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THE STRUCTURE OF PLANKTON COMMUNITIES

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Interactions of herbivorous copepods with their phytoplankton food depend on the size composition of organisms in both trophic levels. A simulation model is used to analyse these size-dependent relations with the following conclusions.

1. Relative size structure of herbivores and their food is more important than total biomass of each trophic level in determining modes of transfer from plants to herbivores. In nearly all cases, in the model, food limitation affects reproduction or the first feeding stage of the nauplii.
2. No single factor emerges as predominant in determining the size structure of both populations.
3. The nature of predation on the herbivores is at least as important in determining both phytoplankton and herbivore size composition as physical or nutrient parameters.
4. The magnitude of the population of the larger herbivores such as *Calanus*, important as food for fish, depends on their coexistence with the smaller copepod species which control the smaller phytoplankton.
5. Stress on the system, if it affects adversely the smaller herbivores, can lead to the breakdown of the *Calanus*-diatom component.
6. Prediction of the population structure for both plants and herbivores may be a more attainable objective of theory and more practically important than prediction of total biomass at each trophic level.

INTRODUCTION

The structure of an ecosystem may be described in relatively static terms by the species composition. Some of the best descriptions in this form were made many years ago. Hardy's (1924) classic description of the complex food web from phytoplankton to fish is a good example. The problem with such detailed portrayal of structure lay in the fact that our knowledge of the dynamic processes determining rates of grazing or predation was, and still is, much more scanty. Thus, with the development of an interest in trophic dynamics (starting with Lindemann 1942) there has been a corresponding simplification in the representation of ecosystems. It has become common practice to define the food web in terms of biomass, organic matter or energy in various very general trophic categories such as herbivores or primary carnivores. This approach, although it can indicate general features, ignores the species composition and, especially, the age structure of populations. Thus the recent generality in the study of ecosystem dynamics has an associated aura of unreality; describing an ecology without species.

A practical disadvantage of biomass models derives from the need to compare theory and observation. Often it is found that the biomass of a trophic level may vary considerably over short periods of time, or distances in space (Fasham & Pugh 1976; Denman 1976). This variability can make it almost useless to compare observations with a theory which portrays the planktonic world as smooth curves representing biomass changing only with time and not with space (Steele 1974*b*). One alternative is to attempt to simulate the observed spatial variability (Steele & Henderson 1977). Another approach, followed here, is to simulate the internal structure of one or more trophic levels. The value of a comparison with observations will depend on the variability of data presented in terms of population structure rather than biomass. The former method of presentation is commonly used in describing communities. At its simplest this may be seen in the frequent use of percentages to express relative species composition or age structure. At a greater level of sophistication it has led to a proliferation in indices of diversity which permit the comparison of mixed populations independently of the fluctuations in their total biomass or numbers (Pielou 1975). The problem with this approach is that it is difficult, if not impossible, to relate these percentages or diversity indices to the dynamics of the populations they represent. This is a symptom of the dichotomy between studies of static structure and of the dynamics of interactions through several trophic levels.

The problem is threefold. First there is a need to find a small number of indices which represent the variety of species at any trophic level but these indices must also be related to the dynamics of these species. Secondly, in terms of the dynamics, these indices must define some factors which differentiate between species in a trophic level, whereas in biomass models it is only the average response of a trophic level that is needed. Lastly, if the first two conditions are fulfilled, the theory will be more complicated than that for a biomass model of the same system and this complexity could make the model too unwieldy for useful insights.

The planktonic ecosystems in the sea have formed the basis for many theoretical studies, mainly in terms of biomass (see for example, Riley, Stommel & Bumpus 1949; Steele 1958; Walsh 1976) but also with some separation of a herbivore species into size or age classes (see for example, Cushing 1959; Steele 1974*b*). For the estimation of rates of growth, these earlier theories had available only a few laboratory studies on very few species: Ketchum's (1939) measurements of phosphate uptake by the diatom *Phaeodactylum tricornutum*, Marshall & Orr's (1955) work with the copepod *Calanus finmarchicus*. Over the last few years there has been an increasing effort to extend the range of experimental work in these areas. As a result the nature of the differences between species at the same trophic level can now be considered.

The general relation of growth rates and metabolic rates to size of organism has been widely accepted (Zeuthen 1947; Fenchel 1974; Banse 1967). For marine plants and animals the dependence of grazing and predation on relative size of animal to its food is often used as a working hypothesis for food chain relations (Ryther 1969; Parsons & Lebrasseur 1970). Based on these general concepts, we shall use recent information in an attempt to model the interrelations of phytoplankton and zooplankton where more than one species of each is involved. The main simplifying assumption is that in both cases a 'species' can be defined by its size. All phytoplankton cells with the same volume per cell are taken as a 'species' and defined by the diameter, D, of a sphere with the same volume as the cells; a zooplankter is defined by its initial (egg) and final (adult) masses (expressed as carbon). The critical assumption is that, in each case, differences in metabolism can be related to size. For a plant cell, nutrient uptake, respiration and sinking are related to the parameter, D. For a copepod, food intake, respiration and excretion rates are determined by its mass, m. Further, for a particular animal, the rate of intake of phytoplankton is a function of its own mass and the size composition of the phytoplankton.

The basis for each of these assumptions will be discussed in detail but some of the relations will be simplified to bring out their main features. This is necessary if the ecological bases for the interactions are to be kept in the foreground and not lost in the intricacies of programming. A further justification for such simplifications arises from the fact that, although plant-herbivore interaction is the central interest, we must include nutrient concentration and carnivore predation. Both these factors can have a significant effect on size structure of the populations. The predators may be as important as any other factor in selecting which of two or three competing zooplankton species survives or dominates. Yet we have relatively little information on this aspect. For this reason it would be pointless to go into too great detail on some of the characteristics of the plants or herbivores.

One form of elaboration has been eschewed. The structure of the physical environment has been kept as simple as possible. Thus we shall be emphasizing the biological interactions and ignoring the ways in which horizontal and vertical variability affect the planktonic ecosystem (see Platt & Denman 1975; Steele & Mullin 1976). This simplification is based on the desire to explore some aspects of community structure rather than provide a predictive tool.

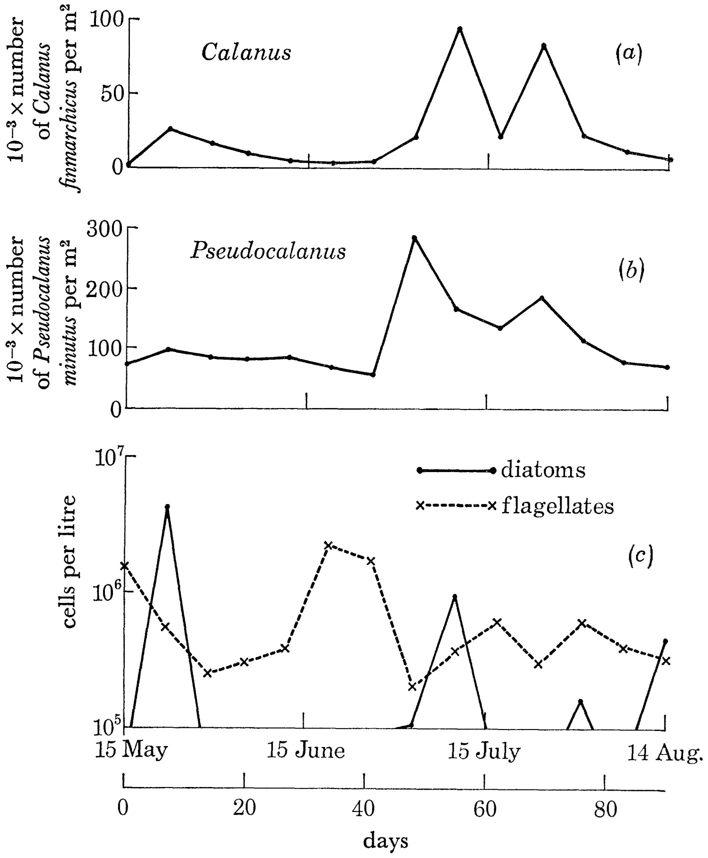

FIGURE 1. Numbers of all stages of *Calanus finmarchicus* under a m^2 in Loch Striven during 1933 (from Marshall, Nicholls & Orr (1934)); (*b*) numbers of all stages of *Pseudocalanus minutus* under a m^2 (Marshall 1949); (*c*) numbers of diatoms and small flagellates per litre (Marshall, Nicholls & Orr 1934).

OBSERVATIONS ON PLANKTON POPULATIONS

The best way to define the problem is to describe certain observations which will provide a general background and, in some cases, a specific test of the theoretical models. The central part of this study concerns the population structure of filter-feeding copepods and the relative abundance of species which, at any developmental stage, differ markedly in body size. We shall simulate the changes over 100 days of populations of two or three species, depicting the complete size structure of each population. Although there are numerous studies of plankton communities we know of only one which gives sufficient detail on temporal variation of population structure of two species – the work by Marshall, Nicholls and Orr in Loch Striven on the west of Scotland during 1933. This provides data at weekly intervals on numbers of all stages of *Calanus finmarchicus* (Marshall, Nicholls & Orr, 1934), of *Pseudocalanus minutus* (Marshall 1949), and of several other, usually less abundant, species. The vertical net used had an 0.16 m^2 opening and a 68 μm mesh. By assuming a filtering efficiency of 50 %, the total numbers of the two main species under a square metre can be derived from their data (figure 1*a* and *b*). Marshall *et al.* state that when diatoms were plentiful the filtration efficiency was very low and so some population levels will be underestimated. Of more interest are the relative numbers of each stage (figure 2). These show differing patterns for each species but, for *Calanus*, a similarity in the sequence of stages during successive 'outbursts', which is not strongly affected by rather large fluctuations in abundance. An adequate representation of copepod populations should attempt to reproduce this type of information and possibly, for particular conditions, the observed sequence of developmental stages through an outburst.

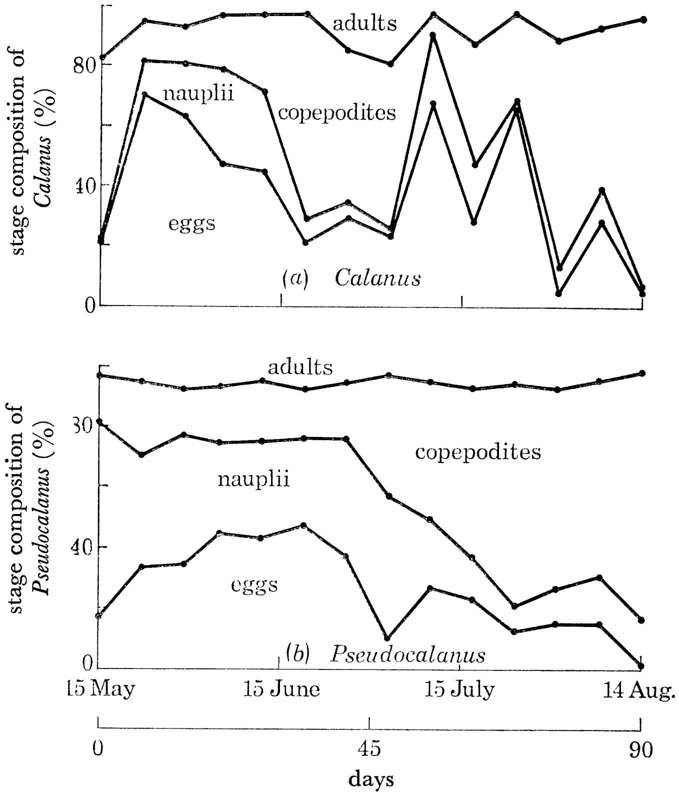

FIGURE 2. Percentage composition of (*a*) *Calanus* and (*b*) *Pseudocalanus* in Loch Striven.

Information on phytoplankton was from centrifuged water samples and shows a sequence of diatom and µ-flagellate blooms related to the periods of growth and decline of *Calanus* (figure 1*c*). The dominant diatom in the initial bloom was *Skeletonema costatum* whose average diameter is about 10 µm. The µ-flagellates were probably in the range 2–5 µm (Marshall & Orr 1955).

These studies do not provide a detailed size structure for the phytoplankton, a procedure which was technically difficult to achieve at that time. Recent applications of electronic particle counters can provide volume distributions of particles (Sheldon & Parsons 1967) over a broad range of particle size expressed as equivalent spherical diameter. The particles measured will include non-living material as well as phytoplankton cells but in relatively eutrophic waters these distributions in the range 2–150 µm should be closely related to the size distribution of the phytoplankton. At the same time the use of large plastic enclosures

(Menzel & Case 1977; Gamble, Davies & Steele 1977) permits the study of community development over periods of about one month. From studies in Saanich Inlet, Vancouver Island (Takahashi *et al.* 1975) particle size distribution in two such enclosures (figure 3) shows conditions before (day 2), at the peak (day 11) and immediately after (day 25) the spring outburst. The peak was dominated by *Thalassiosira* spp. and afterwards µ-flagellates were the main component. This sequence is similar in character to that observed in Loch Striven. Parsons & Lebrasseur (1970) have stressed the importance of size structure in this area, as a determining factor for the development of juvenile salmon.

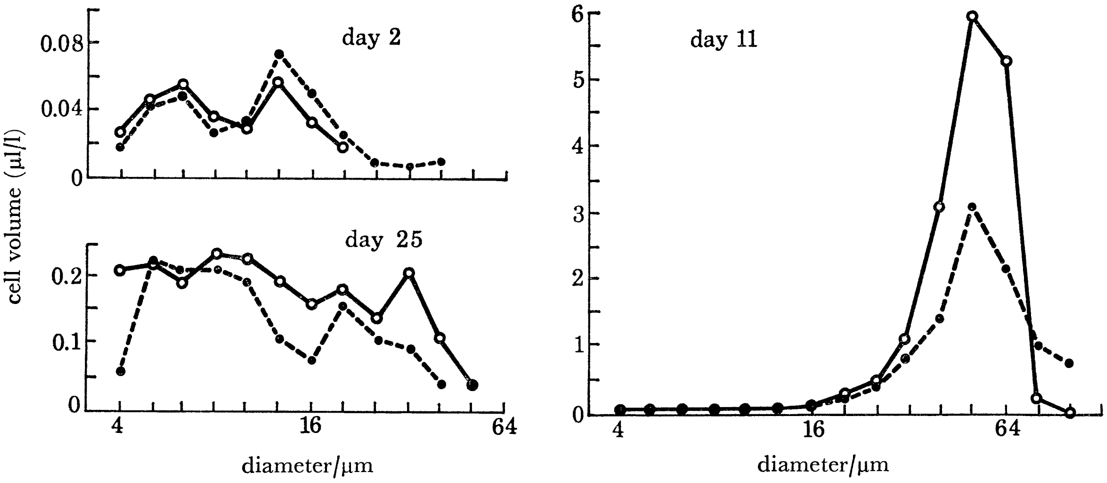

FIGURE 3. Particle size distributions in two large plastic enclosures in Saanich Inlet, Canada (Takahashi *et al.* 1975).

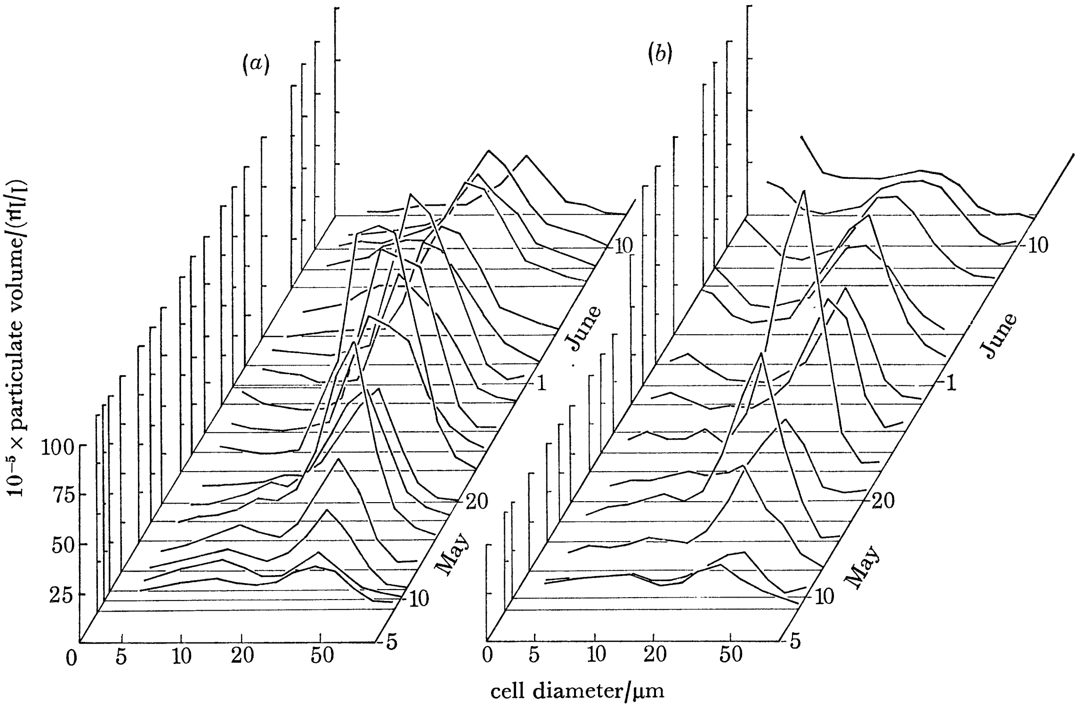

FIGURE 4. Particle size distributions in two enclosures (*a*) and (*b*) in Loch Ewe, Scotland, during May–June, 1974 (Gamble *et al.* 1977).

In another sea loch on the west of Scotland, Loch Ewe, enclosure experiments produced generally similar sequences of cell size (figure 4) (Gamble *et al.* 1977), with the diatom *Cerataulina bergonii* dominant initially in both bags. Later, however, there were differing degrees of dominance with μ-flagellates predominant in (*b*) but significant quantities of small diatoms also present in (*a*). Associated with this divergence in response were differences in the numbers of herbivores in the two enclosures (particularly *Pseudocalanus*) and also in predators (the ctenophore *Bolinopsis*). These extra features suggest that, as well as effects arising from the physical or nutrient environment, the structure of higher trophic levels will play a role in determining the phytoplankton species composition (Gamble *et al.* 1977).

These data indicate the importance of studying not merely total biomass of trophic levels but also population structure. They suggest that certain recognizable sequences in relative composition can occur and these sequences may be more regular than the changes in biomass. Further, there are indications of interactions between phytoplankton and herbivores dependent on size composition as much as on total biomass. The definition of these interactions as a function of organism size, is the subject of the succeeding sections.

The components of the system

The general food web (figure 5) has been kept as simple as possible but the quantitative description of the system necessarily requires close study of the details of each interaction. This section can be regarded as a very selective review of phytoplankton and zooplankton dynamics, as these relate to size structure. For each component, (*a*) to (*o*) (figure 5), a mathematical formulation is derived and, where necessary, numerical values given for the coefficients. The evaluation of the final 'model', as a simulation of the ecosystem, depends critically on these details but the main features are summarized in the final part (*p*) of this section. A list of the symbols used is given in the appendix.

(*a*) *Physical aspects*

The simplest vertical structure for the physical environment (figure 6) is obtained by assuming a two-layered sea with the division between the two layers occurring in the seasonal thermocline. There is a mixing rate, M, defined as the fraction of the upper layer exchanged with the lower each day. This removes plants from, and introduces nutrients to, the upper layer. The animals which can migrate vertically are considered to be independent of vertical motion. It is assumed that the layers are well mixed and the lower layer is sufficiently deep for the nutrient concentration in it to be constant and the concentration of plants to be negligible. It is assumed that one nutrient is limiting and this is taken to be nitrogen with no distinction made between nitrate and ammonia. On this basis the model describes changes in the upper layer only.

The depth of the upper mixed layer, z_e, is assumed sufficiently great for all plant growth to occur within this layer. Incident radiation, I_0, is assumed constant with time. The only depth-dependent factor which is variable is the attenuation coefficient, k. It is assumed that this depends on the chlorophyll *a* concentration, χ (mg/m³), where

$$k = A\chi + B.$$

A value for $B = 0.1$ is used here to give a maximum depth of 46 m for the 1% light level (the usual definition of the euphotic zone). This corresponds to the maximum transmission observed in the relatively turbid waters of the northern North sea (Steele & Baird 1962). A value for $A = 0.02$ is taken from Aruga & Ichimura (1968). These values, and the relation for photosynthetic rate (section *c*) are based on light measurements in lumens rather than the more recent quanta measurements for A (Tyler 1975).

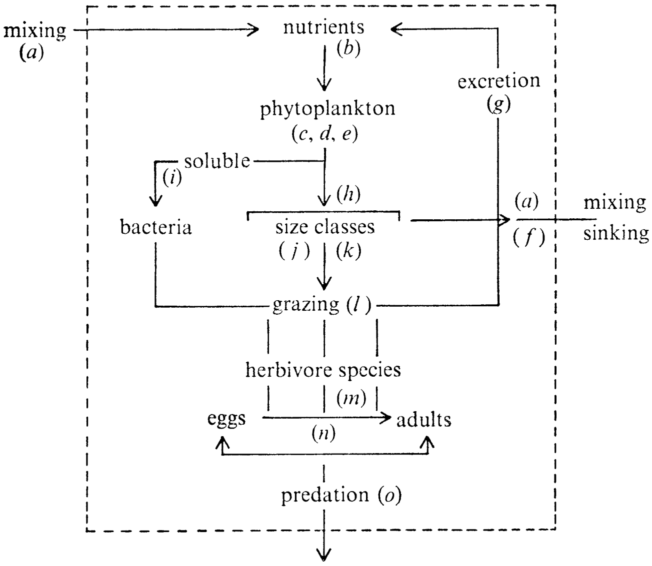

Figure 5. The main processes simulated in the computer model (letters indicate sections of the text (p. 492 to p. 510)).

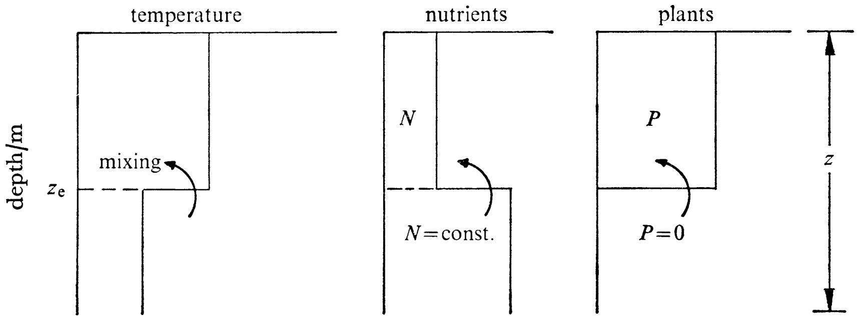

Figure 6. Vertical structure used in the model.

(*b*) *Nutrient uptake*

As before (Steele 1974*b*) it is assumed that all plants and animals have a fixed C:N ratio. For convenience this is taken as 7:1 so that, effectively, 100 mg C ≡ 1 mmolN. This excludes changes occurring in this ratio which may be related to species composition (Gamble *et al.* 1977). This simplifying assumption ignores the concept developed by Droop (1974) of a variable nutrient pool within the plant cell, acting as an intermediate stage between uptake and growth. It allows the kinetics of nitrogen uptake to be used as a factor determining the rate of photosynthetic fixation of carbon. The accepted form for the former is (Dugdale 1967):

$$\frac{V_{\max} N}{k_s + N}$$

where $V_{\max}$ is the maximum rate of uptake when there is no nutrient limitation and k_s is the nutrient concentration at which uptake is half the maximum rate. In this model $V_{\max}$ will be replaced by a parameter, C, expressing maximum growth in carbon units as a function of mixed layer depth and attenuation coefficient.

(*c*) *Photosynthetic rate in the euphotic zone*

Photosynthesis is a function of light which, in turn, varies with depth in the sea. Given the simplifications in figure 6, an average value is needed of photosynthetic rate for the upper layer in the absence of nutrient limitation.

If radiation, I, as a function of depth is given by

$$I = I_0 \, \mathrm{e}^{-kz},$$

then the relation for photosynthetic rate, P_h (Steele 1962) is

$$P_h = \frac{2P_{\max} I}{I_0} \exp\,(1-2I/I_0),$$

where $P_{\max}$ = max photosynthetic rate (at $I = \frac{1}{2}I_0$). From these

$$\int_0^{z_e} P_h \,\mathrm{d}z = \frac{P_{\max}}{k} [\exp\,(1-2I/I_0)]_{z=z_e}^{z=0}.$$

If one assumes $I \ll I_0$ at z_e then the average photosynthetic rate, C, in the euphotic zone is

$$C = \frac{1}{z_e}\int P_h \,\mathrm{d}z = \frac{P_{\max}}{kz_e}(\mathrm{e}-\mathrm{e}^{-1}) = \frac{2.58P_{\max}}{kz_e}.$$

It is necessary to determine a value for $P_{\max}$. Steele (1962) used 0.066 mg C/mg plant C per hour, as an average for the daylight hours. Parsons & Takahashi (1973*b*) give 4 mg C/mg Chl per hour as the maximum value for growth. The maximum used here (see later section) for the Chl:Carbon ratio is 1:30, which converts the Parsons & Takashi value to 0.133 mg C/mg C per hour. If the average for daylight hours is one-half this value, this would give 0.067; effectively the same as the earlier estimate.

The critical time of year in northern latitudes is taken as the spring outburst, which occurs in April–May, when the day length is 13–16 hours, and gives an average value of

$$C = \frac{2.5}{kz_e}$$

This value has been derived independently of cell diameter, D. Laws (1975) suggests a dependence of the form $D^{-\frac{1}{3}}$. Parsons & Takahashi (1973*a*) indicate that, under certain light conditions, $V_{\max}$ could increase with cell size. Since other factors contribute greater decreases in population growth with increased cell diameter it is assumed here that C is independent of diameter.

(*d*) *Half-saturation coefficient*

There has been some disagreement about the dependence of k_s on cell size (Parsons & Takahashi 1973*a*, 1974; Hecky & Kilham 1974). Attempts to obtain a single relation that can apply anywhere may not be justified but the intent here is to study changes in time for particular areas, rather than to compare average conditions in widely differing environments.

With this restriction some relation of k_s to D appears appropriate. The data in figure 7 indicate that such a relation cannot be defined exactly. If it is assumed that the effect is related to the ratio of volume (growth) to surface area (uptake) then k_s would be proportional to D and we shall use

$$k_s = \delta D.$$

The distinction between uptake and growth will complicate the application of k_s values in the model (Droop 1974). Thus, in the experiments, the k_s values from uptake experiments at higher nutrient concentrations may be too large for growth rates (Dugdale 1976). Two values will be used; the minimum from the observation given by $\delta = 0.015$; and an intermediate value of $\delta = 0.030$ to show the effects of an increase in k_s (figure 7). The effects of nutrient limitation are most significant after the spring outburst when nutrient concentrations are low.

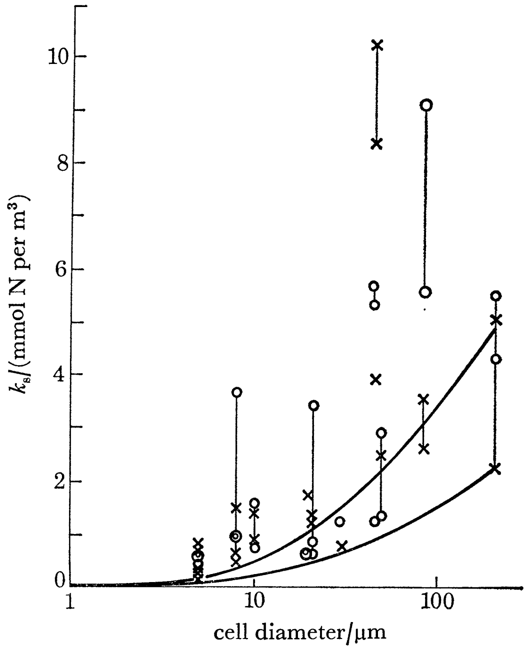

FIGURE 7. Nitrate (×) and ammonium (○) half-saturation constants from Parsons & Takahashi (1974). The lines indicate the two responses used in the model (see p. 494).

Thus the critical values of k_s will be associated with species later in the season which may be expected to have a below average value of k_s (Dugdale 1967). For this reason $\delta = 0.015$ is used for the standard run.

(*e*) *Chlorophyll: carbon ratio*

Carbon is used as the basic unit in the model but chlorophyll is needed to determine the attenuation coefficient, k. Further, chlorophyll, rather than carbon, is the commonly used index of phytoplankton populations. Thus it is necessary to define the ratio of these parameters. Ignoring variations in light, it will be assumed (Steele 1962) that the chlorophyll content of the cell is dependent on nutrients. The simplest assumption is that the ratio chlorophyll: carbon is proportional to

$$N/(k_s+N)$$

so that it has its maximum value, $\chi_{\max}$ when nutrients are plentiful. Thus for a given cell size with population, P, in carbon units (mg C/m^3) its standing stock in chlorophyll units (mg/m^3) is

$$\chi = \frac{\chi_{\max} PN}{k_s + N}.$$

This will be related to cell diameter through k_s. A value of $\chi_{\max} = 0.033$ is used here.

(*f*) *Sinking rate*

Sinking rate, S, of phytoplankton cells is related both to cell size and to growth rate (Eppley, Holmes & Strickland 1967). The relation with size might be expected to follow Stokes Law with $S \propto D^2$, but observations (Eppley *et al.* 1967) show that it is nearer $S \propto D$. This may be due to the fact (Strathmann 1967) that carbon content of the cell per unit cell volume decreases as cell volume increases.

The dependence of sinking rate on growth rate may, in turn, depend on rate of nutrient uptake (Steele & Yentsch 1960). Eppley (personal communication) has suggested the form

$$S \propto 1 - N/(k_s + N) = k_s/(k_s + N).$$

The combined contributions of growth rate and size to sinking rate gives

$$S = V\delta D^2/(\delta D + N),$$

where V determines the sinking rate when $N = 0$. From Eppley *et al.* (1967) non-growing cells 10 μm in diameter have a sinking rate of 1 m/day; thus $V = 0.1$.

In nutrient poor waters, nutrient depletion in the water near the cell wall may decrease the rate of nutrient uptake calculated on the basis of nutrient concentration at a distance from the cell. This can be overcome by the cell sinking through the water. Munk & Riley (1952) calculated this effect for cells of different shapes and diameters and concluded that absorption rate always decreased with increasing size. Pasciak & Gavis (1974), following Munk & Riley, derived a term

$$P^1 = \frac{ak_s}{D^2 V_{\max}} (1 + bDS),$$

where the larger the value of P^1 the smaller the effect of depletion. The definitions already used for terms in P^1 give

$$P^1 = c/D(1 + 4.5\ 10^{-5} D^3/(0.015D + N)),$$

where a, b and c are arbitrary constants.

This form of relation has a minimum for some intermediate cell diameter, dependent on N and should be most severe for N very small when the minimum value is given by $D = 180$ μm. Thus again the effect will be a decrease in absorption rate with increasing cell size.

This effect might be used to account for some of the observed decreases in uptake with cell size which are incorporated here by making k_s proportional to D. However, the exact determination of the size-sinking-absorption effect is difficult to formulate precisely and so it is ignored here, or assumed to be part of the k_s variation.

(*g*) *Respiration rate*

The parameters k_s and S vary with cell size and this will result in a decrease in population growth rate with increasing cell diameter. On this basis alone, the phytoplankton population would always be dominated by the smallest cells. Respiration rate per unit carbon, R, is the size-dependent factor likely to have the opposite effect on growth rate, based on the general relation found for other organisms; that respiration is more nearly proportional to surface area than to volume or mass. For phytoplankton cells this would make

$$R \propto D^2/D^3 = D^{-1},$$

if the carbon content of cells were a fixed proportion of cell volume. Strathmann (1967) has shown that

cell carbon $\propto$ (cell volume)$^{\beta}$ where β lies between 0.7 and 0.9. Thus $R \propto D^{2-3\beta}$,

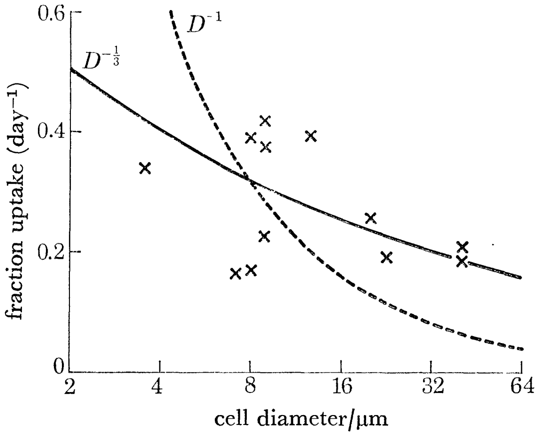

FIGURE 8. Respiration data recalculated from Eppley & Sloan (1965) with two curves used in the model (see p. 496).

and this gives rather wide limits of $D^{-0.1}$ to $D^{-0.7}$. The available data for this relation are inconclusive. From Eppley & Sloan (1965), by using their cell volume data (Eppley & Sloan 1966), figure 8 suggests that a weaker relation than D^{-1} would be appropriate and $D^{-0.33}$ will be used. Because the respiration-size relation is critical in determining population growth of the smaller cells, D^{-1} will also be used to demonstrate the effect of this size factor. From figure 8, $R = 0.3$ approximately at 10 µm cell size. Since these experiments were done at 21 °C, and the spring temperature in the North Sea is about 10 °C a value for R of 0.15 is assumed. This gives

$$R = 0.32D^{-0.33}$$

or

$$R = 1.5D^{-1.0}$$

as the alternative formulations.

(h) *Phytoplankton population size distribution*

At this stage it is useful to bring together the various factors affecting size distribution, excluding grazing. If P is the carbon content of a population with diameter D, then growth rate (= photosynthetic rate – respiration rate – sinking rate – mixing rate) may be represented as

$$\frac{1}{P}\frac{\mathrm{d}P}{\mathrm{d}t} = \frac{CN}{\delta D+N} - aD^{-\alpha} - \frac{V^*\delta D^2}{\delta D+N} - M,$$

where a, α specify the alternative forms of respiration, and

$$C = 2.5/kz_e,$$

$$k = 0.02\chi + 0.1,$$

$$S = 0.015,$$

$$V^* = 0.1/z_e \text{ determines fractional loss from a mixed layer } z_e.$$

Then, $$\mathrm{d}P/\mathrm{d}t = 0 \quad \text{for} \quad CN - a\delta D^{1-\alpha} - aND^{-\alpha} - V^*\delta D^2 - M(\delta D + N) = 0.$$

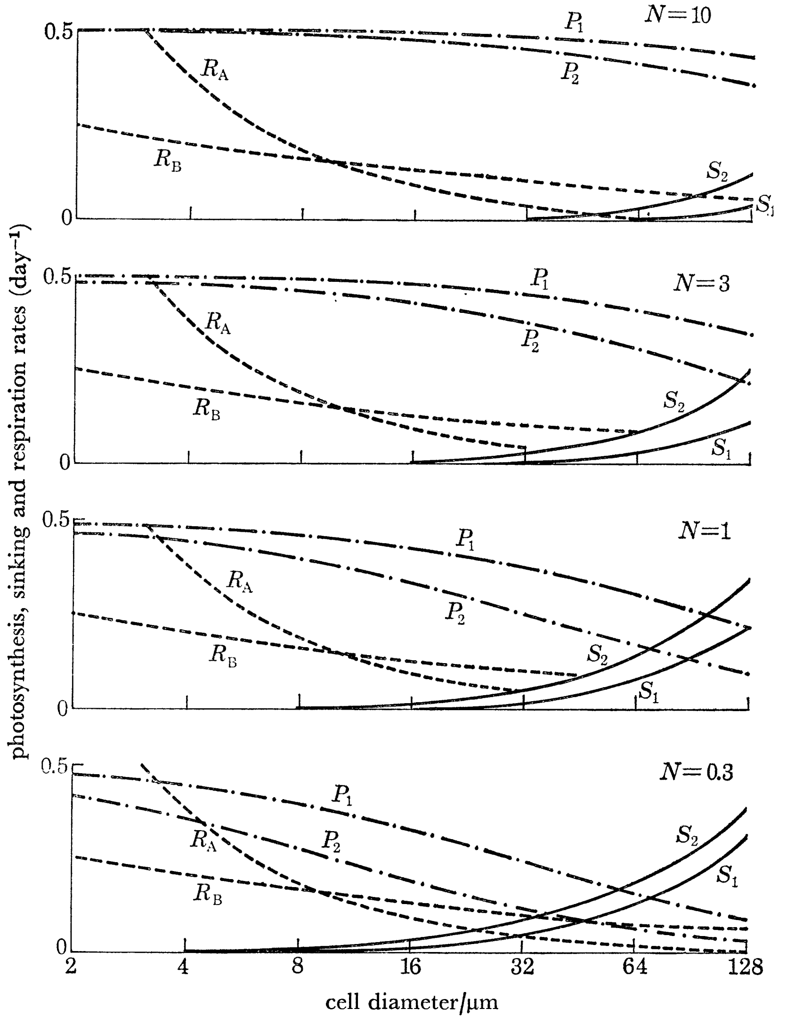

FIGURE 9. Photosynthesis, sinking and respiration rates, for varying nitrate concentrations. P_1, S_1 are photosynthesis and sinking with $k_s = 0.01\ D$; P_2, S_2 with $k_s = 0.03\ D$. R_A, R_B are respiration expressed as $1.5\ D^{-1}$ and $0.32\ D^{-0.33}$ respectively.

Approximately, the upper and lower diameter for cells showing zero growth will be defined by

$$D_{\min} = (a/C)^{1/\alpha}, \; D_{\max} = (CN/V^*\delta)^{\frac{1}{2}}.$$

Thus the cell size below which growth will be negative is determined predominantly by the ratio of respiratory coefficient and maximum growth coefficient. This emphasizes the importance for the smaller cells of the function used for respiration. D_{min} is effectively independent of nutrient concentration, sinking rate or half saturation coefficient but will increase with increasing z_e. The maximum diameter for a cell showing positive growth will decrease with nutrients and is determined by k_s. The above values for C and V^* give

$$D_{\mathrm{max}} = (25N/k\delta)^{\frac{1}{2}}$$

and show that D_{max}, in this formulation, is independent of the thickness of the upper mixed layer, z_e, because a decreased sinking loss due to greater thickness is balanced by the decrease in growth rate. Thus one has the counter-intuitive conclusion that variations in mixed layer thickness would affect the smaller rather than the larger cells.

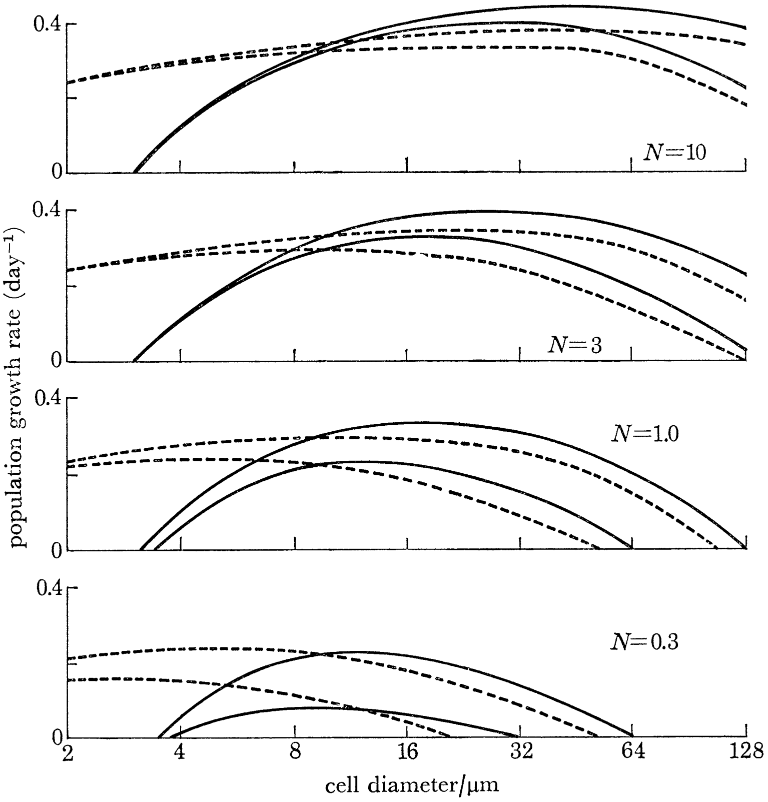

FIGURE 10. The phytoplankton population growth rate for varying nitrate concentrations determined from photosynthesis–respiration–sinking (see figure 9). —— $R = 1.5\ D^{-1}$, – – – $R = 0.32\ D^{-0.33}$. The upper lines in each case are for $k_s = 0.01\ D$; the lower $k_s = 0.03\ D$.

To illustrate these interactions, figures 9 and 10 show how population growth rate is determined by the various processes. The alternative choice of respiration functions gives either a dome-shaped growth response, so that these processes will be highly size selective, or a flatter response which can be affected to a greater extent by other factors such as grazing. It is possible that the growth response could be derived by slightly different assumptions. With some increase in the photosynthetic rate with cell size, and assuming that respiration rate is independent of cell size (Eppley, personal communication), similar flat-topped responses could be obtained which would retain the essential dependence on nutrient concentration. The effect which grazing will have on phytoplankton size distribution depends on the choice between a dome-shaped or a flat-topped growth curve rather than on the specific form for respiration or photosynthesis.

One major feature of the phytoplankton has been ignored here – the formation of chains of diatoms. These chains will increase the apparent particle size and alter sinking and grazing rates so that a cell volume made up of a number of individual cells will have different characteristics from those of a single larger cell. A population of particles comprised of diatoms with varying chain lengths could have a flatter growth curve than would result for a population of single cells. The consequences, however, might still be represented within the range of responses shown in figure 10.

(*i*) *Soluble excretion and bacterial production*

One complicating factor in describing size distribution of material available to the grazers arises from the excretion of soluble organic matter by the phytoplankton. On the one hand this could be related to phytoplankton cell size thus altering their size distribution; on the other hand utilization of this material by bacteria will produce a potential food source. The bacteria themselves would probably have a diameter of less than 2 μm but their accumulation on larger pieces of matter, organic or inorganic, could increase the effective size of particles available for grazers. In this study, bacterial synthesis will generally be ignored, but as a naive representation, we shall consider the consequences of excretion of 10 % of the products of photosynthesis by all phytoplankton cell sizes: this soluble organic material being utilized by a bacterial population with a 2 μm diameter.

(*j*) *Zooplankton grazing*

From the previous section it is apparent that any herbivore species will need to capture food of a wide range of sizes and the limiting factor for its growth may be the ability to feed on low concentrations of small cells which occur when nutrients are limiting. This could place larger animals at a disadvantage if we assume that there is some interrelation between size of copepod and size of cells which it can capture efficiently. The complications in specifying this interaction arise from the other assumption, that the animals' feeding behaviour will also depend on the total food taken in over the whole range of cell sizes.

At this point it is necessary to make some fundamental simplifying assumptions. (i) The feeding behaviour of a herbivorous copepod of mass m (expressed as μg C) is independent of its species and depends only on the phytoplankton abundance and size composition. In the range of masses where, say, *Calanus* and *Pseudocalanus* overlap, their feeding behaviour will be indistinguishable, and so the differences between the species will arise only from their differing initial and final masses. (ii) The change in feeding behaviour with increasing mass is a smooth progression with a generally increasing efficiency for larger cells. This ignores morphological changes occurring in a copepod as it develops through discrete stages. Especially it ignores the transformations in feeding apparatus which occur when it passes from naupliar to copepodid stages. (iii) The species are considered to be completely herbivorous, feeding by filtration of water. This ignores evidence that *Calanus*, in the laboratory, can feed on smaller animals and so could be a predator on the early stages of its own or other species (Corner, Head, Kilvington & Pennycuik 1976). The justification for the last simplification rests on lack of evidence that this species is carnivorous during the main periods of growth.

(*k*) *Size selection of cells*

The filtering apparatus is composed of setae with setules on them, figure 11. Different parts of the filter may have different selection characteristics depending on the spacing between setules and between setae. The simplest, and very idealized, picture of a part of the filter is that of a fan, figure 12*a*. There has been discussion of whether the opening of this fan can be adjusted by an individual animal to give differing filtration dependent on the size of cells in the water (Wilson 1973; Boyd 1976; Steele & Mullin 1976). At present it appears simplest to assume that for a copepod in a particular stage of growth, the shape of the fan is fixed, but as it grows, the shape may change.

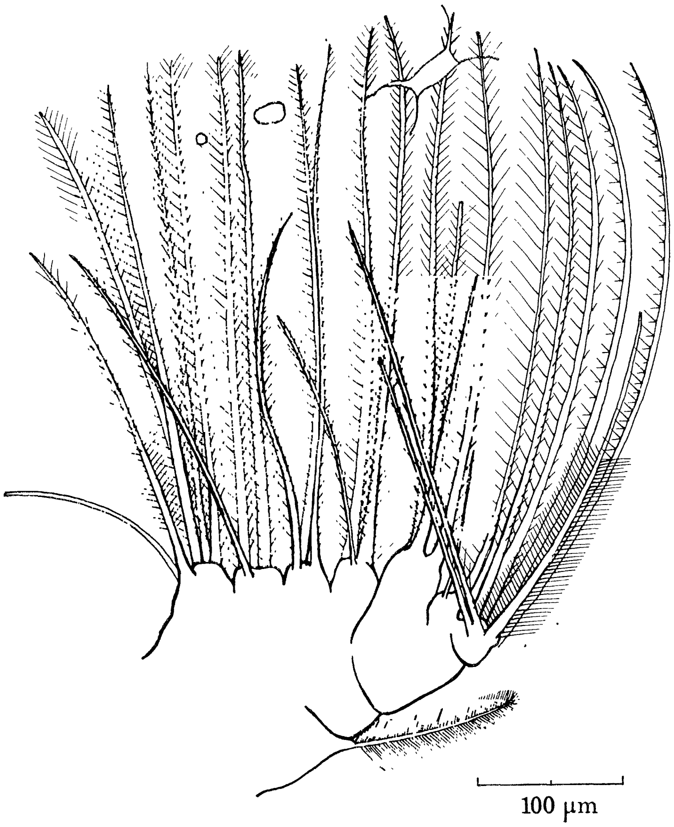

FIGURE 11. An illustration of a filtering appendage of *Calanus helgolandicus* with three cell sizes shown: a μ-flagellate, a coccolithophore and a diatom (from Marshall & Orr 1955).

Consider one segment of a fan. The area A_D between two limbs which will catch particles of diameter D is, approximately,

$$A_D = \tfrac{1}{2}D^2\theta \quad \text{for} \quad D < l\theta,$$

where θ is the angle between the segments and l is the length of the segments. Assuming isometric growth (but see p. 502) the filtering area, as a function of D, alters in the manner shown, figure 12*b*. For small cells the filtering area is independent of animal growth. Thus a large animal with a proportionately higher metabolic rate would present the same area for capture of small cells as a small animal. This is likely to be an unsatisfactory strategy for large copepods such as *Calanus*. Using the idealized fan design, a copepod, as it grows, could solve this problem in two ways: (i) it could introduce extra setae into the fan (figure 12*a*). If this were done to allow the filtering of small cells to increase as l^2 (figure 12*b*, curve 2), then the number of extra setae would be proportional to l. The consequence would be that the area of material in the filter would increase as l^3 rather than l^2. (This would cause a rapid increase of drag with size). Morphologically such an increase in numbers of setae is not possible during the copepodid stages but there is usually a marked elaboration in the filtering structure at the last naupliar stage (Marshall & Orr 1955); (ii) an alternative method of increasing filtration of small cells during growth would be to decrease θ or, more realistically, to have the spacing of the setae in figure 11 increase at a rate less than the linear increase of the animal. Measurements of the maxillae for two copepods show that the setae increase in length as the dimensions of the animal L but (figure 13) the length of the filtering appendage increases at a lower rate, approximately (and for simplicity) $L^{\frac{1}{2}}$; thus early copepodid stages have relatively larger filters than late stages.

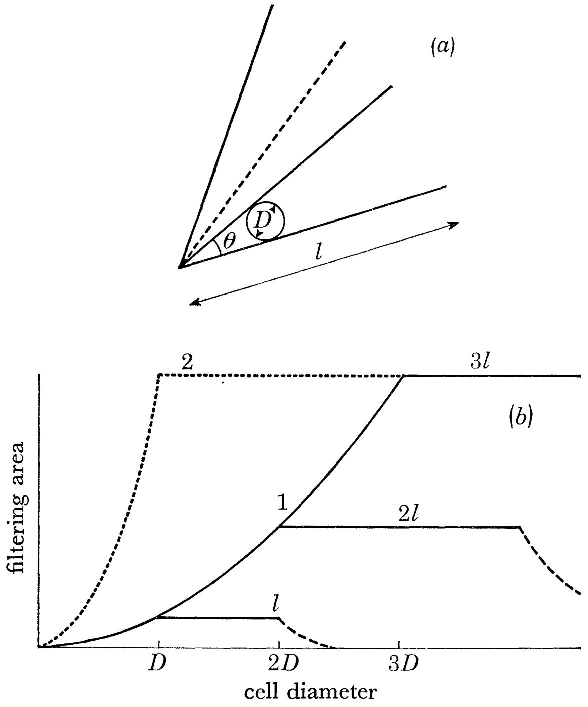

FIGURE 12. (*a*) A segment of a fan showing dimensions. (*b*) (1) Area for capture of cells as a function of diameter (D), for different sizes of fan (l). (2) The effect of adding extra segments (– – –) in the position indicated in (*a*).

There must be some upper limit to the size of particle which an animal can not only capture but also ingest (cf. Wilson 1973). Many copepods appear to be able to break open and ingest parts of larger cells but there should be some limit to this effect. The early naupliar stages are about the same size as a large diatom. Thus for large D relative to L the efficiency of capture must decrease. None of the available experimental work considers the efficiency with which small animals feed on various sizes of large cells, so there are no data to support this part of the development of the selection process. However, for the general relation between size of copepod and ingestion efficiency on different sizes of particles, the upper part of the curve needs to be estimated (figure 12*b*). The most economic assumption is that for D large relative to l, filtration will decrease as D^{-1}.

The fan concept illustrates the main problems of size selection facing a copepod as it grows but is obviously too simple a representation. The filter can also be regarded as composed of a number of fans or as a net with variable mesh size (Nival & Nival 1973, 1976) producing a selection curve which would be a function of cell diameter, D, and length, l, and would include the decreasing efficiency for large cells.

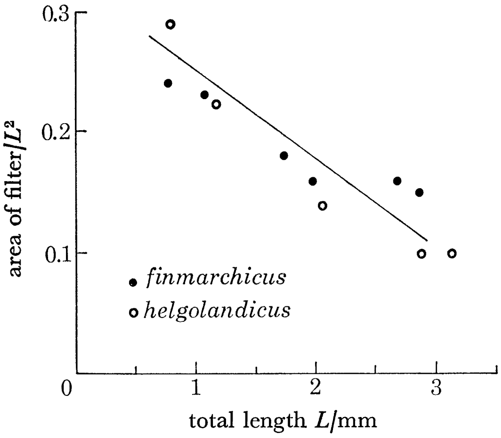

FIGURE 13. Relation of (area of filter)/L^2 to L, where L is animal length.

This curve can be expressed in terms of two parameters, l, a scale length for the filter, and $\lambda = D/l$, in the form

$$F = l^2 S_e(\lambda),$$

where max $(S_e) = 1$ and F can be considered as relative ingestion rate for unit velocity of flow through the mesh and unit particle concentration at diameter D.

A general function for $S_e(\lambda)$ is

$$S_e(\lambda) = \exp[-(\ln\lambda)^2/\mu],$$

which can be interpreted as assuming that, for any animal, the ability to catch cells is log-normally distributed so that a cell with half the optimum diameter has the same selectivity as one with double the optimum diameter. By varying μ, narrow- and broad-band filters can be derived. This functional form is used but the choice of μ $(= 2.5)$ for most runs is made so that the relation approximates to the simpler form (figure 14*a*)

$$S_e = 2\lambda/(1+\lambda^2).$$

With this relation, for $D \ll l$, F increases as l and so lies between curves (1) and (2) in figure 12*b*. For $D \gg l$, $F \propto 2l^3/D$ and so decreases as D^{-1}.

In relation to the model it is best to express l, the filter dimension, in terms of the animal's dimension, L. The simplest relation is to take $l \propto L$. The alternative, corresponding to the reduced rate of increase in spacing of the filter, is $l \propto L^{\frac{1}{2}}$. The former gives $F_{\max} \propto L^2$, the latter $F_{\max} \propto L$. These two cases can be combined by taking

$$F_\beta = L^\beta S_e(D/L^{\beta/2}) \quad \beta = 1, 2.$$

In practice it is necessary to scale the value of L so that L is defined as

$$L = D_m m^{\frac{1}{3}},$$

where m is mass of the copepod (in μg C) and D_{m} is cell diameter (μm) at which $S_{\mathrm{e}} = 1$ for an animal with $m = 1$. In the model, the range for m is 0.1 to 100 μg C, and for D it is 2.5–125 μm. With $D_{\mathrm{m}} = 10$, and $\beta = 2$, the ratio D/L can vary between 0.05 and 25. With $D_{\mathrm{m}} = 200$, and $\beta = 1$, $D/L^{\frac{1}{2}}$ varies between 0.08 and 13.6. These choices of D_{m} (figure 14*a*) ensure that ingestion rate is about the same at the upper and lower ends of the size scale for phytoplankton. In the first case ($\beta = 2$) it is apparent that a large animal feeding on small cells, or a small animal feeding on large cells, would obtain a very poor relative food intake. In the second case ($\beta = 1$) the intake would be much improved. For an intermediate size of cell with L increasing by a factor of less than 10, variation in intake would be less than a factor of two, which indicates that a copepod could complete its growth cycle on a single species of phytoplankton. As an example, the selection curves for $\beta = 2$, are derived (figure 14*b*) for three different sizes of animals.

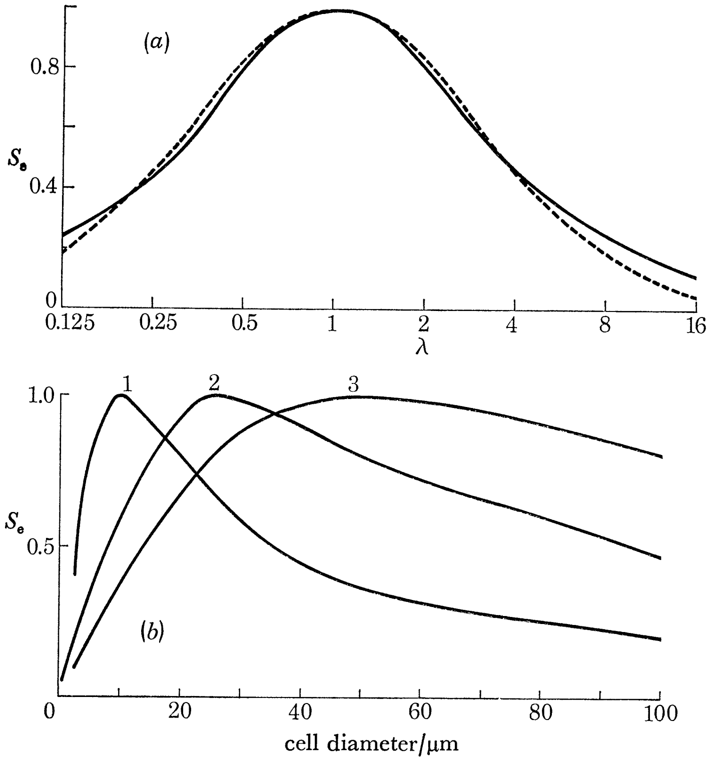

FIGURE 14. (*a*) The selection function $S_{\mathrm{e}}(\lambda)$ with alternative formulations: ——, $2\lambda/(1+\lambda^2)$; – – – $\exp[-(\ln\lambda)^2/\mu]$. (*b*) Examples of the selection curves for $D_{\mathrm{m}} = 10$, $\mu = 2.5$, and for three sizes of animal (1) $m = 1$, (2), $m = 10$, (3), $m = 100$ μg C.

At the moment, experimental evidence to decide between the various alternatives is inconclusive. Studies of the growth of *Calanus* spp. on a range of diets (Paffenhöfer 1971) gives rates proportional to $m^{\frac{2}{3}}$. This would support the L^2 form ($\beta = 2$). For the actual selection function, the experimental evidence supports the general concept, for any size of animal, of an increasing efficiency of retention with increasing cell size. The upper limit and decline for large cells is not known. Experiments with *Calanus finmarchicus* in the Clyde (Steele, unpublished) indicated a roughly linear increase from zero up to 80 μm cell diameter. Similar results (Frost 1972) were found with *Calanus pacificus*. *Calanus plumchrus*, however, although showing an increase with cell size (Frost unpublished) appears able to filter efficiently very small cells. It is known that *C. plumchrus* has a very much finer mesh than other calanoids of its size and this may be related to its environment in the open north Pacific where small cells may be the only food source (McAllister, Parsons & Strickland 1960; Parsons 1972). This example indicates the care needed in defining a 'copepod' too generally. *C. plumchrus* will be considered as a special case where the spread of the selection curve is larger than for the other calanoids (p. 518).

This discussion of filtration efficiency has the implicit assumption that there is the same rate of flow of water through all parts of the filter. The mechanisms for producing the flow of water (Marshall & Orr 1955) may not give uniform flow, and mucus secretions by phytoplankton cells may clog the filter as they do with a plankton net, thereby altering the filtration characteristics. Further, the decreased porosity of the finest parts of the filter could decrease the flow and increase the drag. This factor could provide a lower limit to the general fineness of the filter and so to the animal's ability to catch the smallest cells. Beyond this the animal can be expected to vary the flow rate depending on the concentration, and possibly the size, of cells. This factor complicates the interpretation of the experimental results mentioned earlier, and must be treated separately.

(*l*) *Energy expended in filtration*

Following Lam & Frost (1976) and Lehman (1976), it will be assumed that the main energy expenditure of the animal, above some basal or standard metabolic rate, arises from the drag of the filtering appendages as water flows through them. This permits a direct relation between energy intake and metabolic losses of energy.

The drag of the filter will be of the form $C_D A_f V_e^2$ where A_f is the area of the material of filter presented to the flow, V_e is the average velocity of flow through the filter and C_D, the drag coefficient, is some function of Reynolds Number, $Re = dV_e/\nu$. Here d is the average diameter of the setules and setae and ν is the kinematic viscosity of sea water. The rate of energy expenditure by the animal in overcoming drag is, then, drag × velocity $= C_D A_f V_e^3$.

Any exact consideration of Reynolds effect is impossible because of the great variability in d and the fact that the filter also has high frequency transverse vibrations (Marshall & Orr 1955), but for $d = 10^{-2}$ cm, $V_e = 1$ cm/s, $\nu = 10^{-2}$ g cm^{-1} s^{-1}, $Re = 1$. Thus (Hoerner 1952) the type of drag might be between viscous and laminar. This implies that $C_D \propto Re^{-\gamma}$, $0.5 \leqslant \gamma \leqslant 1$. It appears unlikely that turbulent drag with $C_D \propto Re^0$ would be appropriate.

From the preceding section the surface area A_f of material of the filter appendages may increase as L^2. If the area is increased more rapidly at the change from naupliar to copepodid stage or by increased length of setae or setules, then $A_f \propto L^{1+\beta}$ where $1 \leqslant \beta \leqslant 2$.

Thus the energy term is of the form

$$L^{(1+\beta-\gamma)} V_e^{3-\gamma}.$$

There are obvious simplifications in calculation by taking $\gamma = 1$ rather than having the exponent of V_e lie between 2.5 and 2.0 and so this term becomes

$$L^{\beta} V_e^2.$$

Again for simplicity we shall take $\beta = 1$ for F_1 and $\beta = 2$ for F_2, but use the above form in the intermediate calculations.

(*m*) *Growth rate*

It is assumed that all particles captured by the animal are ingested. A fixed fraction, 0.3, of this ingested material is excreted in particulate form as faecal pellets which, since they have a high sinking rate (Smayda 1970) are lost from the system. The assimilated material is used to meet metabolic losses from some basal or standard rate, assumed to be of the form QL^2, plus the energy cost of feeding. The nutrients associated with these losses are returned to the water (50 % in the upper layer). Any excess after meeting these losses goes to growth.

From previous sections, the total carbon assimilated by an animal with characteristic length L will be of the form

$$aL^\beta V_e \pi(L),$$

where

$$\pi(L) = \int_D S_e(L, D)\, P(D)\, \mathrm{d}D,$$

and a is an undefined constant.

π combines the selection curve with the carbon distribution as a function of diameter.

Thus growth rate, G, can be expressed as

$$G = aLV_e\pi = cL^\beta V_e^2 - QL^2,$$

where c is an undefined constant.

At this point we make a critical assumption about the response of the animal to variation in food supply. We postulate that (at any food concentration) the copepod will 'choose' the value of V_e which maximizes growth, G, below some maximum rate (see Lam & Frost 1976; Lehman 1976). A similar assumption has been used by Ware (1975) for pelagic fish. There are attractions in a possible evolutionary derivation of this assumption but it is best to regard it as an optimum strategy within the context of the model. On this basis, optimum velocity is given by

$$V_{\mathrm{opt}} = \frac{a}{2c}\pi$$

and

$$G = \frac{a^2}{4c} L^\beta \pi^2 - QL^2$$

so long as G is less than the maximum rate.

From the form of this equation for G, the optimum growth rate, the actual velocity V_{opt} need not be known. Also the two constants, a, c can be replaced by one, $E = a^2/2c$.

For limiting food (π small, $G < G_{\max}$) the efficiency of growth is defined as

$$\frac{\text{growth}}{\text{assimilation}} = \tfrac{1}{2} - QL^{2-\beta}/E\pi^2.$$

If $\beta < 2$ then efficiency will decrease with increasing size but will be constant for $\beta = 2$. Since standard metabolism is generally a minor fraction of total metabolism for small active poikilotherms this effect may not be marked.

From the preceding equations it will be seen that the optimum velocity is proportional to available food. The energy expended on overcoming drag is always exactly half the energy assimilated, and the rate of assimilation,

$$A_S = EL^\beta\pi^2 \quad \text{for} \quad \pi < \left[\frac{2(G_{\max}+Q)}{EL^{\beta-2}}\right]^{\frac{1}{2}}.$$

To maintain this relation the animal responds to a decrease in food concentration by decreasing the rate of flow through the filtering appendages. It should be pointed out that this velocity V_e is different from the swimming speed of the animal, which can also move through the water without filtering and with a relatively low drag (Vlymen 1970).

It is assumed that there is some maximum growth rate probably dependent on rate of digestion (Lehman 1976). A further assumption is that this rate is proportional to L^2 rather than L^3 (Lam & Frost 1976). This choice is based on the growth of *Calanus* in the laboratory (Paffenhöfer 1971). When food is plentiful, the copepod can then reduce V_e so that it takes only enough food to maintain maximum growth

$$G_{\max}L^2 = aL^\beta V_e\pi - cL^\beta V_e^2 - QL^2.$$

The rate of assimilation is then

$$A_S = E\pi^2L^\beta\left(1-\left\{1-\frac{2(G_{\max}+Q)}{E\pi^2L^{\beta-2}}\right\}^{\frac{1}{2}}\right),$$

when
$$\pi > \frac{(2G_{\max}+Q)^{\frac{1}{2}}}{EL^{\beta-2}} = \pi_c.$$

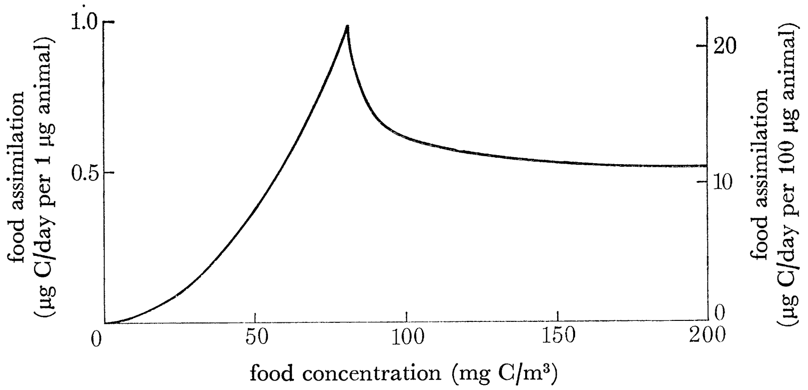

FIGURE 15. Rates of food assimilation as a function of optimum food concentration.

These relations define the metabolism of any copepod as a function of its size and available food which, in turn, is a function of cell diameter. The relation of assimilation A_S to available food π (figure 15) has a highly unrealistic cusp at π_c. This formulation is modified and simplified from that of Lam & Frost (1976). To eliminate the cusp these authors introduced a maximum assimilation rate. This has not been done here: partly because of the difficulty in determining this rate which, experimentally, is very dependent on the physiological condition of the animals (Frost 1972) and partly because this formulation simplifies the theory and keeps the number of constants to a minimum. Apart from the standard rate, Q, there are only two such constants $G_{\max}$ and E. For a particular environment $G_{\max}$ can be determined from the minimum period required for an animal to complete its growth phase; we use 30 days for *Calanus* in Scottish waters. Given $G_{\max}$, Q and a choice of β, then E can be determined from the relation for π_c. For the particular cell size which is optimal for selection by a copepod, $S_e = 1$ and $\pi = P$, the carbon concentration of the plant population. Thus π_c is the minimum carbon concentration which permits maximum animal growth to take place. We have used a value of 80 mg C/m³.

If size of cells for a particular animal were suboptimal, then the carbon concentration for maximum growth would be increased; thus for $S_e = 0.5$, $P = 160$ mg C/m³. From the point of view of the phytoplankton, there would be less grazing pressure on these cells and so a potentially larger population would be possible. This emphasizes the critical rôle of the selection curve S_e in determining the interactions between phytoplankton and herbivores and so the population structure for each.

The most significant feature of assimilation as a function of food (figure 15) is that, for low π, the rate increases more rapidly than π. It has been shown (Steele 1974*a*; Oaten & Murdoch 1975) that this condition is necessary for population stability in very simple prey–predator theories although it is not a necessity for more complex descriptions of this process (Evans 1977; Steele 1976). This functional response at low food concentrations is similar in form to the 'S-shaped' curves of Holling (1965) although derived quite differently. In earlier theories of planktonic herbivore grazing (Steele 1974*a*) a threshold food concentration, below which grazing ceased, was used to produce the same type of effect. The evidence for this has been questioned (Frost 1975) and so the present formulation provides a sounder basis for this functional response.

(*n*) *Reproduction*

So far only growth of copepods has been considered, between some initial and final masses which define the species. When the final mass is attained we assume the animal remains at this mass and all excess of assimilated food over metabolic requirement goes to the formation of eggs. The mass (as carbon) of eggs is the same as that which would have gone to growth. During the period of development from the egg to the start of feeding at naupliar stage 3 (8 days in the model) the offspring are subject to metabolic losses and predation.

Again this is a simplified picture since some copepods, such as *Calanus* spp., release the eggs to the water whereas others, such as *Pseudocalanus* spp., carry the eggs in a sac and only release them as nauplii.

(*o*) *Predation*

Predators on the copepods, in reality, will consist of numerous species each of which will interact with the numbers and size distribution of their prey. Thus, the representation of this prey–predator relation should be, in principle, similar to that used for the plant-herbivore system. Since it has been decided to close the system at this level, it is necessary to simplify the interactions as far as possible. This implies that we make the predator system largely independent of the prey, giving it predefined characteristics.

There are three features (out of many) which need to be considered. (*a*) Different types of predators are likely to have preferences for certain sizes of prey. (*b*) The numbers of predators can depend on the total numbers (or biomass) of prey available. (*c*) The numbers of predators will change with time. Each of these features will be interactive but here must be considered as partially or wholly independent.

(*a*) As with copepods themselves, it may be assumed that any individual predator will have an optimum size of prey. For invertebrate predators, Reeve & Walter (1972) have demonstrated that *Sagitta hispida* have an optimum food particle size which increases as *Sagitta* grows. For the largest *Sagitta* used in their experiments, the preferred food particle appeared to be relatively small (equal fractions of the nauplii and copepodids of *Acartia tonsa*). From stomach contents of the larger *Sagitta elegans* collected in the North Sea Rakusa-Suszczewski (1969) showed that the size of food increased with size of *Sagitta* ranging from *Oithona* spp. to *Calanus* *finmarchicus*. Ctenophores which capture their prey with mucous nets may be expected to be much less selective in their mode of feeding (J. C. Gamble, personal communication), but the escape ability of the prey from the mucous nets and tentacles may increase with prey size. Thus invertebrate predation might be expected to decrease with increasing size of the prey.

Predation by fish will cover the whole size range of herbivores. Fish larvae immediately after hatching are known to need small food items such as copepod eggs and nauplii (Jones 1973). On the other hand, mature herring prefer the largest copepods (Hardy 1924) and their growth rate decreases with decreasing abundance of *Calanus* (Steele 1965). On this basis, it is reasonable to assume that predation pressure from fish may tend to increase with size of copepod.

There may be also temporal differences in the predation pattern. For example, in the North Sea there is evidence (Steele 1974*b*) that predation by fish may occur predominantly in the spring and early summer, with invertebrate predation replacing the fish in late summer and autumn.

As the simplest assumption, we shall take a predation rate independent of the masses of the copepods and so dependent only on numbers

$$\mathrm{d}Z/\mathrm{d}t = -aZ \quad (a \text{ is an arbitrary positive constant}), \tag{1}$$

where Z is population density of a cohort of copepods of mean mass m. This appears unbiased since it is independent of the mass of the copepod. However, the impact of predation on biomass of the cohort depends on both the growth rate and predation rate. For a given cohort with biomass $B_{\mathrm{s}} = Zm$

$$\frac{\mathrm{d}B_{\mathrm{s}}}{\mathrm{d}t} = Z\frac{\mathrm{d}m}{\mathrm{d}t} + m\frac{\mathrm{d}Z}{\mathrm{d}t},$$

$$\frac{1}{B_{\mathrm{s}}}\frac{\mathrm{d}B_{\mathrm{s}}}{\mathrm{d}t} = \frac{1}{m}\frac{\mathrm{d}m}{\mathrm{d}t} + \frac{1}{Z}\frac{\mathrm{d}Z}{\mathrm{d}t}.$$

If we assume here that growth rate into the adult size category is proportional to $m^{\frac{2}{3}}$ (i.e. $= bm^{\frac{2}{3}}$) then, for B_{s} representing the adult population

$$(1/B_{\mathrm{s}})\,(\mathrm{d}B_{\mathrm{s}}/\mathrm{d}t) = bm^{-\frac{1}{3}} - a$$

and $(1/B_{\mathrm{s}})\,(\mathrm{d}B_{\mathrm{s}}/\mathrm{d}t)$ will decrease with increasing m and be negative for sufficiently large m or small b. This will tend to give a bias against those animals which have a larger final size.

On the other hand, if we make predation take the form

$$\mathrm{d}Z/\mathrm{d}t = -am^{-\frac{1}{3}}Z, \tag{2}$$

then the proportional change in biomass of adults is $(b-a)m^{-\frac{1}{3}}$.

This still decreases with increasing m, but a positive or negative value will depend on changes in b only (i.e. on availability of food for the particular size of copepod) rather than on the size of the copepod. Relation (2) can be regarded as the pattern which might be associated with predation by small invertebrates. On the other hand (1) is a pattern biased against the larger copepod species and could be more appropriate for fish. Both will be used in the simulation.

(*b*) Formulations (1) and (2) are derived for fixed (or steady-state) populations of predators. In the nature of the interaction one would expect numbers of predators to fluctuate in a manner dependent on both prey numbers and their size. In particular, such a relation is integrative, in the sense that numbers of predators at any time depends on the past history of the prey population. To simulate this, however, would require a complete description of the interactions.

The problem may be partially simplified by considering first an instantaneous relation and later a temporal sequence independent of prey numbers. The former can be considered as a functional response and the latter a numerical response (Holling 1965). It has been stressed elsewhere (Steele 1976; Steele & Mullin 1977) that, in a simple 'biomass' type of model, the assumptions about changes in predator numbers as a function of prey numbers may be of critical importance to the ability of the model to reach a reasonable steady state after an initial perturbation (such as a spring outburst). Graphically, this depends on whether predation is assumed to increase faster or slower than B_s. The former relation will make the system more stable but the latter may destabilize it. A slightly simplified and more extreme form is used here, exp $(Z_0 B_s)$, where the predation term for (1) would be

$$m\,\mathrm{d}Z/\mathrm{d}t = aB_s \exp{(Z_0 B_s)}.$$

With $Z_0 > 0$ this will give an increasing curve; with $Z_0 < 0$, there will be a maximum value for $m\,\mathrm{d}Z/\mathrm{d}t$ at $B_s = a/Z_0$. This could correspond to the concept of a predetermined predator population.

(*c*) Lastly, the population of predators will change with time as a consequence of its own population dynamics as well as of its food intake. This is most likely to be significant during the spring when, initially, predators, like the other populations, will be at a low level. For the overwintering copepods to have survived until the spring it is necessary to assume that predation has been negligible. Thus, at the start of the spring outburst one could take predator populations as effectively zero. This is likely to be so for the invertebrate predators, but for fish it will not be true as regards numbers. However, for the pelagic migratory fish the alternative assumption, that they do not move into the feeding area until their food supply has begun to grow, provides a similar effect – that predator populations will increase in number during the spring. There is some evidence of this for North Sea herring and a similar assumption is used for the Peruvian anchovy (Walsh 1976).

A formulation for this:

$$T^2/(T_0^2+T^2)$$

will give a predation rate increasing with time T_s and the 50 % increase occurring at $T = T_0$.

These forms of predation give a general formulation

$$\frac{1}{Z}\frac{\mathrm{d}Z}{\mathrm{d}t} = -(H+H_* m^{-u})\,\mathrm{e}^{Z_0 B_s}\,T^2/(T_0^2+T^2).$$

The standard run (figure 17), to be described in detail later, includes terms for a functional and numerical response (figure 16*a*, *b*). The herbivore biomass without these terms (figure 16*c*) has some initial quantitative differences but the results converge at later times. The introduction of the extra terms eliminates the unnatural drop in biomass at the start of the run, so that a smaller and thus more realistic initial value can be used. It also permits a more rapid population increase which is more in line with some field observations in early spring in the North Sea (Steele & Henderson 1977). It is for this reason that the extra terms are included in the simulations.

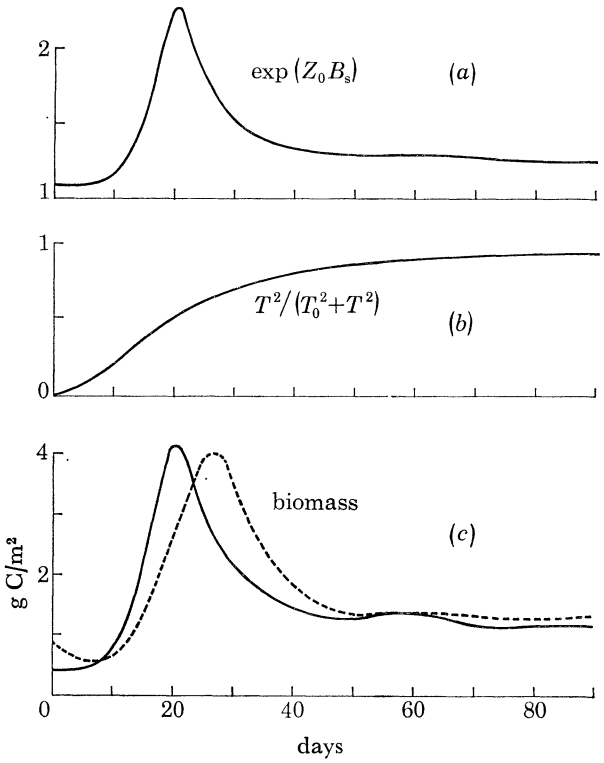

Figure 16. The changes in predation rate used in the model, (*a*) as a function of herbivore biomass and (*b*) as a function of time. (*c*) —— gives the total biomass of herbivores using the responses (*a*) and (*b*); - - - gives the biomass with $Z_0 = 0$, $T_0 = 0$.

(*p*) *Summary of the theory*

This completes the review of the processes used to describe the nutrient–plant–herbivore–carnivore dynamics and interactions. For each component there are not only a considerable number of coefficients to be determined, but numerous alternative functional responses. For each trophic level a large number of simplifying assumptions have been made and several functional relations predetermined. For each level, however, a choice between two responses has been left in. These choices are intended to exemplify the possible range of responses.

For phytoplankton the relation of respiration rate to cell size appears critical, so two functional forms are included D^{-1}, $D^{-\frac{1}{3}}$. The former gives a dome-shaped relation of population growth to cell size; the latter a much flatter response. It is possible that the latter is nearer the truth and it will be used as the basic postulate with the former as an alternative. For grazing by copepods there are two critical factors, the relation of grazing potential to size of animal, as L or L^2; and the shape of the selection curve in relation to the structure of the filtering appendages. These have been combined into a choice between two strategies which could be termed L^2 or L. The former is used as a first choice for the, perhaps arbitrary, reason that, in the growth equation, all terms are proportional to L^2.

The third factor, predation, will be considered as either constant over all sizes of copepod; or decreasing as $m^{-\frac{1}{3}}$. Since fish may be the most important predators during the spring outburst, the former is used as the basic formulation.

It will be apparent that there is some degree of imprecision in all the formulae derived here and this must be borne in mind when the results of the model are being interpreted.

Computer simulation†

The computer simulation is merely a technique for calculating, for particular values of the coefficients, the consequences of the assumptions derived in the preceding section. The outline of the simulation is given to indicate the general processes and the form used to present the results. Copies of the computer program have been deposited in the archives of the Royal Society and the British Library, Lending Division.†

It is necessary to divide the phytoplankton into discrete groups with diameters

$$D(I+1) = 2^{\frac{1}{3}}D(I).$$

This division corresponds to the categories used in the particle counters. For each group there will be a phytoplankton population $P(I)$ defined as the carbon content (mg C/m^2) of phytoplankton with diameter $D(I)$. This differs from the presentation by the particle counters which is in terms of cell volume. As discussed earlier the carbon:volume ratio decreases approximately as $D^{-0.8}$ (Strathmann 1967) so that cell volumes would give a representation biased to the larger cells. Twenty categories are used for $P(I)$ but the smallest, $P(I) = 2$ μm, is reserved for 'bacteria'. The overall level of phytoplankton abundance will be presented as chlorophyll concentration (mg/m^3).

Similarly for mass of a copepod, twenty separate categories are used with

$$m(J+1) = m(J)+m(J)^{\frac{2}{3}}.$$

This is derived from the assumption that maximum growth is proportional to $m^{\frac{2}{3}}$. A particular species is defined by an initial and maximum mass category. Three 'species' are used in the model. *Calanus* sp. is defined as having initial and final masses of 0.32 μg C and 106 μg C. *Pseudocalanus* sp. has 0.10 and 12 μg C respectively. These are the two main species which will be considered. For a third species, *Oithona*, very little is known about its feeding behaviour and metabolic rates but it will be included for certain runs with masses of 0.1 and 1.6 μg C. For simplicity the eggs are assumed to have the same mass as the first feeding naupliar stage, and metabolic loss during development to the feeding stage is accounted for as loss of numbers.

Because of the division of the copepods into discrete size classes, growth is considered as a transfer from one class to the next. If, during some time interval ΔT, an animal in category J would have increased its mass by $\Delta m(J)$ then a fraction

$$F(J) = \Delta m(J)/(m(J+1)-m(J)) = \Delta m(J)/m(J)^{\frac{2}{3}} \tag{3}$$

of the population will be transferred into $m(J+1)$. This is a necessary artificiality but it will have a tendency to smear out population size distribution since, potentially, an animal entering a size category at time T could leave at time $T+\Delta T$. Because of the assumption that all three species will have the same feeding and metabolic rates when they are the same mass, this relation (3) applies to all three species. Further, from the assumption that maximum growth is proportional to $m^{\frac{2}{3}}$, $F(J)$ will have $G_{\max}$ as its maximum value; otherwise it will fall below this depending on the size and concentration of cells present. For this reason $F(J)$ is a useful indicator of the effect that the phytoplankton size structure has on growth of animals of different sizes. It will display the consequences of the choice of selection curve, and will be

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† Copies of the computer program may be purchased from the British Library, Lending Division, Boston Spa, Wetherby, West Yorkshire LS23 7BQ, U.K. (reference SUP 100 23).

used in the presentation of results. The numbers of the three species in a mass category is $Z(K, J)$ with $K = 1$–3. Again, the assumption that predation is dependent only on size of copepod means that the rates apply equally to all three species. For each species total biomass (as g carbon/m²) in the euphotic zone can be calculated as

$$B_s = z_e(\sum_J Z(K, J)\, m(J)),$$

and this will be presented as a summary of the course of development of each species. The population structure of *Calanus* and *Pseudocalanus* will be given as percentage composition of stages with the relation of mass to stage derived from Marshall (1949) and Marshall & Orr (1955).

The flow diagram (figure 5), summarizes the main processes used within this system. The governing equations can be expressed as

$$\begin{aligned} \Delta N/\Delta T &= -\sum_I \text{nutrient uptake by } P(I) + \sum_J \text{nutrient excreted by zooplankton} \\ &\quad + \text{nutrient mixed into upper layer}, \\ \Delta P(I)/\Delta T &= \text{particulate production by } P(I) - \sum_J \text{grazing by zooplankton} \\ &\quad - \text{sinking of } P(I) - \text{mixing out of } P(I), \\ \Delta Z(K,J)/\Delta T &= \text{recruitment from } Z(K, J-1) - \text{loss to } Z(K, J+1) - \text{predation}. \end{aligned}$$

RESULTS

The output from the computer simulation will be presented in three sections. The first will discuss the main effects of the different formulations, indicating the general nature of the conclusions. The second will demonstrate the comparison with the Loch Striven data. The third will discuss the implications for other areas and problems, and consider the limitations implicit in the present simulation.

By their nature, simulation techniques lack the generality of mathematical solutions and, for any run, show the response for one particular choice of numerical values for the parameters. There are 25 parameters which define the functional responses and 45 numbers to define the initial concentrations of nutrient, plants and herbivores. The possible runs are effectively unlimited in number and a choice must be made for a large proportion of these. The choice made here is to consider an open sea environment with relatively high concentration of deep water nitrate (10 mmol/m³), a deep mixed layer (40 m) and a fairly high rate of mixing (2 % exchange per day). Over a period of 100 days in spring this generates a primary production of about 100 gC/m²). The reason for this choice is that we know that a well stratified upper layer will develop considerable vertical structure of nutrients and plants, thus contradicting the simplifying hypotheses made about the physical and biological environment. The probable effects of this will be considered in the last section. For many of the other parameters the basis for choosing a single value has been discussed earlier and these are summarized in the appendix.

A further choice concerns the time of year to be simulated. The greatest changes occur during the spring and we start the runs at the point where a separate upper mixed layer has recently formed; primary production is beginning; the overwintering copepods of the two species *Calanus* and *Pseudocalanus* have gone into the adult stages and will start reproduction when food is available; and the predator populations are very low. The initial numbers of each herbivore species are chosen so that each population has approximately the same rate of growth, and initial herbivore biomass is about 0.4 g C/m^2. Phytoplankton carbon is assumed to be evenly distributed among the size classes with 5 μg C/m^3 in each class giving 100 μg C total.

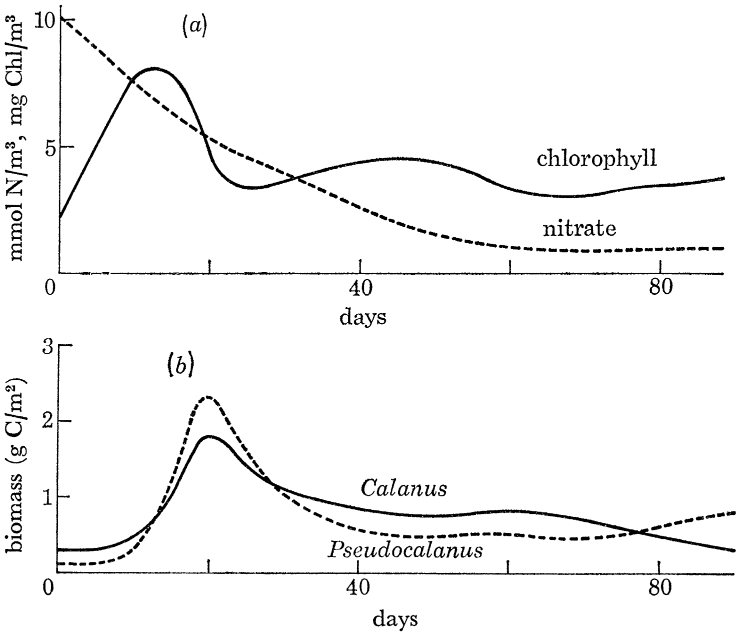

Figure 17. (*a*) The basic run with changes in time of nitrate and chlorophyll. (*b*) The basic run with changes in time of biomass (g C/m^2) of *Calanus* and *Pseudocalanus*.

For the basic run (figures 17–19) we have chosen (i) $D^{-\frac{1}{3}}$ for phytoplankton respiration; (ii) the L^2 relation for grazing and growth of herbivores; (iii) no mass dependence of predation. The output is presented in the usual form (figure 17) of nutrient, chlorophyll and herbivore concentrations. From day 1 to about day 15 phytoplankton population growth depends mainly on their own dynamics. From about day 10 to day 20 the phytoplankton population is sufficiently large that zooplankton growth, for all size classes, is at a maximum. Thereafter plants and copepods interact significantly, not only in terms of overall population levels but, particularly, in terms of size composition. Comparing figure 9 with figure 18*a* it is apparent that the phytoplankton distribution is significantly altered by grazing. The earlier peak of larger cells could correspond to the diatom outburst in the spring: the later peak of very small cells has a diameter appropriate to the general group termed μ-flagellates. The effect of grazing, in this run, is to emphasize these two size categories. Further runs will deal with the factors determining the split into two separate sizes.

In turn the growth of the herbivores is very much determined by the phytoplankton distribution. The size distribution is presented as percentage of total numbers in various stages (figure 19). After the initial period of reproduction, the largest numbers are in the non-feeding stages (egg to nauplius 3) until the later part of the run when the copepodites become a significant proportion of the population. The reason for this can be seen (figure 18*b*) from the changes in G (growth rate/m^2). After the period of plentiful food for all sizes of animal

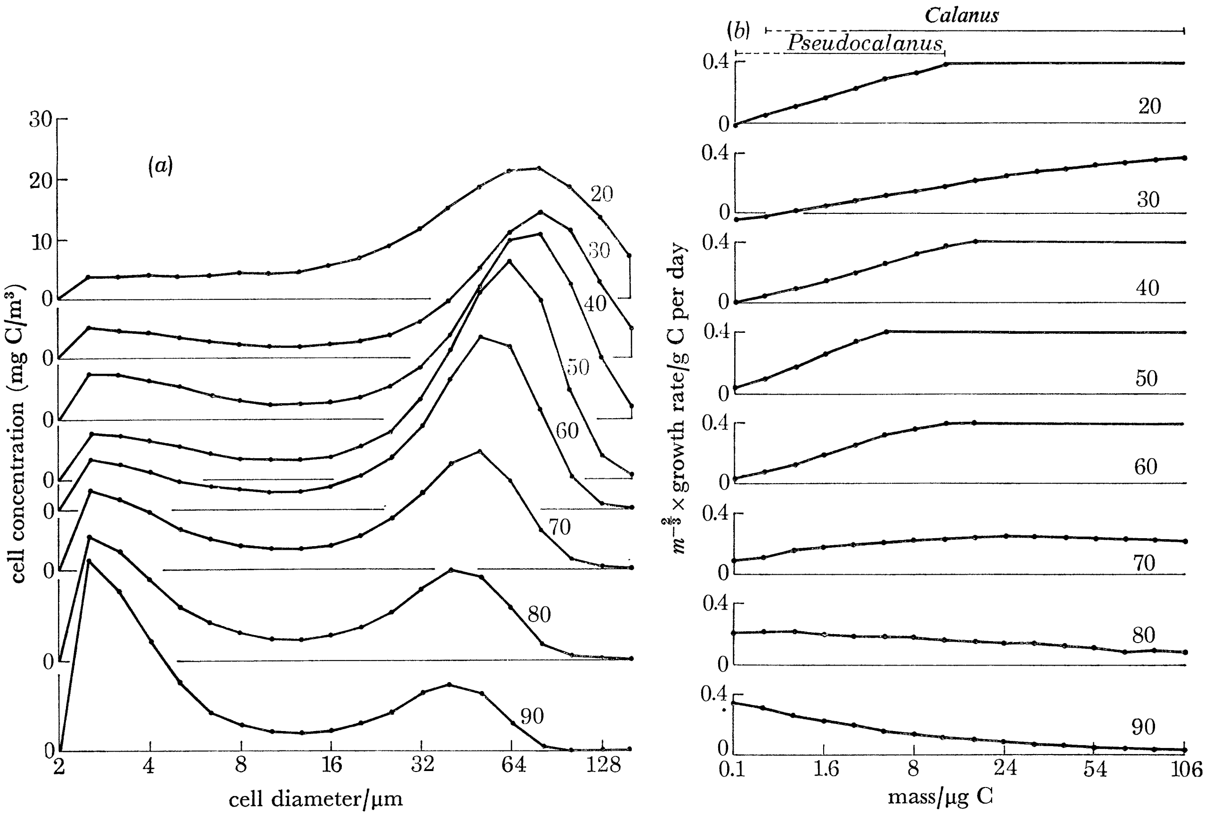

FIGURE 18. (*a*) Size composition of the phytoplankton from 20 to 90 days during the basic run (each point gives the concentration in that discrete size category). (*b*) Growth rate (g C/day) × $m^{-\frac{2}{3}}$ for each size category of herbivore on the same days.

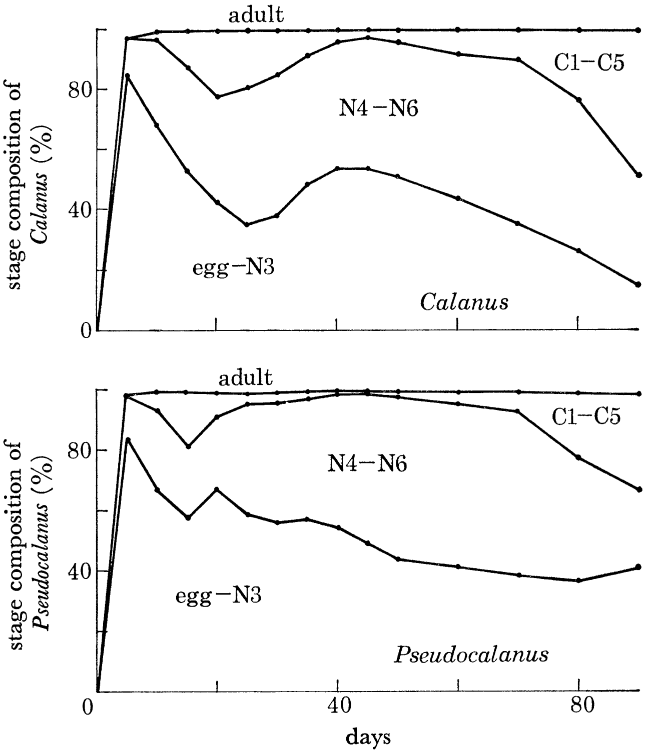

FIGURE 19. The percentage composition of *Calanus* and *Pseudocalanus* in the basic run.

($G = G_{\max} = 0.4$) food for the smallest size categories becomes limiting because the phytoplankton are dominated by large cells. Conversely food for reproduction by the adults is effectively unlimited until day 60. For these reasons, immediately after day 20, there is a large production of eggs – N3 which will have a very slow or, especially for *Pseudocalanus*, zero growth rate until day 70. Thereafter food for the adults becomes limiting, and is more limiting for *Calanus* than *Pseudocalanus*. These detailed features are peculiar to this run of the computer model but they illustrate the interactions of size distributions of phytoplankton and herbivores. Especially they point to the concept that limitation on a species is not on the population as a whole but on particular stages in the life cycles; and the critical stage can change depending on the size structure of the food supply. The effect of alternative formulations on this interaction will be considered in subsequent runs.

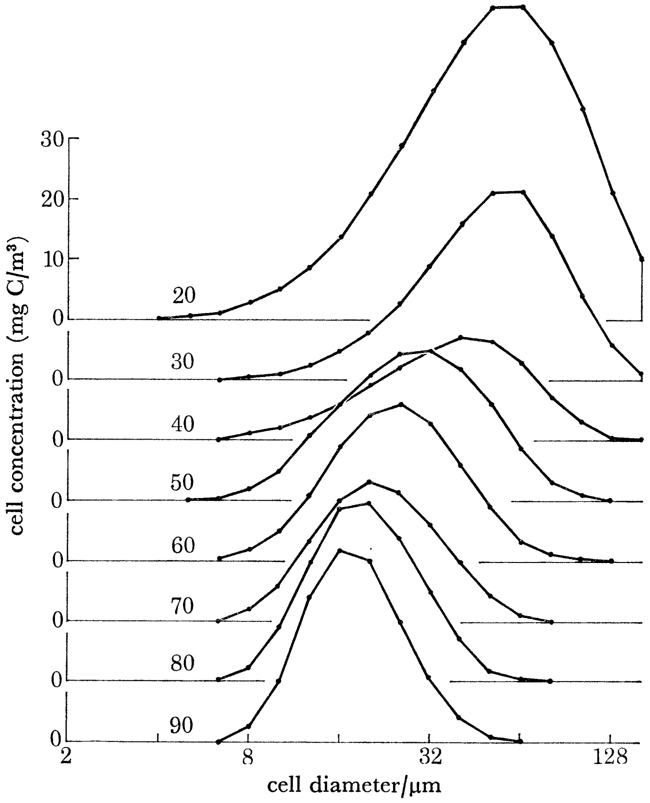

FIGURE 20. Phytoplankton size distribution from 20 to 90 days when $D^{-\frac{1}{3}}$ replaced by D^{-1} in the respiration term.

The marked effects of grazing on phytoplankton size structure depend on the use of the 'flat-topped' response ($D^{-\frac{1}{3}}$). When this is replaced by the dome-shaped phytoplankton growth (D^{-1}) in figure 10 the size structure is relatively uninfluenced by grazing (figure 20) but, because of the larger cells, *Calanus* predominates in the herbivore population. The growth response with D^{-1} in the respiration term can be used to indicate the effect of physical environment factors. If the depth of the mixed layer is halved (20 m) then the peak of the dome is shifted from 16 μm to 5 μm and, in consequence, after the spring outburst, *Pseudocalanus* predominates. Thus differences in the physical environment can affect the size distributions of plants and in consequence the populations of copepods. Similarly, a decrease in mixing rate by decreasing nutrient input and so nutrient concentration in the upper layer, will tend to produce populations with smaller cell size. This raises the question of whether physical factors such as mixed layer depth or vertical mixing rate are the predominant causes of changes in population structure as postulated, implicitly, by Laws (1975) who ignored grazing and considered only mixed layer depth, light and mixing rate as the predisposing factor. The main evidence against this arises from the experiments in deep plastic enclosures. The major effect of stress, whether caused by pollutants (Thomas *et al.* 1977) or grazing (Gamble *et al.* 1977) is to change the size composition of the phytoplankton, usually towards dominance by μ-flagellates (see figure 4). Since the physical environment in stressed and control enclosures will be the same, the changes must be due to chemical or ecological factors. For this reason, although physical factors obviously play a significant rôle, we shall concentrate on the effects of ecological interactions.

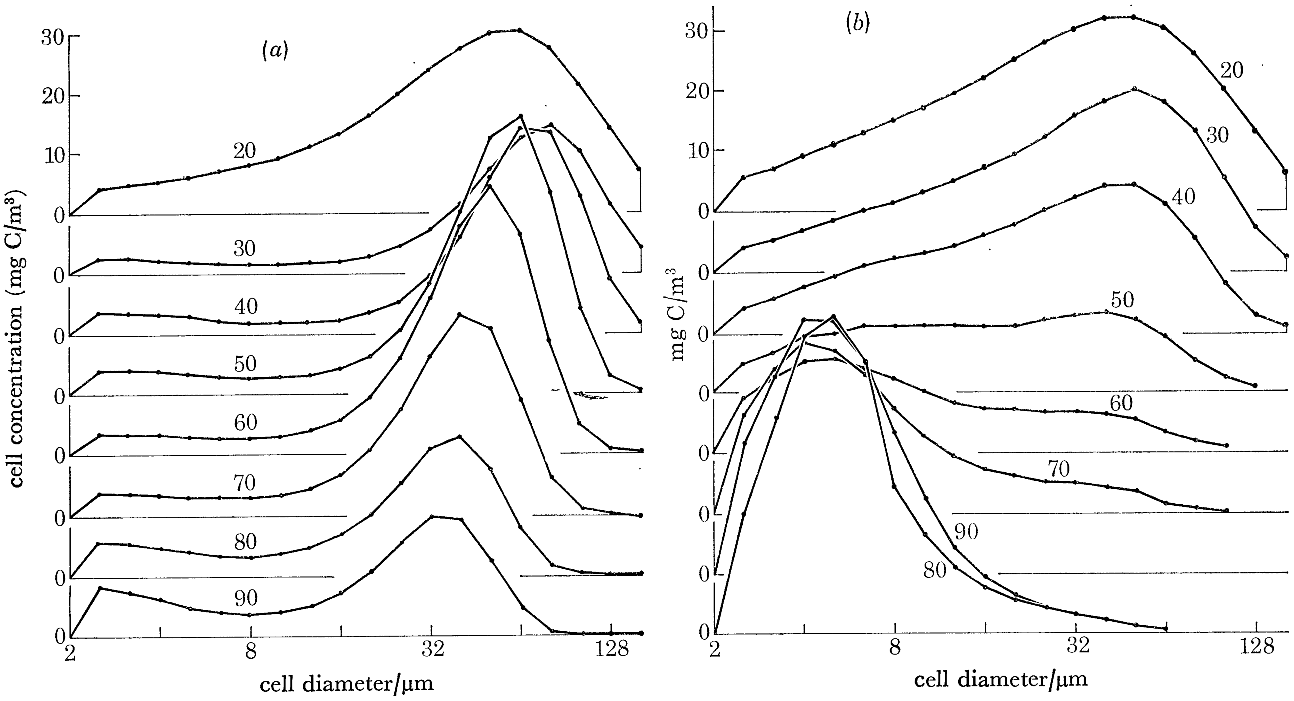

FIGURE 21. (*a*) Phytoplankton size distribution from 20 to 90 days when *Calanus* is omitted in the basic run. (*b*) Phytoplankton size distribution from 20 to 90 days when *Pseudocalanus* is omitted in the basic run.

From the basic run, one way to demonstrate the effects of grazing on the phytoplankton is to remove, in turn, *Calanus* and *Pseudocalanus* (figure 21). Removal of the large copepod produces an increase in large cells and vice versa. In the latter case (figure 21*b*) when *Pseudocalanus* is removed the effect is most extreme with a late and very large outburst of small cells, shown by the chlorophyll increase (figure 22*b*), and a decline in the *Calanus* population towards extinction at 100 days.

Thus, in the model, there is a balance between grazing and phytoplankton growth in terms of size structure. If this balance is upset a breakdown can result with total phytoplankton increasing and the herbivore population decreasing. This imbalance results, not from some general defect in feeding behaviour, but from a mis-match in sizes of the two components. For example, when *Pseudocalanus* is absent the phytoplankton gradually shifts, with declining nutrients and grazing by *Calanus*, toward small cells (figure 21*b*). These cells are not efficiently grazed by adult *Calanus* (figure 14*b*), so that food becomes limiting to adults, their reproductive rate declines, and so does population size. The available nutrients accumulate in the smallest cells and the stock of phytoplankton actually begins to increase again after nutrients have levelled off at a low concentration. This imbalance is not evident when *Calanus* is absent (figure 22*a*), though there is a striking shift in size composition of the phytoplankton toward larger cells (figure 21*a*). Thus the presence of a population of *Pseudocalanus* is essential for the survival of *Calanus* but not vice versa.

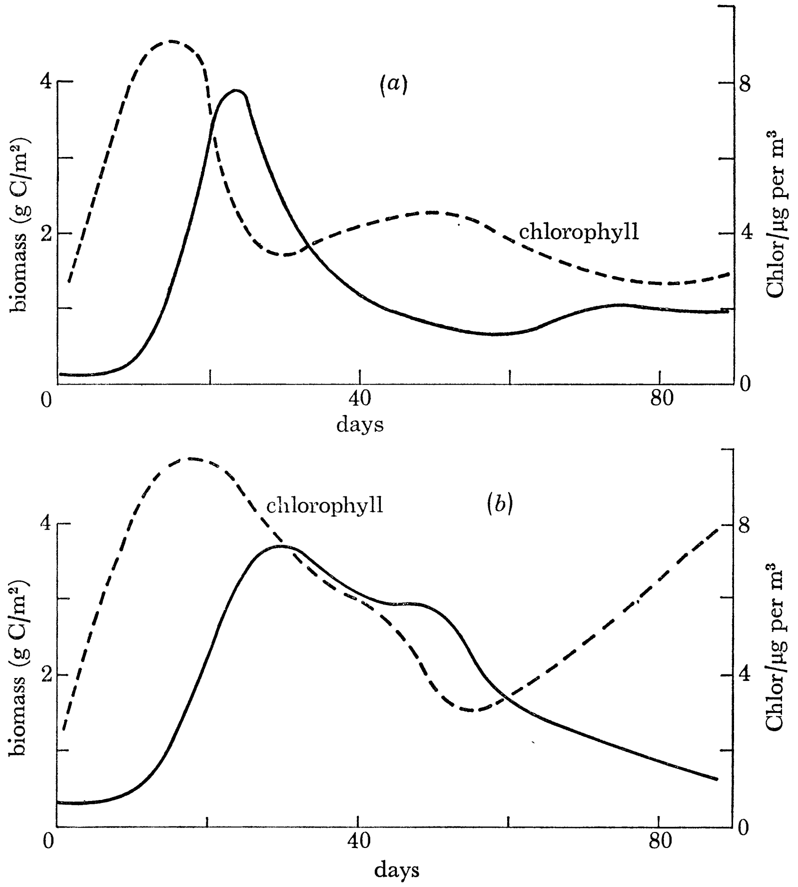

FIGURE 22. (*a*) Chlorophyll:herbivore changes with time when *Calanus* is omitted from the basic run. (*b*) Chlorophyll:herbivore changes with time when *Pseudocalanus* is omitted from the basic run.

These conclusions depend on the choice of values for a relatively large number of parameters. Especially relevant is μ ($= 2.5$) which defines the width of cell size selection in the feeding of the herbivores. Figure 14*b* shows the overlap between adults of the 'species' used here. If the value of μ is increased then the overlap becomes greater till, for large μ, there is effectively no size selection and the two herbivores would be competing for all the available food. An increase in μ (figure 23) removes the bimodal phytoplankton distribution (compare with figure 18*a*) but also produces a decline in *Calanus* after the spring outburst. If, with $\mu = 20$, the model is run with only *Calanus* present, then it does well (biomass at 90 days is 1.62 g C/m²). Thus its elimination in the presence of *Pseudocalanus* is the result of competition. Similar results were obtained in an earlier model (Steele 1974*b*). With a different grazing function, discrete cohort structure of the herbivores and a single phytoplankton food supply, *Calanus* performed well unless *Pseudocalanus* was introduced when *Calanus* was eliminated after the spring outburst.

These effects of changes of μ are in general agreement with the niche width concept (MacArthur 1970) where too great an overlap will eliminate some species. On this basis an increase in the size range of particles captured by *Calanus* does not help *Calanus* to survive over the whole season, if the smaller species have a similar increase. If, however, competition takes some other form, or if exclusion is determined by other factors such as temperature, then a *Calanus* with a wide range of food selection would survive where particle size is generally small.

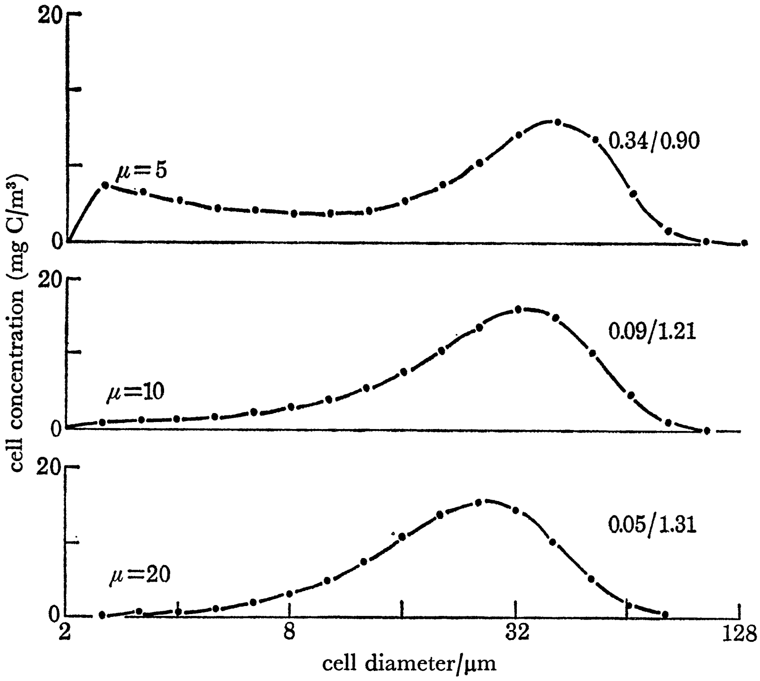

Figure 23. Simulations at 90 days with a range of selection curves for herbivore grazing (the ratios are biomass *Calanus/Pseudocalanus*).

These results correspond with the general features of plankton distribution in the North Pacific Ocean where the species *Calanus plumchrus* has the requisite fine filter (Frost unpublished) and where also *C. plumchrus* occurs as a dominant in the earlier part of the productive season and the smaller species only appear after *C. plumchrus* has stopped feeding and returned to deeper water.

From figure 23, for mixed populations to occur after the spring outburst, $\mu \leqslant 5.0$. Further, only for $\mu \leqslant 5.0$ do bimodal phytoplankton populations occur implying a link between the existence of mixed populations at both trophic levels. The value of $\mu = 2.5$ used in the other runs emphasizes the smaller phytoplankton peak but should not affect the general nature of the conclusions.

The removal of *Calanus* or *Pseudocalanus* is an extreme case but different forms of predation will tend to have this effect. Quantitative variation in predation may occur due to changes in the numbers of predators present, and this can be simulated by doubling and halving the coefficient (H) for the size-independent predation function (figure 24). This has marked effects on size composition of the phytoplankton and on the species composition of the herbivores. The elimination of *Calanus* by 90 days would be expected from the greater severity of this form of predation on larger copepods (see p. 508).

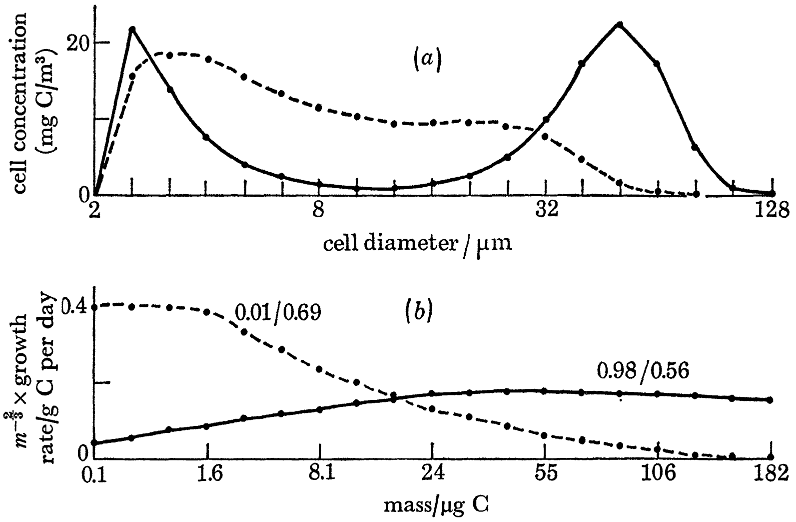

FIGURE 24. (*a*) Size composition at 90 days of phytoplankton with predation rate doubled (– – –) and halved (——). (*b*) Growth rates ($\times m^{-\frac{2}{3}}$) at 90 days of size categories of copepods for the two predation rates. The ratios (*Calanus*/*Pseudocalanus* biomass) indicate the effects on the herbivore populations.

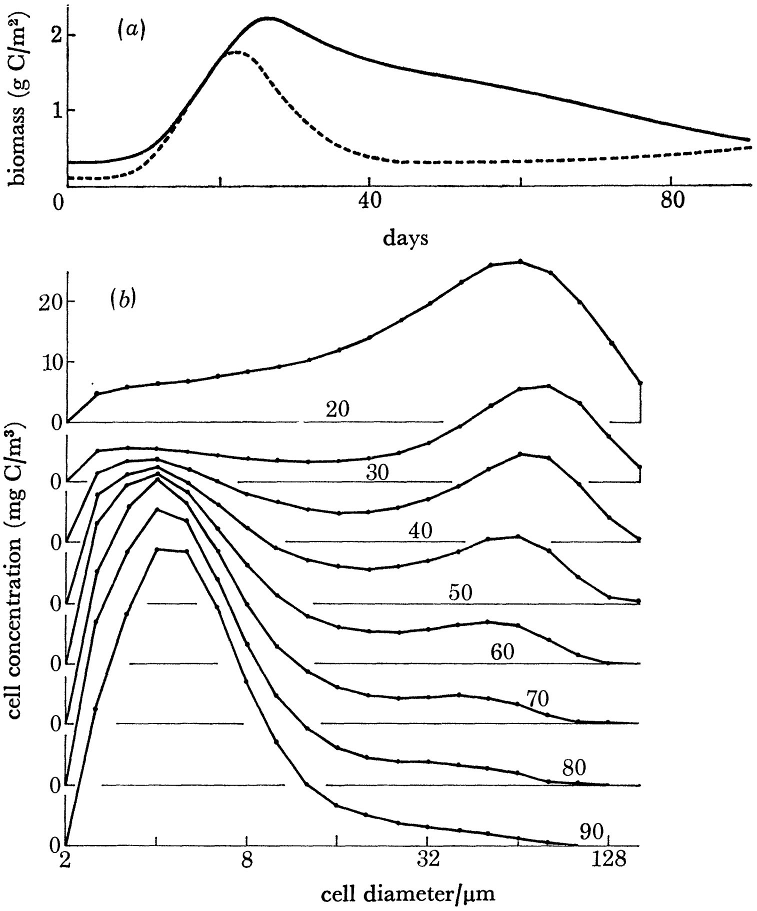

FIGURE 25. (*a*) Effect of using predation as a function of mass ($m^{-\frac{1}{3}}$), *Calanus* (——) and *Pseudocalanus* (– – –) biomass. (*b*) Effect of using predation as a function of mass ($m^{-\frac{1}{3}}$), phytoplankton size distribution 20–90 days.

There may be qualitative differences in predators and this can be simulated by changing to a predation rate dependent on mass as $m^{-\frac{1}{3}}$ instead of the mass independent relation used in figure 18. Then, as expected (figure 25) *Calanus* does rather better than in the basic run. Again, the pattern of cell sizes is altered towards that observed when *Pseudocalanus* was absent. Thus changes in predation pattern will produce marked changes in phytoplankton species composition. In this way not only are environmental stresses transferred up the food web, but quantitative and qualitative changes at higher trophic levels can be transferred downwards.

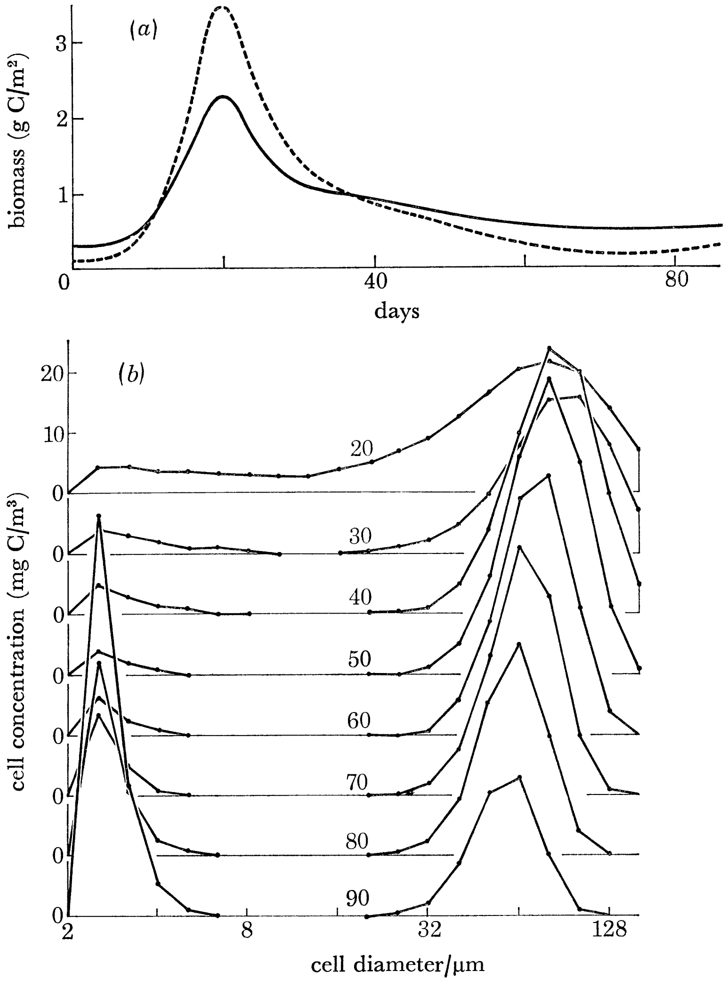

FIGURE 26. (*a*) The effect of replacing the *L* grazing relation by the $L^{\frac{1}{2}}$ form, *Calanus* (——) and *Pseudocalanus* (– – –) biomass. (*b*) The effect of replacing the *L* grazing relation by the $L^{\frac{1}{2}}$ form, phytoplankton size distribution 20–90 days.

Lastly, we can change the formulation of the grazing interaction using the $L^{\frac{1}{2}}$ rather than the *L* relation. This slightly alters the relative proportions of *Calanus* and *Pseudocalanus* (figure 26) and emphasizes the separation of the phytoplankton population into two distinct size groups, but the general pattern of development of plants and animals is not greatly dissimilar from the basic run.

These few examples use the main options for functional responses derived in the preceding sections. They demonstrate the main conclusions from numerous other runs: (1) that size structure plays a fundamental rôle in determining interactions between trophic levels; (2) that no single factor, phytoplankton photosynthesis, herbivore grazing or predation, by itself is predominant in determining these size structures and (3) that the effects of size dependence move both ways, up and down the trophic structure.

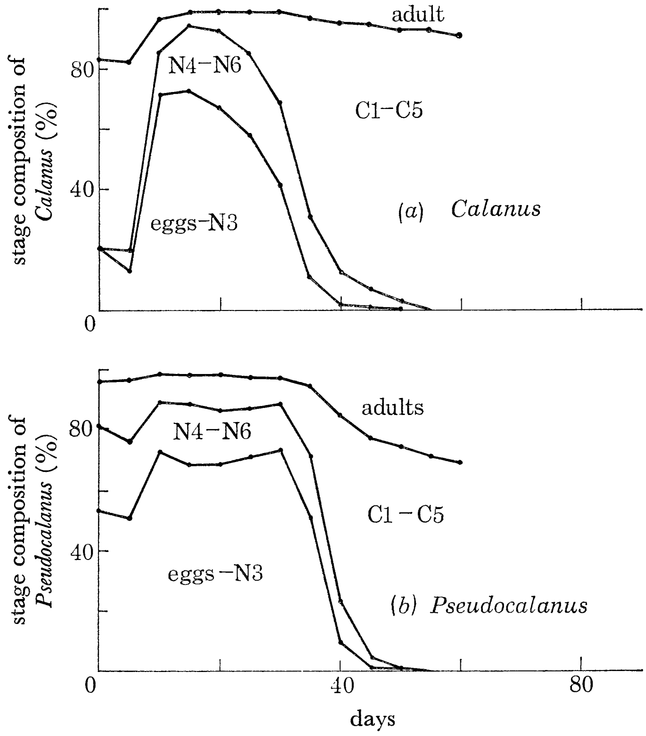

FIGURE 27. Percentage composition of herbivore grazers with initial conditions for the phytoplankton where small cells dominate (*a*) *Calanus*, (*b*) *Pseudocalanus*.

COMPARISON WITH OBSERVATIONS

A comparison of the stage composition of the herbivores in the basic run (figure 19) with the Loch Striven data (figure 2) shows some similarities and some differences. For *Calanus*, theory and observation both give the same marked change in composition at the start of an outburst but thereafter the theoretical bias to small stages is not seen in the observations. The generally smoother response of *Pseudocalanus*, in the data, is reflected in the model but again there are differences later in the relative abundance of small stages. Also the biomass in the model is larger and this probably reflects the highly eutrophic environment being simulated.

Because of the unavoidable paucity of data on the environment in these early observations it is difficult to determine appropriate values for some of the parameters. This permits too many degrees of freedom and so only two changes were made from the basic run. First, the initial age structure of the two copepods was changed to match that given in Marshall *et al.* (1934). This adjustment had negligible effect on the predicted age structures. Second, to decrease the production, the initial nutrient levels in both upper and lower layers were reduced to 5 mmolN/m^3; more important, the initial size composition of the phytoplankton was changed to give a dominance (in carbon units) of small cells. This corresponds to the observation (figure 1*c*) that before each outburst, flagellates are common. With these changes, a rather different structure appears (figures 27 and 28). There are three linked features; relatively small cells predominate; the growth rate of very small herbivores remains high at the end of the phytoplankton outburst in contrast to the standard run; the later dominance of small herbivore stages, observed in the standard run, disappears because of lack of reproduction by the adults.

For the first 30–50 days of this run, the output (figure 27) gives a better comparison with observation (figure 2) than did the standard run. Within this time limit, the model can be said to simulate closely the observations in terms of composition. This occurs without a very good correspondence between total numbers or biomass in theory and data.

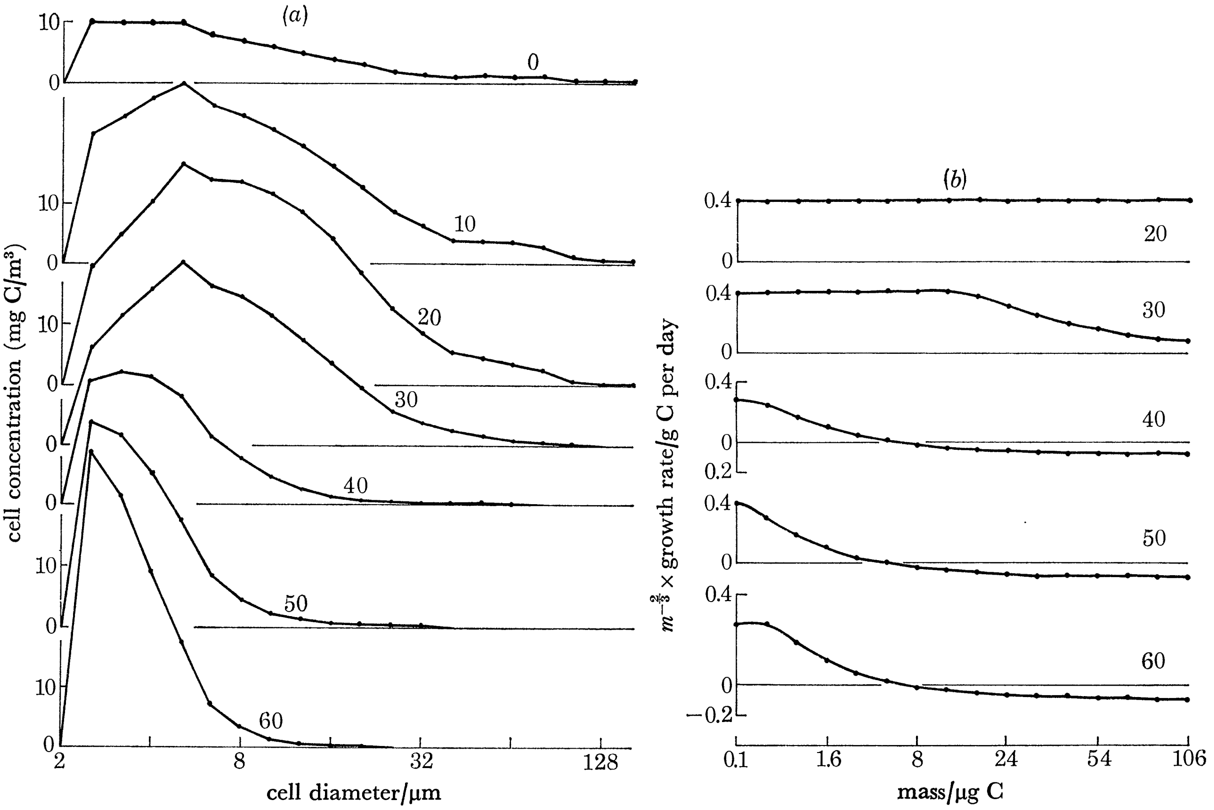

FIGURE 28. (*a*) The size composition of the phytoplankton for figure 27. (*b*) Growth rates of copepods.

After 40 days the model populations of both copepods tend toward zero, whereas the field populations do not. This may be attributed to deficiencies in the model which could be corrected by further manipulation of the parameters but it may also provide insight about the local environment in Loch Striven. The main deficiency in the model is that there is no thermocline layer with low light and intermediate nutrient concentration. After an outburst when surface nutrients are low, the chlorophyll maximum is found in this layer. From the derivation of sinking rate as a function of cell size and nutrient concentration one would expect to find larger cells aggregating in the thermocline region and this is borne out by some observations in Loch Striven (Marshall & Orr 1930) and elsewhere. Not only would this aggregation provide food for the larger copepods but, when more rapid mixing occurs, it could seed the upper layer with diatoms and nutrients so producing the next outburst of diatoms (see figure 1*c*).

Evidence for a diatom aggregation in the thermocline is sparse (Malone 1971) but theory would predict not only that this should occur but that it would be critical for the continued reproduction of *Calanus* populations in regions such as Loch Striven. The results given here imply that the successive growth periods of *Calanus* in Loch Striven will depend on recurrence of high mixing and Marshall & Orr (1927) propose that these successions may result from periods of strong northerly winds.

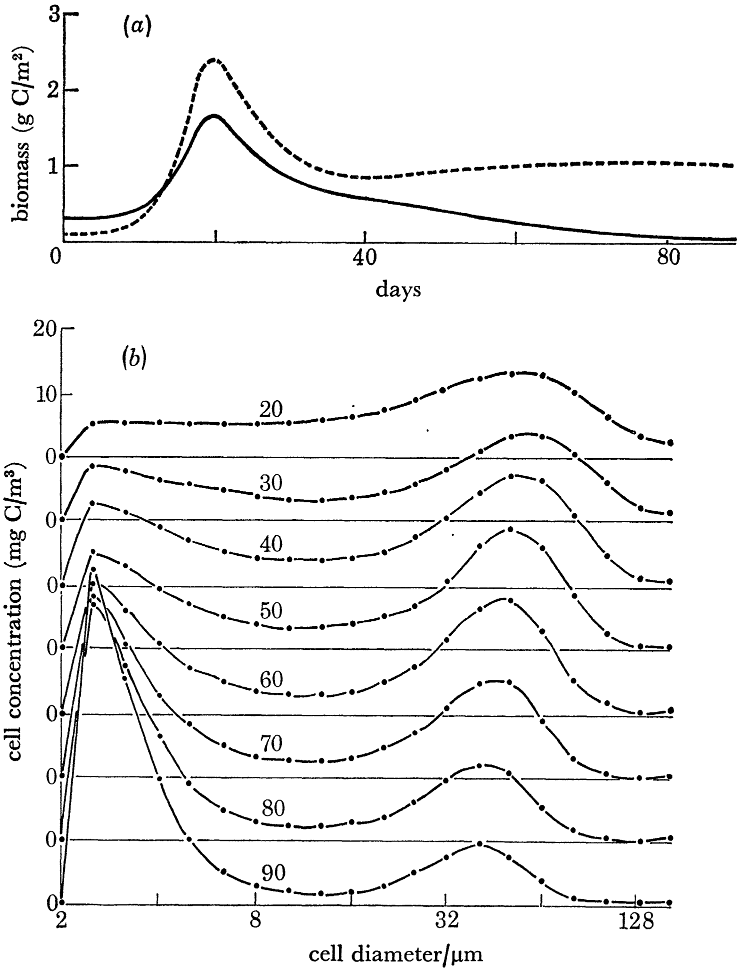

FIGURE 29. (*a*) Effect of increasing sinking rate and decreasing growth of larger cells (by increasing k_s) on *Calanus* (——) and *Pseudocalanus* (– – –) biomass. (*b*) Effect of increasing sinking rate and decreasing growth of larger cells (by increasing k_s) on phytoplankton size distribution over 20–90 days.

The Loch Striven simulations reveal one general problem with the theoretical development. If the rate at which nutrients are introduced to the mixed layer is decreased, by decreasing the mixing rate or the deep-water nutrient concentration, then the populations of *Calanus* and *Pseudocalanus* both tend to zero. In former theories (Steele 1974*b*), dealing with a single phytoplankton category, breakdown was prevented by the introduction of a threshold below which grazing on phytoplankton carbon as a whole was zero. This general effect has already been introduced here through the shape of the assimilation curve (figure 15). The difficulty here is not in the general level of phytoplankton abundance but the domination of the population by very small cells. This could be corrected if the 'dome-shaped' phytoplankton growth response were used. Given this response, the rate of mixing can be reduced to one-quarter of the normal level used here with the effect of accentuating the dominance of *Pseudocalanus* which can still act as a control on phytoplankton abundance. This solution to the problem in Loch Striven seems unacceptable for the same reason which suggested that the flat topped response was the more appropriate. Smaller cells in the range 2–5 μm are commonly found in oligotrophic conditions. Thus the resolution of this difficulty requires additional factors. The use of a broader selection curve, as proposed for '*C. plumchrus*', would permit animals of the size used here to feed effectively on the smallest cells but appears to prevent coexistence of different herbivore species. There is, however, a further factor which has been ignored so far; the existence of smaller species of copepod and other small species which may graze effectively on cells of less than 10 μm. We have restricted discussion so far to two species, partly for simplicity, partly because their feeding and metabolism are relatively well studied. In Loch Striven and nearly all other inshore areas smaller, cyclopoid, copepods, such as *Oithona* spp. are numerically dominant, and often about ten times as numerous as *Pseudocalanus*. Their maximum mass is approximately one-fifth to one-tenth that of *Pseudocalanus* but this will still make their food requirements comparable with, and sometimes greater than, that of the larger copepods. Their mode of feeding and even whether they are herbivorous or carnivorous, is ill-defined (Marshall 1949; Gauld 1966), but it is likely that they, or some of the many other small herbivores (including invertebrate larvae) extend the grazing range to cover the smallest cell sizes. Their existence in the plankton and their probable effect on controlling the smallest phytoplankton cell populations emphasizes the conclusion, derived for *Pseudocalanus*, on the interaction of grazing control by smaller and larger species. Pteropods which obtain their food by collecting particles on a mucous sheet (Morton 1954) may take a wider range of particle sizes than copepods. Although not generally dominant in the North Sea, the species *Limacina retroversa* can be very abundant at times, replacing copepods as the main grazer (J. A. Adams, personal communication). This fits in with the response expected for a grazer with a wide spectrum of food sizes.

For the Loch Ewe environment (figure 4 and p. 491), *Oithona* and *Pseudocalanus* are the dominant species with *Calanus* virtually absent. Thus the model developed here does not apply explicitly, but the general conclusions about the ability of predator variation to affect not only herbivore but also phytoplankton population structure, provide a general description of the effects observed experimentally (Gamble *et al.* 1977).

Alteration of the ecosystem

Although we are interested in naturally induced variations in the ecosystem there is a desire to understand how our own actions may alter it, and a hope that a theoretical approach can help in such understanding. For this reason we shall select variations in the parameters which may illustrate the possible responses to a variety of stresses.

For phytoplankton, the ability to take in nutrients from a very dilute solution is essential to their growth. A critical parameter is the half saturation coefficient, $k_s = \delta D$. In the theory developed here, an increase in δ will not only decrease growth of the larger cells but also increase sinking rate through its dependence on nutrients. Since this aspect of the uptake is assumed dependent on enzymatic action at the cell surface, it would appear sensitive to stresses such as metal or oil pollution which may affect cell surface conditions.

The effect (figure 29) of doubling δ ($= 0.03$) is, however, much less than might be deduced from the relations for cell dynamics by themselves (figure 8). There is some increase in small cells above that observed in the basic run but such an increase is, in part, balanced by an increase in *Pseudocalanus* relative to *Calanus*. Thus the effects of the change in cell dynamics are ameliorated by changes in the herbivores, emphasizing the conclusion that an understanding of the effects of stress on phytoplankton communities cannot be deduced from a study of the effects on phytoplankton species in isolation.

Another possible stress effect is the release of quantities of soluble organic matter by the phytoplankton. This effect, which occurs naturally (Fogg 1975) has been ignored so far. We assume that, under certain conditions, 10% of the photosynthesized material is released, with the same C/N ratio as other components of the system. These go into a soluble pool from which they are assimilated by bacteria with a cell diameter of 2 μm. In fact some of the main compounds released by the phytoplankton may contain little or no nitrogen (Fogg 1975) so that the bacteria must compete with the phytoplankton for the inorganic nitrogen. Also 2 μm may be closer to the upper limit of bacterial diameter, than to the mean. Thus this addition to the simulation is a very simplistic picture of the bacterial cycle. The effect of this contribution to the smallest particle size category (2 μm) is to increase the bias in favour of *Pseudocalanus* so that after 90 days the *Calanus* is only 70% of its value without bacteria. Otherwise the runs do not look very different.

Alternatively or additionally pollutants, or other factors, may affect the herbivores directly. Reeve, Gamble & Walter (1977) have shown from experiments that metal pollutants exert a greater stress on smaller animals than on larger ones. In particular this can affect grazing and reproduction. It is not possible to simulate this exactly in the model but the removal of *Pseudocalanus* (figure 21*b*) indicates the general nature of the consequences predicted by the model. After the outburst there is an accumulation of small cells giving another chlorophyll maximum with a consequent decline to extinction in *Calanus*.

(*a*) *Experimental enclosures*

Experiments with copper polluted enclosures (at 10 μg/l) were conducted at Saanich Inlet, Vancouver Island. In these enclosures, production rates are very high so that changes are accelerated. During spring when grazing has a limited effect on the phytoplankton there was a marked change within 10 days in size structure, with *Chaetoceros* spp. dominant in the controls but replaced by μ-flagellates in the polluted enclosures (Thomas & Seibert 1977). This implies direct effects of copper on the diatoms with no control on the μ-flagellates by grazing. In the autumn, with more herbivores, principally *Pseudocalanus*, there was a similar but less marked size change arising twenty days after addition of copper, with smaller cells in the treated enclosure compared with the control. Further, there was a marked decline in copepod numbers particularly *Pseudocalanus* but less so for *Calanus* (Gibson & Grice 1977). Lastly, at the end of the period there was an increase in chlorophyll in the treated enclosures compared with the control (Thomas *et al.* 1977). The general similarities between this sequence and those derived theoretically when grazing by smaller copepods is eliminated (figure 21*b*) suggests that, as well as direct impact of copper on the phytoplankton, effects on the smaller copepods may also determine phytoplankton population structure (Reeve *et al.* 1977).

The effects of copper on phytoplankton composition in the autumn were much less severe than in the spring. This may be, in part, because grazing by copepods, as suggested by figure 29, can modify the potential changes in phytoplankton species. In similar enclosure experiments in Loch Ewe, west Scotland, where herbivore populations were well established in the enclosures before copper was added, the effects were even less than in Saanich.

(*b*) *Changes in the North Sea*

The North Sea ecosystem has shown many changes in plankton population structure in the years 1960–70. Over the same period there have been significant changes in the physical environment (Dickson, Lamb, Malmberg & Colebrook 1975) and dramatic changes in the fisheries. The question raised is whether all these changes are interrelated and whether a sequence of cause and effect has occurred up or down the food chain.

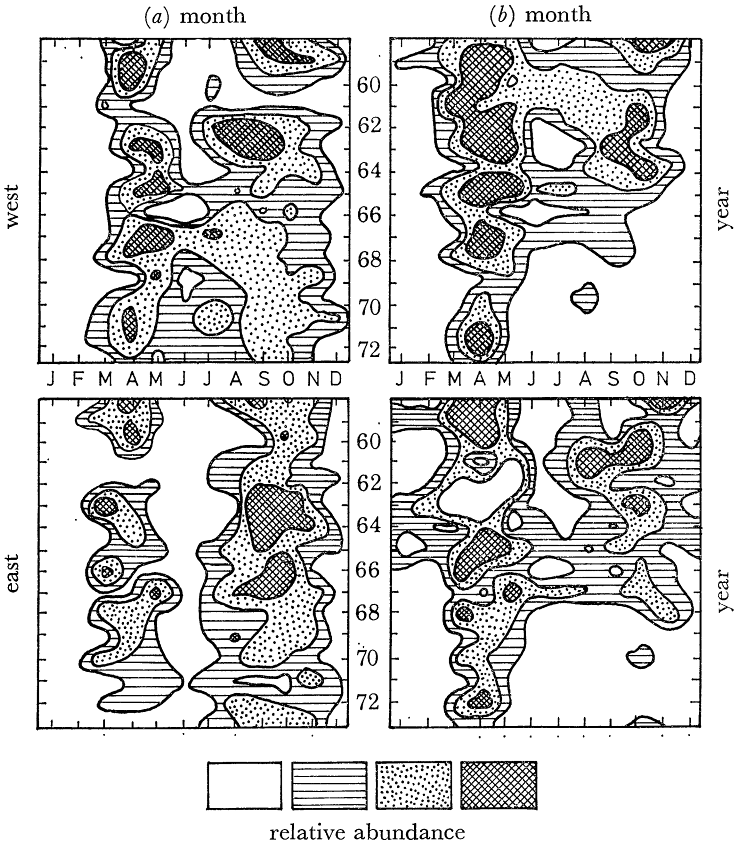

FIGURE 30. Continuous Plankton Recorder data on relative abundance of phytoplankton from eastern and western parts of the central North Sea (Reid 1977, see pp. 526–527). (*a*) Phytoplankton colour, indicative of small cells, (*b*) diatoms.

A major source of evidence comes from the Plankton Recorder (Hardy 1939) which samples with a 250 μm mesh, which was intended to simulate the filtering action of herring. It catches the larger zooplankton quantitatively (adult *Pseudocalanus* and copepodite stages of *Calanus*) but not the smaller species. It also catches larger diatoms, particularly chain forming species, and the colour (greenness) of the netting is noted as an indication of smaller phytoplankton whose mucous excretions cause them to adhere to the material of the net. An example of the data for the central North Sea (figure 30) shows the general sequence of a population of large diatoms in the spring followed by an apparently smaller cell size in summer (Reid 1977).

Further, there is a temporal trend over the 16 years with a decline in diatoms in late spring and early summer and some indication (from this and other areas) of an increase in the smaller cells.

The zooplankton shows a general decrease in numbers over the North Sea (Colebrook 1977) but for the central area this decrease is dominated by changes in *Pseudocalanus* rather than in *Calanus* (figure 31). Although we lack direct evidence for the smallest phytoplankton and zooplankton, these changes are consistent with results of the model in that a marked decline in *Pseudocalanus* would permit an increase in small cells with a reduction in large cells and, in turn, some effect on *Calanus* later each season. Any marked decrease in productivity, or environmental changes such as a shallowing of the mixed layer which would decrease phytoplankton cell size, would also tend to increase the smaller zooplankton at the expense of the larger species. Similarly an increase in phytoplankton cell size should favour the larger herbivores. This is in contradiction with the pattern recorded in the central North Sea. Thus, in the context of the model, explanations may be needed from within the trophic structure.

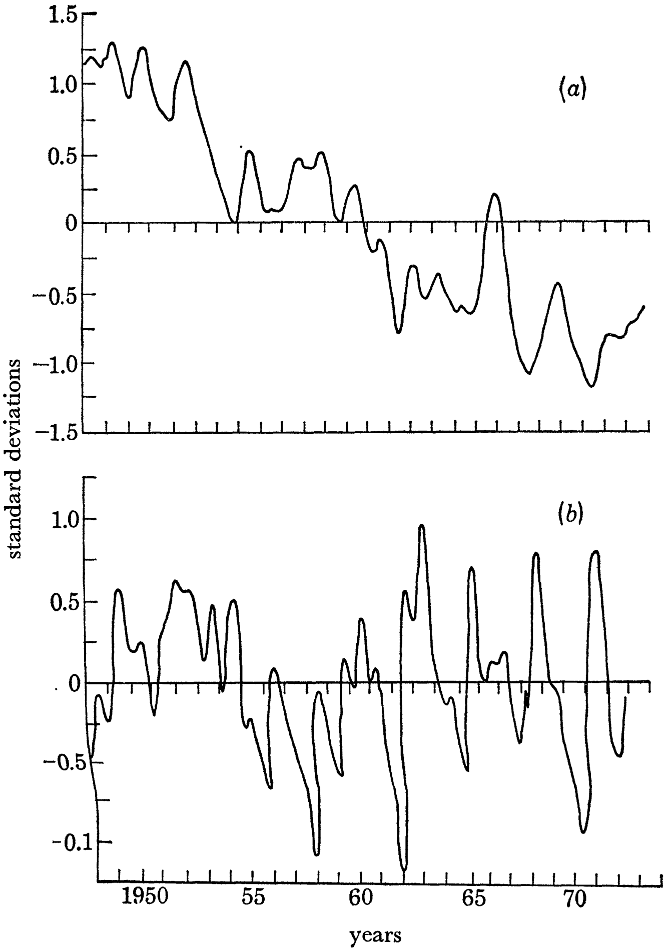

Figure 31. Continuous Plankton Recorder data on *Pseudocalanus* and *Calanus* (standard deviations from the annual mean) from the central North Sea (Colebrook 1977).

In general, we have shown that quantitative or qualitative changes in predation pattern will induce marked alterations in phytoplankton size composition. Within the theoretical framework, the observed changes could result from a relative change in predation pressure from the larger to the smaller copepods. Such a change could have occurred during 1960–70 as a result of the massive decline in herring stocks (Burd 1977). It would require, however, a concomitant increase in predation in the smaller copepods. From the same Plankton Recorder data (Colebrook 1977) there has been a general decline in Chaetognatha over the same period although it is not impossible that other invertebrate predators have increased.

There are, however, other changes which must be considered. During the same period, there have been large increases in demersal fish stocks arising from increased survival of the larvae and juveniles. These larvae, and possibly the juveniles, feed on planktonic crustacea during the spring outburst with the smallest larvae eating the smallest stages, followed by a progressive increase in size of food as the larvae grow (Jones 1973).

As stressed in earlier work (Steele 1965, 1974*b*) the commercial yield of fish from the North Sea appears to utilize fully the energy transferred through the food chain. In those calculations both phytoplankton and herbivorous zooplankton were considered as single units with the latter divided arbitrarily into two food sources, for fish and invertebrate predators respectively. It was noted that the fish appeared to predominate in the earlier, and invertebrates in the later part of the productive season. The reasons for this temporal sequence are more apparent from the theory used here. It also explains, qualitatively, how the two can change in importance after the spring outburst. In this way, in any year there could be a change in the balance of large vertebrate and small invertebrate predators. Because we are looking only at periods of 100 days it does not explain, directly, how year-to-year changes occur unless one assumes that there are longer-term changes in environmental events or predator structure, which influence the within-year pattern. This assumption underlies the interpretation of North Sea trends, suggested here.

In either case, this study of complementary chains within the food web emphasizes the fact that changes in commercial yield at the top of the web are more likely to result from changes in the structure of the web than from alterations in the total energy flow through it. For these reasons, the calculation of potential yields with altered distributions of fishing effort between species, will depend on some knowledge of the impact such changes have on the component of energy flow going to the smaller organisms.

These comments do not indicate a particular explanation of North Sea changes, but support the general conclusion that observed changes in ecosystem structure may be caused as much by changes at higher trophic levels as by environmental factors. Even more, it emphasizes that an understanding of events in a food chain, larger diatoms – *Calanus* – herring, requires a knowledge of changes occurring in the other components, flagellates – *Pseudocalanus/Oithona* – small invertebrate predators. The energy flow through the former is a direct function of that through the latter. In a field study of the pelagic food web in the Straits of Georgia, British Columbia, combined with feeding experiments, Parsons & Lebrasseur (1970) showed that juvenile salmon fed best off *Calanus plumchrus* and less well off *Pseudocalanus minutus*. On the other hand, an important part of the food chain for larval fish survival is nanophytoplankton → microzooplankton → larval fish. Thus Parsons and Lebrasseur recognize two food chains with significant consequences for the nature and quantity of the commercial yield of fish.

More generally it has been pointed out by Ryther (1969) that the open ocean supports a food chain that is composed of relatively small sizes at each trophic level so that the commercial harvest occurs at a higher trophic level and is correspondingly small compared with the area of the open oceans. In inshore waters the value of the commercial harvest depends on that part of the food chain composed of larger organisms. It would appear that, rather than regarding this as an alternative to the 'small' chain, the larger chain must be considered as a complement to the smaller and very dependent on it. Experimental studies in enclosures show that, under stress, even highly eutrophic systems will revert to the smaller components. Such stresses can arise as easily, if not more easily, from perturbations at higher trophic levels as from environmental factors, natural or man-induced. These speculations would tend to amplify rather than alter comments based on a simpler picture of the structure of marine ecosystems (Steele 1974*b*). It is possible that, instead of producing a breakdown of a food web, the effect of perturbations may be to convert it to a less structured form based on smaller components. Within the context of our present knowledge, it is not yet possible to say whether this could occur in large areas of our coastal environment.

Conclusions

Size has been used as the basis for species discrimination in this model. It occurs as a component in three ways. (1) There are 'static' descriptions of the size distribution of the population at any instant. (2) There are the dynamics of growth: for the phytoplankton as a size-dependent rate of increase *within* each size category; for the herbivores as size-dependent rate of exchange *between* size categories. (3) Lastly, there is the size dependence of the phytozooplankton grazing relations.

(1) The descriptions of populations as numbers in various size or age categories together with transfer rates between categories form the basis for many general ecological descriptions of populations epitomized by the Leslie matrix (Williamson 1972).

(2) The relation of growth and metabolic rates to size has also been used to make general comments on energy flow rates in different communities (Zeuthen 1947; McNeill & Lawton 1970; Fenchel 1974).

(3) Lastly, the relation of predator size to prey size has been used to determine, for example, possible numbers of trophic levels (Hutchinson 1959).

Population dynamics has been viewed normally in terms of operations on numbers of organisms, and energy flow studies confined to the exchanges between trophic levels using biomass as the unit for description of a population. Any combinations relating size and energy have been at a very general level. The development of experimental work on plankton now permits a more detailed examination of possibilities arising from the combination of considering populations as transformers of energy and as numbers of organisms.

The primary conclusion, within the context of a model incorporating both size and energy flow, is that size structure is at least as important and probably more significant than total biomass of a population, in understanding the exchange of energy between trophic levels. Thus a breakdown of the transfer of plant to herbivore energy arises when the herbivore population is of the wrong size. The failure of a particular herbivore population is related to absence of the right size of food at a particular stage of its development, rather than a generally low rate of energy intake over the whole life cycle. Such deprivation occurs at the extremes of its size range either as lack of food for the adults, preventing reproduction, or as lack of food for the first feeding stage after development from eggs to nauplii.

These conclusions on the critical periods involving reproduction are in general agreement with terrestrial ecological studies, particularly on birds (Lack 1966). The arguments based on size/energy relations may have some relevance to carnivore–herbivore events in terrestrial systems, but certainly are not applicable to insect–plant interactions on land; this is not merely because of the obvious disparity in sizes but also because of the biochemical coevolution (Feeny 1975) in such systems; grazing is not appropriately expressed as energy transfer. Once again (Steele 1974*b*) it may be that the plant–herbivore system in the sea is best compared with the herbivore–carnivore interaction on land.

From those runs of the model where several of the critical parameters were varied, no single factor emerged as predominant in determining size structure. A large number of those factors, both physical and biological, could be varied to a point where the multi-species system tended to break down. For many of these parameters our knowledge is insufficient to define a numerical value within sufficiently narrow limits. Further we have ignored seasonal factors such as temperature or day length which could determine some aspects of development of particular species. Thus there appears to be some justification in dividing copepod species into three groups defined by their adult masses ('Oithona' = 1 μg C, '*Pseudocalanus*' = 10 μg C; '*Calanus*' = 100 μg C). The spacing of these categories may have evolved in relation to a niche width defined in terms of their size selection of food, permitting two or three of the categories to coexist. Within each category there are, in reality, several species with different seasonal or geographical patterns and these variations are completely outside the scope of this theory.

Because energy is transferred predominantly in one direction, plants → herbivores → carnivores, it might appear that the determination of size structure will also be transferred upwards from physical and chemical factors to various trophic levels. The model indicates that factors at higher trophic levels are at least as important as physical or nutrient parameters in determining population structure. The predation functions used here have a basically simple dependence on biomass so that at the trophic level of organization they do not exert any obvious control over the stability of the whole system (Steele 1976). Changes in size dependence of the predation function have, however, marked consequences, not only at one but also at two trophic levels lower.

Most of the effects described in the model occur after the period when phytoplankton is generally abundant. During the spring outburst larger cells are generally plentiful but later, because of the nutrient kinetics incorporated in the model, smaller cells will have an advantage and this in turn will tend to support smaller herbivores. Thus, *a priori*, one could expect a combination of small cells and small animals during summer. The fact that this does not necessarily occur in the model, depends on the details of the nutrient kinetics of the plants and the size selection by the copepods. In the context of this model, the continued existence of growing and reproducing populations of larger copepods depends on their coexistence with smaller species which control the smaller phytoplankton. Thus the presence of these smaller species is necessary for growth of *Calanus* spp., but not necessarily vice versa.

Environmental alterations which stress the system can be put in two general categories: physical or nutritional changes affecting the phytoplankton. Such stresses may tend to produce conditions favouring smaller cells and these in turn will alter the herbivore dominance in favour of smaller animals. Thus

$$\text{stress} \rightarrow \text{small cells} \rightarrow \text{small herbivores}. \tag{1}$$

Secondly, alterations which affect the herbivores directly, or indirectly, by changing the predator pattern can alter the balance between large and small herbivores. Decrease in small herbivores is particularly effective in stressing the rest of the system. This leads to a combination

$$\text{small cells} \leftarrow \text{large herbivores} \leftarrow \text{stress.} \tag{2}$$

A comparison of (1) and (2) shows how different types of stress can produce quite different patterns of size distribution in the combined plant and herbivore populations. These effects would not necessarily be apparent nor the different causes distinguishable in the general biomass data. Such a qualitative analysis may have a rôle in investigating the possible causes of observed changes in the natural communities.

This provides an example for the general but tentative conclusion that prediction of certain features of population structure for parts of a food web may be a more attainable objective of theory and more practically important, than attempts to predict total biomass.

APPENDIX

(Values for the standard run are given, where appropriate.)

$a, b, c, \alpha, \beta, \gamma$	used as temporary, undefined, constants
A	effect of chlorophyll on k (0.02 m^2/mg Chl)
A_D	area of fan that can retain cells of diameter D
A_s	rate of assimilation of food (as carbon)
B	attenuation with zero chlorophyll (0.1 m^{-1})
B_s	biomass of a copepod cohort with mass m and numbers Z
C	maximum photosynthetic rate in the euphotic zone (2.5 mg C/mg C per day)
C_D	drag coefficient
D	cell diameter (μm); $D(I)$ are categories in the simulation
D_m	scale factor to define D for which $S_e = 1(10)$
D_{min}, D_{max}	lower and upper limit for positive population growth
E	factor determining A_s (0.15×10^{-3})
F_1, F_2	relative ingestion rates
G	maximum growth rate for a given π ($G \leqslant G_{max}$)
G_{max}	maximum growth rate for unlimited food (0.4)
H, H_*, u	constants determining predation as a function of m (0.1, 0, 0)
I	radiation at depth z
I_0	incident radiation; just below the sea surface (Langleys)
k	attenuation coefficient (m^{-1})
k_s	half-saturation coefficient
L	characteristic length, proportional to $m^{\frac{1}{3}}$
l	length of setae in filtering apparatus
d	average diameter of the setae
M	mixing rate (0.02 day^{-1})
N	concentration of inorganic nitrogen; nitrate plus ammonia (mmol/m^3)
P	phytoplankton carbon concentration (mg C/m^3); $P(I)$ defines quantity in $D(I)$
P_h	photosynthetic rate (mg C/mg C per h)
P_{max}	maximum value of P_h
Q	basal metabolic rate (0.09)

R	respiration rate (mg C/mg plant C per day)
Re	Reynolds number
S	sinking rate of phytoplankton cells (m/day)
T_0	constant determining time course of predation (20 days)
V	maximum sinking rate ($N = 0$) (0.1 m/day)
V^*	V/z_e
V_e	velocity of water flow through filter
V_{max}	maximum rate of nitrogen uptake
V_{opt}	value of V_e for which growth is maximum
m	mass of a copepod expressed as μg C; $m(J)$ are categories in the simulation
Z	number of copepods per m^3
z_e	upper later thickness (40 m)
Z_0	constant determining dependence of predation on total biomass (0.2)
$Z(K, J)$	number of Kth species in Jth category
δ	half saturation as a function of diameter (0.015 mmolN/m^3 per μm)
θ	angle between two segments of a fan
λ	D/L
λ^*	$D/L^{0.5}$
μ	variance of log-normal selection curve (2.5)
ν	kinematic viscosity
π	food available to animal of size L
π_c	minimum value of π for which $G = G_{max}$ (81 mg C/m^3)
χ	chlorophyll a (mg/m^3)
χ_{max}	maximum chlorophyll:carbon ratio (0.033)

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