The size-based dynamics of plankton food webs. I. A simulation model of carbon and nitrogen flows

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Abstract. A general, size-based simulation model is developed to investigate the dynamics of carbon and nitrogen flows in plankton communities. In the model, community structure and transfer processes are all size-dependent, and all model parameters are determined by body size, using empirically determined relationships calculated from published data. Major flows include carbon fixation, release of photosynthetically produced dissolved organic carbon (PODOC), nitrogen uptake, respiration, excretion, predation, senescence and sinking. Because the model is based on general ecological principles and not on a specific ecosystem or data set, it can be used to simulate interactions within plankton communities of any ecosystem. The structure of the model can easily be altered to incorporate fewer or more size classes, or different size ranges of organisms. The program adjusts interactions between different components to allow for changes in the number of size classes, and new parameters are estimated, based on mean organism size. A standard simulation is described, which serves as the basis for comparing output from a sensitivity analysis. The model is robust with respect to most parameters. Important factors which affect model output include estimates of various rate parameters (which may be altered by environmental effects), shapes of initial biomass distributions (seeding effects), and wet mass to carbon conversion functions. The model is a useful tool to assist in analysing and interpreting carbon and nitrogen flows in planktonic ecosystems.

Introduction

Planktonic ecosystems commonly are described by compartmental models, each compartment representing a trophic level or taxonomic group (e.g. Steele, 1974; Wroblewski, 1977; Kiefer and Atkinson, 1984; Newell and Linley, 1984; Jones and Henderson, 1987). Such models primarily are descriptive, because the most important components of the ecosystem are represented by compartments, and interactions are described by linking compartments. However, when using these models as the basis for dynamic simulation models (e.g. Moloney et al., 1986), a number of problems are encountered. For example, unrealistic lumping of all phytoplankton sizes with widely disparate rates of growth and metabolism often results in the use of inappropriate rate parameters. In a model of a planktonic ecosystem in an enclosed water column Andersen et al., (1987) found it necessary to divide the phytoplankton compartment into diatoms and flagellates, which in turn necessitated subdividing zooplankton herbivores into copepods and appendicularians. Despite this added complexity, they concluded that further subdivision probably was necessary to make the model output more realistic. This is a problem commonly encountered with species- or trophic-level-based compartment models, and has the effect of making models increasingly unwieldy and parameter estimation very difficult, especially if there are not sufficient data available from which to estimate the parameters.

The above approach develops models from specific data sets. An alternative approach is to develop a generic model of planktonic ecosystems (Platt et al.,
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1981), which is based on general ecological principles. This is the approach that has been used in this study. The most universally applicable system property that has been identified is the influence of organism size on rates of processes in and interactions among planktonic (and other) organisms (Peters, 1983; Dickie et al., 1987). The structure of marine pelagic food webs is largely dependent on organism size (Sheldon et al., 1972, 1977; Platt and Denman, 1978; Silvert and Platt, 1980; Cousins, 1985; Platt, 1985). Furthermore, rates of many processes occurring in planktonic ecosystems are body-size dependent (e.g. Peters, 1983; Moloney and Field, 1989). This means that problems of parameter estimation are obviated to a large extent by using an independent criterion, viz. body size, to estimate nearly all parameters. Organism size thus serves as a convenient theoretical and practical basis for developing a system model of a marine plankton community.

Cousins (1980) developed a trophic continuum model in which an ecosystem is divided into three basic components (autotrophs, heterotrophs and detritus), with each component representing a size continuum from small to large organisms or particles. The trophic continuum model can be used to describe processes occurring in planktonic/pelagic ecosystems (Cousins, 1985), and appears to be universally applicable as a descriptive model. However, system dynamics of planktonic communities throughout the world's oceans vary. Simulation models are required which can be used to investigate factors affecting community structure and dynamics, and thus serve as a basis for exploring the functioning of marine planktonic ecosystems.

This paper describes the structure and functioning of a size-based simulation model of carbon and nitrogen flows in plankton ecosystems. In contrast to size-based energy flow models (Silvert and Platt, 1980; Parkin and Cousins, 1981), this model simulates flows of carbon (C) and nitrogen (N) through plankton communities. The double currency is necessary because, although N is usually believed to be the limiting nutrient in marine ecosystems, C also can limit growth of bacterioplankton, and there are close couplings between growth of bacterioplankton and phytoplankton. Output from the model is used to demonstrate a standard simulation, which serves as the basis for a sensitivity analysis. The aim of our study was to simulate the general features and processes of plankton communities in a generic model, and then apply this model to a variety of planktonic ecosystems. This paper is the first of two. In the second paper (Moloney et al., 1991) the model described here is used to simulate the standing stocks and size structures of two coastal and one oceanic ecosystem in the southern Benguela region, and using the simulated carbon and nitrogen flows to investigate the roles of different sizes of organisms in carbon transfer and nitrogen regeneration, and to identify the most important pathways of carbon transfer to pelagic fish.

Method

Model description

The model described below represents a plankton community occurring in the 1004
surface waters of the ocean in a region of the water column in which light is assumed to be non-limiting. The spatial extent of the model plankton ecosystem is assumed to be one cubic metre, because of the small sizes of most of the components of the model community. The physical environment has been deliberately kept constant, in order to make the model as simple as possible, and to assess the dynamics of the carbon and nitrogen flows based only on physiological and trophic processes. In this respect, the simulation model more closely resembles a micro- or mesocosm experiment than it does conditions in the open ocean.

The model plankton community consists of autotroph and heterotroph continua (which are divided into size classes), a detrital pool and dissolved nutrient pools (Figure 1). Thus the model is essentially a compartmental model, rather than the continuous trophic continuum described by Cousins (1980, 1985) and Parkin and Cousins (1981). The discrete form of the model was chosen to reduce complexity. The model differs also from the trophic continuum model in that the detrital pool is not divided into size classes. In simulations of plankton communities in the euphotic zone (e.g. Moloney et al., 1991), it has been assumed that most detrital material sinks from the model system; consequently it was not necessary to increase complexity by including detrital size classes. For simulations of communities at great depths or below the euphotic zone, this assumption would be invalid, and particle sizes of the detrital pool may be very important in determining vertical flux and regeneration of nutrients.

In the simulations described below, the autotroph and heterotroph continua respectively comprise organisms in size ranges from 0.2 to 200 μm ESD (equivalent spherical diameter) and 0.2 to 2000 μm ESD (Figure 1, Table 1), and are divided into size classes using a logarithmic scale. In these examples a logarithmic base of 10 is used, because the resulting size classes are similar to traditional categories described by Sieburth et al. (1978), and the total number of size classes is manageable for the sensitivity analysis (see below). However, in subsequent analyses we have found that a smaller logarithmic base of 5 is more realistic (Moloney et al., 1991). The size classes have been named according to the convention described by Sieburth et al. (1978) (Table 1). For simplicity, organisms >2000 μm ESD have not been included. Because of this, the time horizon of the standard simulation was set at 20 days. In general, the small sizes of model organisms result in rapid population changes, and simulations are mostly executed over periods of <30 days (Moloney et al., 1991). Large fauna are difficult to incorporate in simulations, because of the large temporal and spatial scales required to adequately describe their behaviour (Field et al., 1985; Fenchel, 1987). Micro- and meso-plankton populations may fluctuate many times in a time period during which large zooplankton and fish populations grow slowly. If the entire size range from bacteria to fish is included in a deterministic, spatially homogeneous simulation, it is found that the time horizon is either too short to adequately simulate large organisms, or, if their standing stocks are initially large, they exert an unrealistic controlling force on the small organisms, preventing these from increasing (personal observations). Consequently, it is inappropriate to include the entire size spectrum in a deterministic simulation.
Fig. 1. Diagrammatic representation of the model plankton community, and the flows of carbon and nitrogen. Bullets represent the size classes of autotrophs, and hexagons the size classes of heterotrophs.
Table I. Categorization of the model community on the basis of size and trophic function

<table>
<thead>
<tr>
<th>Trophic category</th>
<th>No of size classes</th>
<th>Model compartment</th>
<th>Size range (μm ESD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autotrophs</td>
<td>3</td>
<td>Pico-phytoplankton</td>
<td>0.2–200</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Nano-phytoplankton</td>
<td>0.2–2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Net-phytoplankton</td>
<td>2–20</td>
</tr>
<tr>
<td>Heterotrophs</td>
<td>4</td>
<td>Bacterioplankton</td>
<td>0.2–200</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Nanoflagellates</td>
<td>2–20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Microzooplankton</td>
<td>20–200</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mesozooplankton</td>
<td>200–2000</td>
</tr>
</tbody>
</table>

model. Large mobile organisms may be better represented by stochastic or spatially heterogeneous models with longer time horizons.

Organism sizes are expressed in linear dimensions as ESDs. An average size is calculated for each size class using a geometric mean:

$$ESD_{\text{average}} = \sqrt{ESD_{\text{min}} \times ESD_{\text{max}}}$$ (1)

Spherical volumes are calculated and the conversion from volume to wet mass is 1 pg = 1 μm$^3$, assuming a specific density of one. Peters (1983) used factors of between 0.1 and 0.3 to convert from wet to dry mass, and 0.4 to convert from dry mass to C mass. His conversions from wet mass to C mass were thus between 0.04 and 0.13. An intermediate factor of 0.07 is used here. However, it should be noted that the equations of Strathmann (1967) for marine phytoplankton do not use a linear conversion as assumed above, but one of body mass to the power 0.75. Taguchi (1976) estimated a similar relationship for marine diatoms. No equivalent relationship presently exists for bacterioplankton and zooplankton, and the effect of these dissimilar conversion factors will be investigated in the sensitivity analysis.

In contrast to Cousins' (1985) model, the model described below simulates flows of carbon and nitrogen instead of energy flows. Consequently, the trophic continuum model has been adapted to include dissolved C and N pools in addition to the detrital pool (Figure 1). Because the model uses a double currency, it is necessary to relate the fluxes of C and N. This is done by assuming constant C:N ratios for different trophic categories: six for autotrophs (Strickland, 1960), four for bacteria (Fenchel and Blackburn, 1979; Gray et al., 1984) and 4.5 for bactyvorous protozoa and micro/mesozooplankton (see Omori, 1969; Gorsky et al., 1988). This may not always be realistic, but mechanisms causing different rates of uptake and/or release of C and N are complex and poorly understood (Terry, 1982; Syrett, 1981). Furthermore, the Redfield ratio for phytoplankton is commonly used to convert C estimates to N and vice versa (see Goldman et al., 1979), indicating that many ecologists implicitly assume constant C:N ratios in their calculations. Mass units are mg C m$^{-3}$ and mg N m$^{-3}$.
Major flow pathways are represented diagrammatically in Figure 1. Autotroph C is obtained by carbon fixation during photosynthesis, and N through uptake from solution. C is released as PDOC (photosynthetically produced dissolved organic carbon), and further C losses occur as a result of respiration, grazing, senescence and sinking (Figure 1). Uptake and ingestion respectively by bacterioplankton and grazers results in autotroph C entering the heterotroph continuum. Bacterioplankton obtain C and N from solution, whereas large heterotrophs obtain them by ingesting particulate material. Heterotrophs incur C and N losses as a result of egestion, respiration, excretion and predation. The detrital pool consists of faecal material and senescent phytoplankton cells, which sink out of the model system. The dissolved C pool is supplied by autotrophs through the excretion of PDOC and the lysis of senescent phytoplankton cells, and sustains losses to bacterioplankton. The dissolved N pool is separated into new N (nitrate) and regenerated N (ammonia, urea) pools (Dugdale and Goering, 1967), in keeping with most recent laboratory and field studies of the nitrogen dynamics of plankton communities. Both lose N to autotrophs and bacterioplankton. In addition, bacterioplankton take up N from organic sources resulting from the lysis of senescent phytoplankton cells. C fixed during photosynthesis and the input of new N are the only external inputs to the model system. Regenerated N results from the cycling of reduced N by heterotroph size classes. Rates of change of standing stocks of biotic and abiotic compartments are determined by rates of input and output of C and N to and from each compartment. Diurnal effects are not included in the model. Mass flows are described by linear and non-linear functions (described below), and the rates of change of standing stocks are described by differential equations (Table II) which are solved numerically using a second order Runge–Kutta method (Lapidus and Seinfeld, 1971). The model consists of a computer program written in True Basic, and may be used on any IBM-compatible microcomputer.

Primary production

Many factors can limit phytoplankton growth (see Raymont, 1980). In the model

Table II. Differential equations describing rates of change of state variables

<table>
<thead>
<tr>
<th>Equation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>dANj/dt</td>
<td>nitrogen uptake–senescence–grazing–sinking</td>
</tr>
<tr>
<td>dHCj/dt</td>
<td>ingestion/uptake–egestion–respiration–predation</td>
</tr>
<tr>
<td>dHNj/dt</td>
<td>ingestion/uptake–egestion–excretion–predation</td>
</tr>
<tr>
<td>dDETj/dt</td>
<td>faeces–sinking</td>
</tr>
<tr>
<td>dPDOCT/dt</td>
<td>PDOC production by autotrophs–uptake by bacterioplankton</td>
</tr>
<tr>
<td>dDOC/dt</td>
<td>lysis of senescent phytoplankton cells–uptake by bacterioplankton</td>
</tr>
<tr>
<td>dNEWN/dt</td>
<td>(upwelling/mixing/diffusion)–uptake by bacteria and phytoplankton</td>
</tr>
<tr>
<td>dREGN/dt</td>
<td>excretion by heterotrophs–uptake by bacterioplankton and phytoplankton</td>
</tr>
<tr>
<td>dDON/dt</td>
<td>lysis of senescent phytoplankton cells–uptake by bacterioplankton</td>
</tr>
</tbody>
</table>

AC = autotroph carbon, AN = autotroph nitrogen, HC = heterotroph carbon, HN = heterotroph nitrogen, DOC/DON = dissolved organic carbon/nitrogen, DET = detrital carbon and nitrogen, NEWN = new nitrogen (nitrate), REGN = regenerated nitrogen (ammonia, urea), PDOC = photosynthetically produced dissolved organic carbon, j = size class subscript.
described here, only nitrogen is limiting; thus the model describes the carbon and nitrogen flows of a hypothetical eutrophic zone plankton community in which light and other nutrients are not limiting. This should be borne in mind when extrapolating from the simulation results to field conditions, because other factors (e.g. light) may be important in the field, and will modify the results accordingly. Primary production rates are assumed to be limited by N uptake rates, which are governed by Michaelis–Menten kinetics (MacIsaac and Dugdale, 1969), although this is probably an oversimplification for detailed understanding (see Shuter, 1978; Eppley, 1981; Morita, 1984; Nissen et al., 1984). However, for the purpose of general ecological models, the Michaelis–Menten model is sufficient (Raymont, 1980):

\[ V_j(\text{day}^{-1}) = V_{\text{max},j}(\text{day}^{-1}) \frac{N (\text{mg m}^{-3})}{K_N(\text{mg m}^{-3}) + N (\text{mg m}^{-3})} \]  

(2)

where \( V_j \) is the mass-specific uptake rate for size class \( j \), \( V_{\text{max},j} \) is the maximum mass-specific uptake rate, \( K_N \) is the half saturation constant, and \( N \) is the ambient N concentration. \( V_j \) and \( N \) are variables, and \( V_{\text{max},j} \) and \( K_N \) are size-dependent parameters. N uptake rates are thus modified by ambient N concentrations; if \( N \) is large \( V_j \) tends to \( V_{\text{max},j} \), and if \( N \) is small \( V_j \) is slower than \( V_{\text{max},j} \). Net C fixation rates (\( P_j \)) are calculated as the specific uptake rate (\( V_j \)), calculated in equation (2), times the C standing stock (\( B_j \)) in each size class \( j \)

\[ P_j (\text{mg C m}^{-3} \text{ day}^{-1}) = V_j (\text{day}^{-1}) \times B_j (\text{mg C m}^{-3}) \]  

(3)

Net C fixation rates are thus determined by N uptake rates. Gross C fixation is estimated as the sum of the net photosynthetic rate (equation 3), the respiration rate (equation 9) and the PDOC production rate (see below).

**PDOC production**

Phytoplankton exude some variable fraction of primary production as PDOC (Berman and Holm-Hansen, 1974). The percentage of primary production released in this fashion may be relatively large, with estimates ranging up to 70% (Johnson et al., 1981; Lancelot, 1983), although it is very difficult to measure, because the labile fraction of PDOC is rapidly taken up by bacteria. PER (percentage extracellular release) has been related to ambient N concentrations, with large PER (70%) associated with relatively low concentrations (<10 \( \mu \text{g} \text{ at } \text{l}^{-1} \)) and small PER (15%) with high concentrations (28 \( \mu \text{g} \text{ at } \text{l}^{-1} \)) (Azam et al., 1983). However, the situation is far more complex. PER is affected also by other factors such as light, age of cells and species composition (Lancelot, 1983; Zlotnik and Dubinsky, 1989). N concentrations and PER are correlated (Azam et al., 1983), but the relationship cannot be interpreted as being causative, so N levels alone cannot be used to predict PER. Many authors assume a constant value for PER. Although this is probably not realistic at all times, a constant fraction of 15% has been used in the model. This fraction refers only to the labile
portion, because the refractory material has a much longer residence time (for review, see Lucas, 1986). It is assumed that only the labile fraction is important on the time scales that are used in the simulations. The effect of varying the value of PER is investigated in the sensitivity analysis.

**Senescence**

Phytoplankton cells that senesce and lyse provide a potential source of organic nutrients for bacterioplankton. Very little is known about the factors causing cell senescence and the rates at which it occurs (Raymont, 1980). In the model, senescence and lysis of phytoplankton cells are simulated by a simple, two-step process. In the first step, phytoplankton biomass becomes non-living, particulate C and N (POC and PON), which are not immediately available to bacterioplankton:

\[
\text{OC/PON production (mg C/N m}^{-2} \text{ day}^{-1}) = \text{senescence rate (day}^{-1}) \times B_0 (\text{mg C/N mg}^{-3})
\]

The senescence rate is assumed to be proportional to autotroph growth and respiration rates. In the second step, the particulate material is transformed into dissolved C and N as a result of cell lysis:

\[
\text{DOC/DON production (mg C/N m}^{-2} \text{ day}^{-1}) = \text{lysis (day}^{-1}) \times \text{POC/PON (mg C/N mg}^{-3})
\]

The proportion of senescent cells that lyse (due to physical factors and bacterial activity) is assumed to be a constant proportion of the particulate material. Equations (4) and (5) have the effect of reducing the rate at which particulate autotroph material is made available to bacterioplankton as dissolved organic C and N, simulating the slower breakdown of refractory compounds compared with the utilization of labile PDOC and DIN.

**Heterotroph uptake/ingestion**

Two sources of input to heterotroph compartments are simulated. Bacterioplankton take up N from solution (organic and inorganic N) in much the same way as do phytoplankton, and are assumed to obtain C solely from the PDOC and DOC pools. As most particulate carbon (POC), such as faecal material and senescent phytoplankton cells, sinks rapidly (see below), it is consequently assumed that bacterial utilization of POC occurs below the euphotic zone. A direct pathway from POC to bacteria is therefore not included in the model. Uptake of both C and N is governed by Michaelis–Menten models; equation (2) for N (Monod, 1949) and equation (6) for C (Parsons and Strickland, 1962):

\[
V_j (\text{day}^{-1}) = V_{max}(\text{day}^{-1}) \frac{(\text{PD}O\text{C} + \text{DOC}) \text{ (mg m}^{-3})}{K_s (\text{mg m}^{-3}) + (\text{PD}O\text{C} + \text{DOC}) \text{ (mg m}^{-3})}
\]
where \( V_j \) is the mass-specific growth rate of bacteria as determined by C availability, \( V_{\max} \) is the size-dependent maximum uptake rate as in equation (2), PDOC and DOC are the ambient dissolved C concentrations and \( K_s \) is the size-dependent half-saturation constant for PDOC uptake (assumed equal to \( K_s \) for N uptake times the C:N ratio for bacterioplankton). Bacterioplankton growth \( (P_j') \) is thus limited by C or N, depending on which uptake rate \( V_j \) (equation 2 or 6) is slower:

\[
P_j' \text{ (mg C/N m}^{-3}\text{ day}^{-1}) = V_j \text{ (day}^{-1}) \times B_j \text{ (mg C/N m}^{-3}\text{)}
\]

(7)

This appears to be realistic when C is limiting, because Kirchman et al. (1990) have shown that uptake of ammonium by bacteria from the subarctic Pacific is limited by carbon availability, as has been assumed above. However, when nitrogen is limiting, carbon uptake may be underestimated by the model, because bacteria may not modulate their rates of carbon uptake sufficiently only to meet their biosynthetic or bioenergetic demands (Tempest and Neijssen, 1978), and 'excess' carbon may be taken up.

Particle-feeding heterotrophs obtain C and N by ingestion of autotrophs or heterotrophs. Food available to each size class of predator is calculated on a size basis; predators may ingest a range of food-particle sizes, dependent on their own sizes (see below). Ingestion rates are a function of prey concentration and prey size. Various models have been used to relate ingestion rates to prey densities (see Mullin et al., 1975). Most of these models have a maximum or saturation rate at high prey densities, and a density-dependent rate at low prey densities (Mullin et al., 1975). A Michaelis–Menten model for ingestion has been used in the simulations:

\[
\text{ingestion}_{ki} \text{ (day}^{-1}) = I_{\max} \text{ (day}^{-1}) \frac{(B_k' - \text{refuge}_k)}{K_k + \sum_{r=\min}^{\max} (B_r' - \text{refuge}_r)}
\]

(8)

where the specific ingestion rate of size class \( k \) by size class \( j \) is determined by the maximum mass-specific size-dependent ingestion rate of size class \( j \) \( (I_{\max}) \). \( B_k' \) is the standing stock of size class \( k \) available to size class \( j \), the 'refuges' refer to threshold standing stocks below which predation on that size class ceases, and \( r \) represents the range of size classes available to each predator class \( j \). In the simulations described below, each predator size class is assumed for simplicity to prey only on the size class (autotrophic or heterotrophic) immediately smaller than itself. \( K_k \) is the half-saturation constant dependent on the size of prey \( k \) (see below).

**Egestion**

Heterotrophs do not absorb all they ingest. A proportion of ingested material is released as faeces. Hall et al. (1976) were not able to show any size-dependence of absorption efficiencies, which are assumed to be 85% for N absorption of all
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particle-feeding heterotrophs (Dagg, 1976; Barthel, 1983; Miller and Landry, 1984) and 100% for bacteria, because bacteria do not produce faecal pellets.

*Respiration*

C losses as a result of respiration are modelled as a constant fraction of size-class standing stock:

\[
\text{respiration (mg C m}^{-3} \text{ day}^{-1}) = R_f (\text{day}^{-1}) \times B_j (\text{mg C m}^{-3})
\]  

(9)

where \( R_f \) is the mass-specific size-dependent respiration rate, and \( B_j \) the C standing stock of size class \( j \). Respiration rates change during feeding and other activities, but these effects are not included in the model. This may result in an underestimate of respiratory losses, but is probably only important for large size classes of heterotrophs, because motility of protozoans requires an insignificant fraction of their energy budget (Fenchel and Finlay, 1983).

*Excretion*

Metabolic C losses through respiration are matched by equivalent N losses in order to maintain constant C:N ratios for heterotrophs. The required excretion rates are calculated as:

\[
\text{excretion (mg N m}^{-3} \text{ day}^{-1}) = R_f (\text{day}^{-1}) \times B_j (\text{mg N m}^{-3})
\]  

(10)

where \( R_f \) is the same as for equation (9), and \( B_j \) is the N standing stock in size class \( j \). For bacteria this may not be realistic. Bacteria can take up N and C separately, because the dissolved pools consist of both inorganic and organic material, and a variety of different substrates. Bacterial C and N uptake rates are therefore not necessarily coupled, as is assumed here. When N is limiting, bacteria may conserve this nutrient. An alternative approach to modelling this process would be to consider only the net uptake of N, i.e. assume that bacteria only take up sufficient N for their requirements, and excrete none. However, this approach makes the *a priori* assumption that bacteria excrete no nitrogen at all, which is not true (see Kirchman et al., 1989). The real situation is probably intermediate between these two extremes. As it stands (equation 10), the model may overestimate N excretion by bacteria.

*Sinking*

C and N losses through sinking of phytoplankton are calculated as:

\[
\text{sinking losses (mg C/N day}^{-1}) = [\dot{S}_j (\text{m day}^{-1}) - D (\text{m})] \times B_j (\text{mg C/N})
\]  

(11)

where \( \dot{S}_j \) is the sinking velocity of size class \( j \), \( D \) is the depth of the water mass/euphotic zone in question, and \( B_j \) is the C/N standing stock of size class \( j \).
Estimation of model parameters

Many of the processes described above are size-dependent and parameters thus vary between size classes. Allometric equations describing the size-dependence of nitrogen uptake rates, ingestion rates and respiration rates of plankton organisms over a wide range of body sizes have been described previously (Moloney and Field, 1989). However, other factors cannot be described by the general allometric models, because they are not related to intrinsic processes and do not scale in the same fashion with body mass. Such factors often depend on the organism’s interaction with its environment. This section uses published data to derive empirical models relating particle size to three ecological processes in the plankton environment.

Half-saturation constants for nitrogen uptake

Phytoplankton and bacterioplankton rely on the uptake of dissolved nutrients for growth. The uptake process has been described by Michaelis–Menten models (equations 2 and 6), which have two parameters, the maximum uptake rate \( V_{\text{max}} \) and the half-saturation constant \( K_s \). It has been shown that \( V_{\text{max}} \) is body-size dependent, with small organisms having faster mass-specific uptake rates than large organisms (Moloney and Field, 1989). The ability to take up nutrients at low ambient nutrient concentrations is determined by \( K_s \), which also is dependent on body size; small cells are more proficient (i.e. have smaller \( K_s \)) than are large cells (Eppley et al., 1969; Gray et al., 1984). This is important in environments where nutrients are scarce (Gray et al., 1984). To quantify this relationship, cell diameters (\( \mu m \)) and \( K_s \) values (\( \mu g \text{ at } l^{-1} \)) for NO\(_3\) and NH\(_4\) uptake were obtained from Table 2 of Eppley et al. (1969). Cell volumes were calculated using the formula for a sphere, and converted to pg carbon using the equations of Strathmann (1967). \( K_s \) values for NO\(_3\) and NH\(_4\) were averaged, giving one \( K_s \) value for nitrogen uptake per species. \( K_s \) values were plotted against phytoplankton cell mass for cells ranging from \( \sim 4 \) to 200 \( \mu m \) ESD, using logarithmic scales. A functional linear regression (Ricker, 1984) was fitted to the log-transformed data (Figure 2), and this regression model is used to calculate \( K_s \) values for different size classes in the simulations.

Half-saturation constants for ingestion

In Michaelis–Menten ingestion models (equation 8), ingestion rates at low prey densities are determined by half-saturation constants \( K \) (equivalent to \( K_s \) above, but termed \( K \) throughout to avoid confusion). \( K \) is the ratio of the maximum uptake rate to the maximum clearance rate for filter feeders (Fenchel, 1980b). Because both these rates scale to predator body size, the effect of predator size on \( K \) cancels, and \( K \) is predator-size independent (Fenchel, 1980a). However, there is evidence to suggest that \( K \) is affected by prey size, and this relationship can be used to estimate the values of \( K_s \) for different sizes of prey. A half-saturation constant of \( 5 \times 10^8 \) bacteria ml\(^{-1}\) has been estimated for microflagellates feeding on bacteria (Fenchel, 1982). Using an average bacterial cell size of
0.11 μm³ and a conversion of 1 μm³ = 0.1 pg C (Laake et al., 1983), this was converted to a $K$ value of 55 mg C m⁻³. Prey sizes (μm ESD) and half-saturation constants (μm³ l⁻¹) of ciliates were obtained from Fenchel (1980c); only prey >2 μm were used, because ciliates probably do not feed on small, free-living bacteria in open waters (Fenchel, 1980c). In addition, food particle sizes and half-saturation constants for ingestion were obtained for copepods Calanus pacificus (Frost, 1972), Euchaeta elongata (Yen, 1983) and Oithona nana (Lampitt and Gamble, 1982), and a euphausiid Euphausia lucens (Stuart, 1986). All prey sizes ($n = 30$) were expressed as pg C, using Strathmann’s (1967) conversions from volume to carbon when necessary, and half-saturation constants were expressed as mg C m⁻³. A functional linear regression was fitted to the log-transformed data (Figure 3). There is much scatter about this regression, and more data are required. However, there has been no previous attempt to relate half-saturation constants for ingestion to prey sizes over a large size range of organisms, and the relationship presented in Figure 3 is useful for
calculating half-saturation constants for a wide size range of predator and prey organisms.

In contrast to the relationship between $K$ and prey size described above, intraspecific feeding studies have shown that large prey items are more susceptible to predation at low concentrations than are small prey items (Paffenhofer, 1971; Frost, 1972, 1975; Boyd, 1976; Cowles, 1979; Fenchel, 1980a; Capriulo, 1982; Quetin and Ross, 1985). A similar trend was found for the threshold feeding response of the copepod C.pacificus, the threshold occurring at progressively lower concentrations as the sizes of food particles increase (Frost, 1975). This implies that $K$ should decrease as prey size increases for a constant predator size, which is the reverse of the pattern found here for a range of species (Figure 3). Individual predators apparently utilize prey items at the large end of their prey size range more efficiently than small prey items, but for the general interspecific trend, $K$ values increase as prey size increases.

**Sinking velocities**

The rate at which organisms and particles sink through the water column to some extent depends on particle size, although sinking velocities also are affected by factors such as buoyancy, shape, orientation and physical features of the water column (Anderson et al., 1985). Measured sinking rates of live phytoplankton cells ($S_p$) are much slower than are those of faecal and detrital material ($S_F$), presumably because of buoyancy mechanisms operating in live cells (Smayda, 1970). Regression models relating sinking velocities to particle sizes were estimated for phytoplankton cells and for faecal pellets. Sinking rates (m day$^{-1}$) of particulate organic carbon and phytoplankton in three discrete size classes were obtained from Burns and Rosa (1980). Geometric mean sizes were estimated for each size class, and sizes were converted to carbon masses (pg C) using an average conversion of 1 $\mu$m$^3$ = 0.07 pg C (Peters, 1983; Moloney and Field, 1989). Sinking rates of particulate carbon (Bienfang, 1985) were similarly treated ($n = 4$), and cell carbon (pg) and sinking rates (m day$^{-1}$) of 29 species of nutrient-replete marine phytoplankton were obtained from Bienfang and Harrison (1984). The data for live cells were combined into one data set ($n = 36$). Logarithmic values of sinking rates (m day$^{-1}$) and particle volumes ($\mu$m$^3$) for faeces of gelatinous zooplankton ($n = 232$) were read from Figure 2 of Bruand and Silver (1981), and the data were converted to a linear scale. Sinking velocities of both living and dead particles increase with increasing cell/particle size. Power functions were fitted to both sets of data (Figures 4 and 5).

Values of allometric and other regression parameters that are used to calculate parameters used in the simulation model are presented in Table III. Resulting size-dependent parameters for autotrophs and heterotrophs in the simulation model are presented with associated size classes and C masses in Tables IV and V. There is a large difference in rate parameters between the smallest and largest organisms, highlighting the necessity for some form of size differentiation among system components. For example, autotrophs comprise three size classes, with 13-fold differences in rate parameters between the
C.L. Moloney and J.G. Field

Fig. 4. Regression model relating sinking velocities of live phytoplankton cells to cell mass. See text for data sources.

Fig. 5. Regression model relating sinking velocities of faecal material to particle volume. Data from Bruland and Silver (1981).

smallest and largest size classes (Table IV). Such differences are realistic. Specific growth rates of 8.9 day⁻¹ have been calculated for pico-phytoplankton (Douglas, 1984), whereas net-phytoplankton growth rates are usually <1 day⁻¹ (Parsons et al., 1984). Prey-size dependent half-saturation constants (equation 8) for prey size classes (autotrophs and heterotrophs) are presented in Table VI, together with the food web matrix describing trophic interactions between predator and prey size classes in the model.

Results

Standard simulation

A standard simulation was performed to demonstrate the output of the model, and to serve as a basis for comparing output from a sensitivity analysis. Values assigned to standing stocks in each model compartment at the start of a simulation, to some extent, determine the behaviour of the model system. In executing simulations, it was found that large autotrophs generally had to be
### Table III: Summary of some of the regression models used to calculate values of size-dependent parameters in the simulation models

<table>
<thead>
<tr>
<th>Process</th>
<th>Regression model</th>
<th>Parameters</th>
<th>Units</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nitrogen uptake</td>
<td></td>
<td>$V_{max} = aM^p$</td>
<td>$\mu g C^\text{day}^{-1} \cdot mg Nm^{-3}$</td>
<td>3.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$K_{max} = aM^{aK}$</td>
<td>$\mu g C^\text{day}^{-1}$</td>
<td>2.15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$l_{max} = bM^{b}$</td>
<td>$\mu g C^\text{day}^{-1}$</td>
<td>0.38</td>
</tr>
<tr>
<td>Ingestation (phytoplankton and bacterioplankton)</td>
<td></td>
<td>$R_{s} = aM^{a}$</td>
<td>$\mu g C^\text{day}^{-1}$</td>
<td>63</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$S_{s} = bM^{b}$</td>
<td>$\mu g C^\text{day}^{-1}$</td>
<td>-0.25</td>
</tr>
<tr>
<td>Ingestion (particle-feeding heterotrophs)</td>
<td></td>
<td>$R_{i} = aM^{a}$</td>
<td>$\mu g C^\text{day}^{-1}$</td>
<td>54</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$S_{i} = bM^{b}$</td>
<td>$\mu g C^\text{day}^{-1}$</td>
<td>0.88</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$S_{j} = cM^{c}$</td>
<td>$\mu g C^\text{day}^{-1}$</td>
<td>1.14</td>
</tr>
<tr>
<td>Sinking (live phytoplankton cells)</td>
<td></td>
<td>$S_{m} = dM^{d}$</td>
<td>$\mu g C^\text{day}^{-1}$</td>
<td>-0.25</td>
</tr>
<tr>
<td>Sinking (faecal and detrital material)</td>
<td></td>
<td>$S_{f} = eM^{e}$</td>
<td>$\mu g C^\text{day}^{-1}$</td>
<td>0.42</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$S_{2} = fM^{f}$</td>
<td>$\mu g C^\text{day}^{-1}$</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$S_{3} = gM^{g}$</td>
<td>$\mu g C^\text{day}^{-1}$</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$S_{4} = hM^{h}$</td>
<td>$\mu g C^\text{day}^{-1}$</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$S_{5} = iM^{i}$</td>
<td>$\mu g C^\text{day}^{-1}$</td>
<td>0.38</td>
</tr>
</tbody>
</table>

Regressions for $V_{max}$, $l_{max}$, $S_{s}$, $S_{i}$, and $S_{j}$ were obtained from Molenoy and Field (1989), the remainder are described in the text. See equations (1) to (11) for explanations of symbols and units.
### Table IV. Autotroph size classes, model parameters and initial standing-stocks

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Pico-phytopl. (0.2–2 μm)</th>
<th>Nano-phytopl. (2–20 μm)</th>
<th>Net-phytopl. (20–200 μm)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average ESD (μm)</td>
<td>0.63</td>
<td>6.3</td>
<td>63</td>
<td>This study</td>
</tr>
<tr>
<td>Cell mass (pg C)</td>
<td>0.088</td>
<td>16</td>
<td>2800</td>
<td>This study</td>
</tr>
<tr>
<td>Uptake rate $V_{max}$ (day$^{-1}$)</td>
<td>6.6</td>
<td>1.8</td>
<td>0.50</td>
<td>Moloney and Field (1989)</td>
</tr>
<tr>
<td>Respiration (day$^{-1}$)</td>
<td>3.1</td>
<td>0.86</td>
<td>0.23</td>
<td>Moloney and Field (1989)</td>
</tr>
<tr>
<td>Senescence (day$^{-1}$)</td>
<td>0.66</td>
<td>0.18</td>
<td>0.050</td>
<td>This study</td>
</tr>
<tr>
<td>Lysis (day$^{-1}$)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>This study</td>
</tr>
<tr>
<td>$K_s$ (mg N m$^{-3}$)$^*$</td>
<td>0.0068</td>
<td>1.2</td>
<td>54</td>
<td>This study</td>
</tr>
<tr>
<td>Sinking (m day$^{-1}$)</td>
<td>0.000058</td>
<td>0.010</td>
<td>0.96</td>
<td>This study</td>
</tr>
<tr>
<td>PER (day$^{-1}$)$^b$</td>
<td>0.15</td>
<td>0.15</td>
<td>0.15</td>
<td>This study</td>
</tr>
<tr>
<td>Initial values (mg C m$^{-3}$)</td>
<td>0.5</td>
<td>5</td>
<td>50</td>
<td>This study</td>
</tr>
</tbody>
</table>

* $K_s$ values are half-saturation constants for nitrogen uptake.

**PER is percentage extracellular release of carbon fixed by phytoplankton.

### Table V. Heterotroph size classes, model parameters and initial standing-stocks

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Average ESD (μm)</td>
<td>0.63</td>
<td>6.3</td>
<td>63</td>
<td>630</td>
<td>This study</td>
</tr>
<tr>
<td>Cell mass (pg C)</td>
<td>0.088</td>
<td>9.3</td>
<td>9300</td>
<td>930000</td>
<td>This study</td>
</tr>
<tr>
<td>Uptake $V_{max}$ (day$^{-1}$)</td>
<td>6.6</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Moloney and Field (1989)</td>
</tr>
<tr>
<td>Ingestion $I_{max}$ (day$^{-1}$)</td>
<td>–</td>
<td>36</td>
<td>–</td>
<td>1</td>
<td>Moloney and Field (1989)</td>
</tr>
<tr>
<td>Respiration (day$^{-1}$)</td>
<td>3.1</td>
<td>8.0</td>
<td>1.4</td>
<td>0.25</td>
<td>Moloney and Field (1989)</td>
</tr>
<tr>
<td>$K_s$ (mg N m$^{-3}$)$^*$</td>
<td>0.0068</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>This study</td>
</tr>
<tr>
<td>Absorption (day$^{-1}$)</td>
<td>1.0</td>
<td>0.85</td>
<td>0.85</td>
<td>0.85</td>
<td>This study</td>
</tr>
<tr>
<td>Initial values (mg C m$^{-3}$)</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>This study</td>
</tr>
</tbody>
</table>

* $K_s$ values are half-saturation constants for nitrogen uptake by bacterioplankton.
initialized with larger standing stocks than small autotrophs, to prevent small autotrophs from dominating. This is consistent with field observations of the seeding crop of newly upwelled waters in the southern Benguela, in which large phytoplankton (mainly in the form of resting spores) dominate the initial biomass (G. Pitcher, personal communication). In the standard simulation the values of the initial standing stocks in the autotroph size classes were set with large cells dominating (Table IV), whereas the heterotrophs were arbitrarily assigned small, equal values for each size class (Table V). For simplicity, new N concentrations were initialized at a value of 10 mg-at N m\(^{-3}\), to simulate the development and decay of a plankton bloom after an upwelling or mixing event. Regenerated N, DON, DOC and PDOM pools were initialized with zero concentrations, but the pools subsequently receive inputs from biotic compartments during growth. The standard simulation was run for 20 days, this being the shortest period in which population cycles of all size classes could adequately be represented. Short time scales also are appropriate for subsequent verification of the model (see Moloney et al., 1991), because the model was developed in parallel with mesocosm experiments using organisms <200 \(\mu\)m (Painting, 1989). The simulation was kept as simple as possible by assuming that PER was constant at 15% of primary production, and by excluding sinking and senescence of phytoplankton cells. Realistic simulations are described elsewhere (see Field et al., 1989; Painting, 1989; Moloney and Field, 1991; Moloney et al., 1991).

Changes with time of the standing stocks of all model compartments in the standard simulation are presented in Figure 6. The autotroph community increases to a maximum of \(~900\) mg C m\(^{-3}\) after 1 day, and undergoes a number of fluctuations before decreasing to \(<50\) mg C m\(^{-3}\) by day 20 (Figure 6a). Model pico-phytoplankton undergo seven pronounced fluctuations during that period, whereas nano- (Figure 7b) and net- (Figure 7c) phytoplankton display only one bloom each. The model heterotroph community displays similar fluctuations to the autotroph community (Figure 6b), with most peaks due to the nanoflagellates (2–20 \(\mu\)m). The fluctuations observed in the simulated communities can be explained in terms of grazing pressure and nutrient limitation. For example, pico-phytoplankton growth is limited by nitrogen availability when N concentrations decrease to near-zero after 1 day (Figure 6c). Pico-phytoplankton standing stocks then decrease as a result of predation by heterotrophic
Fig. 6. Output of the standard simulation. Changes with time of the standing stocks of (a) autotrophs, (b) heterotrophs, (c) dissolved nitrogen pools and (d) dissolved carbon pools. See Table III for size-class names.
nanoflagellates, which also prey on the bacterioplankton (Figure 7a). The fluctuations of the heterotrophic nanoflagellate (2–20 μm) standing stock (Figure 6b) closely follow those of their pico-plankton prey, lagging by ~0.2 days (Figure 7a). The nano-phytoplankton (2–20 μm) bloom is grazed down by micro-zooplankton (20–200 μm) (Figure 7b), which also prey on the nanoflagellates. Net-phytoplankton standing stocks increase much slower than those of pico- and nano-phytoplankton, and their growth in the standard simulation...
occurs in steps (Figure 7c). These steps are the result of temporary reductions in net-phytoplankton growth rates, caused by competition with smaller phytoplankton for nitrogen. The decreased growth rates of net-phytoplankton (i.e. the 'steps') correspond to times when pico- or nano-phytoplankton standing stocks are at a maximum (Figures 6a and 7c). Net-phytoplankton and micro-zooplankton are grazed down by meso-zooplankton (Figure 7c). The meso-zooplankton in the model have no predators, and their standing stock starts to decrease slowly after day 19, as a result of carbon and nitrogen losses through respiration and excretion.

**Sensitivity analysis**

Platt et al. (1981) list four areas in which model sensitivity should be tested: (i) sensitivity to parameters; (ii) sensitivity to initial values; (iii) sensitivity to functional form; and (iv) sensitivity to model structure. In the sensitivity analysis described below, all four areas of sensitivity are explored to some extent. A 'brute-force' approach is used, whereby parameters are varied one at a time and the effect on output of the standard simulation assessed (Platt et al., 1981). This is done descriptively, and a number of different qualitative responses of the simulations have been identified. Some factors that may produce these responses are summarized in Table VII. A detailed representation of output of the sensitivity analysis is presented by Moloney (1988).

(i) Sensitivity to parameter values. Values of allometric parameters were halved and doubled for each parameter in turn, and results were compared with those of the standard simulation. The fluctuations in standing stocks of biotic compartments observed in the standard simulation were repeated in the sensitivity analysis output, but the time scales and magnitudes of standing stocks varied. Most of the changes were predictable. For example, doubling the value of the nitrogen uptake rate, $V_{\text{max}}$, resulted in phytoplankton and bacterial standing stocks increasing faster than in the standard simulation, and the converse was true when $V_{\text{max}}$ was halved. Doubling the ingestion rate, $I_{\text{max}}$, of predators allowed small predators to attain large standing stocks, but large predators did not flourish, because the fast predation rate prevented their phytoplankton prey from increasing. When $I_{\text{max}}$ was halved, the durations of the phytoplankton and bacterioplankton blooms increased. The magnitudes of standing stocks were affected by the values of the respiration rate parameters $R_V$ and $R_r$, as would be expected. When the respiration rates of predators were doubled, the durations of the blooms of their prey increased. Thus the parameters that affect predation rates or predator standing stocks influence the time scales of prey population fluctuations. Altering the value of the allometric exponent from the assumed value of $-0.25$ (Moloney and Field, 1989) had a small effect on standing stocks. When $b$ was increased to $-0.17$, small organisms were favoured, because their rate parameters were faster relative to those of large organisms. The reverse was true when $b$ was decreased to $-0.33$. Largest organisms then had the fastest relative rates, and standing stocks of net-
Table VII. Summary of effects that may be achieved in simulations by altering the values of certain parameters of the model (note that the 'effects' may occur in nature if some factor other than those included in the model were to influence the 'sensitive' parameters)

<table>
<thead>
<tr>
<th>Effect</th>
<th>Sensitive parameter(s) and/or assumptions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Change the values of standing stocks</td>
<td>Change the values of rate parameters</td>
</tr>
<tr>
<td></td>
<td>Change the values of absorption efficiencies A</td>
</tr>
<tr>
<td>Change bacteroplankton standing stocks</td>
<td>Change the values of PER</td>
</tr>
<tr>
<td></td>
<td>Include 'refuge' densities (see text for explanation)</td>
</tr>
<tr>
<td>Change the relative magnitudes of</td>
<td>Change the growth rates of pico-phytoplankton</td>
</tr>
<tr>
<td>standing stocks</td>
<td>Change relative sizes of starting values</td>
</tr>
<tr>
<td></td>
<td>Assign relatively larger carbon values to small organisms than large organisms (use non-linear wet mass:carbon conversion functions)</td>
</tr>
<tr>
<td>Accelerate or delay the rates of bloom</td>
<td>Change the values of nitrogen uptake rates $V_{\text{max}}$</td>
</tr>
<tr>
<td>'increases'</td>
<td>Change factors affecting $N$ uptake rates $V$ (i.e. change $N$ concentrations and/or $K_N$ values)</td>
</tr>
<tr>
<td>Change the durations of 'blooms'</td>
<td>Change the values of absorption efficiencies $A$</td>
</tr>
<tr>
<td></td>
<td>Drastically alter the magnitudes of starting values</td>
</tr>
<tr>
<td>Stabilize predator--prey oscillations</td>
<td>Change the values of maximum ingestion rates</td>
</tr>
<tr>
<td></td>
<td>Change factors affecting ingestion rates $I$ (change prey concentrations and/or $K$ values)</td>
</tr>
<tr>
<td></td>
<td>Change the respiration rates of heterotrophs $R_1$</td>
</tr>
<tr>
<td></td>
<td>Change the absorption efficiencies $A$</td>
</tr>
<tr>
<td></td>
<td>Include diurnal effects</td>
</tr>
</tbody>
</table>

phytoplankton and microzooplankton increased, whereas the other biotic components decreased.

The half-saturation constants in the nitrogen uptake function (equation 2) and the ingestion function (equation 8) are calculated using two parameters for each function (Table III). The effects of doubling and halving these parameters were compared with output of the standard simulation. Changing the nitrogen uptake parameters had very little effect, whereas altering the values of the ingestion parameters had a pronounced effect. When the ingestion parameters were altered in such a way as to make the net effect one of increasing predation rates (i.e., $iK_{s1}$ and $iK_{s2}$ were halved, see Table III), the most obvious effect was to decrease the standing stocks of net-phytoplankton and their meso-zooplankton predators. When these parameters were doubled, the standing stocks of net-phytoplankton and meso-zooplankton increased. Only these two components were affected substantially, indicating that in the standard simulation grazing is an important factor limiting net-phytoplankton growth.

Absorption efficiencies determine the proportion of ingested food that may be used for maintenance and growth. When the $N$ absorption efficiencies ($A$) of heterotrophs were altered, the effects were predictable. A reduced efficiency of 45% slowed down predation rates because predator standing stocks took longer
to increase. Furthermore, the maximum standing stocks of predators were reduced. Conversely, the maximum possible (see below) absorption efficiency of 88% increased predation rates and predator standing stocks, whereas an efficiency of 60% resulted in an effect intermediate between the previous two. Thus, as $A$ decreases the durations of the blooms of the biotic components increase, and the lag before they develop decreases. N absorption efficiencies >88% could not be used, because they resulted in the unrealistic accumulation of carbon in certain model components (see below for details).

Changing the value of PER affected only the bacterioplankton population, which increased when PER was increased, because more carbon (the limiting nutrient for bacterioplankton growth at the start of the standard simulation) was made available. However, for much of the simulation nitrogen was the limiting nutrient for bacterioplankton growth, so changing the value of PER did not substantially affect simulation results.

(ii) Sensitivity to initial values. Initial values assigned to standing stocks at the start of each simulation may be important in determining model output. A number of simulations were executed in which the initial biomass spectra were altered. There were some differences (mainly quantitative) between the outputs of different simulations. These included changes in the magnitudes of standing stocks and in the time scales of model-population increases. The size class that was affected most by altering initial values was the net-phytoplankton size class, which took a long time to increase when initiated with a small standing stock. Consequently, the meso-zooplankton size class which preys on the net-phytoplankton and micro-zooplankton had to rely almost exclusively on the latter for food, depressing the growth of the meso-zooplankton. In a simulation in which new N pools are not renewed, i.e. when new N concentrations decrease to zero, starting values assigned to the net-phytoplankton will be important. It was found that small changes in the initial values of the small size classes in the standard simulation altered the response of the model. The small size classes are predator-controlled to a large extent, and the dynamics of any size class depends on the dynamics of the size classes above and below it in the 'food chain'. 'Seeding' effects can therefore be very important in the standard simulation.

(iii) Sensitivity to functional form. Linear conversions have been used to convert wet mass to C for autotrophs and heterotrophs in the standard simulation. However, volume:carbon relationships for phytoplankton are non-linear, and the following relationships have been estimated for diatoms:

$$W \text{ (pg C)} = 0.378 \, V(\mu m^3)^{0.758} \text{ (Strathmann, 1967)}$$

$$W \text{ (pg C)} = 0.26 \, V(\mu m^3)^{0.74} \text{ (Taguchi, 1976)}$$

and for non-diatom phytoplankton:

$$W \text{ (pg C)} = 0.347 \, V(\mu m^3)^{0.866} \text{ (Strathmann, 1967)}$$
The non-linear equations of Strathmann (1967) are widely used to calculate phytoplankton C from cell volumes, whereas linear conversions commonly are used for heterotrophs (e.g. Rodriguez and Mullin, 1986). Because the model uses size classes and not weight classes, it is confusing to use different conversions. Heterotrophs could then ingest autotroph and heterotroph prey of the same physical size but with different C masses. Furthermore, allometric equations typically use C masses as an indicator of organism size, and autotrophs and bacteria of the same physical size would have different C masses and thus different physiological rates. The effect of using the assumed linear conversion for all groups was compared with a simulation in which equation (12) was used for autotrophs and heterotrophs. In the simulation the standing stocks of small organisms increased, whereas those of large organisms were depressed. The non-linear conversion resulted in increased C masses for small organisms, whereas large organisms were assigned smaller C masses, the changeover occurring at 1066 μm³ (12.7 μm ESD). If a non-linear conversion were used for phytoplankton and a linear conversion for all heterotrophs, as is usually the case, this would substantially affect the differences in uptake rates between similar-sized autotrophs and bacteria. Thus C masses in the standard simulation are underestimated for small autotrophs and overestimated for large autotrophs, resulting in an overestimate of growth rates of pico-phytoplankton in the standard simulation. Consequently, equation (12) has henceforth been adopted as the standard conversion from volume to carbon for autotrophs and bacterioplankton. The reason why autotrophs should display a pronounced non-linearity between volume and C mass, whereas heterotrophs apparently do not (see Gorsky et al., 1988), is unclear. Studies by Putt and Stoecker (1989) indicate that the standard conversion of 0.07–0.11 pg C μm⁻³ for ciliates also is an underestimate, and the value should be at least twice as large. It is possible that a non-linear conversion should be applied to all organisms, or at least to unicellular heterotrophs as well as phytoplankton, but such a conversion has not yet been calculated for heterotrophs, possibly because a large enough size range has not been studied.

Predators often display a threshold response in their feeding behaviour; feeding may cease when the density of prey items falls below a threshold value (e.g. Frost, 1975). Such a functional response has been included in the structure of the ingestion functions in the simulation model (equation 8), but the threshold concentrations (or ‘refuges’) were set to zero in the standard simulation, to reduce model complexity. However, the effect of including a threshold density of 5 mg C m⁻³ for ingestion of all prey size classes was investigated, and it was evident that the simulation output stabilized when threshold densities were included, and the fluctuations in model standing stocks were dampened. This result is more realistic than that of the standard simulation, and henceforth, small threshold densities (Table VII) have been included in the model (Moloney et al., 1991). However, the inclusion of thresholds in the ingestion function of the model may result in the unrealistic ‘creation’ of matter, because populations maintained at refuge biomasses continually drop below these biomasses during computations for each time step (through respiration, excretion, etc.), and are
then reinstated by the model. In the process, biomass losses from living compartments are added to abiotic pools, and the same biomass reinstated to the biotic compartment by the computer program, thereby artificially adding N and C to the model environment. In nature, energy storage mechanisms and the development of dormant stages at times when food is scarce may circumvent these problems, but it was impractical to include such detail in the model. The larger the refuge biomass, the greater the respiratory and excretory losses (which are functions of biomass, equations 9 and 10). To minimize this unrealistic effect, we have deliberately used very small values for the refuge biomasses (Moloney et al., 1991).

(iv) Sensitivity to model structure. C and N flows through the biotic compartments were related by assuming that each compartment maintained a constant C:N ratio. Thus C and N were excreted and/or egested in amounts that kept the C:N ratios of donor and recipient compartments constant. However, relating the flows in this manner can result in inconsistencies, which are not immediately apparent. For example, in the model, zooflagellates (C:N = 4.5) ingest pico-phytoplankton and bacterioplankton. Assuming an absorption efficiency A of 90%, the carbon and nitrogen fluxes through the zooflagellate compartment can be calculated in two ways (Figure 8). Assuming a C absorption efficiency of 90% (Figure 8a), the amount of pico-phytoplankton carbon (C:N = 6) absorbed by zooflagellates is estimated to be 5.4 units for every six units ingested. In order to maintain a constant C:N ratio of zooflagellates, the amount of nitrogen absorbed must be in the correct proportion. Thus absorbed pico-phytoplankton N is 5.4 × 4.5 = 1.2 units, a greater amount than the 1 unit that was ingested. If an N absorption efficiency of 90% is used, 0.9 N units of bacterioplankton (C:N = 4) are absorbed (Figure 8b). To maintain a C:N ratio of 4.5 for zooflagellates, a corresponding amount of C (i.e. 4.5 × 0.9 = 4.05 units C) must be absorbed, and C is 'created' in this calculation. In general, N absorption is often more efficient than C absorption (Dagg, 1976), so the calculation in Figure 8(b) is probably more realistic than the one in Figure 8(a), provided the N absorption efficiency is not larger than the ratio of the C:Ns of the prey and predator (respectively 4 and 4.5, setting a maximum limit of 88.9% for A in Figure 8b). Thus when calculating mass budgets where prey and predator have different C:N ratios, caution should be exercised, and careful checks made to see that the second law of thermodynamics is not violated.

Detrital material is assumed to sink rapidly in all simulations, and is lost from the model environment. Live phytoplankton are buoyant, and sink much less rapidly than dead material (Figures 4 and 5). Sinking losses of living phytoplankton were not included in the standard simulation, but the effect of including them was assessed by assuming a 20 m deep euphotic zone, and calculating the rate of loss of autotroph C and N through sinking (equation 11). Phytoplankton sinking losses have very little effect on standing stocks of autotrophs <20 μm, and changing the values of the sinking parameters has no further effect. This is because the small autotrophs have very slow sinking velocities (Table IV). However, net-phytoplankton and their grazers are
affected dramatically by the inclusion of sinking losses, with standing stocks barely increasing before decreasing to zero. Thus sinking of large-celled phytoplankton is likely to be an important factor in the vertical flux of living organic material in a stable water column. The sinking velocities used here are applicable only to a water body in which water densities are uniform and there is no upward transport, so the loss rates are not completely realistic. However, the result is consistent with that of Michaels and Silver (1988), who found that net-phytoplankton were the dominant living source of export material from oceanic systems.
All processes in the model are assumed to occur continuously, i.e. there are no diurnal effects. Obviously this is not realistic. The assumption that photosynthesis is averaged over a day gives an indication of the magnitude of primary production, but does not reflect the true dynamic pattern. The effect of including a simple diurnal pattern was assessed by assuming that carbon is fixed by autotrophs for one half of every day, but all other processes remain unchanged throughout the day. This resulted in a jagged, diurnal pattern with fluctuations occurring on a time scale of <1 day being superimposed on the relatively smooth fluctuations of model standing stocks over periods of >1 day (e.g. Figure 7b and c). The effect was more pronounced for small organisms than for large organisms. For example, pico-phytoplankton oscillated more frequently than in the standard simulation. Because no carbon was fixed during the ‘night’ but respiration continued, autotroph standing stocks took longer to increase than in the standard simulation, which also affected the rate of increase of heterotroph grazers. The model functions and parameters are for daily not hourly changes, and it is inappropriate to introduce the detail required to simulate diurnal effects in the model at this stage, given its limited resolution.

In the standard simulation, the logarithmic base used to calculate size class limits was set to 10, and traditional size groupings were used. Additional simulations were carried out in which the number and size range of size classes in the model community was altered. By increasing the number of size classes within a fixed size range, the structure of the model became more complex. Predators were able to utilize more than one size class, and competition for nitrogen between phytoplankton size classes became more pronounced. Successions involving different sizes of organisms occurred, but not necessarily in a sequence from small to large organisms.

It is often assumed that predators are roughly an order of magnitude larger than prey items (Sheldon and Kerr, 1972; Sheldon et al., 1977; Azam et al., 1983; Moloney and Field, 1985), which would support the use of a log-scale of 10 for separating size fractions in the plankton. In order to find out whether this general rule is supported by empirical evidence, prey sizes for different sizes of predator were obtained from the literature, and average ESDs were estimated for each predator and prey species. ‘Prey’ in this context was assumed to comprise all potential food items, and includes autotrophs, heterotrophs and detritus. Data used are summarized in Table VIII. The ESD of the copepod *Pseudocalanus minitus* (Table VIII) was estimated by assuming a wet mass:carbon conversion of 7% (Peters, 1983), and approximate volumes of the three copepod species obtained from Cowles (1979) were calculated using dimensions estimated from diagrams in Newell and Newell (1963). Relationships between individual predator and prey sizes were established as simple proportions (Table VIII). Minimum, optimum and maximum prey:predator size ratios (mean ±95% CI) were calculated as 0.04 ± 0.04 (n = 15), 0.06 ± 0.04 (12) and 0.13 ± 0.04 (13) respectively. Thus each predator ingests, on average, prey organisms ranging from 4 to 13% of its body size calculated in linear dimensions, or from 0.002 to 0.06% of predator mass, the latter range spanning
### Table VIII. Summary of predator sizes (μm ESD) and estimated minimum, optimum and maximum food-particle sizes (μm ESD)

<table>
<thead>
<tr>
<th>Predator</th>
<th>Prey size</th>
<th>Ratio&lt;sub&gt;min&lt;/sub&gt;</th>
<th>Ratio&lt;sub&gt;opt&lt;/sub&gt;</th>
<th>Ratio&lt;sub&gt;max&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monostega sp. (μFlag)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-</td>
<td>0.07</td>
</tr>
<tr>
<td>Actinomonas sp. (μFlag)</td>
<td>5&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1-2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-</td>
<td>0.2-0.4</td>
</tr>
<tr>
<td>Cyclidium glaucoma (Ci)</td>
<td>10&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.2&lt;sup&gt;f&lt;/sup&gt;</td>
<td>0.4&lt;sup&gt;i&lt;/sup&gt;</td>
<td>2&lt;sup&gt;f&lt;/sup&gt;</td>
</tr>
<tr>
<td>Colpoda steini (Ci)</td>
<td>12&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.4&lt;sup&gt;f&lt;/sup&gt;</td>
<td>1.1&lt;sup&gt;e&lt;/sup&gt;</td>
<td>2&lt;sup&gt;f&lt;/sup&gt;</td>
</tr>
<tr>
<td>C. cucullus (Ci)</td>
<td>18&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.2&lt;sup&gt;f&lt;/sup&gt;</td>
<td>0.4&lt;sup&gt;e&lt;/sup&gt;</td>
<td>1&lt;sup&gt;f&lt;/sup&gt;</td>
</tr>
<tr>
<td>Glaucoma scintillans (Ci)</td>
<td>35&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.1&lt;sup&gt;f&lt;/sup&gt;</td>
<td>0.4&lt;sup&gt;e&lt;/sup&gt;</td>
<td>4&lt;sup&gt;f&lt;/sup&gt;</td>
</tr>
<tr>
<td>Colpidium campylum (Ci)</td>
<td>35&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.1&lt;sup&gt;f&lt;/sup&gt;</td>
<td>0.4&lt;sup&gt;e&lt;/sup&gt;</td>
<td>2&lt;sup&gt;f&lt;/sup&gt;</td>
</tr>
<tr>
<td>C. colpoda (Ci)</td>
<td>40&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-</td>
<td>0.4&lt;sup&gt;e&lt;/sup&gt;</td>
<td>-</td>
</tr>
<tr>
<td>Euplotes moebius (Ci)</td>
<td>50&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1&lt;sup&gt;f&lt;/sup&gt;</td>
<td>5&lt;sup&gt;e&lt;/sup&gt;</td>
<td>10&lt;sup&gt;f&lt;/sup&gt;</td>
</tr>
<tr>
<td>Styloynchia mytilus (Ci)</td>
<td>50&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-</td>
<td>10&lt;sup&gt;e&lt;/sup&gt;</td>
<td>-</td>
</tr>
<tr>
<td>Blepharisma americanum (Ci)</td>
<td>60&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1&lt;sup&gt;f&lt;/sup&gt;</td>
<td>6&lt;sup&gt;e&lt;/sup&gt;</td>
<td>10&lt;sup&gt;f&lt;/sup&gt;</td>
</tr>
<tr>
<td>Paramecium caudatum (Ci)</td>
<td>70&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.2&lt;sup&gt;f&lt;/sup&gt;</td>
<td>1&lt;sup&gt;e&lt;/sup&gt;</td>
<td>6&lt;sup&gt;f&lt;/sup&gt;</td>
</tr>
<tr>
<td>Bursaria truncatella (Ci)</td>
<td>400&lt;sup&gt;a&lt;/sup&gt;</td>
<td>10&lt;sup&gt;f&lt;/sup&gt;</td>
<td>35&lt;sup&gt;e&lt;/sup&gt;</td>
<td>80&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td>Pseudocalanus minutus (Co)</td>
<td>570&lt;sup&gt;a&lt;/sup&gt;</td>
<td>4&lt;sup&gt;d&lt;/sup&gt;</td>
<td>25-57&lt;sup&gt;c&lt;/sup&gt;</td>
<td>100&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>C. chilenensis (Co)</td>
<td>880&lt;sup&gt;f&lt;/sup&gt;</td>
<td>12&lt;sup&gt;c&lt;/sup&gt;</td>
<td>-</td>
<td>57&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Centropages brochiiatus (Co)</td>
<td>880&lt;sup&gt;f&lt;/sup&gt;</td>
<td>10&lt;sup&gt;c&lt;/sup&gt;</td>
<td>-</td>
<td>50&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Eucalanus inermis (Co)</td>
<td>920&lt;sup&gt;f&lt;/sup&gt;</td>
<td>8&lt;sup&gt;c&lt;/sup&gt;</td>
<td>-</td>
<td>57&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a</sup>Ratios of food size: predator size are given as Ratio<sub>min</sub>, Ratio<sub>opt</sub> and Ratio<sub>max</sub>.<sup>b</sup>μFlag, microflagellates; Ci, ciliates; Co, copepods. Newell and Newell (1963); Poulet (1973); Cowles (1979); Figures 6 and 7 in Fenchel (1980b), Fenchel (1980c), Fenchel (1984).
some two orders of magnitude. Optimum prey sizes are estimated to be 6% of predator linear dimensions or 0.006% of body mass. Thus, although the general 10% rule is not unrealistic, on a more detailed scale it appears that a log-scale of 5 may be more appropriate than one of 10 when considering interactions in plankton communities. In practical terms the log-scale of 5 is preferred because it allows for the separation of autotrophic and heterotrophic nanoflagellates from other ‘nanoplankton’. Nanoflagellates are generally <5 µm (Fenchel, 1982), whereas ciliates, for example, can range from ~10 to >50 µm (Fenchel, 1980c). These two groups play different roles in the marine pelagic environment.

Adopting a log-scale <5, e.g. 2, resulted in an unmanageable number of size classes. Organism size is probably not continuous in nature. In benthic environments, it has been found that sizes of organisms fall into discrete size categories (Schwinghamer, 1981; Warwick, 1983), and this also may be true for pelagic environments (e.g. Sprules et al., 1983). A log-scale of 5 appears to be realistic in separating trophic categories in the plankton, although further, detailed studies are required.

Discussion

The structure of the model described here is largely hypothetical; the model is essentially a synthesis of hypotheses describing important biological processes occurring in plankton communities, using organism size as a basis. This is the essence of a mechanistic-type approach (Price, 1986; Schoener, 1986), in which a number of processes affecting size classes (or populations) are modelled (e.g. nitrogen uptake and respiration), as well as interactions between size classes (e.g. predation), and the resultant ecosystem/community structure assessed. However, by using organism size as the basis for structuring the communities and determining the model parameters, the model has been made more general than is usually the case for a reductionist model (Belovsky, 1986). This combination of reductionism and holism (Platt et al., 1981) makes the model particularly useful for exploring the systems properties of plankton communities.

There are obvious drawbacks to generalizing biological and ecological processes. For every general rule that is formulated, there will always be a species or group of organisms which have specialized in such a fashion as to negate the rule. In the model presented in this paper, maximum rates of transfer processes have been calculated using allometric equations (Moloney and Field, 1989), and factors modifying the maximum rates, e.g. half-saturation constants and sinking rates, which are also body-size dependent, have been calculated using regression models described above. These empirical relationships between organism size and various model parameters will not apply in all cases. However, they are not intended for use by biologists studying details of the biology of individual species. They have been developed to assist us in estimating parameters for use in ecological models of plankton communities. These size relationships are objective estimators of ecological parameters, and
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therefore have wide-ranging applications in the study and understanding of pelagic ecosystems. By formulating and quantifying the relationships, the estimation of parameters for use in ecological models has been made a more rigorous process than was common in the past.

The behaviour of the model populations has been shown to be complex and sometimes unpredictable—characteristic features of biological systems. This is partially the result of using non-linear functions to describe some of the flows of C and N through the model community, in contrast to most other whole-system models, which usually abandon non-linearity because linear transfers between state variables are analytically easier to handle. However, this may result in over-simplification, and it is believed that non-linearity is an integral part of complex systems (Prigogine, 1987). The advantage of our approach to analysing complex, dynamic biological systems is that it is possible to incorporate many complex interactions in the analysis (see Lehman, 1980; Lehman and Sandgren, 1985; Pengerud et al., 1987), and although the model becomes more complex, it becomes more realistic on a time scale of interest to plankton ecologists (see DeAngelis, 1988).

In the standard simulation, the model was deliberately simplified to test the validity of the size-based approach to modelling plankton communities. Furthermore, we only used parameter values for which objective, size-based estimates were available. It is therefore not surprising that the output is not fully realistic. Oscillations in population standing stocks are commonly observed in nature (see Moloney et al., 1991), but the magnitude and frequency of these oscillations in the standard simulation is probably not realistic. Thus the very large, fluctuating standing stocks of pico-phytoplankton and heterotrophic nanoflagellates, and the near disappearance of bacterioplankton from the model system for considerable periods would not be expected in nature. However, by assigning values to a few parameters identified by the sensitivity analysis as being important (Table IX), a more realistic output than that of the standard simulation can be obtained (Figure 9). In these results the standing stocks of the pico-phytoplankton (0.2–2 μm) have been reduced by including a senescence rate (Figure 9a and b), and additional ‘blooms’ of bacterioplankton and nanophytoplankton occur as a result of including a small refuge biomass. Bacterioplankton standing stocks attain larger values than in the standard

<table>
<thead>
<tr>
<th>Assumption/parameter value</th>
<th>Standard</th>
<th>Sensitivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Refuge biomasses (mg C m⁻³)</td>
<td>0</td>
<td>0.5 (for each model size class)</td>
</tr>
<tr>
<td>Sinking losses of phytoplankton (% day⁻¹)</td>
<td>None</td>
<td>0.003 (0.2–2 μm), 0.05 (2–20 μm), 5 (20–200 μm)</td>
</tr>
<tr>
<td>Phytoplankton senescence (day⁻¹)</td>
<td>0</td>
<td>Assumed 10% of N uptake rate</td>
</tr>
<tr>
<td>Lysis of senescent phytoplankton (% day⁻¹)</td>
<td>0</td>
<td>50%</td>
</tr>
</tbody>
</table>
Fig. 9. Comparison of output from the standard simulation with output from a sensitivity analysis simulation in which various parameters have been altered (see Table IX).
simulation (Figure 9c and d), because additional organic nutrient pools are introduced to the model environment through senescence and lysis of model phytoplankton. These DOC and DON pools are used exclusively by bacterioplankton. Thus the magnitudes of the oscillations of the standard simulation may be reduced by assigning 'realistic' parameter values to sensitive processes.

The model focuses on the dynamics of biological processes occurring in the plankton. Consequently, the physical environment was kept as simple as possible. The effects of light and nutrients other than nitrogen on the growth of phytoplankton were kept constant. Furthermore, the physical structure of the water body was assumed to be stable, whereas turbulence and other physical factors may be important in determining interactions within a plankton community. However, despite these discrepancies, some important features of system behaviour are apparent in the output of the standard simulation. The fluctuations displayed by the model populations decrease in frequency and increase in duration as the sizes of the organisms increase. For example, in the standard simulation net-phytoplankton undergo one bloom of ~20 days duration, whereas pico-phytoplankton bloom seven times, with each bloom lasting ~1 day (see Figure 6). This effect in which different time scales apply to different size fractions of the plankton is important, and one that often may be overlooked when designing and carrying out sampling programmes in the plankton. Similar short-term fluctuations have been noted in ammonium uptake and regeneration rates by plankton organisms <2 μm (Wheeler et al., 1989).

The size-basis of the simulation model makes it a true generic representation of the dynamics of plankton communities. It is very simple to alter the number of size classes and the size range of each size class in the model (e.g. by changing the logarithmic base from 10 to 5). Because interactions are determined on a size basis, the necessary links between different components of the model are altered by the computer program when the number of size classes is changed. Furthermore, although there are a large number of parameters in the model, most parameters are objectively estimated from size relationships, and there is no need to estimate new parameters for each new component of the model. It has been shown elsewhere (Moloney, 1988) that the model is robust with respect to most of its parameters, because most changes that occur on altering parameter values are only quantitatively, not qualitatively different, and are predictable. The most important factors to which model output is sensitive are the shape of the initial biomass spectrum, the values of threshold concentrations in the ingestion function, and wet mass:carbon conversion functions (Table VII). Thus the model can be fine-tuned by changing values of these parameters. In addition, the model can be tuned to mimic field measurements, by altering parameter values to allow for the effect of factors not included in the model (see Figure 9; Field et al., 1989; Painting 1989; Moloney and Field, 1991; Moloney et al., 1991). In this regard, the parameters that are most likely to be useful in mimicking environmentally induced changes are maximum growth, ingestion and respiration rates, which should change with different environmental temperatures, and nutrient concentrations and input rates, which allow for differences in the nutrient regimes among different ecosystems.
Simulation models may be used as tools to understand and analyse system behaviour (see Field et al., 1989; Wulff and Ulanowicz, 1989; Moloney and Field, 1991). Furthermore, they can be useful in assisting in the interpretation of data from field studies (see Painting, 1989). This model, based primarily on body size criteria, obviates many of the problems of parameter estimation common in ecological modelling studies. As a result, model output can be validated against any system study or data series, because parameters in the model are not specifically related to any ecological system. The model can therefore be applied to any plankton community, to test hypotheses regarding structure and functioning of different systems. This is a major advantage over most previous models which are largely area or system specific, and whose predictive capacities are often in question. In this regard, predictions made by the model allow rigorous tests of hypotheses and, more pragmatically, model predictions can be used to direct field research, to either invalidate or further strengthen current theory.

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