot{I}_m/\dot{F}_m$, being independent of the weight, W, of the animal, and $[\dot{A}_m]$ being proportional to $\dot{I}_m/W^{2/3}$, where the proportionality factor involves the energy gain per unit weight of particles. In microbiological studies K has become known as the saturation constant.

3. The observation that at a constant food density X, the growth curve for Daphnia magna closely resembles a von Bertalanffy curve (Kooijman & Metz, 1984) suggests that the decline in growth with age is due to the increasing metabolic needs of the animal. This is confirmed by the results of the feeding experiments with Daphnia reported in Fig. 2. In these experiments the length of the animals was monitored during growth at two levels of chlorella densities which were alternated after one, two or three weeks at 20°C. The curves without shift represent least squares adaptations of the von Bertalanffy growth curves. The curves in the other figures represent the expected growth for animals changing their growth regime momentarily to the same parameters as the ones without shift. We can conclude that daphnids retain their ability to grow, and that larger daphnids adapt more gradually to a new growth regime. This will be explained by a weight related storage.

Full-grown animals still reproduce abundantly, suggesting that at constant food density the storage utilization rate $\dot{C}$ falls into a part $\kappa\dot{C}$ spent on growth and routine metabolism, and a part $(1-\kappa)\dot{C}$ spent on reproduction. The balance equation for the storage S is $\dot{S} = \dot{A} - \dot{C}$.

3a. Growth is given by $\eta\dot{W} = \kappa\dot{C} - \dot{M}$, where η is the energy requirement per unit increase of weight, and $\dot{M} = \zeta W$ the routine metabolic rate, which is taken to be proportional to weight. Since $\dot{C}$ is an unknown function of S and W, we substitute $\dot{C} = \dot{A} - \dot{S}$ and assume that, at constant food density, the storage, which depends on W, is in a pseudo-equilibrium S^*, i.e. it can be written as a function of f and W, so $\dot{W} = (\kappa\dot{A} - \dot{M}) / (\eta + \kappa(dS^*)/(dW))$.

If growth is of the von Bertalanffy type, i.e. $\dot{W}$ is a weighed difference between $W^{2/3}$ and W, S^* has to be proportional to W. We assume that it is also proportional to f, giving $S^* = [S_m]\, fW$, where the parameter $[S_m]$ can be interpreted as the weight-specific maximum storage. Substitution of this equilibrium storage in the growth equation gives the growth rate as a function of f and W. Following the diagram of Fig. 1, however, we do not want it as a function of f, but as one of the state variable S. The observations in Fig. 2 also show that a sudden change in f does not produce a sudden change in $\dot{W}$. We therefore substitute $f = [S]/[S_m]$, where [S] is the weight-specific storage, i.e. $[S] = S/W$, which gives

$$\dot{W} = \frac{[S]}{[S] + \eta/\kappa} \frac{[\dot{A}_m]}{[S_m]} W^{2/3} - \frac{\zeta/\kappa}{[S] + \eta/\kappa} W$$

So the maximum weight W_m of an adult is given by $W_m^{1/3} = \kappa[\dot{A}_m]/\zeta$, and the maximum growth rate by $\dot{W}_m = (4/27)\, W_m\, (\zeta/\kappa)/([S_m] + \eta/\kappa)$, which is reached in animals of weight W_m 8/27 for $f = 1$.

The storage utilization rate now becomes

$$\dot{C} = \frac{[S]}{[S] + \eta/\kappa} \left\{ \frac{\eta}{\kappa} \frac{[\dot{A}_m]}{[S_m]} W^{2/3} + \frac{\zeta}{\kappa} W \right\}$$

If we substitute this in the storage balance equation, we have

$$\dot{S} = [\dot{A}_m] W^{2/3} \left\{ f - \frac{1}{[S_m]} \frac{[S]\eta/\kappa}{[S] + \eta/\kappa} \right\} - W \frac{[S]\,\zeta/\kappa}{[S] + \eta/\kappa}$$

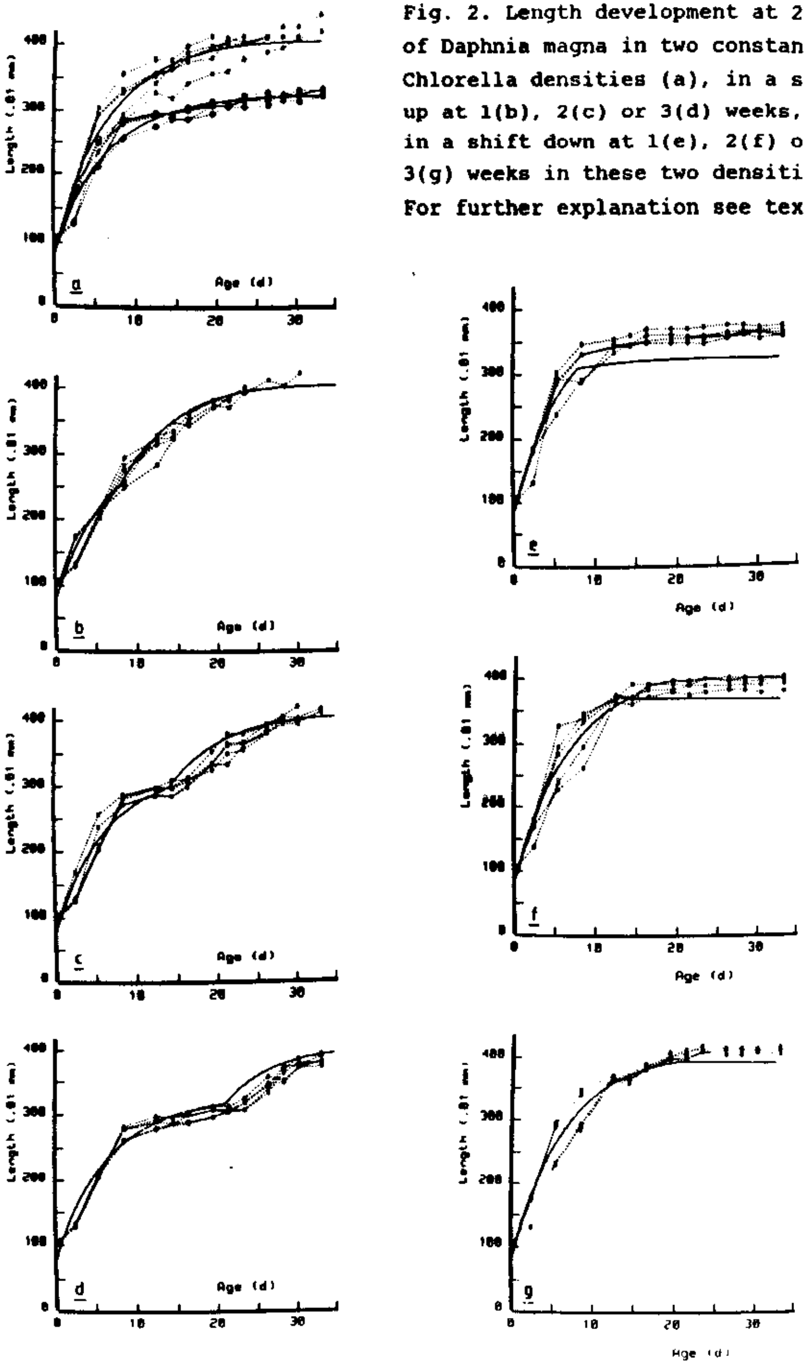

Fig. 2. Length development at 20°C of Daphnia magna in two constant Chlorella densities (a), in a shift up at 1(b), 2(c) or 3(d) weeks, and in a shift down at 1(e), 2(f) or 3(g) weeks in these two densities. For further explanation see text.

When given in the dynamics of the weight-specific storage, $[\dot{S}] = \dot{S}/W - S\dot{W}/W^2$, this simplifies to $[\dot{S}] = [\dot{A}_m]W^{-1/3}\{f - [S]/[S_m]\}$.
If storage decreases to less than $S = W^{4/3}([S_m]/[\dot{A}_m])\,\zeta/\kappa$ the animal can no longer fulfil its metabolic needs in this regime, because $\kappa\dot{C} < \dot{M}$. The results presented in Fig. 2 suggest that κ will increase to $\kappa\dot{C} = \dot{M}$, from which follows that $\kappa = (\zeta/[S])([S_m]/[\dot{A}_m])W^{1/3}$, and so $\dot{C} = [S]([\dot{A}_m]/[S_m])W^{2/3}$.
Under poor feeding conditions, therefore, the animal decreases its utilization rate and ceases growing. Without any food uptake, the storage is emptied by a first-order process down to $S = W^{4/3}\,\zeta\,[S_m]/[\dot{A}_m]$, corresponding to $\dot{C} = \dot{M}$. It will then die of starvation. In the non-growth region of the storage, where W is a constant, its balance equation therefore is $\dot{S} = [\dot{A}_m]W^{2/3}\{f-[S]/[S_m]\}$.
When given in the dynamics of the weight-specific storage, this again gives $[\dot{S}] = [\dot{A}_m]W^{-1/3}\{f - [S]/[S_m]\}$, which means that the dynamics of the weight-specific storage is the same whether the animals are growing or not. The only difference is that maintenance is at the expense of growth when the animals are growing, and of reproduction when they are not.

3b. As stated above, the energy spent on reproduction equals $(1-\kappa)\dot{C}$. In daphnids, the energy seems to be converted into young in female animals if the weight of the animals exceeds a treshold value W_J, (Kooijman & Metz, 1984). At this weight, there is no obvious change in growth. (The von Bertalanffy curves fit well in the entire weight range). This suggests that during the pre-reproductive period, the gonads receive an inflow of energy for their ripening.

4. Daphnids normally reproduce parthenogenetically; female diploid adults beget female diploid offspring without intervention by males (Taub, 1982). The occurrence of males will be discussed in the section on starvation. The reproduction process in daphnids is coupled with the moulting cycle. The latter depends on temperature, but not on the feeding status. At 20°C Daphnia magna moults every 2 or 3 days. Just after moulting, eggs are deposited in the brood pouch and develop without food supply (Green, 1956) into young, which are released just before moulting. During this period the adult restores its energy reserves, so the energy chanelled into reproduction can be regarded as being constant (Tessier & Goulden, 1982). If, at constant food density, growth is of the von Bertalanffy type from birth onwards the weight-specific storage of the young should equal that of the adult.

Tessier et al., 1983, actually observed that the storage in the form of triglycerides in young depends on the adult's feeding success; young born of well-fed adults survived for twice as long when starved as did the offspring of starved adults. So the energy investment per young is $W_b\ (\omega + [S])$, where the parameter ω can be interpreted as the weight specific energy requirement for the formation of offspring tissue, W_b being weight of a young at birth (The length of Daphnia magna at birth is 0.8 mm).

The reproduction rate for growing animals now becomes

$$\dot{R} = \frac{1-\kappa}{W_b}\ \frac{1}{[S] + \omega}\ \frac{[S]}{[S] + \eta/\kappa}\ \{ \frac{[\dot{A}_m]}{[S_m]}\ \frac{\eta}{\kappa}\ W^{2/3} + \frac{\zeta}{\kappa}\ W\}$$

For non-growing ones, we have

$$\dot{R} = \frac{1}{W_b}\ \frac{1}{[S] + \omega}\ \{ [S]\ \frac{[\dot{A}_m]}{[S_m]}\ W^{2/3} - \zeta\ W\}$$

The maximum reproduction rate, which is reached for animals of weight W_m for $f = 1$, then becomes $\dot{R}_m = (1-\kappa)(\zeta/\kappa)(W_m/W_b)/([S_m]+\omega)$.

We have now completed the quantitative description of the arrows in Fig. 1, in terms of the state variables weight, W, and storage S. We can summarize this description in the state space representation, given in Fig. 3. At constant food density, an individual has weight W_b at birth and moves along a line through the origin, as indicated, but does not leave the growth region. This situation will be discussed in the next section. More generally, we can state that, if a population experiences a period of constant food density, all individuals will gather on a line through the origin, regardless of their food history. If the population has experienced higher food densities in the past, there may be a group weighing more than $(f\kappa[\dot{A}_m]/\zeta)^3$, unable to grow, but still able to reproduce. For low food densities, $f < \kappa$, there may be another group weighing more than $(f[\dot{A}_m]/\zeta)^3$ that will eventually die of starvation. This situation will also be briefly discussed. On basis of the (ultimate) reproduction and survival behaviour at fixed food densities, we can classify them into the categories mentioned in Fig. 3. Lines of equal growth and reproduction in the state space are given in Fig. 4.

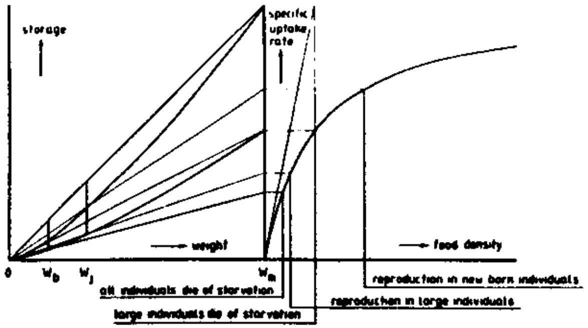

Fig. 3 State space representation of an ectotherm. For an increasing storage at given weight, there is a region in which an animal cannot exist due to starvation (upperbound $S=\kappa[S_m]W^{4/3}/W_m^{1/3}$), a no-growth region (upperbound $S=[S_m]W^{4/3}/W_m^{1/3}$), a growth region (upperbound $S=[S_m]W$) and a region an animal can not reach. For further explanation see text. In this figure, the value for κ has been chosen 1/2.

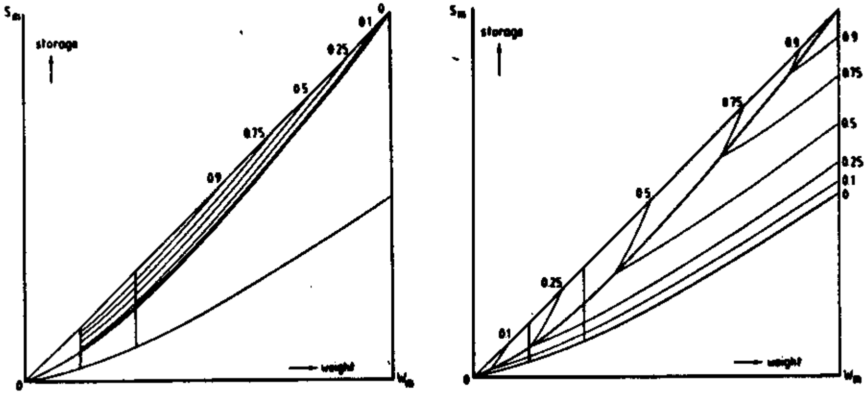

Fig. 4. Lines of equal growth (left) and reproduction (right). In this figures, the following choices have been made: $\kappa=1/2$, $[S_m]\ \kappa/\eta=10$ and $[S_m]/\omega=5$. The numbers indicated along the lines are fractions of maximum growth and reproduction.

SOME PHENOMENA UNDER CONDITIONS OF CONSTANT FOOD DENSITY

Utilization rate can be measured indirectly as respiration rate. It is not at all clear, however how oxygen consumption and carbon dioxide production rates exactly relate to the energy flows under consideration, even for animals with empty guts. Storage materials are usually classified as proteins, glycogen and triglycerides. Growth and reproduction result in formation of tissues also consisting of these components, possibly in other proportions. Although the preservation of energy and oxygen, nitrogen and carbon may be negligible in comparison with the amounts of storage materials used during the measurement of the respiration rate, the energy involved in this preservation process is not. The energy channelled into reproduction can be quite substantial, as has been found for crustaceans (Kmeleva, 1972 gives 0.5 time the utilization rate) and especially for daphnids (Richman, 1958, gives up to 0.8 times the utilization rate).

The energy gain from the utilization of storage materials depends on their composition. For aquatic animals Brafield & Llewellyn, 1982, give the conversion heat loss in joules =
(11.16x mg O_2 cons.) + (2.62x mg CO_2 prod.) - (9.41x mg NH_3 prod.).

If the composition of storage material remains the same, the conversion of oxygen consumption into energy involves a constant factor.

This means that at constant food density, the respiration rate can be written as $aW^{2/3} + bW$, where the quotient of the regression coefficients b/a equals $(\zeta/\eta)\ [S_m]/[\dot{A}_m]$, see Fig. 5. The fit is quite satisfactory.

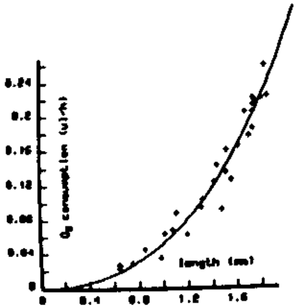

Fig. 5. Respiration rate of Daphnia pulex with few eggs at 20°C as a function of length. Data are from Richman, 1958, table 5. The fitted curve is $0.0336\ L^2 + 0.01845\ L^3$, and is indistinguishable from the curve $0.0516\ L^{2.437}$.

The curve usually fitted to respiration size data is the allometric one, aW^b, see e.g. Richman, 1958, who found b=0.88 and Kersting & V.d. Leeuw-Leeghwater, 1976, who found b=0.82 for Daphnia pulex. As is obvious from Fig. 5, the data can never tell the difference between the two curves. See Kooijman, 1984, for a more extended discussion.

At constant food density, the equilibrium storage equals $[S_m]fW$, for which the growth equation can be solved, resulting in

$$W^{1/3}(a) = W_\infty^{1/3}\ (1-be^{-\dot{\gamma}a}),\ \text{where } W_\infty^{1/3} = \kappa\ f\ [\dot{A}_m]/\ \zeta,\ b = 1-W_b^{1/3}/W_\infty^{1/3},$$

$\dot{\gamma} = (\zeta/\kappa)/\{3(\eta/\kappa + [S_m]f)\}$ and a the age.

The rate $\dot{\gamma}$ therefore decreases with increasing food density, owing to the presence of a storage. Reanalysis of the data on daphnid growth at different chlorella densities of Kooijman & Metz, 1984, reveals a significantly increased goodness of fit, compared with the situation without storage, $[S_m]=0$; see Fig. 6. Note that the inverse rate $\dot{\gamma}$ depends linearly on the asymptotic length: $1/\dot{\gamma} = 3\eta/\zeta + 3([S_m]/[\dot{A}_m])W_\infty^{1/3}$. The quotient of the slope parameter and the intercept, $(\zeta/\eta)\ [S_m]/[\dot{A}_m]$, should equal the quotient of the regression coefficients corresponding to W and $W^{2/3}$ respectively for the respiration rate as a function of weight, as we have seen before.

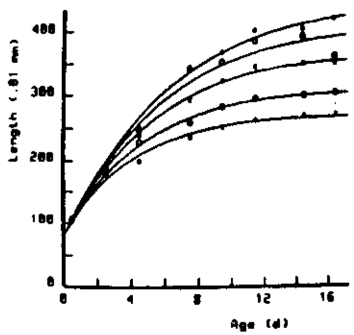

Fig. 6. Lenght L of Dapnia magna as a function of age a for various Chlorella densities X at 20°C. The fitted curves have the form $L = fL_m - (fL_m-L_b)\exp\{-a\dot{\gamma}\}$, where f = .407, .465, .554, .625 and .682 respectively, L_b = .80 mm, L_m = 6.60 mm, $\dot{\gamma} = 1/\{3\eta/\zeta + 3f[S_m]\kappa/\zeta\}$ with η/ζ = 0.672 d and $[S_m]\kappa/\zeta$ = 3.06 d. All parameters have been estimated by nonlinear simultaneous regression, except L_b and L_m, which have been determined from other data.

The duration of the pre-reproductive period, i.e. the age at which weight W_J is reached, is found form $W(J) = W_J$ to be
$J = 3\ (\eta/\kappa + [S_m]f)(\zeta/\kappa)^{-1}\ \ln\{(W_\infty^{1/3} - W_b^{1/3})/(W_\infty^{1/3} - W_J^{1/3})\}$
for $f \geq (\zeta/\kappa)W_J^{1/3}/[\dot{A}_m]$. At lower food densities, the weight W_J will not be reached.

Like the respiration rate, the reproduction rate can be written as $aW^{2/3} + bW$ at constant food density, where b/a also has the interpretation $(\zeta/\eta)\ [S_m]/[\dot{A}_m]$. Khmeleva, 1972, found for crustaceans that the relation between weight and reproduction is similar to that between weight and respiration. For Daphnia magna it is illustrated in Fig. 7.

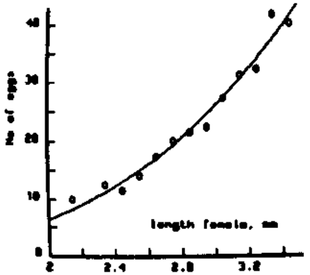

Fig. 7. Number of eggs in brood pouches of Daphnia magna, sampled from a wild population. The data are from Green, 1954. The fitted curve is $-1.01\ L^2 + 1.295\ L^3$.

Although the fit is satisfactory, particularly because nothing is known about the feeding history of the wild population sampled, this regression cannot contribute to the estimation of the energy budget parameters; even a small change in the shape of the curve has a large effect on the regression parameters. In Fig. 7, these parameters even fall outside the relevant range.

At constant food density, but for unknown food history of the population, an optimum relationship of reproduction rate to individual weight will, in principle be established. For $\kappa < 2/3$, the maximum reproduction for $f < \kappa 3/2$ is $(W_\infty/W_b)\ (\zeta/\kappa)(\omega+[S_m]f)^{-1}\ (4/27)\kappa^{-2}$ for $W^{1/3} = (2/3)\ [\dot{A}_m]f/\zeta$, i.e. it lies on the curve $S = (3/2)\ ([S_m]/[\dot{A}_m])W^{4/3}\ \zeta$ in the state space representation. For $f > \kappa 3/2$, the maximum reproduction occurs for W_m. For $\kappa > 2/3$, the maximum reproduction is $(W_\infty/W_b)(\zeta/\kappa)(\omega + [S_m]f)^{-1}\ (1-\kappa)$ for $W^{1/3} = \kappa f[\dot{A}_m]/\zeta$, i.e. it lies on the curve separating the growth and the no-growth regions in the state space.

Up to now, we have compared the reproduction rates of animals on a line through the origin in the state space. Comparing the reproduction rate of full-grown animals, which are on the curve separating the growth and the no-growth regions, we find that the reproduction rate is linearly proportional to weight, with a proportionality factor of $\dot{R}_m/W_m$.

At constant food density, given the explicit expression for weight as a function of age, we can write the reproduction rate explicitly as a function of age. Although the formulae now become lengthy, it is easy to write out the primary production efficiency on basis of wet weight, defined by $(W_b\dot{R} + \dot{W})/\dot{I}$, and to show that it decreases with increasing food density, because storage increases with food density. This finding

may be the solution to the problem mentioned by Conover, 1978, in his review on this topic, namely that he fails to see why production efficiencies should decrease with increasing food density.

SOME PHENOMENA ACCOMPANYING STARVATION

The storage development at constant food density in an animal of weight W and storage S_o at time zero, in the no-growth region of its state space, is easily found from the balance equation to be

$$S(t) = S_o \exp\left\{-\frac{[\dot{A}_m]t}{[S_m]W^{1/3}}\right\} + \frac{\dot{A}_1[S_m]W^{2/3}}{[\dot{A}_m]}\left(1-\exp\left\{-\frac{[\dot{A}_m]t}{[S_m]W^{1/3}}\right\}\right)$$

Where $\dot{A}_1$ is the influx of assimiliation energy. So in case of starvation, i.e. $\dot{A}_1=0$, the storage decays exponentially: $S(t) = S_o \exp.\{-t/\alpha\}$, where the time constant α can be interpreted as $W^{1/3}\ [S_m]/[\dot{A}_m]$. Figure 8 shows that the dry weight and lipid content of starved Daphnia magna at 20°C actually follows such a decay.

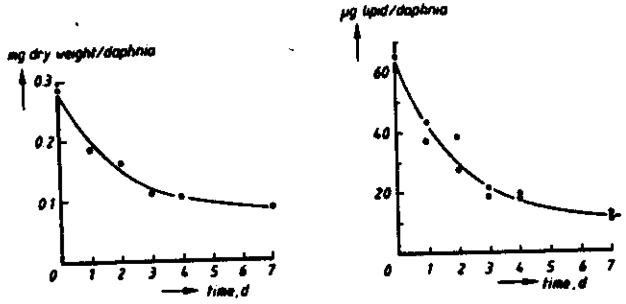

Fig. 8. Dry weight and mean lipid content of starved Daphnia magna at 20°C, measured in groups of 25 animals with a mean length of 3.4 mm. The fitted curves starting from 0.27 mg and 64 µg respectively are exponential decay functions with time constants of 1.99 d and 1.88 d, respectively, with asymptotes of 0.19 mg and 54 µg resp.

From these curves we estimate $[S_m]/[\dot{A}_m]$ to be 0.586 d/mm and 0.552 d/mm respectively. (This type of decay functions has also been found by Richman, 1958, and Lemke & Lampert, 1975, for Daphnia pulex, with twice as large values for $[S_m]/[\dot{A}_m]$). The ratio of the storage at the entry into the no-growth region of the state space and the storage at death by starvation equals κ. The time to death by starvation for the animals was 7 d, so we estimate κ to be about $\exp.\{-7/1.99\} = 0.024$ and $\exp.\{-7/1.88\} = 0.03$, both of which seem to be incredibly small. However, errors in the estimation of the asymptote of the dry weight and lipid content strongly influence this estimation of κ. Estimations based on oxygen consumption or carbon dioxide production rate do not suffer from such errors, because the asymptote is zero.

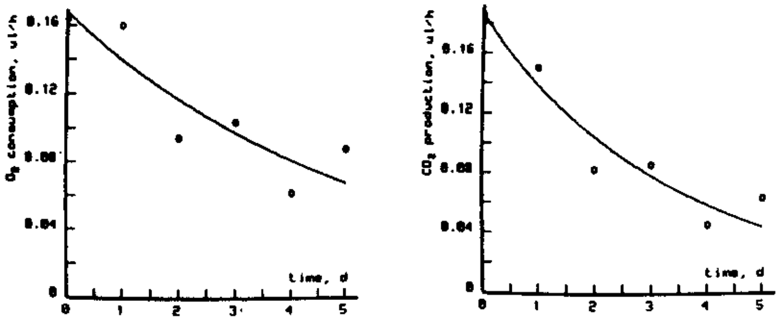

Fig. 9. Oxygen consumption and carbon dioxide production rate in starved Daphnia pulex of 1.62 mm at 20°C. Data from Richman, 1958. The fitted curves starting from 0.167 µl/h and 0.185 µl/h, respectively, are exponential decay functions with time constants of 5.48 d and 3.43 d.

From the curves in Fig. 9, we estimate $[S_m]/[\dot{A}_m]$ to be 3.38 d/mm and 2.11 d/mm. For a starvation time of 7 d, we have $\kappa = \exp.\{-7/5.48\}=0.28$ and $\kappa = \exp.\{-7/3.43\}=0.13$, which seem to be more credible.

If the influx of assimilation energy happens to be less than the routine metabolic rate, the animal will eventually die by starvation. If it is assumed that the storage S_o has been in equilibrium with a higher influx $\dot{A}_o$ experienced earlier, the time until death by starvation is found from $S(t_\dagger) = W^{4/3}\,\zeta[S_m]/[\dot{A}_m]$ to be

$t_\dagger = W^{1/3}\,([S_m]/[\dot{A}_m])\,\ln\{(\dot{A}_0 - \dot{A}_1)/(\dot{M} - \dot{A}_1)\}$,

where as we have stated before, the influxes $\dot{A}$ are assumed to be proportional to $W^{2/3}$, and the routine metabolic rate $\dot{M}$ to W. In case

of starvation, i.e. $\dot{A}_1=0$, the starvation period reduces for

$[S_\dagger] = S(t_\dagger)/W$ to $t_\dagger = ([S_\dagger]/\zeta)\,\ln\{[S_o]/[S_\dagger]\}$.

The number of young born in this period is

$[[S_\dagger]\,\ln\{[S_\dagger]/[S_o]\} + (\omega + [S_\dagger])\,\ln\{(\omega + [S_o])/(\omega + [S_\dagger])\}]\;W/(\omega W_b)$.

Depending on the values of the parameters and especially of κ, the survival time can decrease as well as increase with weight of the animals. This result holds for animals differing in weight, but starting at the equilibrium storage $[S_m]f_oW$, which represents a line in the state space representation. Comparing animals fullgrown at constant food density, we have $t_\dagger = -W^{1/3}\,([S_m]/[\dot{A}_m])\,\ln\kappa$. Such animals are on the curve, separating the growth and no-growth region in the state space representation. So the latter starvation time is the time needed by the animals to cross the no-growth region of the state space. This relation for starvation times can be of use in estimating the parameter κ, if the value for $[S_m]/[\dot{A}_m]$ has been obtained from the analysis of respiration rates or growth curves, as outlined in the previous section.

The starvation times and total number of young born in this period have been determined for individuals of Daphnia magna at 20°C kept without food in two kinds of water derived from groundwater. This had been supplemented with salts to arrive at the major ion concentrations in mmol: Na: 1.19; K: 0.2; Ca: 1.36; Mg: 0.73; Cl: 2.72; SO_4: 0.73; HCO_3: 1.39. Before use, the media were filtered over charcoal and bacterial filters. The two media differed in that one had been kept in stock for several weeks and had been aerated with compressed air from a central supply, whereas the other had not. The results, shown in Fig. 10, indicate that in the water used directly, the animals survived for about 5.5 days irrespective of their length, while in the aerated water, the small ones ($\lesssim$ 2 mm) survived for up to three weeks. The difference may have been caused by the presence of organic matter, possibly arising from microbial degradation of oil residues in the compressed air. This conjecture is supported by the finding that the aerated medium contained 2 mg/l of total organic carbon, whereas the other medium contained only 1.8 mg/l (Most, if not all of which is not biodegradable).

The theory predicts that animals weighing more than $([\dot{A}_m]\,f_s/\zeta)^3$ will fail to survive at input $f_s = X_s/(K+X_s)$. The food density allowing an animal just to survive is known as the threshold food density, and is given by $X_s = KW^{1/3}/([\dot{A}_m]/\zeta-W^{1/3}) = KW^{1/3}/(W_m{}^{1/3}/\kappa - W^{1/3})$. For Daphnia magna fed on the alga Chlorella pyrenoidosa, K equals 1.4×10^5 cells/ml and the maximum length is 6.4 mm, see Kooijman & Metz, 1984.

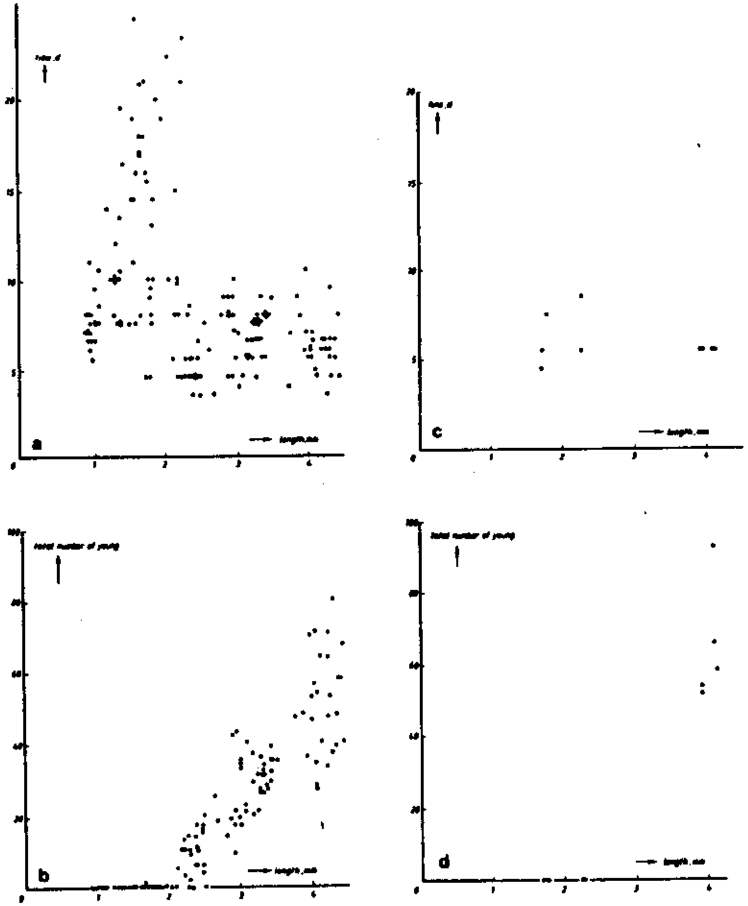

Fig. 10. The survival time of Daphnia magna at starvation after a period of abundant food (Chlorella) and the total number of young of each daphnid born in this period, as a function of length in stocked (a, b) and freshly prepared (c, d) media at 20°C.

If we take κ to be 1/4, we have for an animal of 2 mm length: $X_s \cong 10^4$ cells/ml, which corresponds to 0.1 mg C/l, well within the observed difference in carbon content. In fact, such low threshold food densities pose a practical problem in starvation experiments.

Substituting $W=W_J$ in the formula for the threshold food density, we obtain the threshold food density at which a population can rejuvenate itself. It can be regarded as a lower bound for the threshold food density for the population. It was introduced by Lampert, 1977, who defined it to be such that the biomass of a population remains constant, and so just compensates mortality.

The ingestion rate at the threshold food density is known as the maintenance ration, and is given by $\dot{I}_s = \zeta W \, [\dot{I}_m]/[\dot{A}_m]$; see Kooijman & Metz, 1984. For daphnids about 3 mm long, it equals some 6 chlorella cells a second at 20°C, see Kooijman, 1983. The utilization rate at this ingestion rate eventually becomes equal to the routine metabolic rate, so $\dot{I} = \dot{M} = \zeta W$.

The quotient $\dot{M}/\dot{I}_s$ equals $[\dot{I}_m]/[\dot{A}_m]$, i.e. the conversion factor for food into assimilation energy. Kersting, 1983, inverted this relation by converting the maintenance ration to an energy measure and used the respiration/ingestion ratio to determine the threshold food density. This procedure is valid if it is known how the conversion to an energy measure should be performed for the food and animal species under consideration.

Some species show remarkable adaptations in their life histories to the size dependent effects of a drop in food density. As has been mentioned before, daphnids normally reproduce parthenogenetically. However, large female daphnids start producing males when the food density declines rapidly. This situation usually involves a large variance of weights in the population, because large animals (older ones, grown up at high food density) as well as small ones (new-born animals due to the high reproduction rate) are abundant. They produce no males when food density declines slowly, usually corresponding to a smaller variance of weights, see Kooijman, 1983. After copulation, those females produce winter eggs, which represent a resting stage, see Fig. 11. This behaviour can be understood when we realize that at non-increasing food densities, the small individuals will outcompete the large ones (because of their lower threshold food density) if the variance in weights is large, whereas this mechanism is much less operative if the variance is small.

Fig. 11. Life cycle of Daphnia magna. The female normally produces eggs in a brood pouch (a). The eggs developing into young females, which are released just before moulting (b). Under certain circumstances, eggs develop into males (c), which will copulate with females with empty brood pouches (d). These females then produce two winter eggs (e) in an ephippium, which represents a resting stage (f). For further details, see text.

UNICELLULAR DYNAMICS

The food items ingested by multicellulars usually satisfy all their nutritional requirements although many exceptions to this general rule have been noted. For instance, Checkley, 1980, reports that copepods ingest many more diatoms if these are starved of nitrogen, in order to fulfill their requirement for this element. Scott, 1981, reports that the marine rotifer Brachionus plicatilis requires dissolved vitamin B_{12}. In unicellulars the uncoupling of the various nutritional and energy sources is much more widely spread. The interaction between these inputs will not be discussed here; we will assume that the input of the non-limiting nutrients remains constant. A further essential difference between the dynamics of multicellulars and unicellulars is that in the latter, proliferation is coupled to growth of individuals more directly: the asexual reproduction of unicellulars can usually be well described by a division following attainment of a certain division weight, W_D. For a division into p parts, we have $W_D = pW_b$. In this section we shall consider the implications of the present model for unicellular dynamics, and we shall discuss its relations to relevant results in the extensive literature on this subject. Most of this literature focuses on the description of equilibrium states of chemostats, where the dilution rate, and eventually the population growth rate is constant, in terms of measurable quantities like yield, uptake rate, and cell quota. We shall evaluate these relations on basis of the present model, first for non-conservative substrates, i.e. substrates whose degradation provides the energy necessary for maintenance and proliferation, and secondly for the special case of conservative substrates, here called nutrients, i.e. substrates which provide the chemical elements to be incorporated in the biomass.

The dynamics turns out to be dependent on the scaling of uptake rate of substrates with cell size. We shall consider two scaling relations:

- the uptake is proportional to $W^{2/3}$ because this has been observed to be relevant for ectotherms and
- uptake is proportional to W, because this is the assumption usually made in the literature on unicellular dynamics.

This gives four categories to be studied.

1. Unicellulars feeding by phagocytosis like ciliates probably resemble multicellulars most closely in their dynamics. At constant food density the division interval, D, is easily found from the equation $W(D) = W_D$.

It corresponds to the expression for the length of the juvenile stage in multicellulars, given before for $\kappa = 1$, because no reproduction is involved. In situations where death is not important, the population growth rate at constant food densities is found from $\dot{r} = (\ln p)/D$ for division into p. parts. It results in

$$\dot{r} = \frac{[\dot{A}_m]f - \zeta}{[S_m]f + \eta} \quad (\ln p)/\{3\ (W_\infty^{1/3} - 1) \ln \frac{W_\infty^{1/3} - W_b^{1/3}}{W_\infty^{1/3} - (pW_b)^{1/3}}\ \}$$

where $W_\infty^{1/3} = f[\dot{A}_m]/\zeta$. For $f < (\zeta/[\dot{A}_m])(pW_b)^{1/3}$ the cells will not reach their threshold weight for division. We will see in the next section that in case of an uptake rate proportional to weight instead of surface area, the population growth rate reduces to the first factor.

2. The literature on bacterial dynamics actually assumes that the uptake rate of substrates is proportional to weight, so in the present notation $\dot{I} = [\dot{I}_m]fW$. For bacilli it may be argued that the surface area scales approximately with weight, because the rod diameter is more or less constant. The balance equation for the storage then becomes

$$\dot{S} = W\ \{[\dot{A}_m]f - \frac{[S]}{[S] + \eta} \quad (\frac{[\dot{A}_m]\ \eta}{[S_m]} + \zeta)\}\ \text{for}\ [S] \geq \frac{[S_m]\ \zeta}{[\dot{A}_m]}$$

Growth is given by $\dot{W} = W \dfrac{[S][\dot{A}_m]/[S_m] - \zeta}{[S] + \eta}$. Expressed in the dynamics of the weight-specific storage, $[\dot{S}] = \dot{S}/W - S\dot{W}/W^2$, we have $[\dot{S}] = [\dot{A}_m]\ (f - [S]/[S_m])$. For $[S] \leq [S_m]\ \zeta/[\dot{A}_m]$ the cell dies of starvation.

The population growth rate at constant substrate density is found from $\dot{r} = (\ln 2)/D$, and the division interval D from $W(D) = 2\ W_b$, as before. The result is $\dot{r} = ([\dot{A}_m]f - \zeta)/([S_m]f + \eta)$.
Substitution of $f=X/(K+X)$, reveals the hyperbolic relation between $\dot{r}$ and the substrate density X, which for $\zeta=0$ reduces to the well-known Monod equation $\dot{r}=\dot{r}_m X/(X+K')$ for $\dot{r}_m=[\dot{A}_m]/([S_m] + \eta)$ and $K'=K\eta/([S_m] + \eta)$. It still plays a central role in the literature on microbial dynamics, in spite of the existence of maintenance in bacteria growing on non-conservative substrates having been known for a long time. Pirt, 1965 noticed that the slope of the line in a plot of inverse yield vs inverse population growth rate equals the so-called 'maintenance coefficient' in equilibrium situations.
The yield, Y, defined as the quotient of biomass formed and substrate consumed, is
$Y = \dot{r}/([\dot{I}_m]f) = \dot{r}([\dot{A}_m] - [S_m]\dot{r})/\{\ [\dot{I}_m]\ (\zeta + \eta\dot{r})\}$.

The present model simplifies to the formula in Pirt, 1965, for zero storage, $[S_m] = 0$. In our notation, we have

$\frac{1}{Y} = \eta \dfrac{[\dot{I}_m]}{[\dot{A}_m]} + \dfrac{[\dot{I}_m]\ \zeta}{[\dot{A}_m]\ \dot{r}}$. The parameter $\dfrac{[\dot{A}_m]}{\eta\ [\dot{I}_m]}$ has been called the "true yield" and corresponds to the yield for $\zeta = 0$. Pirt calculated the "maintenance coefficient", corresponding to $\zeta\ [\dot{I}_m]/[\dot{A}_m]$, for two bacterial species growing on two substrates, aerobically and anaerobically, and obtained a range of 0.083 to 0.55 h^{-1} on basis of dry weight (apart from a selomonad that behaved erratically). This wide range is due to differences in the ability of the bacteria to convert the substrate into energy. The corresponding range for the product of the "maintenance coefficient" and the "true yield", ζ/η, confusingly called the "maintenance rate constant" (Gons & Mur, 1975), is 0.0393 - 0.0418 h^{-1}. So, whereas $[\dot{A}_m]$ is highly dependent on the environment, this indicates that the internal parameters ζ and η are essentially constant.
Later, Stouthamer, 1979, 1980 analysed the dependence of the "specific rate of consumption" $\dot{U}$ on the population growth rate $\dot{r}$. The "specific rate of consumption" also known as the "specific uptake rate", is defined as the total substrate (or nutrient) uptake by the biomass, per unit biomass. In the equilibrium situation of a constant substrate density, it is given by $\dot{U}=\dot{r}/Y$. Stouthamer derived a linear relationship between $\dot{U}$ and $\dot{r}$, but he observed deviations which he explained by the growth rate influencing the fermentation pattern. Our model provides an alternative explanation, which can be regarded as a further interpretation of the explanation by Stouthamer, resulting in $\dot{U} = [\dot{I}_m](\zeta + \eta\dot{r})/([\dot{A}_m] - [S_m]\dot{r})$. This hyperbolic relation between $\dot{U}$ and $\dot{r}$ is meaningful only on the interval $\{0,([\dot{A}_m] - \zeta)/([S_m] + \eta)\}$; its asymptote on $\dot{r} = [\dot{A}_m]/[S_m]$ lies outside this interval.
In their study on light-limited growth in algae, Gons & Mur, 1975 and van Liere, 1979, noticed that in an equilibrium situation the intercept of the linear relation between specific light-energy uptake rate and growth rate can be interpreted to be the maintenance rate constant. This relation follows from our model for zero storage, $[S_m] = 0$ and a volume-related input: $\dot{I} = [\dot{I}_m]f\ W$. This relation may be realistic if chlorophyll content is volume related, and the cell is optically thin. In that case, the volume increase of a cell is exponential, as has been found by Donze & Nienhuis, 1973. See Fig. 12. Gons & Mur, 1975 also observed a deviation from linearity for high uptake rates, which they explained by assuming that light energy utilization is less

efficient at higher growth rates. Their data closely obey the hyperbolic relation $\dot{I}/W =$
$[\dot{I}_m]\ (\zeta + \eta\dot{r})/([\dot{A}_m] - [S_m]\dot{r})$ obtained from our model for $[S_m] \neq o$.

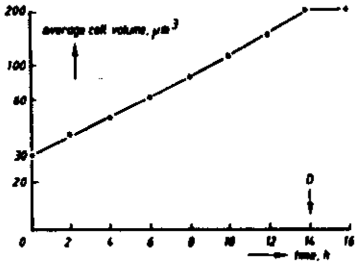

Fig. 12. Exponential volume increase during the light period in Scenedesmus obliquus growing in a synchroneous culture at 20°C. From Donze & Nienhuis, 1973.

See Fig. 13. So this hyperbolic relation affords an alternative explanation for the deviation.

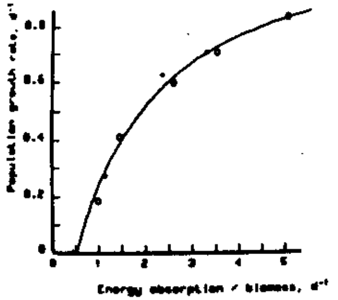

Fig. 13. Relation between biomass-specific energy absorption and population growth rate in Scenedesmus protuberans at 20°C. Data from Gons & Mur, 1975. The dots refer to an illumination of 30 kJ/d and the crosses to 13 kJ/d. The curve is $X = (1+2.284\ Y)/(1.921-1.636Y)$.

3. The literature on nutrient-limited growth of algae is very extensive. As far as I know, it assumes that input is proportional to W, i.e. $\dot{I} = [\dot{I}_m]fW$. There being no routine metabolism for nutrients, we may put $\zeta = o$. It has, however, often been noted that nutrients are excreted. If we assume that the rate of excretion is a fixed proportion, $(1-\kappa)$, of the utilization rate, the resulting balance equations for the storage becomes

$$\dot{S} = [\dot{I}_m]fW - \frac{[S]\ \eta/\kappa}{[S]+\eta/\kappa}\ \frac{[\dot{I}_m]}{[S_m]}\ W.$$

Growth is given by $W = W\ [S][\dot{I}_m]\{[S_m]([S]+\eta/\kappa)\}^{-1}$. Expressed in the dynamics of the weight-specific storage, we have $[\dot{S}] = [\dot{I}_m](f-[S]/[S_m])$. These equations correspond to the formulae presented by Nyholm, 1976, 1977. At constant nutrient concentration, the storage is at its equilibrium value $S^* = [S_m]fW$. If, in this situation, death is not important, the population growth rate can be obtained as before, and results in $\dot{r} = [\dot{I}_m]f/([S_m]f + \eta/\kappa)$.
The first investigator to recognize the importance of storage in nutrient-limited growth of algae was Droop, 1968.
He introduced the concept of cell quota Q, defined as the nutrient concentration in the cell. In the equilibrium situation of a chemostat, this concentration equals the quotient of the substrate consumed and the biomass formed, and so we have $Q=1/Y = [\dot{I}_m]\ f/\dot{r}$. Substitution of $\dot{r}$ gives $Q = [S_m]\ f+\eta/\kappa$. Droop considered the situation of zero loss, i.e. $\kappa=1$, from which it follows that $Q=[S]+\eta$. The parameter η, which we took to be the amount of nutrient required for formation of a unit of biomass, has been called the subsistence quota, or the minimum quota needed for growth to proceed. This is obvious, because $Q=\eta$ implies $[S]=0$. Droop observed a linear relationship between the cell quota and the specific uptake rate $\dot{U}$. In the equilibrium situation of a constant nutrient density, we have $\dot{U} = \dot{r}Q$. Substitution of $\dot{r}$ and $f = (Q-\eta/\kappa)/[S_m]$ gives $\dot{U} = (Q-\eta/\kappa)\ [\dot{I}_m]/[S_m]$, which is linear in Q.

4. The parameter η can be interpreted as the quotient of the amount of nutrients built into the structure of the algae and cell size. Comparing different species, Shuter, 1978, found that the nitrogen and phosphorus contents of algae that do not grow because they are starved of these nutrients, scale with volume to the power 0.709 ± 0.066. This finding suggests that the amount of these structural nutrients is essentially related to surface area. The weight-specific amount of nutrient needed for growth therefore decreases with cell weight. If we assume the uptake of nutrients to be also surface related, i.e. $\dot{I} = [\dot{I}_m]fW^{2/3}$ we have the balance equation $\dot{S} = [\dot{I}_m]fW^{2/3} - \dot{C}$. The utilization rate $\dot{C}$ now relates to growth $\dot{W}$ as $\kappa\dot{C} = 2/3\ \eta W^{-1/3}\ \dot{W}$. Nutrient absorbtion being much more rapid than growth, the storage is at its equilibrium value, S^*, at constant input. Cell growth is usually assumed to be exponential. This implies that S^* scales with $W^{2/3}$, and suggests that $S^* = [S_m]fW^{2/3}$. Writing $\{S\}$ for the surface area-specific storage, i.e. $\{S\}=S/W^{2/3}$, the balance equation is

$\dot{S} = [\dot{I}_m]fW^{2/3} - (\eta/\kappa)W^{2/3}([\dot{I}_m]/[S_m])\ \{S\}/(\{S\}+ \eta/k)$ and

$\dot{W} = W(3/2)([\dot{I}_m]/[S_m])\ \{S\}/(\{S\} + \eta/\kappa)$

When expressed in the dynamics of the surface-specific storage, we have $\{\dot{S}\} = \dot{S}/W^{2/3} - 2/3\ S\dot{W}/W^{5/3}$, so $\{\dot{S}\} = [\dot{I}_m]/(f-\{S\}/[S_m])$.

If death is not important, the population growth rate at constant nutrient concentration is $\dot{r} = 1.5\ [\dot{I}_m]f\{[S_m]f + \eta/\kappa\}^{-1}$.

The yield is given by $Y=\dot{r}\ \{[\dot{I}_m]fA\}^{-1}$ where A is the quotient of the average value of $W^{2/3}$ and of W in the population of cells. If there is any scatter in the threshold weight for division, the distribution of cell sizes at constant nutrient density usually converges rapidly to the stable cell size distribution. This has density $2W_b/W^2$, see Voorn, 1983, so $A = (2/3)\ W_b^{2/3}\ (1-2^{-1/3})\ \{W_b 2\ln 2\}^{-1} \approx 0.1\ W_b^{-1/3}$

The specific uptake rate $\dot{U}$ is $\dot{U} = \dot{r}/Y = ([\dot{I}_m]/[S_m])(Q3/2 - A\eta/\kappa)$ which means that Droop's linearity between $\dot{U}$ and Q still holds.

DISCUSSION

The course of the weight, storage and reproduction rate in an ectotherm containing the parameters $P = \{W_b,\ W_J,\ K,\ [\dot{I}_m],\ [\dot{A}_m],\ [S_m],\ \kappa,\ \zeta,\ \eta,\ \omega\}$ has been described with a set of two coupled differential equations. The parameters involving energy, viz. $[\dot{A}_m]$, $[S_m]$, ζ, η and ω, only occur as ratios in the model, so only nine parameters have to be estimated, and no actual conversion to energy is necessary. Its various aspects have been checked for Daphnia magna feeding on Chlorella. At constant food density the equations for weight, storage and reproduction rate can be written explicitly as a function of age. Even in this case, the storage has an effect on growth and reproduction behaviour, resulting in, e.g., a decrease in production efficiency for increasing food densities. This result contradicts a statement made in Kooijman & Metz, 1984. For zero storage, $[S_m]=0$, the present equations for growth and reproduction reduce to those in Kooijman & Metz, 1983. Apart from the considerations on starvation, no attempt has yet been made to analyse the implications of the model in dynamic environments. For this purpose it is necessary to develop techniques for handling two-dimensional, or, if age is to be included, three-dimensional state spaces for individuals with survival boundaries. As we have shown above, our model can be used to describe nutrient- and light-limited algal growth, and substrate-limited bacterial growth, as well as being able to describe growth in multicellulars. For unicellulars it affords explanations of some observed deviations from current theories. For nutrient-limited algal growth,

the model becomes much simpler involving only the parameters $\{W_b,\ K,\ [\dot{I}_m],\ [S_m],\ \kappa,\ \eta\}$, where W_b disappears when input is weight-related.

A remarkable feature of the reasoning here presented is that, at constant food density, the respiration rate can be written as a weighted sum of a surface area and a weight measure, this sum approximately scaling with $W^{0.8}$ whereas the routine metabolic rate scales with weight for individuals of the same species. The dependence of respiration rate on weight has caught the attention of many research workers in ecophysiology, who usually compare (widely) different species. Their work prompts a study of the implications the model has for the comparison of respiration rates and related variables between species of different sizes. The key to such comparisons is the maximum size a species can reach, which can be written, as has been shown, as a simple function of the parameters. These parameters must therefore vary in a systematic way between species of different size. It has proved to be possible to explain in this way the relations reported in the literature between, on the hand, size of a species and, in the other, ingestion rate, animal abundance, maximum growth rate, respiration rate, reproduction rate, duration of pre-reproductive period, starvation time as well as maximum population growth rate. For further discussions, see Kooijman, 1984.

Our model formulations shows some promise for studies on phytoplankton-zooplankton interactions. Some progress may be expected from a study of population dynamics on a basis of budgets.

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LIST OF FREQUENTLY USED SYMBOLS

Symbol	dimension	interpretation
X, X_s	food (nutrient).length^{-3}	food or nutrient density, threshold-
f		functional response as a portion to its maximum
$\dot{I}, \dot{I}_m, \dot{I}_s$	food (nutrient).time^{-1}	ingestion rate, maximum-, threshold-
$[\dot{I}]$	food (nutrient).length^{-2}.time^{-1}	size specific-
$\dot{A}, \dot{A}_m,$	energy.time^{-1}	assimilation energy rate, maximum-
$[\dot{A}_m]$	energy.length^{-2}.time^{-1}	size specific-
S, S_m	energy (nutrient)	storage, maximum-
$[S], [S_m]$	energy (nutrient).length^{-3}	weight specific-, maximum weight specific-
$\dot{S}$	energy (nutrient).time^{-1}.	storage change rate
W, W_b, W_J	length^3	weight,-at birth,-at the end of the juvenile stage
W_D, W_∞, W_m	length^3	-at division, adult-, maximum-
$\dot{W}$	length^3.time^{-1}	growth rate
$\dot{R}, \dot{R}_m$	time^{-1}	reproductive rate, maximum-
$\dot{M}$	energy.time^{-1}	routine metabolic rate
$\dot{C}$	energy (nutrient).time^{-1}	utilization rate
$\dot{F}_m$	length^3.time^{-1}	maximum filtration or searching rate
K	food (nutrient).length^{-3}	saturation constant
κ		proportion of utilized energy spent on growth and routine metabolism
η	energy.length^{-3}	energy requirement for a unit increase in weight
ζ	energy.length^{-3}.time^{-1}	maintenance energy consumption rate per unit of weight
ω	energy.length^{-3}	energy requirement for a unit increase in offspring tissue

APPENDIX The idea behind the κ-rule.

Blood has a low take-up capacity for energy (or nutrient), but a relatively high transportation rate; Many times an hour it is pumped through the body. Passing along the gut, it takes up any energy delivered there, which is rapidly circulated through the whole body. At separated sites along the vessels, two types of cells are waiting to pick up energy from the blood, the (many) somatic and (few) ovary cells. These cells are not able to react to each other's activities other than through the concentration of energy in the blood. The carriers that remove energy from the blood across the cell membrane, into the two types of cells, have the same activity dependence on the concentration of energy in the blood, but they may have different efficiencies. One might assume that all carriers are identical, but that the numbers of carriers in the membranes of the two types of cells differ. This is the basis of the κ-rule. The efficiency (a number) of the carriers in the ovary cells is controlled by hormones, depending on age, size and environment. For Daphnia, this efficiency seems to be constant as long as feeding states permits. Inside each somatic cell, the energy partition occurs within the same cell, maintenance and growth are natural competing processes. It is therefore reasonable to assume that maintenance is at the expense of growth, not at reproduction as long as energy permits. The hormonal system has to intervene for maintenance to be at the expense of reproduction. It will do so in poor conditions. The main part of the maintenance energy is involved in the course grain regulation of the enzyme system of the cell; i.e. a continuous process of breaking down and building up. This process is closely related to those occurring during cell growth and division. (Observing the oxygen consumption pattern, the energy spent in movement in Daphnia is only of minor importance.) At still other sites along the blood vessels, carriers regulate the energy content of the blood. They can not observe which type of cell removed the energy from the blood nor the energy influx along the gut. They only see the energy content of the blood, the amount of stored energy and the size of the animal. Therefore, $[\dot{S}]$ cannot depent on κ. The size dependence of the energy regulation is plausible, because the stored energy is chemically represented by more or less massive solid lipids, which are deposited on certain surfaces inside the animal. Since these surfaces increase with $W^{2/3}$ and the volume with W in growing animals, the blood has a decreasing ability to reach the stored energy; the lipid layers grow thicker and blood can only reach the outer surface. It is therefore quite natural that $[\dot{S}]$ appears to be proportional to $W^{-1/3}$.