

Reprinted from  
CANADIAN BULLETIN OF  
FISHERIES AND AQUATIC SCIENCES 213

ULANOWICZ, R. E., AND T. PLATT [ED.] 1985. Ecosystem theory for biological  
oceanography. Can. Bull. Fish. Aquat. Sci. 213: 260 p.

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Structure and Equations for a Predictive Model**

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Pages 76-93

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## The Trophic Continuum in Marine Ecosystems: Structure and Equations for a Predictive Model

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### Introduction

The population dynamics and consequently the trophic energetics of simple two and three species systems of predators and prey or parasites and hosts are now considered well established, while the central problem of how very many species interact in a food web remains open (May 1979). This problem has also been expressed in terms of the need to shift from an understanding of single species fisheries to multispecies fisheries (Mercer 1982). Here the development of a multispecies model is first put in the context of an existing model of large ecosystems.

The traditional approach to the study of large, many species, ecosystems has been, since Lindeman (1942), to invoke a particular abstraction, the trophic level, with which to simplify ecosystem food web interactions. An organism would in the trophic level model be apportioned either wholly or in part to a particular trophic level. The green plant is easily identified as trophic level one, organisms which feed on the green plant are assigned to trophic level two and carnivores preying upon these herbivores are placed at trophic level three and so on. It is worth noting at this point that there is only one taxonomic distinction incorporated into this model. The plant kingdom excepting fungi is limited to level one and animal kingdom to trophic levels two and above. Within these kingdoms the trophic level model is truly ataxonomic in that the species identity or even the phylogenetic identity of the organism is subsumed within the operational measure of trophic level content, biomass. Thus all plant species and plant parts are subsumed as plant biomass, all species of herbivores are identified as herbivore biomass and so on.

It is significant that Lindeman believed these categories to be operationally important to the evolution of ecosystems, that is, the efficiency of transfer of energy between trophic levels would become greater the higher the trophic level and that the whole chain of levels would become more efficient as a result of ecological succession. The attraction of these hypotheses was such that Lindeman's methodology (Lindeman 1942) was adopted as the basis for the International Biological Programme (IBP) 1964-74. However by the close of IBP it was evident that trophic levels could not be identified at levels three and above (Heal and Maclean 1975) and consequently Lindeman's hypotheses were not testable for large natural ecosystems.

### Trophic Level: A Non-Predictive Concept

Predictive science is particularly important for ecological modelling. Prediction may not always be possible and the outcome of quite simple system interactions can be chaotic (Lorenz 1982). Peters (1980) argues that trophic level concepts are not predictive and more recently Peters (1983) that allometric models are far more predictive in ecology.

From Fig. 1 we may show formally why the trophic level concept is non-predictive. Consider trophic levels two and three and the flow between them as  $F_2$ . If the trophic level model is to be predictive then the flow,  $F_2$ , is some function,  $f$ , of the biomass at trophic levels two,  $M_2$ , and three,  $M_3$ . By definition the function  $f$  must define the flow  $F_2$  uniquely for each combination of values for  $M_2$  and  $M_3$ .

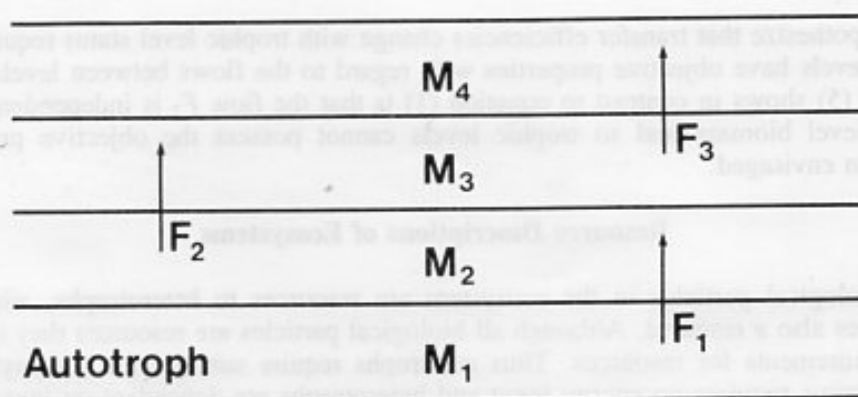


FIG. 1. Trophic level representation.

$$(1) \quad F_2 = f(M_2, M_3)$$

When the flow  $F_2$  is uniquely defined then equation (1) is predictive and consequently the trophic level model can be taken to be predictive.

We may note that a biomass  $M$  is made up of the sum of number of individuals,  $N_i$ , multiplied by their body weight,  $W_i$ .

$$(2) \quad M = \sum N_i \cdot W_i$$

which in continuous form is given by

$$(3) \quad m(n, w)$$

where

$$(4) \quad m = \int_0^{\infty} n w \cdot dw$$

Now, taking the example where  $M_2$  is comprised of zooplankton and  $M_3$  is made up of filter feeding fish, a flow  $F_2$  is established. Suppose as a result of migration these fish are replaced by an equal biomass of large fish which have large mouth parts which do not allow them to feed on zooplankton yet these fish have been feeding, prior to migration, on food at trophic level 2. In the first instance  $F_2$  will have a positive value and in the second it will be zero. Thus the flow  $F_2$  is not uniquely defined and the hypothesis that  $f$  is a function in equation (1), is therefore rejected. However, if the data were left in the form,  $m(n, w)$  for each level, then  $F_2$  may be defined as,

$$(5) \quad F_2 = f(n_2, w_2, n_3, w_3)$$

Here  $F_2$  is uniquely determined in this instance since the flows are dependent on the number and size of particles at both levels and the test as to whether  $f$  is a function is not rejected. To make a predictive model in this form involves adding more variables to equation (5) in situations where  $f$  fails as a function. The number of variables required and the complexity of the function  $f$  will depend on the nature of the prediction being made.

Before ending the discussion of equation (5) it is useful to note that  $n$  is a quantitative variable and that,  $w$ , is a qualitative variable in the context of ecosystems. Thus to define  $M_2$  as a resource to  $M_3$  the quantity,  $n_2$ , at each quality,  $w_2$ , needs to be identified. Similarly to define  $M_3$  as a predatory "force" on  $M_2$  the quantity,  $n_3$ , of organisms at each quality,  $w_3$ , needs to be identified.

To hypothesize that transfer efficiencies change with trophic level status requires that trophic levels have objective properties with regard to the flows between levels. What equation (5) shows in contrast to equation (1) is that the flow  $F_2$  is independent of the trophic level biomass and so trophic levels cannot possess the objective properties Lindeman envisaged.

### Resource Descriptions of Ecosystems

All biological particles in the ecosystem are resources to heterotrophs, which are themselves also a resource. Although all biological particles are resources they differ in their requirements for resources. Thus autotrophs require sunlight for photosynthesis, while detritus requires no energy input and heterotrophs are dependent on ingesting or absorbing particles or dissolved organic matter whose origins are either other heterotrophs, autotrophs or detritus. These latter three categories are considered (Cousins 1980) to be fundamentally distinct trophic categories; they have different properties with respect to time and so are important to distinguish in a predictive model. With time, live organisms grow, feed and reproduce. Detritus will also change its resource status with time. Detritus may be treated as a part of the system which tends to disorder while live organisms maintain their order at the expense of greater disorder in their environment. The minimum set of categories used in the continuum model, autotroph, heterotroph and detritus are also those identified as functional groups (O'Neill 1976; Silvert and Platt 1980).

As we saw earlier, when a heterotroph feeds, the total ecosystem biomass, or biomass at a trophic level is not of interest to that organism, but only the amount of food available to that organism to ingest. For predation, which is where large heterotrophs eat smaller heterotrophs, the prey as a resource to the predator, is limited to the quantity of prey at the size of prey eaten. We may model this process in many species ecosystems as a transfer of energy or individuals, between size classes of organisms. The use of size classes to model feeding relationships in large ecosystems was first used by Elton (1927) and has been recently revived by Platt and Denman (1977) for pelagic systems and by Cousins (1978, 1980) principally for terrestrial systems.

A few simple rules appear to characterise the interactions of food webs when they are analysed by the use of size classes and each rule is discernable in Elton's original size-based description of food web operation. A comparison of these simple rules for terrestrial and pelagic food webs is given in Table 1. Making a predictive model based on

TABLE 1. Simple food web rules and processes.

Rule	Terrestrial <sup>a</sup>	Pelagic <sup>a</sup>	Process
1) Large heterotrophs eat smaller particles	Y	Y	Carnivory Herbivory Detritivory
2) Particles change size with time	Y	Y	Growth Decay
3) Some small particles eat large particles	Y	Y	Parasitism Detritivory
4) Non-particulate plants	Y	N	Herbivory
5) Non-particulate detritus	Y	N	Detritivory

<sup>a</sup>Y = Rule applies; N = Rule does not apply.



these rules therefore requires modelling the processes which are identified as corresponding to each "rule".

As is shown in Table 1 the main difference between terrestrial and aquatic plants is due to the types of green plant in the two systems. In the pelagic case the autotrophs are particulate and equations developed for predation where the heterotrophs are also treated as being particulate can be extended to apply to herbivory. Similarly particulate autotrophs and heterotrophs generate particulate detritus which in total can be viewed as a single particle size spectrum (Silvert and Platt 1980) with material and energy flowing from the small to the large particles. Thus an allometric or species size approach will apply to the whole spectrum including particulate detritus. This is not so in terrestrial systems.

The size of the terrestrial plant is much more variable than pelagic phytoplankton, and more importantly the size *per se* does not constitute an appropriate resource description for heterotrophs feeding on autotrophs again in contrast to the pelagic system. The digestibility of different terrestrial plant parts is very varied as exemplified by the extremes of wood and seeds. Thus while number of phytoplankton particles,  $n_A$ , of particular weights,  $w$ , can describe the quantity of autotroph resources of different qualities, for the terrestrial plant the quality of the resource is described by  $v$ , the digestibility (see below) of a particular plant material and the quantity or the mass of that material present.

Figure 2 shows a comparison of the resource descriptions of the mass distribution of terrestrial autotroph material and the number distribution of pelagic autotrophs. The digestibility variable,  $v$ , has the range of values 0 to 1 corresponding to 0 to 100% assimilability of the plant material. The broad categories of plant parts, wood, leaves, and seeds are also important functional categories which have interesting temporal behaviours (Parkin and Cousins 1981). The range of weights of phytoplankton is given as 0 to  $w'$  the largest phytoplankton in the system.

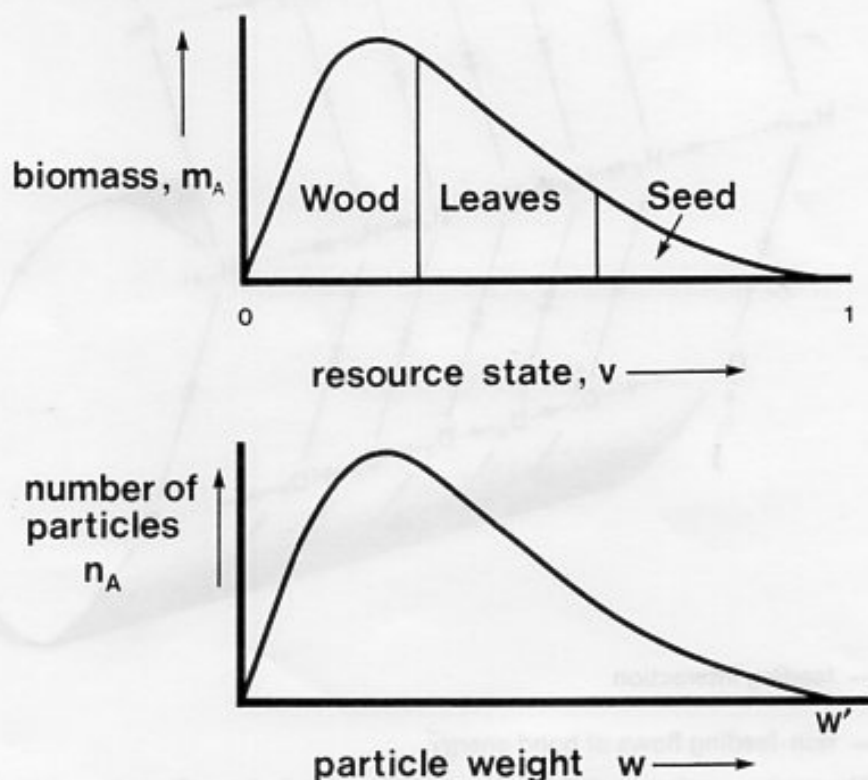


FIG. 2. The terrestrial plant biomass distribution and a phytoplankton number distribution.

### The Trophic Continuum Model

The three fundamental categories of the trophic continuum, autotrophs, heterotrophs, and detritus are those identified above as constituting distinct groups in their requirements for resources and as being distinct in the way that they change resource state with time. Figure 3 represents the trophic continuum as a cylindrical graph which relates the three fundamental categories and also represents changes in resource state occurring within the categories themselves. Row *A* represents the resource states of the many plant species and plant parts which are available for ingestion by heterotrophs. State  $A_{m-1}$  represents all primary products of photosynthesis in the system. States  $A_m$  to  $A_n$  represent the different chemical and structural forms of plant biomass and correspond to  $v$  states or the number distribution of marine autotrophs shown in Fig. 2. Translocation and chemical transformation of the products of photosynthesis create the transfer of material between resource states in the plant. This contrasts to the Lindeman model where biomass only changes state when something is eaten.

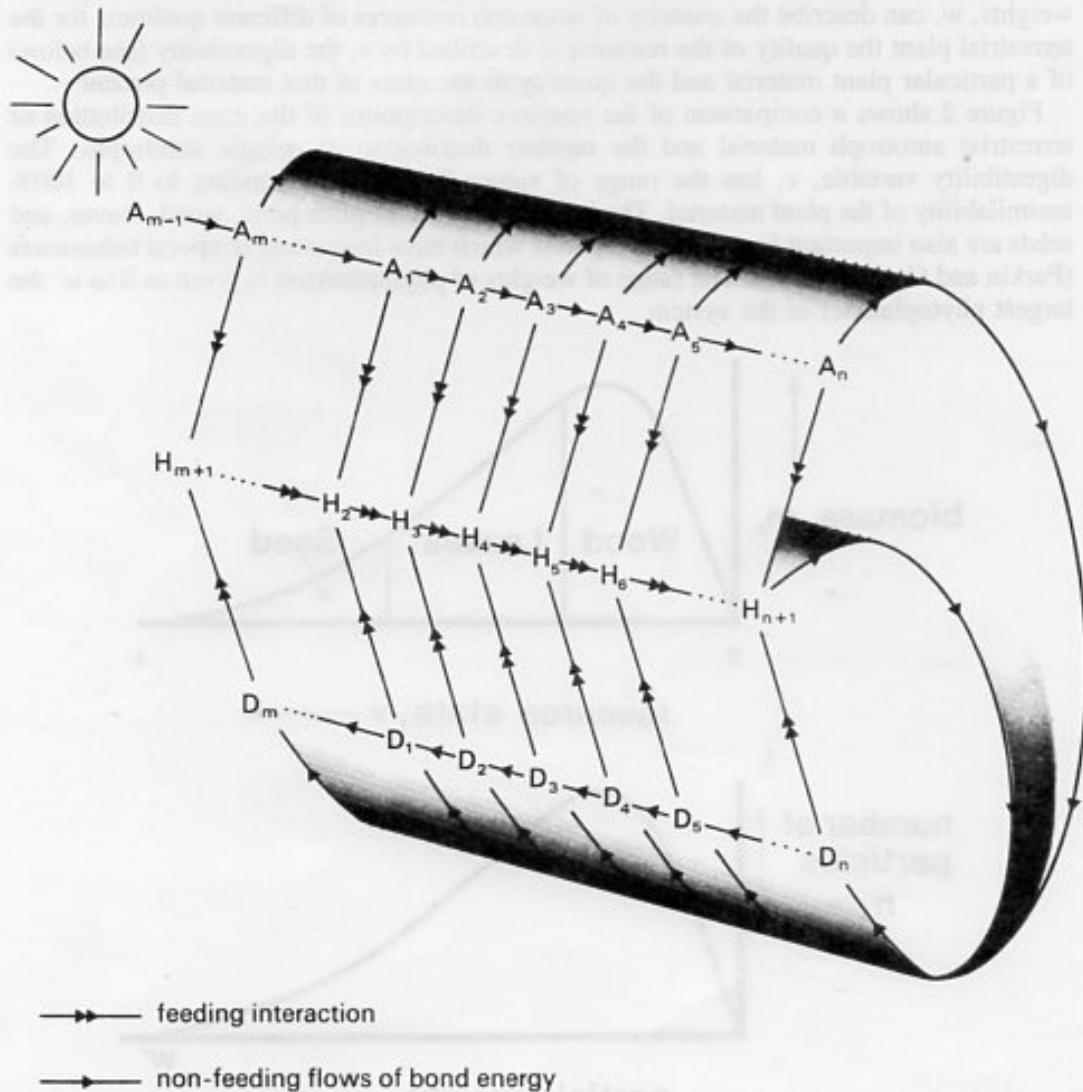


FIG. 3. The trophic continuum showing translocation, chemical transformation within the auto-troph, heterotroph interactions, and detritus fragmentation.

The autotrophs are fed upon by heterotrophs of sizes  $H_m$  (small) to  $H_n$  (large). Feeding interactions (carnivory) also occur between  $H$  states. With time individuals will grow and will therefore change their size category, and therefore alter their resource state in the model which is again in contrast to Lindeman where, of itself, growth does not affect trophic status.

Detritus is also fed upon by heterotrophs and is also generated from both the autotroph and heterotroph compartments of the model. Detritus in the form of carcasses, dung and plant litter as well as exudates and exuviae constitute the variety of states  $D_m$  to  $D_n$ . With time each item of detritus changes its resource state towards the state of greatest dispersal,  $D_m$ . In the pelagic system  $D_m$  represents dissolved organic matter and  $D_n$  the newly dead carcass of the largest heterotroph,  $H_n$  in the system. The trophic continuum shown in Fig. 3 is simplified in that only four routes for the transfer of energy are shown at any single state.

### Marine Systems

The particulate autotrophs and heterotrophs and their particulate litter, carcasses and dung allow each of the autotroph, heterotroph, and detritus resource states of the trophic continuum to be represented by a number distribution of particles of different weights. The autotroph number distribution,  $n_A(w)$ , has already been illustrated in Fig. 2b. Similar distributions for heterotrophs,  $n_H(w)$ , and detritus,  $n_D(w)$  can be defined for the number of heterotroph and detritus particles of different weights,  $w$ .

Figure 4 shows the interactions between these distributions. The figure may be considered as an end view of the cylindrical representation of the trophic continuum of Fig. 3. The three number distributions of particle weight are the resource state distributions of the continuum.

### Predictive Models

The processes by which the particle distributions undergo change with time have been identified in Table 1. These processes occur as an interaction between distributions, together with carnivory, which occurs within the heterotroph number distribution, are shown in Fig. 4; the remaining processes of growth and decay also occur within the distributions but are not shown. Modelling these processes provides a predictive model of the change in the number distributions of autotrophs, heterotrophs, and detritus particle weights.

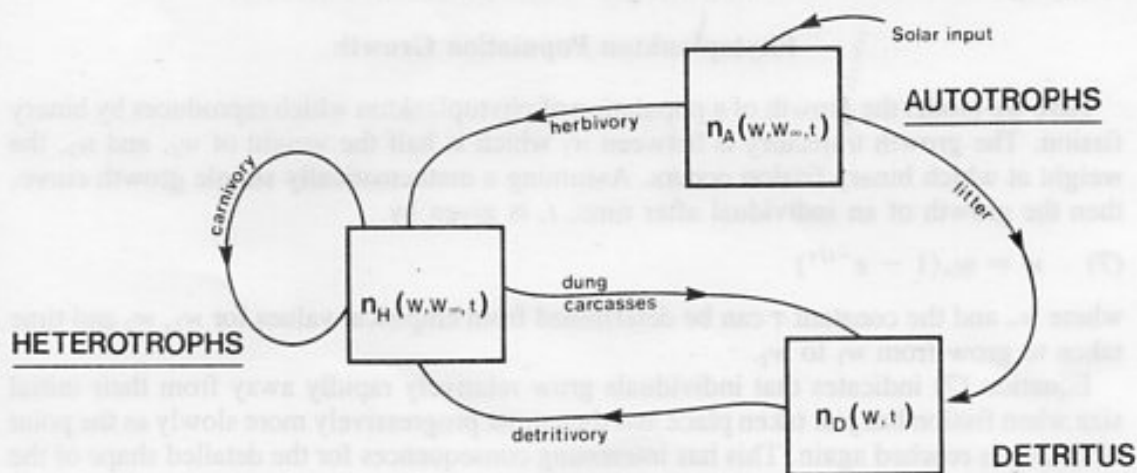


FIG. 4. Inputs and outputs to the functional groups of the trophic continuum.

There is a wide literature relating body size to the processes required for a predictive model. Peters (1983) has assembled over 1000 allometric relationships for various parameters and has reviewed their importance for ecology. He sees these relationships as providing a basis for predictive ecology. The substance of this claim is that by knowing an organism's body weight, predictions can be made about the processes important to its ecology. These include metabolic rate, reproductive rate, mobility, daily food demand, size of food particle eaten, and so on. However, depending on the degree of accuracy required these allometric data may require splitting into the appropriate taxonomic groups such as phyla.

Here we will consider two of the processes in more detail, growth and heterotrophy and also discuss the role of taxonomic groupings in the trophic continuum.

### Growth

Knowing the present state of an ecosystem in terms of the size distribution of particles is useful but needs to be further defined if we are to predict the size distribution at some future time,  $t$ . As noted in Table 1, particles change size, notably live particles grow. Two particles may be the same size at time  $t_0$  but be very different sizes at  $t_1$  because one particle is adult at time  $t_0$  with little prospect of growth and the other is a juvenile on a growth path to being a much larger organism. Thus we need to define the number distribution of particles,  $n$ , as a function of the particles, present weights,  $w$ , and the asymptotic weights,  $w_\infty$  to which they are growing.

$$(6) \quad n(w, w_\infty, t)$$

It is of interest that  $w_\infty$  is, under certain circumstances, the species identity of the particle as is discussed in the taxonomy section below. However, the consideration of the  $w_\infty$  variable does not require the identification of species in the trophic continuum (Cousins 1980) or the biomass spectrum (Platt and Denman 1977). This is because we may make the assumption that there is a continuum of asymptotic species weights between the smallest and largest particle in the ecosystem, just as Platt assumes a continuous distribution of individuals. The  $w_\infty$  variable is vital to the behaviour of the model since it prevents small particles, e.g., bacteria, growing into whales. We might also wish to indicate where species are absent from the continuum of asymptotic adult weights. The inclusion of the adult weight variable  $w_\infty$  allows investigation of the phenomenon of changing diet with changing size which was termed metaphoetesis by Hutchinson (1959).

### Phytoplankton Population Growth

Here we model the growth of a population of phytoplankton which reproduces by binary fission. The growth trajectory is between  $w_1$  which is half the weight of  $w_2$ , and  $w_2$ , the weight at which binary fission occurs. Assuming a mathematically simple growth curve, then the growth of an individual after time,  $t$ , is given by

$$(7) \quad w = w_\infty(1 - e^{-t/\tau})$$

where  $w_\infty$  and the constant  $\tau$  can be determined from empirical values for  $w_1$ ,  $w_2$  and time taken to grow from  $w_1$  to  $w_2$ .

Equation (7) indicates that individuals grow relatively rapidly away from their initial size when fission has just taken place and then grow progressively more slowly as the point of fission is reached again. This has interesting consequences for the detailed shape of the biomass spectrum or number distribution  $n(w, w_\infty, t)$ . For any one species individuals spend more time and are therefore more frequently observed in the larger positions of their



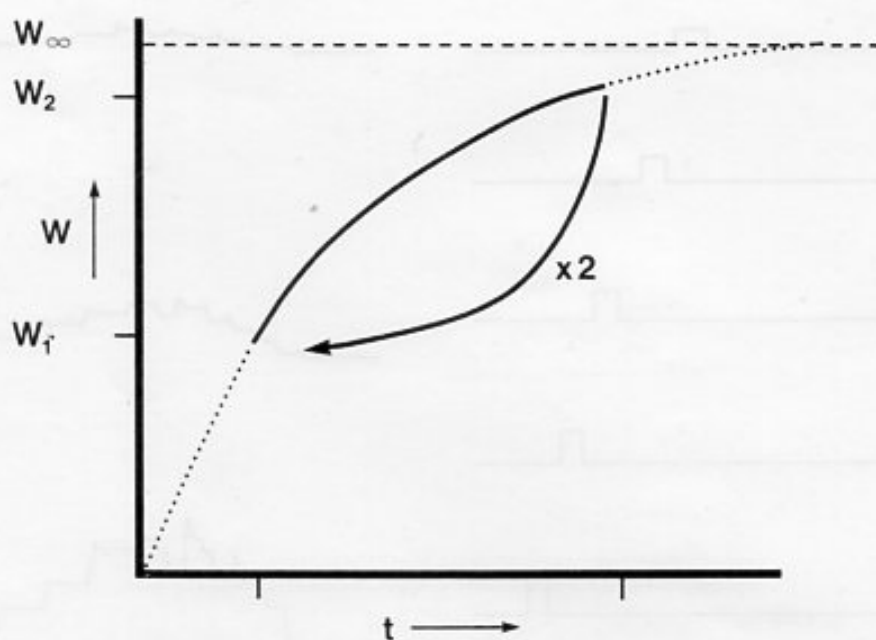


FIG. 5. Growth and binary fission of an individual phytoplankter.

species growth curve. This is in opposition to the general decreasing trend in number of individuals with increasing particle weight first observed by Elton (1927). The resolution of these two processes should produce a "serrated" biomass distribution with exponential growth away from a perfectly flat distribution of logarithmic weight classes.

The creation of a "serrated" particle size distribution is demonstrated by Cousins and Parkin (unpublished data) for a multispecies model of phytoplankton undergoing binary fission. First let us consider the single species case.

From equation (7) for the individual the change in the phytoplankton particle weight distribution  $n_A(w, t)$ , is given by:

$$(8) \quad n_A(w, t) = 2\alpha e^{t/\tau} \cdot n_A(w_0, 0)$$

where

$$(9) \quad \alpha = \frac{w_\infty - w_1}{w_\infty - w_2}$$

The fact that an individual spends more time at larger weights is shown by individuals "bunching" at higher weights in the species distribution,  $n_A$ . Figure 6 shows this effect for a particular set of starting conditions,  $n_A(w_0, 0)$ , where a cohort of individuals is equally distributed over the size range  $w_1$  to some size,  $w_t$ , 10% larger than  $w_1$ . Note that the cohort of individuals becomes narrower and taller prior to fission showing that the same number of individuals are found to be distributed in fewer weight classes.

By taking nine species of different asymptotic adult weights  $w_\infty$ , and giving initial conditions such that the species abundances are proportional to  $1/w_\infty$ , then the growth of the nine species populations is shown in Fig. 7. The population at time  $t$  is given by

$$(10) \quad \sum_{i=1}^q n_i(w, t) = \sum_{i=1}^q 2\alpha_i e^{t/\tau} \cdot n_i(w_0, 0)$$

and generates the serrated curve of particle number against particle weight,  $n_A(w, w_\infty, t)$ . The number of serrations is a function of the number of species present although the

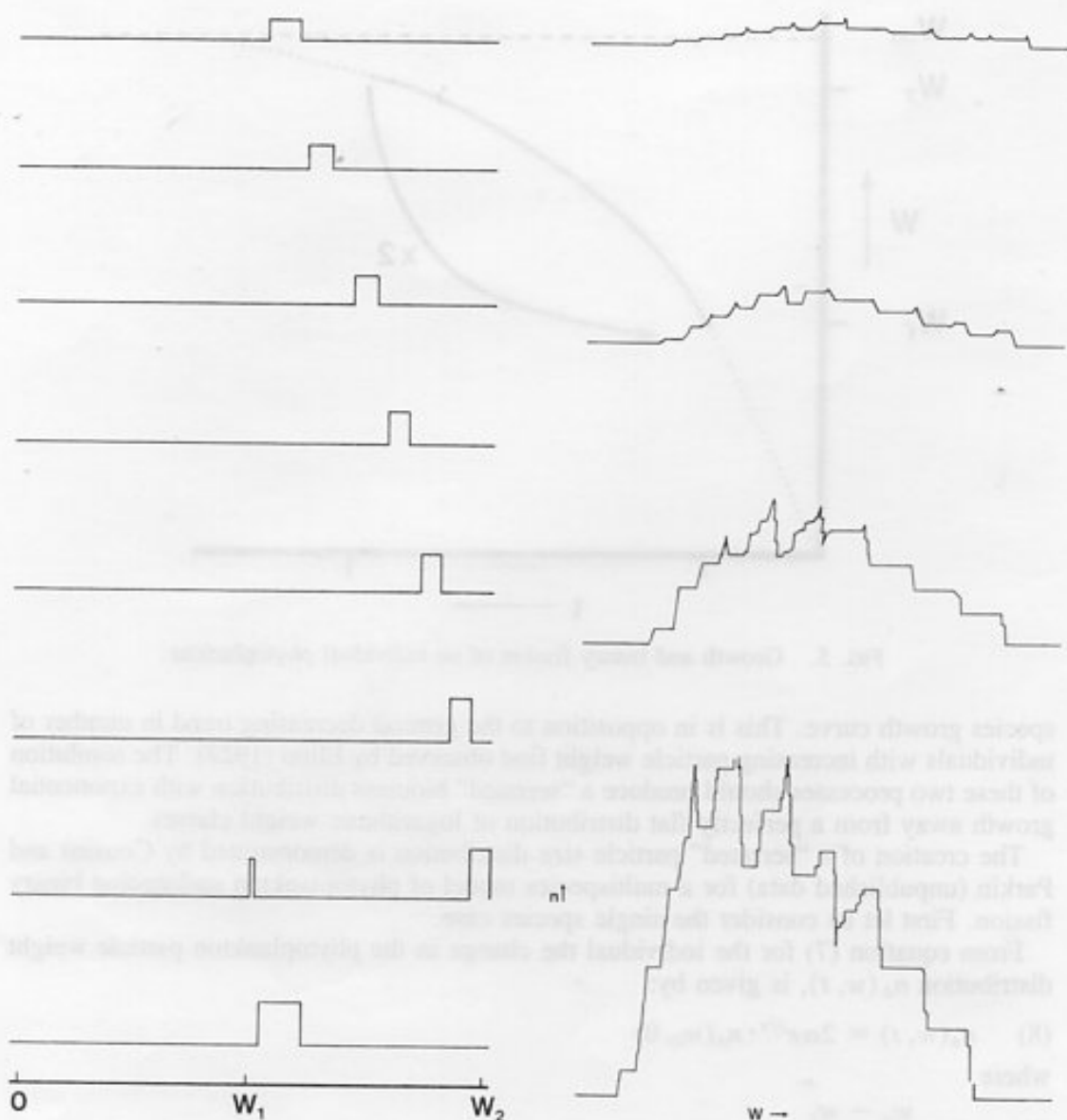


FIG. 6. A cohort of phytoplankton undergoing growth and binary fission.

FIG. 7. Cumulative population growth of nine species of binary fissioning phytoplankters.

complex life-histories of many phytoplankton may create more than one "notch" per species. Detailed phytoplankton number distributions of particle weight do appear serrated at the micro-scale (Sheldon et al. 1972).

### Predation

The study of this form of heterotrophy at the ecosystem level has until recently been limited to trophic level theory. Within this theory there is little if any attention paid to the mechanism of predation itself since the concern is to define organisms as either a level above or below one another dependent on who eats whom. However at the single species level the mechanisms of predation have been much studied and theories of foraging and food capture have been developed. These have been reviewed by Pyke et al. (1977).

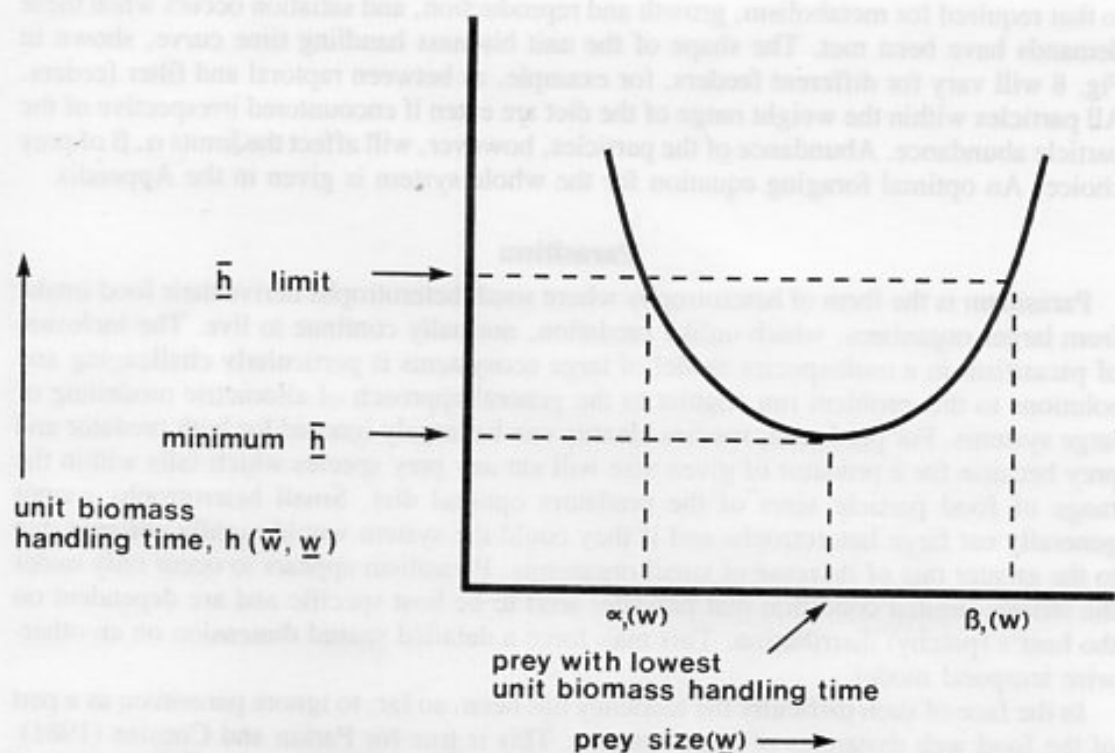


FIG. 8. The time taken for a predator to handle one unit weight of prey biomass for prey of different sizes.

Foraging theory has an allometric basis and can be extended to apply to a large ecosystem containing many species. A general foraging model for free swimming aquatic animals has been developed by Gerritsen (1984).

From optimal foraging theory heterotrophs will encounter other particles at a rate dependent on the abundance of heterotrophs of a given size and the abundance of other particles in the system. A single heterotroph will encounter particles at a rate dependent on the density of particles and the distance travelled by the ingesting organism. Only certain of those encounters will lead to ingestion. Elton (1927) observed that there is both an upper and a lower limit of prey size taken by any predator. The upper limit was determined by the power required by the predator to pursue catch and kill the prey organism while the lower limit is controlled by the inefficiency of collecting small particles even though small particles are likely to be progressively more abundant than large. These phenomena are linked by the concept of handling time which is the time taken to subdue and ingest the particle. The time spent searching for food has been called foraging time. Handling time divided by the weight of the particle gives the unit biomass handling time. This will reach a minimum for the optimal particle size ingested by a particular heterotroph and unit biomass handling times increase for either larger or smaller particles as is shown in Fig. 8. There is a limit shown as a horizontal line above which handling times reduce foraging times to such a degree that food intake is reduced as a whole. Thus, in our model the diet must be satisfied between the limits  $\alpha$ ,  $\beta$  as death by starvation will occur outside this range. The establishment of prey choice by the heterotroph corresponds to Rosen's (at this conference) concept of the organism's questioning the environment. In the model presented here (Parkin and Cousins 1981) the demand for food by a heterotroph, is limited

to that required for metabolism, growth and reproduction, and satiation occurs when these demands have been met. The shape of the unit biomass handling time curve, shown in Fig. 8 will vary for different feeders, for example, as between raptorial and filter feeders. All particles within the weight range of the diet are eaten if encountered irrespective of the particle abundance. Abundance of the particles, however, will affect the limits  $\alpha$ ,  $\beta$  of prey choice. An optimal foraging equation for the whole system is given in the Appendix.

### Parasitism

Parasitism is the form of heterotrophy where small heterotrophs derive their food intake from larger organisms, which unlike predation, normally continue to live. The inclusion of parasitism in a multispecies model of large ecosystems is particularly challenging and solutions to this problem run counter to the general approach of allometric modelling of large systems. For predation, species identity can be largely ignored for both predator and prey because for a predator of given size will eat any prey species which falls within the range of food particle sizes of the predators optimal diet. Small heterotrophs cannot generally eat large heterotrophs and if they could the system would rapidly collapse due to the greater rate of increase of small organisms. Parasitism appears to occur only under the strictly limited condition that parasites tend to be host specific and are dependent on the host's (patchy) distribution. This may force a detailed spatial dimension on an otherwise temporal model.

In the face of such difficulty the tendency has been, so far, to ignore parasitism as a part of the food web dynamics of large systems. This is true for Parkin and Cousins (1981). However a basis for modelling parasite interactions lies in the pattern of distribution of species size,  $w_s$  found in the number distribution  $n(w, w_s, t)$ . The distribution of species size also appears to have an allometric basis (May 1978). Thus rather than treat  $w_s$  as having a continuum of values from the smallest to the largest creature in the system, we should expect a series of discrete values for  $w_s$  akin to Hutchinson's ratios for trophic apparatus (Hutchinson 1959). The importance of parasitism in the food web may be indicated by deep serrations on the particle size distribution curve since like the modest serrations caused by growth, Fig. 7, this is a species based phenomenon.

### Taxonomy

Elsewhere (Cousins 1983) I have concluded that "the discovery of the importance of body size phenomena in trophic ecology is also the rediscovery of the importance of taxonomic ecology. Allometric relationships appear to hold most precisely within taxonomic groups". Thus while the aim of the trophic continuum model is to define the ecosystem with a minimum of taxonomic distinction this is controlled by the precision of the output which is required.

Fenchel (1974) has identified three taxonomic distinctions which apply to the intrinsic rate of natural increase; these are single celled organisms, heterotherms and homeotherms. The identification of the difference between heterotherms and homeotherms was also shown to be of importance to the shape of the growth curve which, through metaphoetesis, is of importance to the food web (Hutchinson 1959). Metaphoetesis is more important in heterotherms than homiotherms where parents forage for their offspring. Phillipson (1981) has considered more extensively the relationship between allometric phenomena and phylogeny. Much finer levels of taxonomic identity are relevant to parasitism. Parasites which are of considerable functional importance to the food web, operate at the species level. But as has been noted, the distribution of species size within taxa offers the potential for allometric generalisation about parasitism.



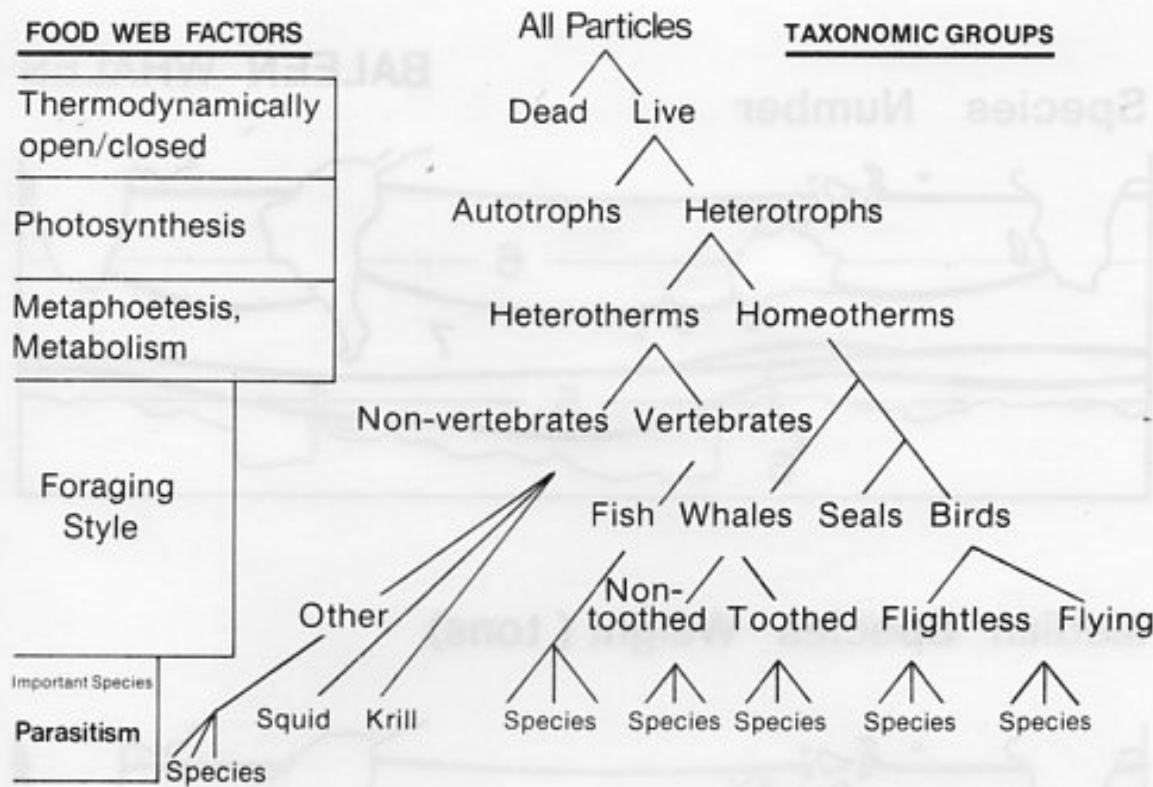


FIG. 9. Taxonomic classifications and their significance to food web factors in the Antarctic food web.

Modes of locomotion and modes of feeding can be functionally important to the operation of the food web. Thus we may wish to distinguish birds from amphibians of the same weight, or filter feeders from raptorial feeders. The degree of taxonomic distinction depends on the question that the model is required to address. Bonner (1981) is concerned with the food web relationships between bird, seal and whale populations as they have been or will be affected by change in whale and krill stocks. A set of taxonomic groups useful in this context is given in Fig. 9. The functional importance of these taxa in the trophic continuum is identified. Each taxon is represented in the trophic continuum model by a number distribution  $n(w, w_{\infty}, t)$  and by allometric characteristics for foraging, reproduction, metabolic rates and so on. Thus the size of food taken by baleen compared to toothed whales is very different and central to the question posed since toothed whales will prey on seals and swimming birds while baleen whales will feed on krill. When baleen whales are separated out some interesting allometric properties emerge as is shown by the trend in species number and baleen diameter with increasing latitude in Fig. 10.

The number distribution of all heterotrophs in the continuum model can thus be seen as the sum of number distributions of various taxa,  $n_i$

$$(11) \quad \sum n_i(w_i, w_{\infty}, t)$$

The cumulative number distribution is a symbolic representation of the predictive model of the trophic continuum which has been developed. These number distributions determine the flows between model compartments and not vice versa. Thus this is a force rather than a flow model.

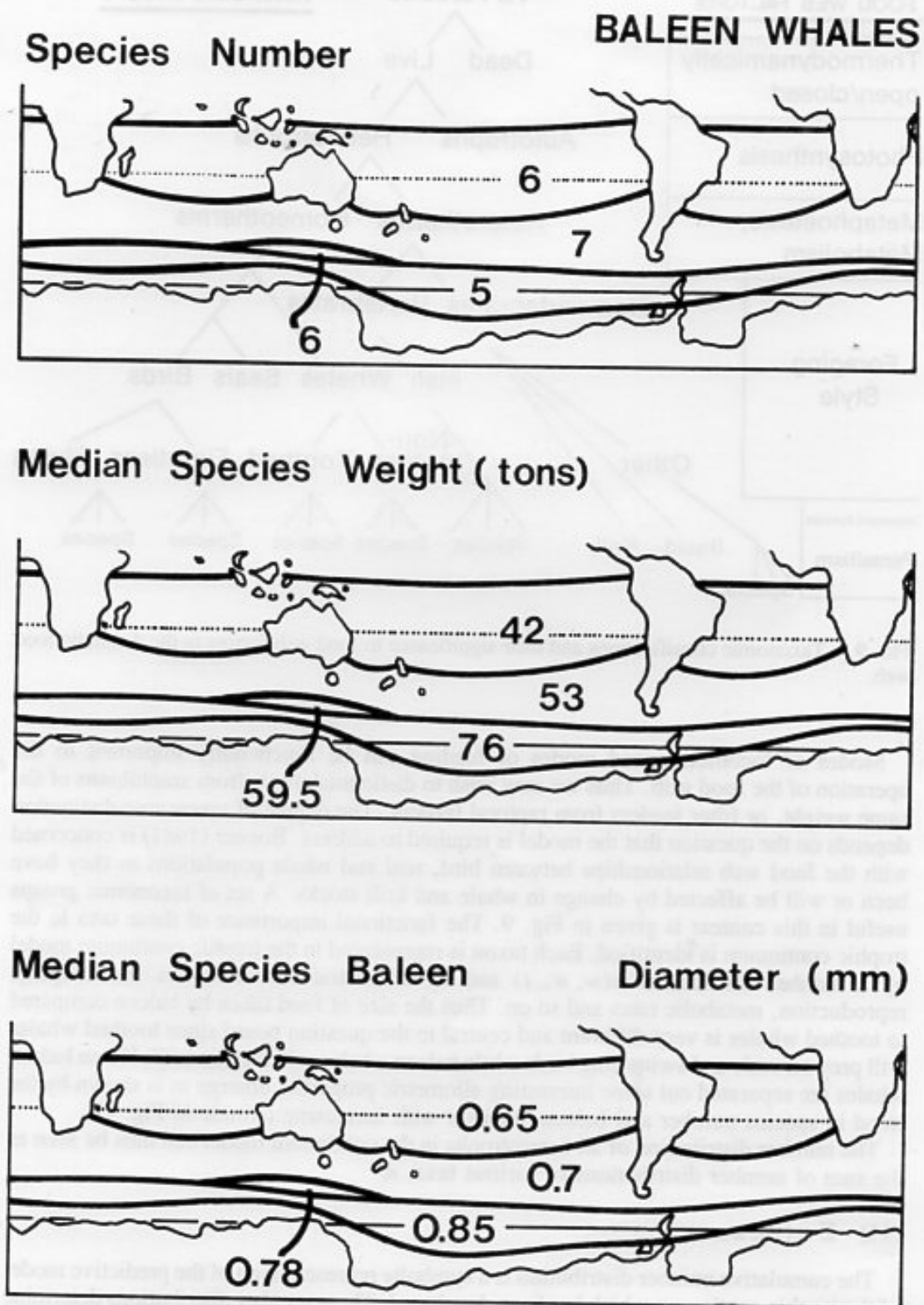


FIG. 10. The distribution of baleen whale species and their characteristics, from Watson (1981).

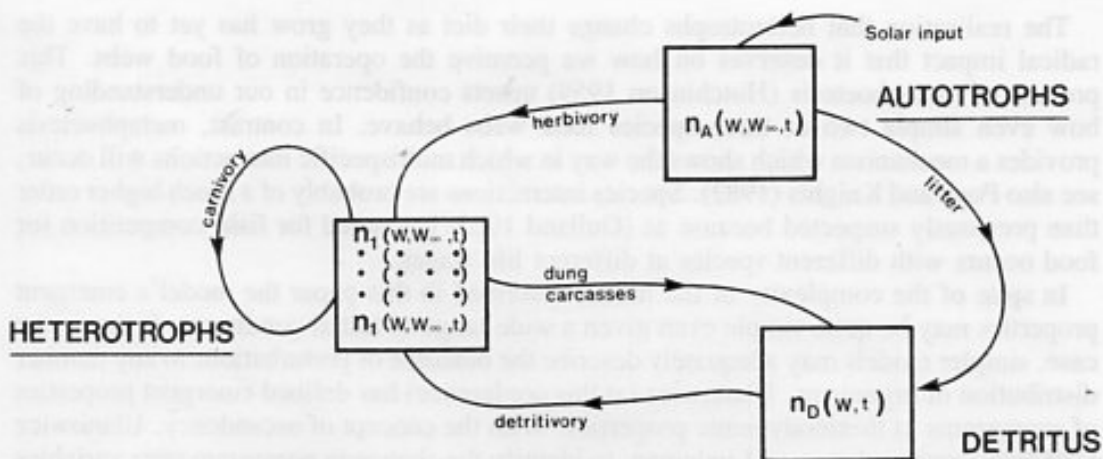


FIG. 11. Inputs and outputs of the functional groups of the trophic continuum showing heterotrophs separated into taxonomic groups.

Since autotrophs and detritus are particulate their number distributions may also be added to equation (14) to give a single particle size distribution for the purpose of modelling heterotrophy. Carnivory arises when the particles in the optimal diet are larger than phytoplankton or detritus particles, but no distinction is necessary in the structure of the model with all particle transfers to heterotrophs classed as heterotrophy, see appendix. The overall structure of the trophic continuum model is shown in Fig. 11.

### Discussion

The development of models of large, multispecies ecosystems is at an early stage appropriate to our present level of understanding of the interactions of multispecies food webs. However, the trophic level concept finds no place in this new analysis. There is no implied criticism of Lindeman's work by that statement since Lindeman's lasting achievement (1942) was to write a highly stimulating paper on the nature of ecological succession using Hutchinson's notation for the trophic level. It is interesting too that Hutchinson's empirical work (1959) on the study of food webs and species assemblies (Hutchinson and MacArthur 1959) has contributed the important concepts of metaphoresis and morphological ratios which are of importance to the allometric analysis of food web properties. But to develop these allometric models unconditionally it has been necessary to show that the concept of trophic level does not carry over into what we may now call allometric ecology.

The structure of the trophic continuum model as described in this paper has been to create a whole ecosystem model based on processes which occur at the micro-scale and which are relevant to food web interactions. The incorporation of organism growth by giving the particle two weight descriptors, its present weight and its asymptotic adult weight, and the inclusion of an optimal foraging strategy as the basis for predation are crucial features of the model developed. The  $w_\infty$  variable provides the option for incorporating species identity into the trophic continuum model if it is required. Where it is not appropriate to identify species, the  $w_\infty$  variable will still ensure that bacteria sized particles will not grow to whale size proportions with the model. When field data is collected some assumptions must be made about the relationship between the observed particle distribution,  $w$ , and  $w_\infty$  the destinations of those particles.

The realisation that heterotrophs change their diet as they grow has yet to have the radical impact that it deserves on how we perceive the operation of food webs. This process of metaphoetesis (Hutchinson 1959) upsets confidence in our understanding of how even simple two or three species food webs behave. In contrast, metaphoetesis provides a mechanism which shows the way in which multispecific interactions will occur, see also Pope and Knights (1982). Species interactions are probably of a much higher order than previously suspected because as (Gulland 1983) has noted for fish, competition for food occurs with different species at different life stages.

In spite of the complexity of the model described in this paper the model's emergent properties may be quite simple even given a wide range of initial conditions. If that is the case, simpler models may adequately describe the outcome of perturbations to any number distribution of organisms. Ulanowicz (at this conference) has defined emergent properties of ecosystems as thermodynamic properties. With the concept of ascendancy, Ulanowicz (1982) is concerned, as was Lindeman, to identify the change in ecosystem state variables which occur during succession or during other forms of ecosystem evolution. It would be useful to examine Ulanowicz's concepts taking body size as the state variable and to examine the properties of the trophic continuum or biomass spectrum as they are affected by succession. Two other thermodynamic questions are of interest, the first is the effect of temperature on the operation of ecosystem processes in an allometric model, and the second concerns the  $m(n, w)$  representation of biomass as a resource descriptor. Here Georgescu-Roegen (1971) stresses that different resource states, in this case values of  $w$ , are analogous to different entropy states.

Platt and Silvert (1981) have sought to explain the importance of organism size in biological processes. It is a substantial achievement that they have established dimensionalism as providing such an explanation. But further challenges exist and there are food web processes which we may call informational which are only partially explained by dimensional analysis of receptor organs Maiorana (1981), although information content is itself dimensionless. While predation may be understood in terms of the relative muscle volumes of predator and prey, parasites cannot overpower their hosts but must find some specialised technique, some species specific information, by which they can defeat the host's defenses. The predator's search for prey *in an environment* is also an information processing problem. While aspects of these information based problems may yield to allometric methods, thermodynamics may also provide analogies which are useful to increase our understanding.

### Acknowledgements

I wish to thank the SCOR workshop organisers for inviting me to attend and I thank Howard Parkin for his help on the diatom model. This research was supported by The Open University.

### References

- BONNER, W. N. 1981. The krill problem in Antarctica. *Oryx* 16: 31-37.
- COUSINS, S. H. 1978. Trophic models — was Elton right? 2nd Int. Cong. of ecol., Jerusalem. Energy Research Group Report 029, The Open University, Milton Keynes, U.K.
1980. A trophic continuum derived from plant structure, animal size and a detritus cascade. *J. Theor. Biol.* 82: 607-618.
1983. An alignment of diversity and energy models of ecosystems. Ph.D. thesis, The Open University, Milton Keynes, U.K.
- ELTON, C. S. 1927. *Animal ecology*. Sidgwick and Jackson, London.
- FENCHEL, T. 1974. Intrinsic rate of natural increase: the relationship with body size. *Oecologia(Berl.)* 14: 317-326.
- GEORGESCU-ROEGER, N. 1971. The entropy law and



- the economic process. Harvard University Press, Cambridge MA.
- GERRITSEN, J. 1984. Size efficiency reconsidered: a general foraging model for free-swimming aquatic animals. *Am. Nat.* 123: 450-467.
- GULLAND, J. A. 1982. Why do fish numbers vary? *J. Theor. Biol.* 97: 69-75.
- HEAL, W. O., AND S. F. MACLEAN, JR. 1975. In W. H. van Dobben and R. H. Lowe-McConnell [ed.], *Unifying concepts in ecology*, p. 89-108. Junk publications, The Hague.
- HUTCHINSON, G. E. 1959. Homage to Santa Rosalia; or why are there so many kinds of animals? *Am. Nat.* 93: 117-125.
- HUTCHINSON, G. E., AND R. H. MACARTHUR. 1959. A theoretical ecological model of size distributions among species of animals. *Am. Nat.* 93: 117-125.
- LINDEMAN, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23: 399-418.
- LORENZ, O. E. 1982. The strange attractor theory of turbulence. *Ann. Rev. Fluid. Mech.* 14: 347-364.
- O'NEILL, R. V. 1976. Ecosystem persistence and heterotrophic regulation. *Ecology* 57(6): 1244-1253.
- MARIOANA, V. C. 1981. Prey selection by sight: random or economic? *Am. Nat.* 118: 450-451.
- MAY, R. M. 1978. The dynamics and diversity of insect faunas. In L. A. Mound and N. Waloff [ed.], *Diversity of insect faunas*. Blackwell Scientific Press, Oxford.
1979. The structure and dynamics of ecological communities. In R. M. Anderson, B. D. Turner, and L. R. Taylor [ed.], *Population dynamics*. Blackwell Scientific Press, Oxford.
- MERCER, M. C. [ED.] 1982. Multispecies approaches to fisheries management advice. *Can. Spec. Publ. Fish. Aquat. Sci.* 59.
- PARKIN, H., AND S. H. COUSINS. 1981. Towards a global model of large ecosystems; equations for the trophic continuum. Energy Research Group Report 041, The Open University, Milton Keynes, U.K.
- PETERS, R. H. 1980. Useful concepts for predictive ecology. *Synthese* 43: 257-269.
1983. *The ecological implications of body size*. Cambridge University Press, Cambridge.
- PHILLIPSON, J. 1981. Bioenergetic options and phylogeny. In C. R. Townsend and P. Calow. [ed.], *Physiological ecology*. Blackwell Scientific, Oxford.
- PLATT, T., AND K. DENMAN. 1977. The organisation of the pelagic ecosystem. *Helgol. Wiss. Meeresunters* 30: 575-581.
- PLATT, T., AND W. SILVERT. 1981. Ecology, physiology, allometry and dimensionality. *J. Theor. Biol.* 93: 855-860.
- POPE, J. G., AND B. J. KNIGHTS. 1982. Simple models of predation in multi-age multispecies fisheries for considering the estimation of fishing mortality and its effects. In M. C. Mercer [ed.], *Multispecies approaches to fisheries management advice*. *Can. Spec. Publ. Fish. Aquat. Sci.* 59.
- PYKE, G. H., H. R. PULLIUM, AND E. L. CHARNOV. 1977. Optimal foraging: A selective review of theory and tests. *Q. Rev. Biol.* 52: 137-154.
- SHELDON, R. W., A. PRAKASH, AND W. H. SUTCLIFFE. 1972. The size distribution of parasites in the ocean. *Limnol. Oceanogr.* 17: 327-340.
- SILVERT, W., AND T. PLATT. 1980. Dynamic energy-flow model of particle size distribution in pelagic ecosystems, p. 754-763. In W. C. Kerfoot [ed.] *Evolution and ecology of zooplankton communities*. The University Press of New England, NH.
- ULANOWICZ, R. E. 1980. An hypothesis on the development of natural communities. *J. Theor. Biol.* 85: 223-245.
- WATSON, L. 1981. *Sea guide to whales of the world*. Hutchinson, London.

## Appendix

The equations presented here form a global model of large ecosystems. The model is specified at any time by number distributions of autotrophs, heterotrophs, and detritus. Dynamic events are determined by a weight dependent appetite function, an optimal foraging strategy, growth, reproduction, and detritus decay terms.

A full description of the model and its derivation is given in Parkin and Cousins (1981).

### Notation

- $n_A$  the number distribution of autotroph particles by weight  
 $n_H$  the number distribution of heterotrophs by weight  
 $n_D$  the number distribution of detritus particles by weight  
 $\phi$  has value 1 when predator is foraging within optimal foraging limits and 0 when outside these limits; see Fig. 8.

- f* the weight of food per unit time derived by a heterotroph of weight *w* while optimally foraging  
*k* the requirement for food per unit time for metabolism, growth and reproduction for a heterotroph of weight, *w*  
*p* predator-prey encounter rate  
*w* the current weight of a particle  
*w<sub>∞</sub>* the asymptotic adult weight of a particle  
 $\alpha$  the minimum particle size ingested to maximise food input per unit time to a heterotroph of size, *w*  
 $\beta$  the maximum particle size ingested to maximise food input per unit time to a heterotroph of size, *w*  
*h* the time taken to handle a unit weight of prey biomass by a heterotroph of weight, *w*  
*d* death rate due to starvation  
*b* a Gaussian distribution function to allocate births to individual weights for a parent heterotroph of weight, *w*  
*r* the number of offspring per individual of reproductive age per unit time  
 $\gamma$  fraction of the asymptotic adult weight at which reproduction begins  
*g* a Gaussian distribution function for allocating dung  
*a* fraction of food assimilated  
*C<sub>F</sub>* natural log of the inverse of the time taken for a particle to fragment to half its present weight

Bar notation: sub bar indicates variable as prey, e.g.,  $\bar{w}$  is the weight of a prey particle, super bar indicates variable as predator, e.g.,  $\bar{w}$  is the weight of the same particle acting as a predator, where both bars are used, e.g.,  $\bar{h}$  this is shorthand for  $h(\bar{w}, \underline{w})$ .

### 1. The equation for the plant (autotroph) is

$$(1) \quad \frac{\partial n_A}{\partial t} = \left( \frac{\partial n_A}{\partial t} \right)_{\text{heterotrophy}} + \left( \frac{\partial n_A}{\partial t} \right)_{\text{growth}} + \left( \frac{\partial n_A}{\partial t} \right)_{\text{litter}}$$

where

$$(2) \quad \left( \frac{\partial n_A}{\partial t} \right)_{\text{heterotrophy}} = -n_A \int_0^{\infty} \bar{\Phi} \cdot \frac{\min \{ \bar{f}, \bar{k} \}}{\bar{f}} \cdot \frac{\bar{p} \left( \int_{\bar{w}}^{\infty} \bar{n} d w_{\infty} \right) d \bar{w}}{1 + \int_{\alpha}^{\beta} \underline{w} \bar{h} \bar{p} \left( \int_{\underline{w}}^{\infty} (n_A + n_H + n_D \dots n_i) d w_{\infty} \right) d \underline{w}}$$

$$(3) \quad \bar{f} = \frac{\int_{\alpha}^{\beta} \bar{P} \underline{w} \int_{\underline{w}}^{\infty} (n_A + n_H + n_D \dots n_i) d w_{\infty} d \underline{w}}{1 + \int_{\alpha}^{\beta} \underline{w} \bar{h} \bar{p} \int_{\underline{w}}^{\infty} (n_A + n_H + n_D \dots n_i) d w_{\infty} d \underline{w}}$$

$$(4) \quad \left( \frac{\partial n_A}{\partial t} \right)_{\text{growth}} = \frac{\partial}{\partial w} \left( \frac{w - w_{\infty}}{t} \cdot n_A \right)$$

$$\left( \frac{\partial n_A}{\partial t} \right)_{\text{litter}} \sim \text{not modelled for marine, only terrestrial plant.}$$

II. The equation for heterotrophs is

$$(5) \quad \frac{\partial n_H}{\partial t} = \left( \frac{\partial n_H}{\partial t} \right)_{\text{heterotrophy}} + \left( \frac{\partial n_H}{\partial t} \right)_{\text{starvation}} + \left( \frac{\partial n_H}{\partial t} \right)_{\text{growth}} + \left( \frac{\partial n_H}{\partial t} \right)_{\text{reproduction}}$$

where,

$$(6) \quad \text{So, } \frac{\partial n_H}{\partial t}_{\text{heterotrophy}} = -n_H \int_0^{\infty} \bar{\Phi} \cdot \frac{\min \{ \bar{f}, \bar{k} \}}{\bar{f}} \cdot \frac{\bar{p}_1 \left( \int_{\bar{w}}^{\infty} \bar{n}_1 dw_{\infty} \right) d\bar{w}}{1 + \int_{\bar{a}}^{\bar{b}} \bar{w} \bar{h} \bar{p} \left( \int_{\bar{w}}^{\infty} (\bar{n}_A + \bar{n}_H + \bar{n}_D \dots \bar{n}_i) dw \right) d\bar{w}}$$

$$(7) \quad \left( \frac{\partial n_H}{\partial t} \right)_{\text{starvation}} = -n_H d \max \left\{ 0, 1 - \frac{f}{k} \right\}$$

$$(8) \quad \left( \frac{\partial n_H}{\partial t} \right)_{\text{growth}} = \frac{\partial}{\partial w} \left( \frac{w - w_{\infty}}{r} \right) \cdot n_H$$

$$(9) \quad \left( \frac{\partial n}{\partial t} \right)_{\text{reproduction}} = br \int_{\gamma w_{\infty}}^{w_{\infty}} \bar{n} d\bar{w} \quad [\bar{w} \text{ is the parent not offspring}]$$

III. The equation for detritus is,

$$(10) \quad \frac{\partial n_D}{\partial t} = \left( \frac{\partial n_D}{\partial t} \right)_{\text{heterotrophy}} + \left( \frac{\partial n_D}{\partial t} \right)_{\text{carcass}} + \left( \frac{\partial n_D}{\partial t} \right)_{\text{dung}} + \left( \frac{\partial n_D}{\partial t} \right)_{\text{fragmentation}}$$

where,

$$(11) \quad \left( \frac{\partial n_D}{\partial t} \right)_{\text{heterotrophy}} = -n_D \int_0^{\infty} \bar{\Phi} \cdot \frac{\min \{ \bar{f}, \bar{k} \}}{\bar{f}} \cdot \frac{\bar{p}_3 \left( \int_{\bar{w}}^{\infty} \bar{n} dw \right) d\bar{w}}{1 + \int_{\bar{a}}^{\bar{b}} \bar{w} \bar{h} \bar{p} \bar{n}_D dw}$$

$$(12) \quad \left( \frac{\partial n_D}{\partial t} \right)_{\text{carcass}} = \int_w^{\infty} n_H dw_{\infty} d \max \left\{ 0, 1 - \frac{f}{k} \right\} + \text{plant litter term}$$

$$(13) \quad \left( \frac{\partial m_D}{\partial t} \right)_{\text{dung}} = g(1 - a) \int_0^{\infty} \min \{ f, k \} \int_w^{\infty} n_H dw_{\infty} dw$$

$$(14) \quad \left( \frac{\partial n_D}{\partial t} \right)_{\text{fragmentation}} = \frac{1}{w} \frac{\partial}{\partial w} (C_F w^2 n_D)$$