

Towards a global model of large ecosystems:
Equations for a trophic continuum

Howard Parkin* and Steven Cousins**

Energy Research Group Report O41,

Open University, Milton Keynes,

MK7 6AA,

U.K.

March 1981

Abstract

Equations are presented for a previously described non-mathematical model of whole ecosystem trophic behaviour based on organism size. The model is specified at any time by number distributions of carnivores, herbivores and detritivores of different sizes and by biomass distributions of autotroph and detritus materials of different resource states. Dynamic events are determined by a weight dependent appetite function, an optimal foraging strategy, growth, reproduction and detritus decay terms. Global modelling of large ecosystems is discussed. It is held to be useful as a framework for detailed studies and to have practical value for ocean fishery management and whole ecosystem toxin impact assessment.

*Howard Parkin,
Engineering Mechanics,
Open University,
Milton Keynes
MK7 6AA,
U.K.

**Steven Cousins
Energy Research Group,
Open University,
Milton Keynes,
MK7 6AA,
U.K.

Contents

1. Introduction
2. Modelling Strategy
3. Structure of the mathematical model
4. Change in the number of carnivores
 - 4.1 Carnivory
 - 4.1.1 Predation with travelling time only
 - 4.1.2 Predation with travelling time and handling time only
 - 4.1.3 Predation with optimal foraging strategy
 - 4.1.4 Satiation, starvation and non-feeding time
 - 4.1.5 The continuous carnivory model
 - 4.2 Starvation
 - 4.3 Growth
 - 4.4 Reproduction
5. Change in the number of herbivores
 - 5.1 Carnivory
 - 5.2 Starvation
 - 5.3 Growth
 - 5.4 Reproduction
6. Change in the number of detritivores
 - 6.1 Carnivory
 - 6.2 Starvation
 - 6.3 Growth
 - 6.4 Reproduction
7. Change in the plant biomass distribution
 - 7.1 Herbivory
 - 7.2 Growth
 - 7.3 Litter
8. Change in the carcass distribution
 - 8.1 Detritivory
 - 8.2 Carcass supply
 - 8.3 Fragmentation
9. Change in the detritus biomass distribution
 - 9.1 Detritivory
 - 9.2 Plant detritus
 - 9.3 Dung
 - 9.4 Decay
10. Recapitulation
11. Discussion

1. Introduction

Modelling whole ecosystem trophic behaviour using the trophic level concept (Lindeman, 1942) has been criticised by various authors (Rigler 1975, Platt and Denman 1977, Cousins 1980) and its demise as a central tenet of ecological energetics has been anticipated by Yodzis (1978) and Orians (1980). Here we attempt a mathematical description of the trophic continuum of Cousins (1980) as applied to a spatially homogenous ecosystem. The trophic continuum is a model of biomass concentration which occurs by a number of mechanisms including feeding. In the model trophic transfers are not equivalent as a change of one trophic level but are dependent on the degree of biomass concentration achieved, that is, dependent upon the size of feeder and size of food. Other mechanisms which create changes in biomass concentration are animal growth, translocation and chemical transformation in the plant and disintegration in detritus. The plant and detritus are treated as distributions of biomasses at different concentrations, referred to as resource states. Herbivory and detritivory are simply food flows to herbivores and detritivores of various sizes from the live plant and from detritus of various resource states.

The model is defined by the number distribution of heterotrophs of different sizes and by a biomass distribution of living plant materials of various resource states and a distribution of detritus of various resource states. Asymptotic animal growth curves, a simple plant growth model and a logarithmic detritus decay curve determine the non-feeding biomass flows across the model's weight class and resource state boundaries. Food flows to heterotrophs are determined by an appetite function dependent on the animals' weight (Fenchel 1974) and by an optimal foraging strategy (Krebs 1978).

Modelling whole ecosystem behaviour using animal size as the central parameter although initiated by Elton (1927) has only recently been revived in a mathematical form by Platt and Denman (1977, 1978) and Silvert and Platt (1978, In Press). Ellis et al (1976) have also

proposed an ecosystem trophic model driven by an organism weight dependent appetite function and which incorporates a feeding strategy sensitive to food abundance. In this paper we pass from the lexical phase (Cousins 1980) to a mathematical description of the interactions of the trophic continuum. The next stage, not considered here, is the investigation of the model's behaviour on a computer. We justify omitting this step at present on three grounds, to enable discussion and criticism of the model structure, to allow the collection of a set of allometric data from a single ecosystem with which to test the model, and last but not least, brevity.

2. Modelling strategy

All flows across system boundaries in the model are required to satisfy the principle of conservation of energy. However, the model's chief system properties are determined by the availability of energy as well as its quantity. The availability of a biomass of organic tissue to a heterotroph species or weight class is affected by the food's fragmentation and dispersal. For instance the availability of prey to a given carnivore depends crucially upon prey size and prey density. There is a correspondence between ecological availability and thermodynamic availability. Traditionally ecologists have limited the discussion of entropy change to photosynthesis and respiration (Morowitz, 1968). Small but calculable changes in entropy are associated with food dispersal and concentration (Cousins, 1978).

It may be possible in future to derive ecosystem structure and dynamics from principles analogous to those of thermodynamics for example to determine an optimal foraging strategy and to allocate assimilated food so gained to maintenance, locomation, growth and reproduction. In the absence of such a grand simplifying theory we content ourselves with piecing together plausible, isolatable model elements. Where choice is necessary elements have been chosen here for their global properties rather than the level

of local resolution they achieve. An instance of this is where we have isolated the internal metabolic processes of assimilation, growth and reproduction from feeding interactions in the ecosystem. Thus an appetite function and constant assimilation fraction tied to a rigid growth curve does not allow second order system behaviours where growth is accelerated or retarded due to prey availability. However the global relationships between food supply and population number is retained by the possibility of starvation if the food requirements of growth are not met. Additionally the identification of all individuals with particular asymptotic growth curves prevents individual members of any weight class growing indiscriminately large. The latter is both a plausible and essential global feature.

In modelling a large ecosystem our dilemma has always been marrying the local and global properties. Our preference for the global automatically leads to some over-specification in the absence of a more profound theoretical synthesis. Whilst we have made every effort to minimise over-specification a residual amount seems to us inevitable and requires the introduction of an extra and thus unnatural degree of freedom. In our case this is achieved by instantaneously neglecting certain metabolic rate constraints within the organism. When energy stores are depleted, so for example, growth continues at a healthy rate until death by starvation intervenes.

3. Structure of the mathematical model

The model is completely specified at any instant in time, t , by a set of seven distribution functions. The total rate of change in time of each distribution is expressed as the sum of the partial rates of change, one for each of the model elements. Since we are considering a homogenous ecosystem the seven distributions are totals for the whole ecosystem area or volume under study. $m_A(v,t)$ is the distribution of the plant biomass over resource value variable, v . The resource value, v , of plant tissue is defined in terms of its assimilable fraction relative to the assimilable fraction of the same biomass of animal flesh. vm_A is thus the flesh equivalent biomass distribution of the plant. That is, the biomass assimilated when a carnivore digests $vm_A dv$ gm of animal flesh is the same as that assimilated when a herbivore digests $m_A dv$ gm of plant tissue at resource value v .

The equation for the plant (autotroph) is

$$\frac{\partial m_A}{\partial t} = \left(\frac{\partial m_A}{\partial t} \right)_{\text{herbivory}} + \left(\frac{\partial m_A}{\partial t} \right)_{\text{growth}} + \left(\frac{\partial m_A}{\partial t} \right)_{\text{litter}} \dots (1)^\dagger$$

where the herbivory term represents the rate of change of $m_A(v)$ due to feeding herbivores; growth is similarly the rate of change of $m_A(v)$ due to photosynthesis, translocation and transformation of its products; losses to litter include leaf-fall and natural death of all or any plant part.

$n_1(w, w_0, t)$ is the population distribution of carnivores over their current weight, w , and their asymptotic adult weight, w_0 .

The equation for carnivores is

$$\begin{aligned} \frac{\partial n_1}{\partial t} = & \left(\frac{\partial n_1}{\partial t} \right)_{\text{carnivory}} + \left(\frac{\partial n_1}{\partial t} \right)_{\text{starvation}} + \left(\frac{\partial n_1}{\partial t} \right)_{\text{growth}} \\ & + \left(\frac{\partial n_1}{\partial t} \right)_{\text{reproduction}} \end{aligned} \dots (2)$$

where carnivory is the reduction n_1 due to ingestion by other carnivores; the starvation term generates losses in n_1 when food requirements are not met; growth is the change in n_1 due to the growth into and growth out of the infinitesimal weight class $n_1 dw$; births are allocated to small weight classes in the model and are driven by the reproduction term.

Similarly $n_2(w, w_0, t)$ is the population distribution of herbivores $n_3(w, w_0, t)$ is that of detritivores of dead animals and $n_4(w, w_0, t)$ is that of the detritivores of dead plant material and dung of all origins.

$$\begin{aligned} \frac{\partial n_2}{\partial t} = & \left(\frac{\partial n_2}{\partial t} \right)_{\text{carnivory}} + \left(\frac{\partial n_2}{\partial t} \right)_{\text{starvation}} + \left(\frac{\partial n_2}{\partial t} \right)_{\text{growth}} \\ & + \left(\frac{\partial n_2}{\partial t} \right)_{\text{reproduction}} \end{aligned} \dots (3)$$

$$\frac{\partial n_3}{\partial t} = \left(\frac{\partial n_3}{\partial t} \right)_{\text{carnivory}} \dots \dots (4)$$

$$\frac{\partial n_4}{\partial t} = \left(\frac{\partial n_4}{\partial t} \right)_{\text{carnivory}} \dots \dots (5)$$

[†] The use of a slightly non-standard notation for the terms on the right of equations 1-7 is to improve the clarity of presentation through the text.

Note that the carnivory term is retained in each case as this refers to the reduction in the number distribution caused by carnivores feeding.

$n_D(w,t)$ is the number distribution of carcasses or carcass fragments

$$\frac{\partial n_D}{\partial t} = \left(\frac{\partial n_D}{\partial t} \right)_{\text{detritivory}} + \left(\frac{\partial n_D}{\partial t} \right)_{\text{carcass}} + \left(\frac{\partial n_D}{\partial t} \right)_{\text{fragmentation}} \dots (6)$$

where detritivory is the change in the distribution due to feeding by detritivores; the carcass term is the increase in the distribution due to heterotroph starvation and natural death although the latter is not included in the current model; the fragmentation term models both putrefaction and fragmentation itself, with the carcass biomass conserved as a larger number of smaller particles. Exuviae are not considered.

$m_D(v,t)$ is the distribution of detritus biomass of resource state, v , defined exactly as for the live plant. Thus vm_D is the flesh equivalent biomass distribution of detritus.

The distribution of detritus biomass of plant and dung is given by

$$\begin{aligned} \frac{\partial m_D}{\partial t} = & \left(\frac{\partial m_D}{\partial t} \right)_{\text{detritivory}} + \left(\frac{\partial m_D}{\partial t} \right)_{\text{plant detritus}} + \left(\frac{\partial m_D}{\partial t} \right)_{\text{dung}} \\ & + \left(\frac{\partial m_D}{\partial t} \right)_{\text{decay}} \dots (7) \end{aligned}$$

where the detritivory term is the loss due to feeding by detritivores; the plant detritus term raises the distribution due to addition of plant litter; 'dung' is the increase in m_D due to defaecation by animal populations; and decay is the movement of biomass to lower resource states caused by putrefaction.

In the proceeding sections these 7 basic equations will be discussed term by term. The carnivory equation, equation (2), is taken first as the modelling of predation is subsequently generalised for herbivory and detritivory.

4. Change in the number of carnivores

4.1 Carnivory

We propose to develop a generalised model of predation which will be applicable to herbivory, detritivory as well as carnivory. It is developed in three stages, the first takes account of travelling time only, the second includes handling time and the third includes optimal foraging. What we call travelling time (Krebs 1978) has been called foraging time (Silvert and Platt, 1978, In press). Our use of the term is defined as the fraction of time spent neither eating or resting where resting includes all non-feeding activities.

To clarify the continuous equations for predation it is simplest to first discuss carnivory for a discrete case with a finite number of prey classes.

4.1.1 Predation with travelling time only

The simplest assumption is that a single predator's encounter rate with prey is proportional to the number of prey present within the given system. This assumption gives the Lotka-Volterra result that the predation rate for the r th prey is $P_r N_r$, where N_r is the number of individuals in the r th weight class and P_r the predation coefficient, a constant for the given system and is the predator - prey encounter rate per unit prey. Under Lotka-Volterra assumptions eating is instantaneous and thus encounter and predation rates are equal.

With l prey classes in the system the total encounter rate of a single predator with prey of any type is $\sum_{r=1}^l P_r N_r$

Unit travelling time is defined as the time between encounters which for 1 predator, 1 prey type is $\frac{1}{P_1 N_1}$

and, $\frac{1}{\sum_{r=1}^l P_r N_r}$

for 1 predator and l prey types.

4.1.2 Predator with travelling time and handling time only

In this section we derive an expression for the flesh equivalent feeding rate of a predator on a prey class.

Unit prey handling time for the rth prey is H_r . The fraction of all encounters when the rth prey are predated will be

$$\frac{P_r N_r}{\sum_{i=1}^{\ell} P_i N_i}$$

so mean unit prey handling time with ℓ prey types is,

$$\sum_{r=1}^{\ell} H_r \cdot \frac{P_r N_r}{\sum_{i=1}^{\ell} P_i N_i}$$

Then mean unit predation time, that is, mean unit travelling time plus mean unit handling time is given by

$$\frac{1}{\sum_{i=1}^{\ell} P_i N_i} + \sum_{r=1}^{\ell} \frac{H_r P_r N_r}{\sum_{i=1}^{\ell} P_i N_i} = \frac{1}{\sum_{i=1}^{\ell} P_i N_i} \left(1 + \sum_{r=1}^{\ell} H_r P_r N_r \right)$$

thus the net predation rate is

$$\frac{\sum_{i=1}^{\ell} P_i N_i}{1 + \sum_{r=1}^{\ell} H_r P_r N_r} \dots (8)$$

and the predation rate on the kth prey is

$$\frac{\sum_{i=1}^{\ell} P_i N_i}{1 + \sum_{r=1}^{\ell} H_r P_r N_r} \cdot \frac{P_k N_k}{\sum_{i=1}^{\ell} P_i N_i} = \frac{P_k N_k}{1 + \sum_{r=1}^{\ell} H_r P_r N_r} \dots (9)$$

For a parallel definition of equation (9) see Silvert and Platt (In press).

These interactions for a carnivore can be generalised for herbivory and detritivory by considering biomass flows. Some instances of herbivory are exactly analogous to carnivory e.g. where herbivores forage for discrete high food value items such as fruit or seeds or

where detritivores forage for carcasses. However, for non-discrete food items further definition of the predation coefficient is required. In order to achieve this we will re-examine the carnivory equation.

For a carnivore the fraction of the time spent travelling is,

$$\frac{1}{\sum_{i=1}^{\ell} P_i N_i} \left/ \left(\frac{1}{\sum_{i=1}^{\ell} P_i N_i} + \frac{\sum_{r=1}^{\ell} H_r P_r N_r}{\sum_{i=1}^{\ell} P_i N_i} \right) \right.$$

$$= \frac{1}{1 + \sum_{r=1}^{\ell} H_r P_r N_r} \quad \dots (10)$$

The fraction of time spent handling the sth prey is

$$\frac{H_s P_s N_s}{\sum_{i=1}^{\ell} P_i N_i} \left/ \left(\frac{1}{\sum_{i=1}^{\ell} P_i N_i} + \frac{\sum_{r=1}^{\ell} H_r P_r N_r}{\sum_{i=1}^{\ell} P_i N_i} \right) \right.$$

$$= \frac{H_s P_s N_s}{1 + \sum_{r=1}^{\ell} H_r P_r N_r} \quad \dots (11)$$

So, $\frac{\text{fraction of time spent handling the sth prey}}{\text{fraction of time spent travelling}} = H_s P_s N_s = R_s$, say.

Since neither H, P, or N depend upon ℓ , this result is independent of the number of prey types, ℓ , and gives an empirical definition of the predation coefficient P_s which can be extended to herbivory or detritivory.

If h_s is the handling time of unit biomass of the sth prey, then $H_s = w_s h_s$ where w_s is the mass of the sth prey.

$$\text{So, } R_s = w_s h_s P_s N_s = h_s P_s M_s \quad \dots (12)$$

where M_s is the total biomass ($N_s w_s$) of the sth prey type.

Equation (12) is now in a general form suitable for application to carnivory, herbivory and detritivory.

$$\frac{\text{Fraction of time spent handling any biomass}}{\text{Fraction of time spent travelling}} = \sum_{s=1}^{\ell} h_s P_s M_s$$

$$\frac{\text{Fraction of time handling + fraction of time travelling}}{\text{Fraction of time travelling}} = 1 + \sum_{s=1}^{\ell} h_s P_s M_s$$

$$= \frac{1}{\text{fraction of time travelling}}$$

So fraction of time spent travelling is $\frac{1}{1 + \sum_{s=1}^{\ell} h_s P_s M_s}$

From (12) the fraction of time spent handling the kth biomass is

$$\frac{h_k P_k M_k}{1 + \sum_{s=1}^{\ell} h_s P_s M_s}$$

If all the time were spent handling the kth biomass with no travelling time then the biomass feeding rate is given by $\frac{1}{h_k}$

But the fraction of time spent handling the kth biomass is given by the preceding expression.

(13) So the actual feeding rate on the kth biomass by a single predator is

$$\frac{h_k P_k M_k}{1 + \sum_{s=1}^{\ell} h_s P_s M_s} \cdot \frac{1}{h_k} = \frac{P_k M_k}{1 + \sum_{s=1}^{\ell} h_s P_s M_s} \quad \dots (13)$$

The flesh equivalent feeding rate for the kth biomass is

$$\frac{v_k P_k M_k}{1 + \sum_{s=1}^{\ell} h_s P_s M_s} \quad \dots (14)$$

where v_k is the resource value of the kth biomass. $v = 1$ for flesh and is $0 < v \leq 1$ for plant and detritus materials.

4.1.3 Predation with an optimal foraging strategy

To implement feeding relations in the model using equation (14) would result in the r th predator feeding on all prey where P_r is non-zero. Here we adopt one of several possible foraging strategies, one which maximises assimilated energy flow to a predator. We define a subset of food types which maximises the rate of flesh equivalent biomass flow to the predator. To simplify the notation for the following proof let, $x_k = v_k P_k M_k$ then from equation (14) total flesh equivalent flows to a predator is

$$F = \frac{\sum_{k=1}^{\ell} x_k}{1 + \sum_{s=1}^{\ell} \left(\frac{h_s}{v_s} \right) x_s}$$

We assume we have found the subset of $n \leq \ell$ food classes which maximises F . If necessary we could rearrange the food class subscripts such that the optimal diet is indexed 1 to n . Addition of one food class will by definition reduce F whilst subtraction of one class will also reduce F or leave it unchanged.

The following inequalities can be deduced.

$$\frac{y - x_p}{\frac{h_p}{v_p} x_p} \leq \frac{y}{1 + z} \quad \dots (15)$$

and,
$$\frac{y + x_q}{\frac{h_q}{v_q} x_q} < \frac{y}{1 + z} \quad \dots (16)$$

where $y = \sum_{s=1}^n x_s$ and $z = \sum_{s=1}^n \frac{h_s}{v_s} x_s$

and $1 \leq p \leq n < q \leq \ell$

Inequality (15) reduces to

$$\frac{h_p}{v_p} \leq \frac{1 + z}{y} \quad \dots (17)$$

and inequality (16) reduces to

$$\frac{h_q}{v_q} > \frac{1+z}{y} \quad \dots (18)$$

combining inequalities (17) and (18) gives

$$\frac{h_p}{v_p} < \frac{h_q}{v_q} \quad \dots (19)$$

This result shows that $\frac{h}{v}$ for each class in the optimal diet, is less than that of any class excluded from it. This simple result allows us to choose the required subset of classes from the $2^{\ell} - 1$ possible non-empty subsets of ℓ classes.

Note that $\frac{h}{v}$ has an empirical interpretation. Since h is the handling time for 1 g of food of resource value v and $\frac{1}{v}$ is by definition that mass of food equivalent to 1 g of animal flesh, $h \cdot \frac{1}{v}$ is the unit flesh equivalent handling time of food at v .

The strategy for the optimal diet of a predator in our model is to first rank foods according to $\frac{h}{v}$ then starting with minimum $\frac{h}{v}$ add successive food classes until F reaches a maximum where addition of a further class would reduce F . The flesh equivalent biomass flow rate to an optimally foraging predator is thus,

$$F_{opt} = \frac{\sum_{k=1}^n v_k P_k M_k}{1 + \sum_{s=1}^n h_s P_s M_s} \quad (n \leq \ell) \quad \dots (20)$$

The relative abundance of foods in different food classes can influence the number of food classes in the diet but from (19) all food classes with $\frac{h}{v}$ less than the maximal $\frac{h}{v}$ in the optimal diet will be included irrespective of their abundance.

Paradoxically it is possible to demonstrate that if a diet contains more than one class of food the class which has lowest $\frac{h}{v}$ doesn't necessarily contribute to the diet at the greatest rate although it is necessarily a member of the optimal subset.

4.1.4 Satiation, Starvation and non-feeding time

A predator may or may not reach satiation when feeding at the rate F_{opt} dependent on the availability of prey at any instant in time. However the optimal foraging rate can be compared to the weight dependent food demand rate, K .

If, $F_{opt} \geq K$ then death rate due to starvation = 0

if, $F_{opt} = 0$ then death rate due to starvation = D

The starvation rate D is the death rate of heterotrophs of a particular mass in the complete absence of food.

Then for $0 < F_{opt} < K$

assuming a simple linear relationship between death rate and degree of satiety then the death rate due to starvation is given by

$$D(1 - \frac{F_{opt}}{K}) \quad \dots (21)$$

This is one instance where we have relaxed the condition of model homogeneity since failure to do this results in all members of a weight class dying simultaneously. The present approach implies a statistical (i.e. patchy) distribution of food shortages.

Heterotrophs continue to forage optimally until their appetite is satisfied they then rest from feeding. The final form of the flesh equivalent biomass flow to a given predator is

$$\min \{F_{opt}, K\} \quad \dots (22)$$

From equation (9) the number of individuals of the k th class eaten by a predator is

$$\frac{P_k N_k}{1 + \sum_{s=1}^n w_s h_s P_s N_s}$$

without satiation and with satiation

$$\frac{P_k N_k}{1 + \sum_{s=1}^n w_s h_s P_s N_s} \cdot \frac{k}{F_{opt}}$$

the two cases can be combined to give the number of prey class k , eaten by a single predator in unit time

$$\frac{P_k N_k}{1 + \sum_{s=1}^n w_s h_s P_s N_s} \cdot \frac{\min \{F_{opt}, K\}}{F_{opt}} \quad \dots (23)$$

Observe that expression (22) can be regained from (23) by multiplying by w_k and summing over k .

4.1.5. The continuous carnivory model

Any large ecosystem will contain carnivores of many different masses. Over a short time interval carnivores of different masses may be preying upon other heterotrophs, be starving or be being predated upon by other carnivores. A continuous model allows the simultaneous operation of these processes as the total rate of change of population number is given by the sum of the partial rates, equation (2). We shall now determine $\left(\frac{\partial n_1}{\partial t}\right)$ carnivory, using equation (23).

The number of individuals of all ages in an infinitesimal weight class is given by $n_1(w, w_0, t) dw_0 dw$. Note that subscript 1 refers to carnivores, 2 to herbivores and 3 and 4 to detritivores. The set of predation coefficients, P , becomes a function $p_1(\bar{w}, \underline{w})$ where \bar{w} is the weight of the ingestor carnivore and \underline{w} the weight of the carnivore ingested. Similarly the unit biomass handling time, h , becomes $h_1(\bar{w}, \underline{w})$. Appetite, K , becomes $k(\bar{w})$ and F_{opt} becomes $f_1(\bar{w}, t)$. To simplify the notation \bar{h}_1 is used for $h_1(\bar{w}, \underline{w})$ similarly \bar{p}_1 for $p_1(\bar{w}, \underline{w})$ and \bar{f}_1 for $f_1(\bar{w}, t)$.

From equation (20) putting $v=1$ and $M_k = w_k N_k$, for carnivores,

$$F_{opt} = \frac{\sum_{k=1}^n P_k w_k N_k}{1 + \sum_{s=1}^n h_s P_s w_s N_s}$$

which in continuous form is

$$\bar{f}_1 = \frac{\int_{\frac{\bar{\alpha}_1}{\bar{w}}}^{\bar{\beta}_1} \frac{\bar{p}_1}{\bar{w}} \int_{\bar{w}}^{\infty} (\underline{n}_1 + \underline{n}_2 + \underline{n}_3 + \underline{n}_4) dw_0 d\bar{w}}{1 + \int_{\frac{\bar{\alpha}_1}{\bar{w}}}^{\bar{\beta}_1} \bar{w} \bar{h}_1 \bar{p}_1 \int_{\bar{w}}^{\infty} (\underline{n}_1 + \underline{n}_2 + \underline{n}_3 + \underline{n}_4) dw_0 d\bar{w}} \dots (24)$$

Notice N_k becomes $(\int_{\bar{w}}^{\infty} (\underline{n}_1 + \underline{n}_2 + \underline{n}_3 + \underline{n}_4) dw_0) d\bar{w}$ which is the number of heterotrophs of masses which lie between \bar{w} and $\bar{w} + d\bar{w}$ irrespective of their age.

The optimisation procedure here reduces to optimising the domain of the integral over prey weight classes. This is achieved by selecting prey of lowest \bar{h}_1 (since $v=1$) for each \bar{w} and progressively adding those of greater \bar{h}_1 until \bar{f} reaches a maximum. Figure 1 shows the optimal domain $\alpha_1(\bar{w})$ to $\beta_1(\bar{w})$ for a single value of \bar{w} .

Here the curve $h(\bar{w}, w)$ has only one minimum and where there is a single interval of integration only. This appears to us a realistic assumption about \bar{h}_1 but the optimisation procedure carries through for any \bar{h} function giving possibly more than one interval in the range of integration. The α_1, β_1 terms are a function of time as they respond to changes in prey abundance.

We now derive the actual rate of change in n_1 taking into account the condition of carnivore satiation. The continuous form of equation (23) is

$$\frac{\min\{\bar{f}_1, \bar{k}\}}{\bar{f}_1} \cdot \frac{\bar{p}_1 (\int_{\bar{w}}^{\infty} (\underline{n}_1 + \underline{n}_2 + \underline{n}_3 + \underline{n}_4) dw_0) d\bar{w}}{1 + \int_{\frac{\bar{\alpha}_1}{\bar{w}}}^{\bar{\beta}_1} \bar{w} \bar{h}_1 \bar{p}_1 (\int_{\bar{w}}^{\infty} (\underline{n}_1 + \underline{n}_2 + \underline{n}_3 + \underline{n}_4) dw_0) d\bar{w}}$$

which is the rate of decline of all heterotrophs of size \bar{w} to $\bar{w} + d\bar{w}$

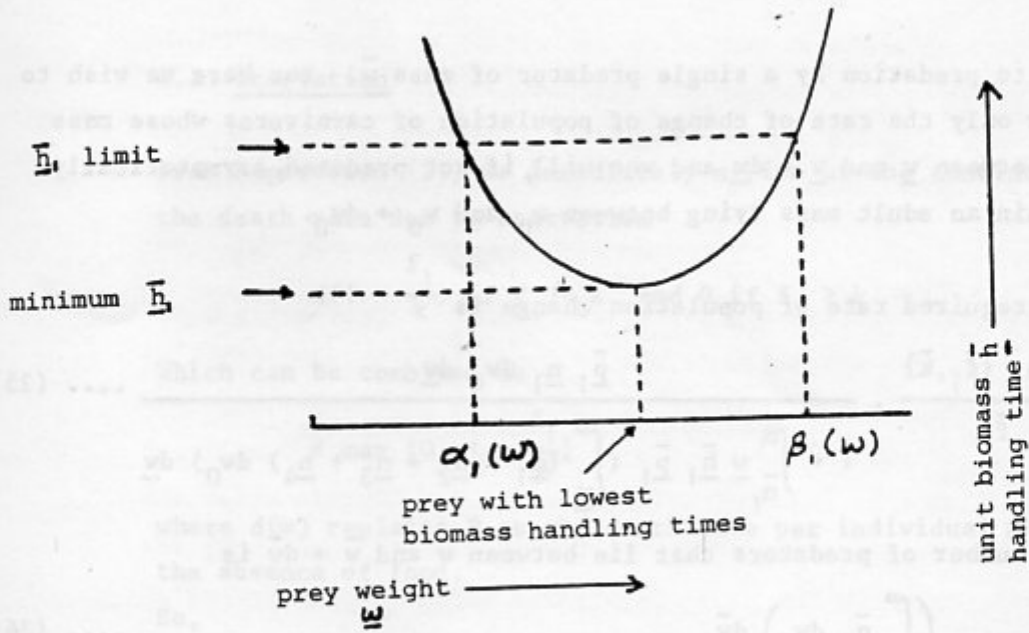


Figure 1 : The optimal foraging domain of a carnivore, \bar{w} .

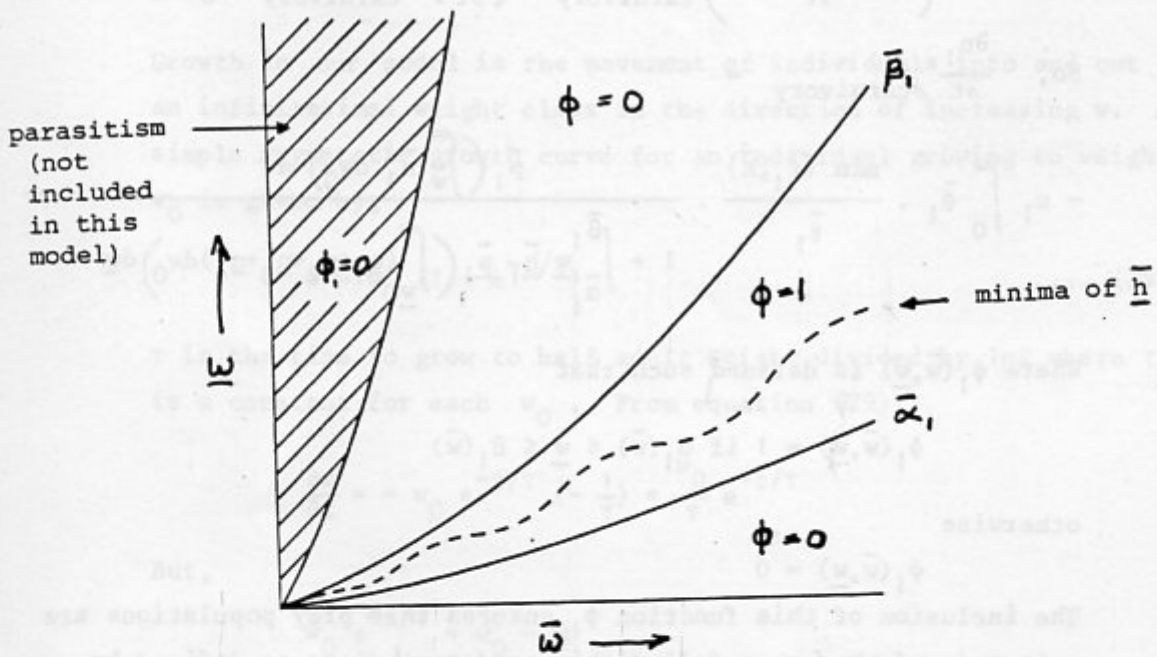


Figure 2 : Predator carnivore - prey carnivore domains of interaction for carnivores of all weights.

due to predation by a single predator of mass \bar{w} . But here we wish to know only the rate of change of population of carnivores whose mass is between \underline{w} and $\underline{w} + d\underline{w}$ and who will, if not predated, asymptotically attain an adult mass lying between w_0 and $w_0 + dw_0$.

The required rate of population change is

$$\frac{-\min\{\bar{f}_1, \bar{k}\}}{\bar{f}_1} \cdot \frac{\bar{p}_1 \underline{n}_1 dw_0 d\underline{w}}{1 + \int_{\alpha_1}^{\beta_1} \underline{w} \bar{h}_1 \bar{p}_1 \left(\int_{\underline{w}}^{\infty} (\underline{n}_1 + \underline{n}_2 + \underline{n}_3 + \underline{n}_4) d\underline{w}_0 \right) d\underline{w}} \dots (25)$$

The number of predators that lie between \bar{w} and $\bar{w} + d\bar{w}$ is

$$\left(\int_{\bar{w}}^{\infty} \bar{n}_1 d\bar{w}_0 \right) d\bar{w} \dots (26)$$

The product of expressions (25) and (26) integrated over all predators \bar{w} is,

$$\left(\frac{\partial(\underline{n}_1 dw_0 d\underline{w})}{\partial t} \right) \text{carnivory} = \left(\frac{\partial \underline{n}_1}{\partial t} \right) \text{carnivory} dw_0 d\underline{w}$$

So, $\frac{\partial \underline{n}_1}{\partial t} \text{carnivory} =$

$$- \underline{n}_1 \int_0^{\infty} \phi_1 \cdot \frac{\min\{\bar{f}_1, \bar{k}\}}{\bar{f}_1} \cdot \frac{\bar{p}_1 \left(\int_{\bar{w}}^{\infty} \bar{n}_1 d\bar{w}_0 \right) d\bar{w}}{1 + \int_{\alpha_1}^{\beta_1} \underline{w} \bar{h}_1 \bar{p}_1 \left(\int_{\underline{w}}^{\infty} (\underline{n}_1 + \underline{n}_2 + \underline{n}_3 + \underline{n}_4) d\underline{w}_0 \right) d\underline{w}} \dots (27)$$

Where $\phi_1(\bar{w}, \underline{w})$ is defined such that

$$\phi_1(\bar{w}, \underline{w}) = 1 \text{ if } \alpha_1(\bar{w}) \leq \underline{w} \leq \beta_1(\bar{w})$$

otherwise

$$\phi_1(\bar{w}, \underline{w}) = 0$$

The inclusion of this function ϕ_1 ensures that prey populations are only reduced when they fall within predators' diets as defined by optimal foraging. This is illustrated in figure 2 where the predation domain for all weight classes is shown. The minima of \bar{h}_1 occur along the dotted line.

4.2 Starvation

From expression (21) we immediately arrive at the continuous form of the death rate due to starvation

$$d(1 - \frac{f_1}{k}) \text{ if } f_1 < k, \text{ and } 0 \text{ if } f_1 \geq k$$

Which can be combined as

$$d \max \{0, 1 - \frac{f_1}{k}\}$$

where $d(w)$ replaces D as the death rate per individual per unit time in the absence of food.

So,

$$\left(\frac{\partial n_1}{\partial t}\right)_{\text{starve}} = -n_1 d \max \{0, 1 - \frac{f_1}{k}\} \dots (28)$$

4.3 Growth

Growth in our model is the movement of individuals into and out of an infinitesimal weight class in the direction of increasing w . A simple asymptotic growth curve for an individual growing to weight w_0 is given by,

$$w = w_0 (1 - e^{-t/\tau}) \dots (29)$$

τ is the time to grow to half adult weight divided by $\ln 2$ where $\tau(w_0)$ is a constant for each w_0 . From equation (29)

$$\frac{\partial w}{\partial t} = -w_0 e^{-t/\tau} (-\frac{1}{\tau}) = \frac{w_0}{\tau} e^{-t/\tau}$$

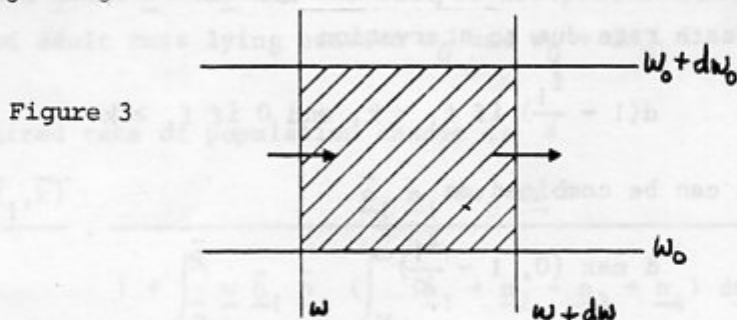
But,

$$w_0 e^{-t/\tau} = w_0 - w$$

so,

$$\frac{\partial w}{\partial t} = \frac{w_0 - w}{\tau} \dots (30)$$

We consider now the change in the number of carnivores which have current weight w to $w + dw$ and which will have adult weights between w_0 and $w_0 + dw_0$ in the time interval dt . From figure 3,



net increase in number of carnivores in the shaded area = number of carnivores which grow in - number of carnivores which grow out

$$\text{So, } \left(\frac{\partial n_1}{\partial t}\right)_{\text{growth}} dw_0 dw dt = \frac{\partial w}{\partial t} (w) dt dw_0 n_1(w) - \frac{\partial w}{\partial t} (w+dw) dt dw_0 n_1(w+dw)$$

$$\text{So, } \left(\frac{\partial n_1}{\partial t}\right)_{\text{growth}} = \frac{-\left(\left(\frac{\partial w}{\partial t} \cdot n_1\right)(w+dw) - \left(\frac{\partial w}{\partial t} \cdot n_1\right)(w)\right)}{dw}$$

$$= -\frac{\partial}{\partial w} \left(\frac{\partial w}{\partial t} \cdot n_1\right)$$

from (30)

$$= \frac{\partial}{\partial w} \left(\frac{w - w_0}{\tau} \cdot n_1\right) \dots (31)$$

The more sophisticated Bertalanffy growth equation (Bertalanffy, 1957)

$$w = w_0 \left(1 - e^{-\frac{(t+c)}{\tau}}\right)^3$$

may be substituted if required. In this case

$$\frac{\partial w}{\partial t} = 3 \left(\frac{w^{2/3} w_0^{1/3} - w}{\tau}\right)$$

and,

$$\left(\frac{\partial n_1}{\partial t}\right)_{\text{growth}} = 3 \frac{\partial}{\partial w} \left(\left(\frac{w - w^{2/3} w_0^{1/3}}{\tau}\right) \cdot n_1\right) \dots (32)$$

4.4 Reproduction

Given the present state of the model, since the population distribution n_1 is only a function of weight and adult weight, only a single reproductive strategy is possible for each adult weight. This

limitation could be partly met by having separate general equations for heterotherms and homiotherms, the latter with parental care included in the equation. Here we neglect parental care. Fertility and size of offspring are assumed to be single functions of adult weight only.

For a given adult weight class, w_0 , the fertility $r(w_0)$ is the number of offspring per individual of reproductive age per unit time. The reproductive weight is defined as $w_0 \gamma(w_0)$. Note that $\gamma(w_0)$ is the fraction of the adult weight at which reproduction begins. $b(w, w_0)$, the birth distribution, is a Gaussian function of w defined such that the fraction of offspring born of weight class, w_0 , whose weight lie between w_1 and w_2 is

$$\int_{w_1}^{w_2} b(w, w_0) dw$$

Note that

$$\int_0^{\infty} b(w, w_0) dw = 1 \text{ for all } w_0$$

The number of reproductively active individuals in an interval dw_0 at w_0 is

$$\left(\int_{\gamma w_0}^{w_0} n_1(\bar{w}, w_0, t) d\bar{w} \right) dw_0 \quad [\bar{w} \text{ is the parent not offspring}]$$

So,

$$\left(\frac{\partial n_1}{\partial t} \right) \text{reproduction} = br \int_{\gamma w_0}^{w_0} \bar{n}_1 d\bar{w} \quad \dots (33)$$

Where $\bar{n}_1 = n(\bar{w}, w_0, t)$.

5. Change in the number of Herbivores

To determine the distribution of herbivorous heterotrophs we now find the expressions for the right hand side of equation (3).

5.1 Carnivory

The change in the number of herbivores due to ingestion by carnivores is given from equation (27) as

$$\left(\frac{\partial n_2}{\partial t}\right)_{\text{carnivory}} = -n_2 \int_0^{\infty} \bar{\phi}_1 \frac{\min(\bar{f}_1, \bar{k})}{\bar{f}_1} \cdot \frac{\bar{p}_1 \left(\int_{\bar{w}}^{\infty} \bar{n}_1 dw_0\right) d\bar{w}}{1 + \int_{\bar{\alpha}_1}^{\bar{\beta}_1} \frac{w}{\bar{\alpha}_1} \bar{h}_1 \bar{p}_1 \left(\int_{\bar{w}}^{\infty} (\bar{n}_1 + \bar{n}_2 + \bar{n}_3 + \bar{n}_4) dw_0\right) d\bar{w}} \dots (34)$$

5.2 Starvation

To find the starvation rate we first have to calculate the rate at which herbivores can feed. In section 4 we generalised carnivory such that the concepts of handling time, travelling time and optimal foraging can be applied to herbivory. Equation (12) is now the defining equation for herbivory where the heterotroph feeding interaction term P_g is now the herbivore feeding interaction term.

We go directly to the continuous form of the feeding equation (20) which becomes

$$f_2 = \frac{\int_{\alpha_2}^{\beta_2} v p_2 m_A dv}{1 + \int_{\alpha_2}^{\beta_2} h_2 p_2 m_A dv} \dots (35)$$

where $f_2(w,t)$ is the flesh equivalent biomass feeding rate under the optimal foraging strategy of an individual herbivore. No bars are needed in this situation as the feeders have weights, w , whilst the food is defined by biomasses of plant state m_A of resource value v . The herbivory coefficient, p_2 , is a function of w and v , $p_2(w,v)$ and similarly for $h_2(w,v)$ the handling time per unit plant biomass.

Thus the corresponding equation to (28) for starvation of herbivores is

$$\left(\frac{\partial n_2}{\partial t}\right)_{\text{starvation}} = -n_2 d \max\left\{0, 1 - \frac{f_2}{k}\right\} \dots (36)$$

5.3 Growth

The corresponding equations to (31) and (32) are

$$\left(\frac{\partial n_2}{\partial t}\right)_{\text{growth}} = \frac{\partial}{\partial w} \left(\frac{w - w_0}{\tau} \cdot n_2 \right) \quad \dots (37)$$

$$\left(\frac{\partial n_2}{\partial t}\right)_{\text{growth}} = \frac{\partial}{\partial w} \left(\left(\frac{w - w_0^{2/3} w_0^{1/3}}{\tau} \right) \cdot n_2 \right) \quad \dots (38)$$

5.4 Reproduction

The corresponding equation to (33) is

$$\left(\frac{\partial n_2}{\partial t}\right)_{\text{reproduction}} = br \int_{w_0}^{w_0} \bar{n}_2 \, d\bar{w} \quad \dots (39)$$

6. Change in the number of detritivores

Again the distribution of detritivorous heterotrophs is provided by finding the expressions on the right hand side of equations (4) and (5).

6.1 Carnivory

The change in the number of detritivores due to ingestion by carnivores is given from equation (27) as

$$\left(\frac{\partial n_3}{\partial t}\right)_{\text{carnivory}} = -n_3 \int_0^{\infty} \bar{\phi}_1 \frac{\min\{\bar{f}_1, \bar{k}\}}{\bar{f}_1} \cdot \frac{\bar{p}_1 \left(\int_{\bar{w}}^{\infty} \bar{n}_1 \, d\bar{w}_0 \right) \, d\bar{w}}{1 + \int_{\bar{\alpha}_1}^{\bar{\beta}_1} \frac{w}{\bar{h}_1} \bar{p}_1 \left(\int_{\bar{w}}^{\infty} (n_1 + n_2 + n_3 + n_4) \, d\bar{w}_0 \right) \, d\bar{w}} \quad \dots (40)$$

Similarly

$$\left(\frac{\partial n_4}{\partial t}\right)_{\text{carnivory}} = -n_4, \dots \quad \dots (41)$$

6.2 Starvation

To calculate the starvation rate we must first find $f_3(w,t)$ the biomass feeding rate upon carcasses by an individual detritivore from equation

(24)

$$\bar{f}_3 = \frac{\int_{\alpha_3}^{\beta_3} \bar{p}_3 \frac{w}{n_D} dw}{1 + \int_{\alpha_3}^{\beta_3} \bar{h}_3 \bar{p}_3 \frac{w}{n_D} dw} \quad \dots (42)$$

The starvation rate for detritivores of plant material and dung requires the calculation of $f_4(v,t)$ the flesh equivalent biomass feeding rate of an individual detritivore.

$$f_4 = \frac{\int_{\alpha_4}^{\beta_4} v p_4 m_D dv}{1 + \int_{\alpha_4}^{\beta_4} h_4 p_4 m_D dv} \quad \dots (43)$$

So starvation, from equation (28), is given by

$$\left(\frac{\partial n_3}{\partial t}\right)_{\text{starvation}} = -n_3 d \max\left\{0, 1 - \frac{f_3}{k}\right\} \quad \dots (44)$$

Repeat this expression replacing subscript 3 by 4 for $\left(\frac{\partial n_4}{\partial t}\right)_{\text{starvation}}$.

6.3 Growth

The corresponding equations to (31) and (32) are

$$\left(\frac{\partial n_3}{\partial t}\right)_{\text{growth}} = \frac{\partial}{\partial w} \left(\frac{w - w_0}{\tau} \cdot n_3 \right) \quad \dots (45)$$

$$\left(\frac{\partial n_3}{\partial t}\right)_{\text{growth}} = 3 \frac{\partial}{\partial w} \left(\left(\frac{w - w_0^{2/3} w_0^{1/3}}{\tau} \right) \cdot n_3 \right) \quad \dots (46)$$

With similar expressions for n_4 .

6.4 Reproduction

The corresponding equation to (33) is

$$\left(\frac{\partial n_3}{\partial t}\right)_{\text{reproduction}} = br \int_{\gamma w_0}^w \bar{n}_3 d\bar{w} \quad \dots (47)$$

and similarly for n_4 .

7. Change in the plant biomass distribution

Our model of autotroph behaviour is not as detailed as the heterotroph models presented above. We have attempted the simplest model which appears to us to establish the global properties of an autonomous plant mediating the solar energy supply to the food demands of herbivores which is perhaps not a botanist's view of the world.

7.1 Herbivory

The change in the plant biomass distribution is derived from the predation equation (27) with plant biomass substituted for heterotroph prey thus,

$$\left(\int_{\underline{w}}^{\infty} (n_1 + n_2 + n_3 + n_4) dw_0 \right) d\underline{w}, \text{ becomes, } m_A dv$$

and subscript 2 replaces subscript 1 since herbivores are the feeders not carnivores, then

$$\left(\frac{\partial m_A}{\partial t} \right)_{\text{herbivory}} = - m_A \int_0^{\infty} \phi_2 \frac{\min \{f_2, k\}}{f_2} \cdot \frac{p_2 \left(\int_w^{\infty} n_2 dw_0 \right) dw}{1 + \int_{\alpha_2}^{\beta_2} h_2 p_2 m_A dv} \dots (48)$$

where ϕ_2 is defined as follows

$$\phi_2(w, v) = 1 \text{ if } \alpha_2(w) \leq v \leq \beta_2(w)$$

otherwise

$$\phi_2(w, v) = 0$$

and where $\alpha_2(w), \beta_2(w)$ are the limits on the range of plant resource states, v , in the optimal diet of a herbivore of weight w .

7.2 Growth

In our representation of plant growth we distinguish between photosynthetic and non-photosynthetic parts of the $m_A(v)$ distribution. In addition we distinguish seasonally replaced and non-seasonal portions of $m_A(v)$. A distribution of plant biomass for all v states is given in figure 4 showing the parts of the plant which are distinguished above.

$$\text{where } M_B = \int_0^{V_G} m_A, \quad M_G = \int_{V_G}^{V_Y} m_A, \quad M_Y = \int_{V_Y}^1 m_A$$

where M_G is the photosynthetic biomass, $M_G + M_Y$ the seasonally replaced biomass and $M_B + M_Y$ the non-photosynthetic biomass. In nature this approximates to the distribution of woody tissue (brown), leaf tissue (green) and high resource value seeds and storage organs (yellow).

For $0 < v < V_G$, let the fractional rate of increase of woody biomass,

$$C_B = \lim_{\Delta t \rightarrow 0} \frac{\frac{\Delta m_A(v,t)}{m_A(v,t)}}{\Delta t} = \frac{1}{m_A} \left(\frac{\partial m_A}{\partial t} \right) \text{ growth} \quad \dots (49)$$

and for $V_G \leq v < 1$, let the fractional rate of increase of non-woody biomass,

$$C_{GY} = \lim_{\Delta t \rightarrow 0} \frac{\frac{\Delta m_A(v,t)}{m_A(v,t)}}{\Delta t} = \frac{1}{m_A} \left(\frac{\partial m_A}{\partial t} \right) \text{ growth} \quad \dots (50)$$

Our further assumption is that C_B and C_{GY} are only a function of t and not v .

Under conditions of light saturation of a closed canopy the energy per unit time captured by the photosynthetic biomass in the ecosystem is given by S . Whilst the upper canopy photosynthesis may be limited by

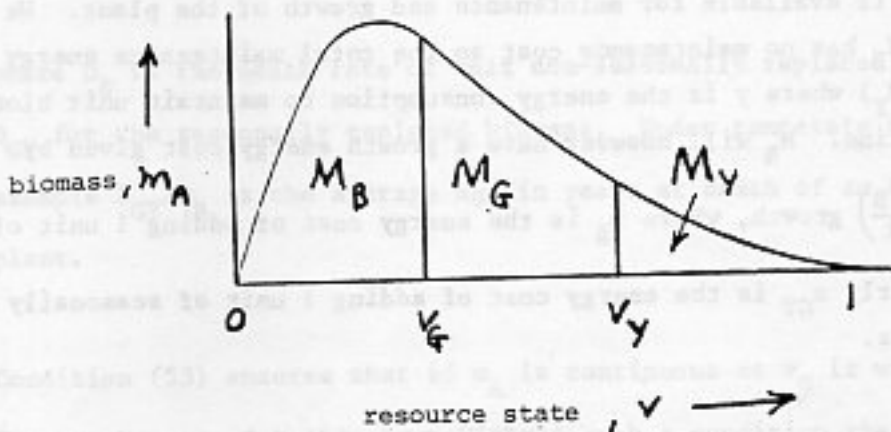


Figure 4 : The plant biomass distribution.

factors other than light availability the plants or plant parts in the lower canopy will through phenological changes or self-shading experience conditions of light deprivation.

When herbivory reduces the photosynthetic mass a lower level of energy fixation will occur given by eM_G where e is the rate of solar energy fixation per unit biomass of photosynthetic material. Allowing for saturation the total energy fixed in the ecosystem is given by

$$\min \{S, eM_G\} \quad \dots (51)$$

which is available for maintenance and growth of the plant. We assume that M_B has no maintenance cost so the total maintenance energy cost is $y(M_G + M_Y)$ where y is the energy consumption to maintain unit biomass for unit time. M_B will however have a growth energy cost given by

$x_B \left(\frac{\partial M_B}{\partial t} \right)$ growth, where x_B is the energy cost of adding 1 unit of biomass.

Similarly x_{GY} is the energy cost of adding 1 unit of seasonally replaced biomass.

Thus,

$$x_B \left(\frac{\partial M_B}{\partial t} \right) \text{ growth} + x_{GY} \left(\frac{\partial (M_G + M_Y)}{\partial t} \right) \text{ growth} + y(M_G + M_Y) = \min \{S, eM_G\}$$

So,

$$\left(\frac{x_B \partial \left(\int_0^{V_G} m_A \partial v \right)}{\partial t} \right) \text{ growth} + \left(\frac{x_{GY} \partial \left(\int_{V_G}^1 m_A \partial v \right)}{\partial t} \right) \text{ growth} + y(M_G + M_Y) = \min \{S, eM_G\}$$

now using equations (49) and (50)

$$x_B C_B \int_0^{V_G} m_A \, dv + x_{GY} C_{GY} \int_{V_G}^1 m_A \, dv + y(M_G + M_Y) = \min \{S, eM_G\}$$

So substituting for the integrals and putting $M_G + M_Y = M_{GY}$ we have

$$x_B C_B M_B + x_{GY} C_{GY} M_{GY} + yM_{GY} = \min \{S, eM_G\} \quad \dots (52)$$

In order to solve for C_B and C_{GY} we require another relationship between them. This is provided by the following continuity condition for m_A at v_G

$$C_B m_A(v_G) - D_B m_A(v_G) = C_{GY} m_A(v_G) - D_{GY} m_A(v_G)$$

whence

$$C_B - D_B = C_{GY} - D_{GY} \quad \dots (53)$$

where D_B is the death rate of unit non-seasonally replaced biomass and D_{GY} for the seasonally replaced biomass. Under temperate conditions for example D_{GY}/D_B is the average age in years at death of an individual plant.

Condition (53) ensures that if m_A is continuous at v_G it will remain so in the absence of herbivory. Without such a condition the standing crop of green plant could increase without a corresponding increase in supportive tissue.

We can now solve for C_B and C_{GY} and substitute them in equations (49) and (50) to yield our plant growth term.

$$\left. \begin{aligned} \left(\frac{\partial m_A}{\partial t}\right)_{\text{growth}} &= \left(\frac{\min\{S, eM_G\} - yM_{GY} + x_{GY}M_{GY}(D_B - D_{GY})}{x_B M_B + x_{GY} M_{GY}} \right) m_A \\ &\quad \text{for } 0 < v < v_G \end{aligned} \right\} (54)$$

$$\left. \begin{aligned} \left(\frac{\partial m_A}{\partial t}\right)_{\text{growth}} &= \left(\frac{\min\{S, eM_G\} - yM_{GY} + x_B M_B(D_{GY} - D_B)}{x_B M_B + x_{GY} M_{GY}} \right) m_A \\ &\quad \text{for } v_G \leq v \leq 1. \end{aligned} \right\}$$

It is instructive to investigate a few implications of these equations in order to confirm that the autotroph dynamics are behaving in a globally plausible manner.

The specific growth rates in the absence of herbivory are given by

$$C_B - D_B = \frac{\min \{S, eM_G\} - yM_{GY} - x_{GY}^M D_{GY} - x_B^M D_B}{x_B^M + x_{GY}^M} \quad \dots (55)$$

$$= C_{GY} - D_{GY}$$

At steady state in the absence of herbivory we can equate these expressions to zero to obtain

$$C_B = D_B \text{ and } C_{GY} = D_{GY}$$

thus for these conditions growth exactly compensates for natural death and litter production, and,

$$yM_{GY} + x_{GY}^M D_{GY} + x_B^M D_B = \min \{S, eM_G\}$$

$$= s \text{ here (see below)} \quad \dots (56)$$

that is the maximal solar input is entirely devoted to maintenance and litter production with no net increase in standing crop. So plant growth is limited by solar input as is desired.

The dynamic behaviour of the autotroph biomass distribution in the absence of herbivory can be investigated by assuming a mathematically simple distribution $m_A(v, t) = \ell(t)$, $0 < v \leq 1$

$$\text{Then for } \ell < \frac{s}{e(v_Y - v_G)},$$

$$\min \{S, eM_G\} = \min \{S, e\ell(v_Y - v_G)\} = e\ell(v_Y - v_G)$$

And by (55)

$$\frac{dl}{dt} = \frac{e(v_Y - v_G) - y(1 - v_G) - x_{GY}(1 - v_G)D_{GY} - x_B v_G D_B}{x_B v_G + x_{GY}(1 - v_G)} \cdot \lambda \dots (57)$$

The numerator of this expression (including λ) represents the solar input less the total maintenance cost and less the energy to replace biomass loss to detritus (each term is measured in unit time) and so the numerator must be greater than zero away from the steady state. Equation (57) then represents a situation of exponential growth of plant biomass.

$$\text{If } \lambda \geq \frac{S}{e(v_Y - v_G)}, \quad \min \{S, eM_G\} = S$$

and by (55)

$$\frac{dl}{dt} = \frac{S}{x_B v_G + x_{GY}(1 - v_G)} - \left(\frac{y(1 - v_G) + x_{GY}(1 - v_G)D_{GY} + x_B v_G D_B}{x_B v_G + x_{GY}(1 - v_G)} \right) \cdot \lambda \dots (58)$$

Thus under conditions of light saturation $m_A = \lambda$ is approaching a limiting value λ_{\max} from below, where,

$$\lambda_{\max} = \frac{S}{y(1 - v_G) + x_{GY}(1 - v_G)D_{GY} + x_B v_G D_B} \dots (59)$$

Rearranging equation (59) we recover our steady state equation (56).

Our choice of $\min \{S, eM_G\} = S$ in equation (56) now becomes clear.

Finally we observe that our plant growth term equation (54) is responsive to overgrazing (low M_G) which produces reduced growth and, in extremis, unnatural plant death.

7.3 Litter

In calculating the losses to detritus we distinguish between seasonally and non-seasonally lost plant parts. We treat woody tissue as being part of the heterotroph until the whole plant dies.

Losses to detritus are

$$\left(\frac{\partial m_A}{\partial t}\right)_{\text{death}} = -D_{B^m A} \quad \text{for} \quad 0 < v < v_G$$

$$= 0 \text{ otherwise} \quad \dots (60)$$

$$\left(\frac{\partial m_A}{\partial t}\right)_{\text{litter}} = -D_{GY^m A} \quad \text{for} \quad v_G \leq v \leq 1$$

$$= 0 \text{ otherwise} \quad \dots (61)$$

8. Change in the carcass distribution

The distribution of dead animal tissue by particle size, w , is determined by the terms in equation (6). We first consider change in the n_D distribution caused by detritivores feeding on carcasses.

8.1 Detritivory

By analogy with equation (27)

$$\left(\frac{\partial n_D}{\partial t}\right)_{\text{detritivory}} = -n_D \int_0^\infty \bar{\phi}_3 \cdot \frac{\min(\bar{f}_3, \bar{k})}{\bar{f}_3} \cdot \frac{\bar{p}_3 \left(\int_{\bar{\alpha}_3}^{\infty} \bar{n}_3 \, d\bar{w} \right) d\bar{w}}{1 + \int_{\bar{\alpha}_3}^{\bar{\beta}_3} \bar{w} \bar{h}_3 \bar{p}_3 n_D \, d\bar{w}} \quad \dots (62)$$

Where ϕ_3 is defined as,

$$\phi_3(\bar{w}, \underline{w}) = 1 \text{ if } \alpha_3(\bar{w}) \leq \underline{w} \leq \beta_3(\bar{w})$$

and $\phi_3(\bar{w}, \underline{w}) = 0$ otherwise

and where $\alpha_3(\bar{w})$, $\beta_3(\bar{w})$, are the limits on the range of carcass particle size, \underline{w} , in the optimal diet of a carcass detritivore of weight, \bar{w} .

8.2 Carcass supply

Carcasses are added to n_D as a result of heterotroph starvation. Natural death is not included in our current model but could be incorporated without difficulty as in equation (60) for the plant. From equation (28)

$$\left(\frac{\partial n_D}{\partial t}\right)_{\text{carcass}} = \sum_{i=1}^4 \int_w^{\infty} n_i dw_0 d \max \left\{0, 1 - \frac{f_i}{k}\right\} \dots (63)$$

8.3 Fragmentation

At the moment of a heterotroph's death the likelihood of its carcass being ingested is dependent only on the weight of the carcass and detritivore abundance. With time however the carcass becomes fragmented (Sih 1980) and suffers putrefaction. We model both these processes as fragmentation, which is defined here as the carcass changing weight class with time but conserving biomass. Janzen (1977) has suggested that the production of toxins by small detritivores effectively allocates the food resource to them only. We model this process of putrefaction by considering the carcasses with time to be progressively fragmented by toxins and so to fall within the foraging range of increasingly small detritivores.

Let us assume a fragmentation rate dw/dt of $-C_F w$

Where $\Delta_{1/2}(w)$ is the time taken for a carcass to fragment to half its weight

$$C_F = \frac{\ln 2}{\Delta_{1/2}}$$

By an exact analogy to the derivation of equation (31) but conserving biomass rather than the number of individuals

$$\left(\frac{\partial (wn_D)}{\partial t}\right)_{\text{fragmentation}} = - \frac{\partial}{\partial w} ((-C_F w)(wn_D))$$

so,

$$\left(\frac{\partial n_D}{\partial t}\right)_{\text{fragmentation}} = \frac{1}{w} \frac{\partial}{\partial w} (C_F w^2 n_D) \dots (64)$$

9. Change in the detritus biomass distribution

The distribution of detritus biomass over resource states, v , is now considered by expanding equation (7).

9.1 Detritivory

By analogy with equation (48) the consumption of detritus by detritivores n_4 is given by

$$\left(\frac{\partial m_D}{\partial t}\right)_{\text{detritivory}} = -m_D \int_0^{\infty} \phi_4 \frac{\min(f_4, k)}{f_4} \cdot \frac{p_4 \left(\int_w^{\infty} n_4 dw_0 \right) dw}{1 + \int_{\alpha_4}^{\beta_4} h_4 p_4 m_D dv} \dots (65)$$

Where ϕ_4 is defined as,

$$\phi_4(w, v) = 1 \quad \text{if } \alpha_4(w) \leq v \leq \beta_4(w)$$

and $\phi_4(w, v) = 0$ otherwise

and where $\alpha_4(w)$, $\beta_4(w)$ are the limits on the range of detritus resources, v , in the optimal diet of a non-carnivorous detritivore of weight, w .

9.2 Plant detritus

At death or leaf fall plant biomass of resource value, v , is assigned to the same v state in the detritus distribution.

$$\left(\frac{\partial m_D}{\partial t}\right)_{\text{plant detritus}} = \left(\frac{\partial m_D}{\partial t}\right)_{\text{death}} + \left(\frac{\partial m_D}{\partial t}\right)_{\text{litter}}$$

from equations (60) and (61)

$$\left.\begin{aligned} \left(\frac{\partial m_D}{\partial t}\right)_{\text{plant detritus}} &= D_B m_A \quad \text{for } 0 < v < v_G \\ &= D_{GY} m_A \quad \text{for } v_G \leq v < 1 \end{aligned}\right\} \dots (66)$$

9.3 Dung

All heterotrophs generate dung which can be defined as the non-assimilated fraction of ingested food materials. Thus dung production is dependent upon, v , the food resource value. Our earlier definition of v is not convenient, as it stands, for comparison with available data from the literature. The resource value, v , was defined such that m g of biomass at v are equivalent to, i.e. (give rise to the same assimilated biomass as) vm g of heterotroph flesh.

Let a_1 be the assimilated fraction of flesh consumption, $v = 1$

let a_v be that of a biomass at v consumed

Then m g of biomass at v produce $a_v m$ g assimilated and mv g of flesh produce $a_1 mv$ g assimilated. So according to our definition

$$a_v m = a_1 mv$$

$$\text{so } a_v = a_1 v \quad \text{and } v = \frac{a_v}{a_1} \quad \dots (67)$$

Thus digestion of mass m g at v gives $(1 - a_v)m$ g of dung. However, empirical input is required to determine the resource state, v' , of this mass of dung. A summary of assimilation fractions a_v is given in Heal and Maclean (1975) from which we may estimate v values for the main trophic groups using equation (67)*. In the absence of more precise information known to us we assume the very simple functional relationship between v and v' namely that $v' = v r_D$ where r_D is a constant. Values of $r_D = 0.33$ appear plausible as r_D lies between $\frac{v_D}{v_C}$ and $\frac{v_D}{v_H}$ i.e. between .25 and .44

*Heal and MacLean give the following values of assimilation; for carnivores $a_C = .8$, for herbivores $a_H = .45$, for detritivores $a_D = .2$ So $v_H = .56$, and $v_D = .25$ and by definition $v_C = 1$.

$$\left(\frac{\partial m_D}{\partial t}\right)_{\text{dung}} = \left(\frac{\partial m_D}{\partial t}\right)_{\text{carnivore dung}} + \left(\frac{\partial m_D}{\partial t}\right)_{\text{herbivore dung}} + \left(\frac{\partial m_D}{\partial t}\right)_{\text{detritivore dung}}$$

$$\left(\frac{\partial m_D}{\partial t}\right)_{\text{carnivore dung}} = g(1 - a_1) \int_0^{\infty} \min\{f_1, k\} \int_w n_1 dw_0 dw \dots (68)$$

where $g(v)$ is a normalised Gaussian function whose maximum value is $g(r_D)$ and $(1 - a_1) \min\{f_1, k\}$ is the mass of dung produced in unit time, by a carnivore of weight, w .

$$\left(\frac{\partial m_D(v)}{\partial t}\right)_{\text{herbivore dung}} = -\frac{1}{r_D} \left(\frac{\partial m_A\left(\frac{v}{r_D}\right)}{\partial t}\right)_{\text{herbivory}} \left(1 - a_1 \frac{v}{r_D}\right) \dots (69)$$

where the increment in the quantity of dung at v is purely a function of herbivory, equation (48), at v -state v/r_D . Similarly for detritivores from equation (65) with a term for carcass detritivores analogous to (68),

$$\begin{aligned} \left(\frac{\partial m_D(v)}{\partial t}\right)_{\text{dung}} &= -\frac{1}{r_D} \left(\frac{\partial m_D\left(\frac{v}{r_D}\right)}{\partial t}\right)_{\text{detritivory}} \left(1 - a_1 \frac{v}{r_D}\right) \\ &+ g(1 - a_1) \int_0^{\infty} \min\{f_3, k\} \int_w n_3 dw_0 dw \dots (70) \end{aligned}$$

For equations (69) and (70) since $0 < v \leq 1$ implies $0 < \frac{v}{r_D} \leq \frac{1}{r_D} > 1$, it is necessary to artificially extend the domain of herbivory and detritivory by setting them equal to zero for $1 < v \leq \frac{1}{r_D}$.

9.4 Decay

In the model the process of decay is characterised by movement of biomass towards the origin ($v = 0$) at a rate proportional to its displacement from the origin. By direct analogy with the derivation of equations (31) and (64) we get,

$$\begin{aligned} \left(\frac{\partial m_D}{\partial t}\right)_{\text{decay}} &= -\frac{\partial}{\partial t} ((-C_D v) m_D) \\ &= \frac{\partial}{\partial t} (C_D v m_D) \dots (71) \end{aligned}$$

10. Recapitulation

We have now completed the description of the seven equations of the trophic continuum. It is inevitable that in making a mathematical model some changes in the original description (Cousins, 1980) will result, although the changes are minor.

The solar input which generates the initial products of photosynthesis now connects with the autotroph over the whole of the photosynthetic region of the plant. Plant products are then translocated and transformed chemically to both higher and lower resource states. The only other change of any magnitude arises from a natural limit on the size of the smallest heterotroph in the system. Because there will be a limit to the size or dilution of food taken by that heterotroph there will be a pool of unusable food in the system. We predict this for all ecosystems not just aquatic ones where it is already well known.

Other changes in the model which appear marked are in fact less so. The use of two detritus equations rather than one is simply because we have not succeeded in modelling organisms which eat both dead plant and animal material. Similarly omnivory is included in the original continuum description of heterotrophs but not in this paper. Detritivory, herbivory, and carnivory flows were also shown in the original model but the calculation of these flows requires that the number of heterotrophs of weight w , be disaggregated into carnivores $n_1(w)$, herbivores $n_2(w)$, and detritivores $n_3(w)$, $n_4(w)$. We should perhaps stress that identification of these trophic groups in a weight class is not a recourse to trophic level concepts.

11. Discussion

Ecosystems are apparently comprised of loosely connected elements. Perhaps for this reason alone ecological research has been successful at the level of the single species, taxon or habitat. There are however a few applications which require analysis of much larger ecological groupings. These include whole system effects of radioactive or biochemical toxins or taking a different example, ocean fishery management (May et al 1979).

Global models have other uses too. The choice of variables investigated at the local level is influenced by the global model held by the investigator. Thus a global model focussed on body size suggests questions to be asked at the local level and also allows local models to fit with each other. Whilst global models have local implications the converse is also true. Optimal foraging strategies studied at the local level of the single species have important implications for global energy flows and biomass distributions. Optimal foraging theory is still at an early stage of development (Krebs, 1978) and what is to be optimised is still a subject of speculation and investigation. Ellis et al (1976) identify rate of energy gain, feeding time minimisation and nutritional balance as candidates. Evans (1976) presents a taxonomy of weather factors which affect prey availability and the energy cost of predator activity which together determine a foraging strategy. It is clear from our trophic continuum model that choosing different parameters to be optimised will generate different whole ecosystem structures. Viewed in reverse, observed whole ecosystem structures may indicate which foraging strategies are consistent at the local level.

Having identified some of the reasons for making global models we now briefly discuss the nature of global models themselves with particular reference to ecological examples. The joint interaction of many subsystems so as to produce structure and function on a macroscopic scale has been identified by Haken (1977) and others as a coherent field of study irrespective of system type. This study of the emergent properties of systems may be considered as the study of global

models per se and our concern here. Behaviours which are of interest in this context include the system's trajectories over domains of attraction, whether there are stable equilibria, bifurcations and catastrophic changes between modes. These behaviours allow us to examine global models relevant to ecosystem dynamics. Clearly the predator-prey limit cycle is a good example of an emergent property of a simple but global ecosystem model. (May 1974). A two species model showing catastrophic change is given by Jones (1975) for the spruce budworm and by Bazin et al (1978) for microbial predation. A two species predator-prey model admitting spatial heterogeneity (Stenseth 1980), demonstrates multiple stable points.

Our sphere of interest is large multicomponent ecosystems. Examples from ecology are Platt and Denman (1977, 1978), Silvert and Platt (1978, In Press), Ellis et al (1976) and Innis (1978). Paradoxically the world models of Forrester (1968) and Meadows et al (1974) do not study global system properties as such but are concerned only to extrapolate the present state of the system in an integrated way. In order to study the global properties of a world model it would be necessary to investigate system trajectories from many starting points and over many timescales appropriate to whole system behaviour. The Forrester model was not structured for this purpose nor is that its function.

Of the large multi-component ecosystem models the most highly developed is the ELM model of the US Grassland Biome study of the International Biological Program (Innis 1978). In that model the abiotic, producer, consumer, decomposer and nutrient subsystems are interactively linked. By the nature of the system being studied the ELM modellers have the advantage that perturbation experiments can be carried out both on the model and on the ecosystem itself. This is in contrast to Forrester's world dynamics where only the model can be perturbed. Like Forrester, ELM uses the SIMCOMP simulation language based upon difference equations. Once again distinctions must be drawn between investigation of the integrated behaviours of the model over the region for which it has been constructed and the set of truly global behaviours. Finite difference equations are not well suited to the latter application.

Three problems in this respect are (i) the global behaviours of difference equations deviate from those of the corresponding differential equations. Whilst quantal processes are more accurately modelled using difference equations, where the level of observer resolution is such that a statistical description is all that is possible, then it is differential equations that best provide the system's functional description (Wiegert, 1975). (ii) rounding errors of the computer simulation can propagate and in the absence of the underlying functional description may do so without the knowledge of the modeller. (iii) difference equations do not allow the investigation of the unstable parts of the system trajectory and so cannot easily detect catastrophic changes. We should stress that we are not trying to criticise ELM which is the most thorough computer model of an ecosystem to date, but only to distinguish model strategies. In this respect Platt and his co-workers and our own work, though at a more rudimentary stage, attempt a truly continuous description of whole ecosystems.

Platt and Denman (1977, 1978) working on pelagic marine ecosystems give an equation for the steady state biomass distribution of organic particles by weight. Their result is in good agreement with the empirical findings of Sheldon et al (1973). Similarly Lurié and Wagensberg (1980) have produced equations for biomass distributions of marine ecosystems derived from entropy considerations only. Such steady state solutions may be considered as referring to the equilibrium point in the system's principle domain of attraction. Dynamic equations are required to investigate behaviours away from the equilibrium point. Silvert and Platt (1978, In Press) attempt a dynamic model and investigate its response to a perturbation in the biomass distribution.

The formation of a global model from isolatable parts is completely specified by the interactions between parts. In the present model these interactions reduce to predation interactions and an energy allocation strategy within the particular plant or animal. Considering heterotrophs the choice is between allocating energy to growth, reproduction, fat deposition and locomotion (McNab 1980). In our model these activities are time invariant functions of food supply to heterotrophs, their current weight and adult weight. We exclude many of the interaction terms of McNab (1980).

At any instant in time the sum of energy expended may be more or less than the assimilated energy intake. In nature this is made possible for the organism by the presence of energy storage, figure 5. For the modeller the energy stores are decoupling points of the system which permit the isolation of the model elements essential to the modelling process. Although short term energy imbalances occur in nature, long term imbalances do not. Again in our model long term imbalances are prevented by starvation using empirical values for both appetite and the starvation rate. Decoupling also occurs between the biotic and abiotic parts of the ecosystem, for example, atmospheric oxygen may be considered as a store or buffer sufficient that it is not rate limiting for respiration.

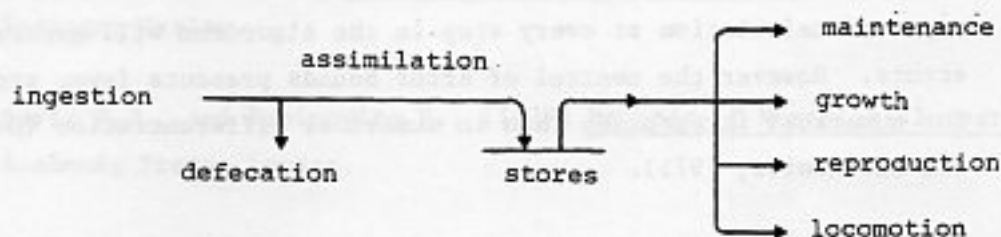


Figure 5 : Energy allocation in the individual organism.

Our model could be further developed in a number of ways. Detailed modelling of the organisms' energy stores (figure 5) and the energy allocation process would produce greater precision. Calow (1976) has for example modelled the relationships between fat storage, growth and reproduction. The role of stored fat may be particularly important for some pesticide studies. The organism's energy allocation strategy would also have to be allowed to vary if the continuum model were used to investigate change over evolutionary time. Structural change in the model may also be required if different foraging strategies are incorporated. Model developments and specialisations are legion; parental care, parasitism, omnivory, homiothermy, heterothermy, above and below ground ecosystems, seasonality, nutrient limits and spatial heterogeneity.

Now let us discuss the mathematical structure of the model and how one might solve the equations. Few equations of interest for the behaviour of ecosystems can be solved explicitly and recourse to numerical methods for their solution is essential. Numerical methods free us to model the system as faithfully as possible rather than attempting to reapply more familiar but less appropriate equations. It is not common for example to include integrals in the modelling of feeding interactions although Cushing (1977) reviews and extends their use to model delays in population dynamics. It is inherently because of delays caused by handling that integrodifferential equations are used in our predation terms. We should also note that delays due to reproduction and growth are directly incorporated into our model by the inclusion of juvenile stages in the specification. One concern in using integrals is whether their repeated calculation at every step in the algorithm will generate errors. However the control of error bounds presents fewer problems for numerical integration than in numerical differentiation (Davis and Rabinowitz, 1975).

The solution of equations 1-7 is an initial-value problem in that given the state of the system at any instant in time its future is completely determined. The specification of the initial state requires inputting number and biomass distributions. Running the model from many initial states allows the study of its global properties. A numerical solution will require using predictor-corrector methods (Lapidus and Seinfeld, 1971). Unlike the Runge-Kutta method, which cannot be used here, a predictor-corrector solution needs an additional numerical technique to calculate initial values of rates of change of the distributions. This additional step would not be a trivial one for a simulation from any particular initial state. However we believe that initialisation errors will not pose a problem if whole ecosystems exhibit strong domains of attraction.

REFERENCES

- Bazin M.J. and Saunders P.J. (1978) Nature 275: 52.
- Bertalanffy, L. von, (1957) Q. Rev. Biol. 32: 217.
- Calow, P., (1977) Adv. Ecol. Res 10: 1.
- Cousins, S.H., (1978) Trophic models - was Elton right? Energy Research group, The Open University, Milton Keynes.
- Cousins, S.H., (1980) J. theor. Biol 82: 607.
- Cushing J.M., (1977) Lecture notes in biomathematics 20 Berlin: Springer-Verlag.
- Davis P.J., and Rabinowitz P., (1975) Methods of Numerical Integration Academic Press, London.
- Ellis, J.E., Weins, J.A., Rodel, C.F., and Anway, J.C., (1976) J. theor. Biol. 60: 93.
- Elton, C.S., (1927) Animal Ecology, Sidgwick and Jackson, London.
- Evans, P.R., (1976) Ardea 64: 117.
- Fenchel, T., (1974) Oecologia (Berl) 14, 317.
- Forrester, J.W., (1971) World Dynamics. Cambridge, Mass: Wright-Allen press.
- Haken, H., (1977) Synergetics: An Introduction Berlin: Springer-Verlag.
- Heal, O.W., MacLean Jr., S.F., (1975). In Unifying Concepts in Ecology (W.H. van Dobben, R.H. Lowe-McConnell eds), pp 89-108. The Hague: Junk publications.

Innis, G.S., (1978) Grassland Simulation Model, Ecological Studies 26
Berlin: Springer-Verlag.

Janzen, D.H. (1977) Amer Nat 111: 691.

Jones D.D., (1975) The application of catastrophe theory to ecological systems. International institute for applied systems analysis,
Laxenburg, Austria RR-75-15.

Krebs, J.R., (1978) In Behavioural ecology an evolutionary approach.
eds J.R. Krebs and N.B. Davies, Oxford: Blackwell Scientific.

Lapidus L., and Seinfeld, J.H., (1971) Numerical solution of ordinary differential equations, Academic Press, New York.

Lindeman, R.L., (1942) Ecology 23: 399.

May, R.M., (1974) Stability and complexity in model ecosystems
Princeton: Princeton University press.9: 188.

May R.M., Beddington, J.R., Clark, W.C., Holt, S.J., and Laws, R.M.,
(1979) Science 205: 267.

McNab, B.K., (1980) Amer. Nat. 116: 106.

Meadows, D.L., Behrens, W.W. III, Meadows, D.H., Naill, R.F., Randers,
J and Zahn, E.K.D. (1974) Dynamics of growth in a finite world.
Cambridge Mass: Wright-Allen press.

Morowitz, H.J., (1968) Energy flow in biology. London and New York:
Academic press.

Orians, G.H., (1980) BioScience 30: 79.

Platt, T., and Denman, K., (1977) Helgol. wiss. Meers. 30: 575.

Platt, T., and Denman K., (1978) Rapp. p. - v Reun. Cons. int. Explor. Mer, 173: 60.

Sheldon, R.W., Sutcliffe, W.H., and Prakesh A., (1973) Limnol Oceanogr. 18: 719.

Sih, A., (1980) Amer. Nat. 116: 281.

Silvert, W., and Platt, T., (1978) Limnol Oceanogr. 23: 813-816.

Silvert, W., and Platt, T., (in press) Dynamic energy-flow model of particle size distribution in pelagic ecosystems.

Wiegert, R.G., (1975) Ann. Rev. Syst. Ecol. 6, 311.

Yodzis, P., (1978) Lecture notes in Biomathematics 25 Berlin: Springer-Verlag.

Acknowledgements

We would like to thank Dr. F. Holroyd and Dr. P. Evans for detailed and constructive comments on earlier drafts of this paper.