

# **Fjordic ecosystem models**

by

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in the Department of Statistics and Modelling Science**

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Finally I would like to thank my parents and the rest of my family for their support over the past few years.

## Abstract

In this thesis a number models of fjordic pelagic ecosystems are developed, tested and analysed.

In Part 1 we develop a strategic simulation model in which we attempt to represent all the major processes in a spatially and temporally consistent way. The result is a model of sufficient detail as to allow agreement with data from the Killary Harbour pelagic ecosystem, yet which is sufficiently simple to allow us to understand what are the key process which govern its behaviour.

From the insights gained from this model, we develop, in Part 2, a revised model which is capable of quantitative agreement with the observed nutrient and plankton dynamics of four contrasting fjordic systems.

In the conditions which prevail in fjordic systems in the western British Isles we find that the flow of nutrient between the fjord and the external coastal water is the critical flux supplying nutrient for phytoplankton growth. We find this flux is sufficiently large that growth is almost always limited by the availability of light rather than nutrients.

Although the persistence of the ecosystem is thus determined by this flux, and although primary productivity is mostly determined by the availability of light; for much of the year primary production is controlled by zooplankton grazing.

Utilising this understanding, we develop a model of strategic simplicity which, although it does not contain a representation of dissolved nutrients, is still capable of quantitative agreement with the observed data.

Finally in assessing what our findings mean for disturbance to these ecosystems, we conclude that the critical disturbances are those which affect the zooplankton grazing rate.

## Preface

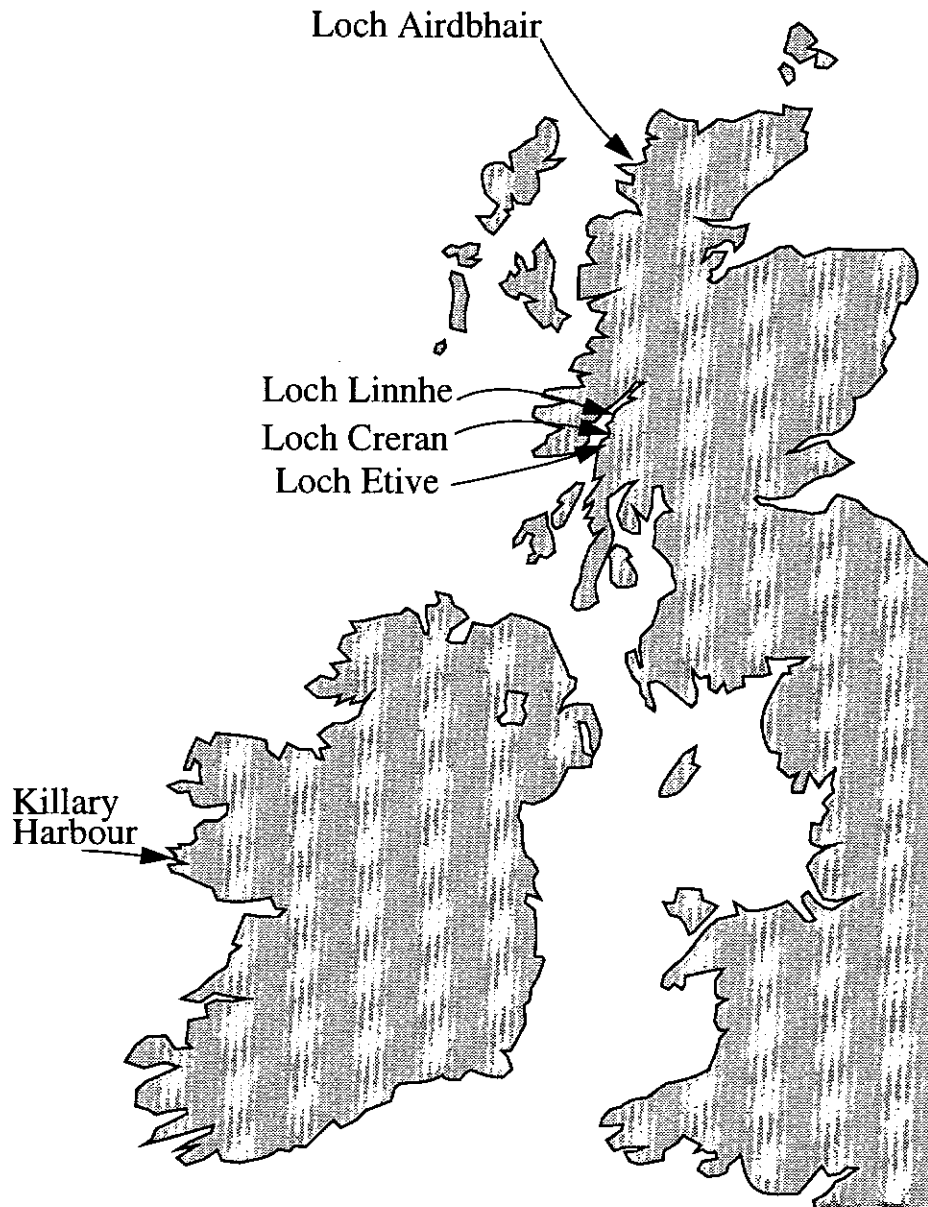
For a considerable time the sea lochs of the west coast of Scotland have been sustainably exploited as a fisheries resource. In recent years as exploitation techniques have become more sophisticated, these systems have become over exploited and as a consequence much of the pelagic and demersal fish together with some benthic invertebrate populations have come under severe pressure.

The development of human activities on, or in the vicinity of, sea-lochs: marine farming, industrial activities, quarrying, agricultural etc. have introduced disturbances which may have consequences for lower trophic levels. Fears have thus been raised that the phytoplankton and zooplankton, which comprise most of the biological activity in a sea loch, will suffer a similar fate to the higher trophic levels.

To address these concerns objectively we must first understand how the ecosystem functions in its unperturbed state. This requires us to quantify how the basic limiting resources, nutrients, light etc., are utilized by and made available to, the various biota. The only practical mechanism available to us for doing this is to build a mathematical model of the ecosystem. To establish its validity we must test any such model against a dataset from a real sea loch - preferably against a number of such datasets.

This thesis reports our attempts to achieve this understanding. Much of

this work is also reported elsewhere (Ross et al. 1992, Ross et al. 1993a, Ross et al. 1993b). It consists of two parts. The first part reports the development and analysis of a "Strategic simulation model" of a sea-loch water column ecosystem - a preliminary model developed and used, to advise on a field programme conducted by the SOAFD Marine Laboratory, Aberdeen on Loch Linnhe (a large, relatively undisturbed, two-basin fjordic sea-loch) throughout 1991. The second part develops this model to the point where it can be used to explain differences between the dynamics of quite different sea-loch systems (by changing system specific parameters only). We incorporate features into this model potentially capable of explaining more subtle differences between these systems. We further develop a minimal 'clone' of this model in Chapter 6. Finally in Chapter 7, we assess the potential consequences of various types of disturbance on these ecosystems.



**The locations of the sea-lochs discussed in this thesis.**

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## **Part 1**

### **A Strategic simulation model of a sea-loch ecosystem**

## Introduction

Our intention in this work is to do a quantitative assessment of the flow of nutrients both within a sea loch and between the loch and connected systems. In so doing we hope to gain a broad understanding of the mechanisms underlying the ecosystem dynamics. To achieve this we need to develop a mathematical model of the ecosystem.

In the development of such models there is an inherent conflict between realism and mathematical tractability. This has often led to some uneasy compromises. Those models which are designed on the basis of realism incorporate a detailed description of both the biological and physical dynamics of a complete ecosystem (Baretta and Ruardij 1987; Nixon and Kremer 1977; Kremer and Nixon 1978; Beyer 1981; Radford 1979; Asknes and Lie 1990). They are usually completely impenetrable by analytic techniques, and moreover raise serious difficulties in their parameterisation. They are frequently so demanding computationally that even comprehensive numerical exploration of their properties is, in practice, impossible. In addition the difficulty of obtaining adequate spatially and temporally resolved data, often results in a model which is effectively untestable. Taken together these features imply that such models are not well adapted to reveal the dynamic mechanisms underlying any predicted behaviour.

A second strategy is to focus on those aspects of the ecosystem which the modeller considers most significant in relation to the question asked. These models provide a fully dynamic description of only a part of the overall system and describe the rest by static "environmental" parameters (e.g. Steele and Frost 1977, Parsons & Tessler 1986, Tett 1986, Tett et al. 1986, Taylor et al. (1992). Such models can provide significant insight into underlying mechanisms, but the results are frequently dependent on initial or boundary conditions, which are hard to determine with acceptable accuracy.

Another approach (Andersen et al. 1987, Andersen and Nival 1989) is to make a complete ecosystem model of an artificial system such as the CEPEX mesocosms. In such circumstances the modeller has clear information about the relatively small number of functional groups in the ecosystem, is not greatly troubled by spatial inhomogeneities, and has plentiful accurate information against which to test his model. Since mesocosms of necessity exclude all exchange processes, spatial structure, and realistic benthos; their resemblance to their real-world analogs is debatable.

In this work it is our aim to construct a fully dynamic model of a marine ecosystem which, while acceptably realistic, is still simple enough to allow us to achieve an intuitive understanding of its mechanisms. Although much sparser than a full simulation model, such a model is necessarily more complex than a traditional "strategic" model in which analytic tractability is achieved by representing only a small number of dynamic interactions. Thus our model, whilst being analytically intractable, is nevertheless sparse enough for comprehensive numerical investigations to be a practical proposition. We shall refer to such models as "strategic simulations".

Our principal motivation in developing this model was our desire to provide informed advice on a field program on Loch Linnhe (a fjordic loch on the west coast of Scotland) during 1991. This program involved the siting of fixed recording apparatus at various points in and around the Loch Linnhe system; backed up by extensive spatial sampling at regular periods during the year. Our two main aims were to advise on which variables should be measured and on the best locations for the fixed recording apparatus. Thus, in contrast to many large ecosystem models, it was formulated before the collection of the data which will ultimately be used to test it.

Although Loch Linnhe is an hydrologically complex two-basin system, we chose to model a single basin and represent the effects of inter-basin coupling heuristically as changes in the environment of the system. This strategy has not only greatly reduced the size and complexity of the model, but also gave us the opportunity to test it against a full year's data on primary and secondary production in Killary Harbour - a single basin system on the west coast of Ireland. The results achieved by this test gave us some confidence in advising on the Loch Linnhe experimental program.

At the time of writing, this program has been completed and the data is currently being processed with a view to testing this model and its successors. Initial results indicate that the field program has benefited substantially from the initial modelling stage.

## Chapter 1 - The Model

### 1.0 Introduction

Having identified that our principal aim is to understand how the system functions, the strategy follows directly. In order to assess the validity of the model used, it must be capable of quantitative comparison with real systems. Yet there is limited value in a model which though behaving in a similar manner to a real system, is so complex it cannot reveal the mechanisms underlying its behaviour. Thus the compromise between sufficient detail for data comparison and sufficient simplicity for model understanding is the key element in the model design.

In this context it is clear that the inclusion of dynamically unimportant detail is undesirable. Some of the existing understanding and information on which model design relies, comes from systems with quite different scale characteristics and may therefore be inappropriate. Indeed a representation of the system that uses inconsistent spatial and temporal scales or biological aggregation, is not only inappropriate, it can potentially be misleading.

To get a good quantitative comparison requires a reasonably accurate description of the important processes. Often the best available information on such processes is obtained from work on different systems and in some cases from the laboratory. Whether or not this is a barrier to a good quantitative comparison depends on the degree to which the critical infor-

mation is scale independent. In any case a model of this type is a good vehicle for exploring the possibilities.

### **1.1 The state variables**

There is considerable evidence that the most commonly limiting nutrient for marine phytoplankton growth is nitrogen Dugdale (1967). In the context of the above stated strategic objectives a natural simplifying assumption is therefore to neglect other nutrients such as phosphorus and silicon, which may in certain circumstances be growth limiting. It is of course impossible to tell whether or not such a simplification is justified in sea-lochs without undertaking a quantitative assessment of the fluxes of these nutrients. We can however obtain some guidance from the time series of phosphate and nitrate measured by Solarzano & Ehrlich (1977a&b), Solarzano & Ehrlich (1979a) and Jones (1979) in Lochs Etive and Creran on the west coast of Scotland.

The data for nitrate shows a very pronounced annual cycle with much lower levels during the summer than the winter. On the other hand levels of phosphate show a markedly less seasonal influence. In addition the mean levels of phosphate are higher with respect of the typical phosphorus to carbon ratio observed for marine phytoplankton than nitrate levels are to the typical nitrogen to carbon ratio. The data of Roden et al. (1987) for Killary Harbour show similar high standing crops of silicates and phosphates with respect to nitrates.

We therefore choose nitrogen as the as the most representative limiting nutrient to phytoplankton growth. Dissolved inorganic nitrogen is found in three basic forms in the marine environment - nitrate, nitrite and ammonium. Nitrate however is the dominant form in sea-lochs (Solarzano and Ehrlich 1977a&b) and hence we choose to neglect the internal differentiation of the inorganic nitrogen pool on the grounds of simplicity. Nitrogen

is taken up by the phytoplankton in dissolved inorganic form and is excreted and lost (due to bacterial activity) by the phytoplankton in organic form. A minimal representation of the phytoplankton nitrogen cycle therefore involves three variables: bound organic nitrogen ( $N_p$ ); dissolved inorganic nitrogen (DIN); and dissolved organic nitrogen (DON).

Very little is known about how competition functions in the marine environment. This together with the tendency of simplistic models of competition to display unstable behaviour, suggests that the representation of each trophic group should cover all organisms which compete for the same resources. Thus we choose the functional groups of phytoplankton, zooplankton and carnivores as representing the biological food web.

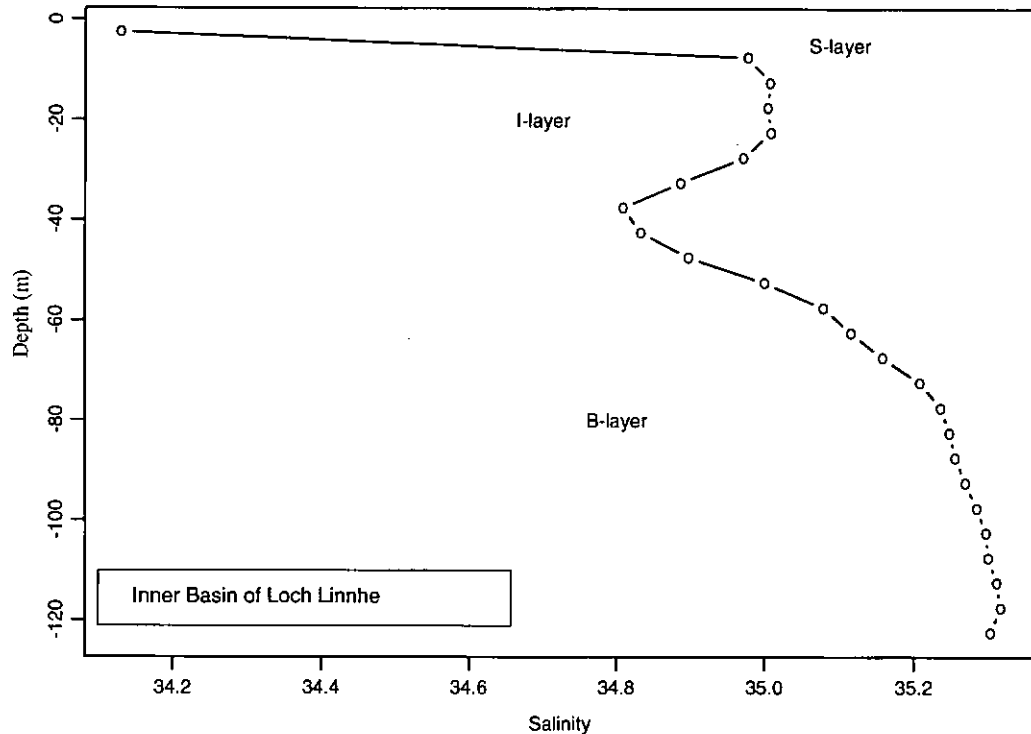
Whereas nitrogen is considered limiting to phytoplankton growth; carbon is generally considered to limit the growth of higher trophic levels. We therefore assume that zooplankton and carnivores are limited by carbon; necessitating the inclusion of the state variables of: phytoplankton carbon ( $C_p$ ); zooplankton carbon ( $C_z$ ) and carnivore carbon ( $C_c$ ). However since we are representing both the carbon and nitrogen cycles, we also need to include zooplankton nitrogen ( $N_z$ ) and carnivore nitrogen ( $N_c$ ) as state variables.

## 1.2 The physical system

The need for simplicity has been a constraint on the number of biological and nutrient variables included in the model. A similar constraint applies to the description of the physical environment in which these variables operate. A fully specified vertical and horizontal model would be not only contain a lot of detail inconsistent with our representation of the biological components, it would seriously undermine the degree to which the model's results can be understood. There are however large water fluxes across the boundaries of the system; raising the possibility that nutrient



fluxes across these boundaries are an important determinant of system behaviour. It is pertinent therefore to represent these effects in a way which accounts accurately for the net flows of nutrient and biological material on the time scales of interest (a few days to a few years) without becoming enmeshed in the complex details of short term tidal flows and eddies.



**Fig.1.1** An example of the vertical salinity profile in the inner basin of Loch Linnhe during August 1990.

Most sea-lochs conform to the classic description of a fjord i.e. have restricting sill at the connecting point with the external coastal water. The sill together with the freshwater run-in dictates the major characteristic of fjordic hydrography: namely a seaward flowing surface layer overlying a lower layer flowing in the opposite direction. In deeper systems there is often a bottom layer of more slowly flushed water at depths considerably greater than the sill depth. The depth of the surface of the sill in fact char-

acterises most strongly the fjordic nature of the system - in a few systems the sill is deep enough (or indeed is non-existent) that the hydrography is typically estuarine (Milne 1972).

The natural layer structure of the system is illustrated in Fig. 1.1 using data from Loch Linnhe during August 1990 (M. Heath pers. comm.). The bottom of the surface (S) layer (at approximately 10m) is clearly seen by the change in salinity gradient. The top of the bottom (B) layer (40-50m), although less distinct, can also be determined by a further change in salinity gradient. The layer lying between these two we term the intermediate (I) layer. The boundary between the S-layer and I-layer is commonly termed the primary pycnocline; the boundary between the I and B layers the secondary pycnocline.

We assume that these layers are well mixed at all times - a drastic simplifying assumption which allows a very simple treatment of the physical processes. Certain factors justify this assumption, within the spatial and temporal scales represented, in loch systems: the restricting sill at the entrance to the loch means a higher current flow over the sill and a higher kinetic energy within the basin of the loch compared to an estuary. In addition there is considerable energy imparted to the system, particularly the S-layer, from the high level of wind induced turbulence typical of these systems. This layer structure together with the hydrodynamic features which we represent in the model is illustrated in Fig. 1.2.

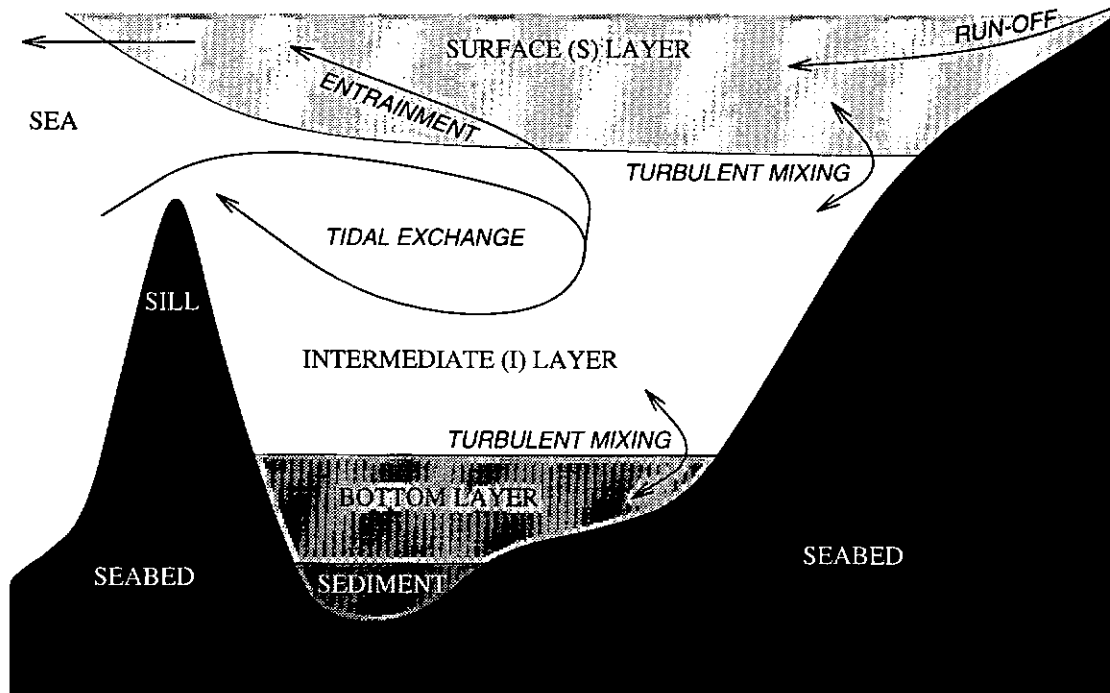


Fig. 1.2. A simple physical model of a sea-loch.

Incoming tidal water is pushed under the less dense surface layer and mixed with the intermediate layer. This tidal inflow moves some I-layer water into the S-layer which in turn pushes an equivalent volume of S-layer water out into the sea - a processes commonly known as entrainment. Freshwater run-off into the S-layer similar displaces a slug of S-layer water into the sea. There is additionally some turbulent diffusion across the pycnoclines owing to the 'discontinuities' in current speed and direction.

In general the bottom layer is held stably in position by its high salinity and consequent high density. However the slow but finite mixing between bottom and intermediate layers implies a slow reduction of salinity and hence stability. Eventually there is sufficient higher salinity coastal water coming across the sill to cause a temporary density inversion, and a consequent breakdown of the lower pycnocline (Fig. 1.3). Such "turnover

events" produce rapid, if temporary, mixing of the bottom and intermediate layers.

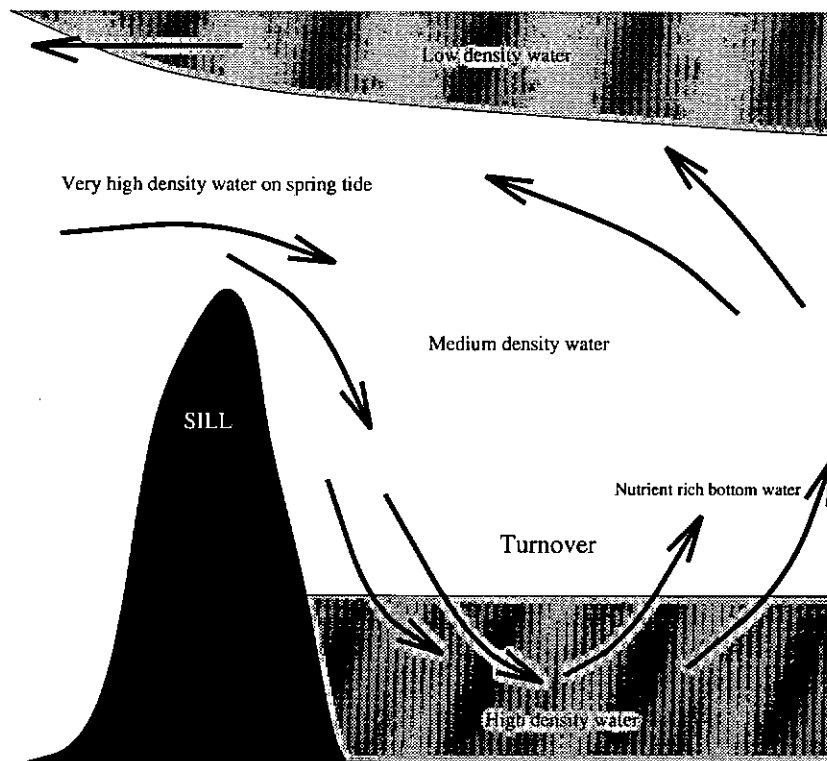


Fig. 1.3. A turnover event caused by an intrusion of high density water on a spring tide.

### 1.2.1 The physical rate equations

We can describe the flow of a material of concentration  $X$  between the various parts of the physical system using simple rate equations.

The average rate of inflow due to tidal flushing from the sea (E) into the I-layer is:

$$W_{XEI} = T_E (X_E - X_I);$$

where  $T_E$  is the total volume of water carried over the sill into the I-layer and  $X_E$  and  $X_I$  are the concentrations of  $X$  in the external coastal water and

in the I-layer respectively.

We assume that a proportion  $\beta$  of this tidal inflowing water is entrained into the S-layer resulting in a total entrainment rate for X of

$$W_{XIS} = \beta T_E (X_I - X_S).$$

Similarly we assume a volume  $T_R$  of freshwater, containing a concentration  $X_R$  of X, runs into the S-layer resulting in an expulsion of  $T_R X_S$  (mgX day<sup>-1</sup>), i.e.

$$W_{XRS} = T_R (X_R - X_S).$$

Likewise we assume that the rate of turbulent mixing across the primary pycnocline, caused by the wind and the residual circulation, is:

$$M_{XIS} = T_{IS} (X_I - X_S),$$

where  $T_{IS}$  is the volume exchanged between the S & I layers. Similarly the mixing rate across the secondary pycnocline is:

$$M_{XBI} = T_{BI} (X_B - X_I),$$

where  $T_{BI}$  is the volume exchanged between the I & B layers. A full listing of the rate equations of the physical processes for DIN (F), DON (D) together with phytoplankton carbon ( $C_p$ ) and nitrogen ( $N_p$ ) is shown in Table 1.1

Tett (1986) suggests that sea-lochs are a sink for phytoplankton. There is one obvious mechanism by which this can occur - phytoplankton which

**Table 1.1 The physical rate equations.**

Symbol	Description	Definition	Units
$M_{CIS} =$	Net flux of $C_p$ from I-layer to S-layer due to mixing.	$= T_{IS}[C_{PI}-C_{PS}]$	mgC day <sup>-1</sup>
$M_{NIS} =$	Net flux of $N_p$ from I to S due to mixing.	$= T_{IS}[N_{PI}-N_{PS}]$	mgN day <sup>-1</sup>
$M_{FIS} =$	Net flux of F from I to S due to mixing.	$= T_{IS}[F_I-F_S]$	mgN day <sup>-1</sup>
$M_{DIS} =$	Net flux of D from I to S due to mixing.	$= T_{IS}[D-D_S]$	mgN day <sup>-1</sup>
$M_{FBI} =$	Net flux of F from B to I due to mixing & turnover.	$= T_{IS}[D-D_S] + T_{TO}(t)[F_B-F_I]$	mgN day <sup>-1</sup>
$W_{CEI} =$	Net flux of $C_p$ from sea (E) into I due to tide.	$= T_E[C_{PE}(t)-\beta C_{PI}-\Omega(1-\beta)C_{PI}]$	mgC day <sup>-1</sup>
$W_{CIS} =$	Net flux of $C_p$ from I to S due to entrainment.	$= \beta T_E[N_{PI}-\Omega N_{PS}]$	mgC day <sup>-1</sup>
$W_{CRS} =$	Net flux of $C_p$ from run-off in to S.	$= T_R[C_{PR}(t)-\Omega C_{PS}]$	mgC day <sup>-1</sup>
$W_{NEI} =$	Net flux of $N_p$ from sea (E) into I due to tide.	$= T_E[N_{PE}(t)-\beta N_{PI}-\Omega(1-\beta)N_{PI}]$	mgN day <sup>-1</sup>
$W_{NIS} =$	Net flux of $N_p$ from I to S due to entrainment.	$= \beta T_E[N_{PI}-\Omega N_{PS}]$	mgN day <sup>-1</sup>
$W_{NRS} =$	Net flux of $N_p$ from run-off in to S.	$= T_R[N_{PR}(t)-\Omega N_{PS}]$	mgN day <sup>-1</sup>
$W_{FEI} =$	Net flux of F from sea (E) into I due to tide.	$= T_E[F_E(t)-F_I]$	mgN day <sup>-1</sup>
$W_{FIS} =$	Net flux of F from I to S due to entrainment.	$= \beta T_E[F_I-F_S]$	mgN day <sup>-1</sup>
$W_{FRS} =$	Net flux of F from run-off in to S.	$= T_R[F_R(t)-F_S]$	mgN day <sup>-1</sup>
$W_{DEI} =$	Net flux of D from sea (E) into I due to tide.	$= T_E[D_E(t)-D_I]$	mgN day <sup>-1</sup>
$W_{DIS} =$	Net flux of D from I to S due to entrainment.	$= \beta T_E[D_I-D_S]$	mgN day <sup>-1</sup>
$W_{DRS} =$	Net flux of D from run-off in to S.	$= T_R[D_R(t)-D_S]$	mgN day <sup>-1</sup>

are moving seaward in the S-layer sink whilst they are doing so, thus concentrating the population near the pycnocline where the water is more slow moving. If the layer is not very well mixed then the loss rate of phytoplankton from the S-layer will be less than bulk water movements imply. Whether the retention is due to large scale phenomena such as this, or due the biomechanics of the phytoplankton/eddy interaction, it is clear that it could play a significant part in determining the nutrient flux. Bearing in mind our strategic objectives, we will incorporate this feature in the model in the simplest possible way by multiplying the phytoplankton exchange equations above by a 'retention factor'  $\Omega$

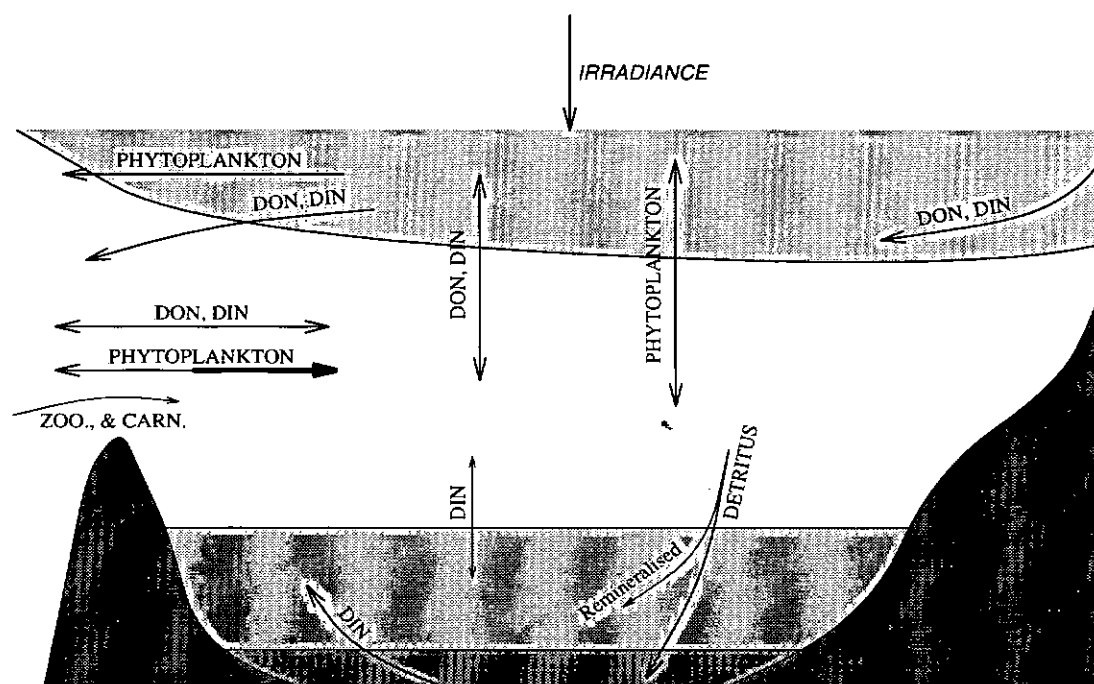
### **1.3 The biological and nutrient dynamics**

One of our principle aims in this work is to understand the broad patterns of nutrient flow around a sea-loch system. The constraints of these strategic objectives necessitates removal of any feature which will not significantly contribute to the net fluxes. The attenuation of incident light within the surface and intermediate layers of these quite brackish systems, means that the bottom layer is a very poor place indeed to conduct primary production. This combined with the slow coupling of the intermediate layer with the bottom layer means that phytoplankton which sink into the B-layer are unlikely to find their way back into the biologically active layers above. We hence neglect any possibility of biological activity within this layer.

Although the sediment is in contact with all water column layers, the effects of wave scouring of sediments in the surface layer, and rapid flushing of the intermediate layer with respect to the bottom layer, suggest that the bottom layer is the important pathway of sediment remineralisation. Pearson (1970) found that the organic component of sediment in contact with the bottom layer of the inner basin of Loch Linnhe was three to four times

greater than that in contact with the intermediate or surface layers (layer as defined above). Thus given the strategic aims, we choose to ignore secondary fluxes such as denitrification and terrigenous PON input, as well as the more complex aspects of sedimentation, particularly sediment burial. We can then simplify our representation of the sediment by regarding it as a well mixed volume coupled to the bottom (B) layer by a first order rate process.

Perhaps the most difficult aspect of modelling an ecosystem so affected by physical processes is describing the way in which the fluxes of the components modelled are influenced by these processes. Whilst it is reasonable to assume that dissolved nutrients are subject completely to bulk water movements, phytoplankton have (depending on their type and size) some movement independent of the prevailing current whether it be active or passive.



**Fig. 1.4** The physical and biological coupling

Phytoplankton are assumed to be active within both upper layers. Since



they do not have a great deal of control over their movement, a uniformly distributed population over the whole biologically active region is implausible. It is necessary therefore to have separate populations in the upper two layers. These are coupled by the mixing and exchange processes described in the previous section, defined in Table 1 and illustrated in Fig. 1.4.

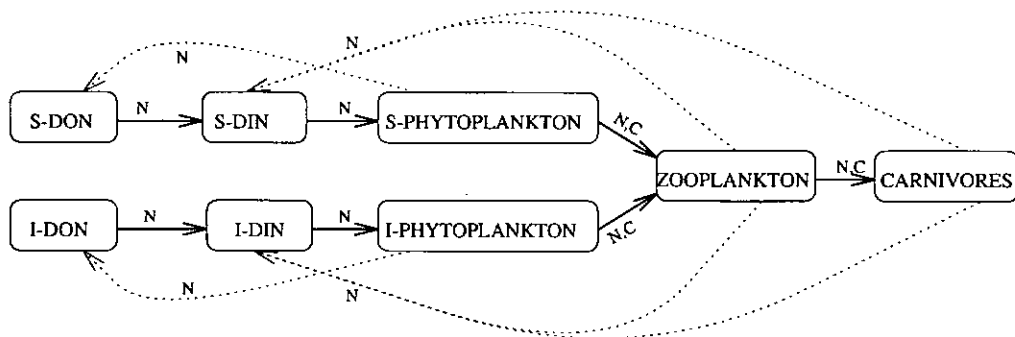
The higher trophic levels have much greater control over their locomotion (e.g. according to Hardy & Bainbridge 1954, small copepods can swim at about  $10 \text{ m hr}^{-1}$ ; and according to Longhurst 1976 large zooplankton can reach speeds in excess of  $100 \text{ m hr}^{-1}$ ). The carnivores in particular are likely to have complete control in the hydrological conditions experienced in a sea-loch. Although small copepods may experience some difficulty in crossing the pycnocline we consider this is unlikely to significantly affect the vertical movements of the trophic level as a whole. We thus consider single population representations to be sufficient.

There is very little guidance in the literature on vertical movements and feeding patterns in relation to any specific factors such as availability of food. We will therefore assume that both carnivores and zooplankton spend a fixed proportion of their time feeding (and excreting) in the S-layer and the remainder in the I-layer. We further assume that the higher trophic categories are fixed within the system and are not subject to bulk water movements.

An illustration of the model nitrogen cycle within the food web is given in Fig. 1.5. The phytoplankton populations of the two upper layers take up nitrogen from the appropriate layer and excrete dissolved organic nitrogen (DON) which remains in the water for a short period before bacterial decomposition returns it to the inorganic state. Mixing carries phytoplankton in both directions across the upper pycnocline, while sinking carries S-layer

er phytoplankton downward into the I-layer, and I-layer individuals across the lower pycnocline where they are assumed to die - adding the labile fraction of their bound nitrogen to the bottom water and the remainder to the sediment.

We assume nitrogen and carbon are assimilated by the zooplankton in the ratio found in the ingested prey, thus potentially causing the N/C ratio of the zooplankton to vary in sympathy with that of the phytoplankton. Excretion from the zooplankton is assumed to be simply DIN and is returned directly to the surface and intermediate pools in the ratio of the times spent in each location. Zooplankton corpses and faecal pellets are assumed to fall rapidly into the sediment. A fast remineralisation process releases a labile fraction of their bound nitrogen directly into the bottom water, and the remainder is added to the sediment.



**Fig. 1.5** The food web.

The excretion products of carnivores are also regarded as inorganic nitrogen which is returned to the DIN pools of the upper two layers in the ratio of the time spent in each. Faeces and corpses fall into the sediment yielding a labile fraction of their bound nitrogen on the way.

Inorganic nitrogen accumulating in the sediment is continuously returned to the productive upper layers at a rate governed by the slowest

processes in the chain, namely the remineralisation rate and the mixing rate across the lower pycnocline. However, when a turnover event occurs, the nutrient rich bottom water becomes thoroughly mixed into the intermediate layer, producing a strong pulse of nutrient into the productive regions. External inputs of nitrogen into the system come from both the sea and the land. Freshwater runs into the surface layer carrying with it a seasonally varying load of inorganic nitrogen<sup>1</sup>. The tides flush seawater carrying both DIN and viable phytoplankton into the intermediate layer. The seaward flows in both upper layers carry bound nitrogen (phytoplankton) as well as dissolved organic and inorganic nitrogen out of the system. The small, seasonally varying, immigration rates of zooplankton and carnivores formally constitute nitrogen inputs, but are more important for their dynamic effects than as a nitrogen source.

### 1.3.1 The balance equations

From the observations and basic assumptions discussed above, we can write down an ordinary differential equation for each state variable in the model.

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1. We ignore the Particulate organic matter (PON) input from freshwater, assuming that riverborne detritus has a high sedimentation rate.

## Carnivores

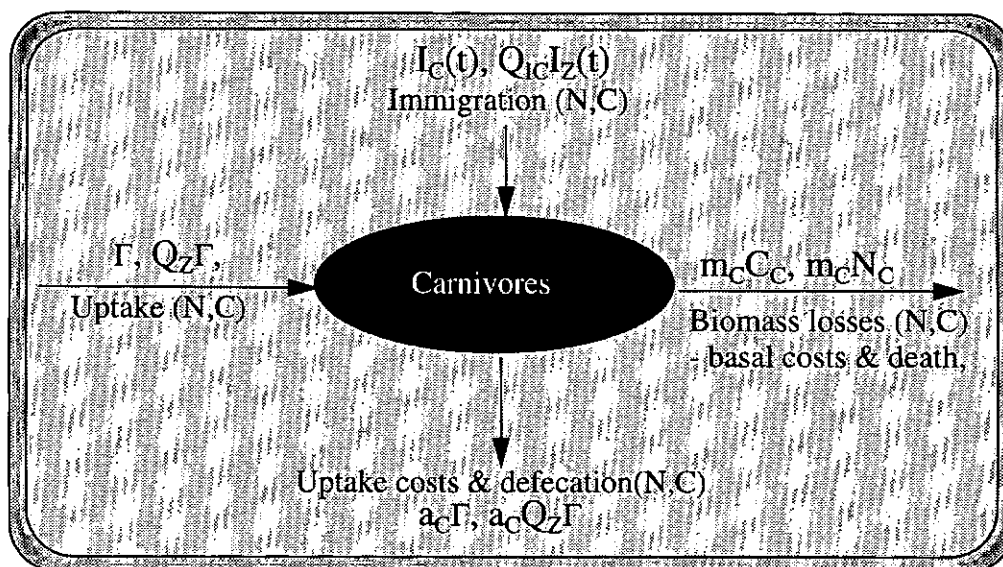


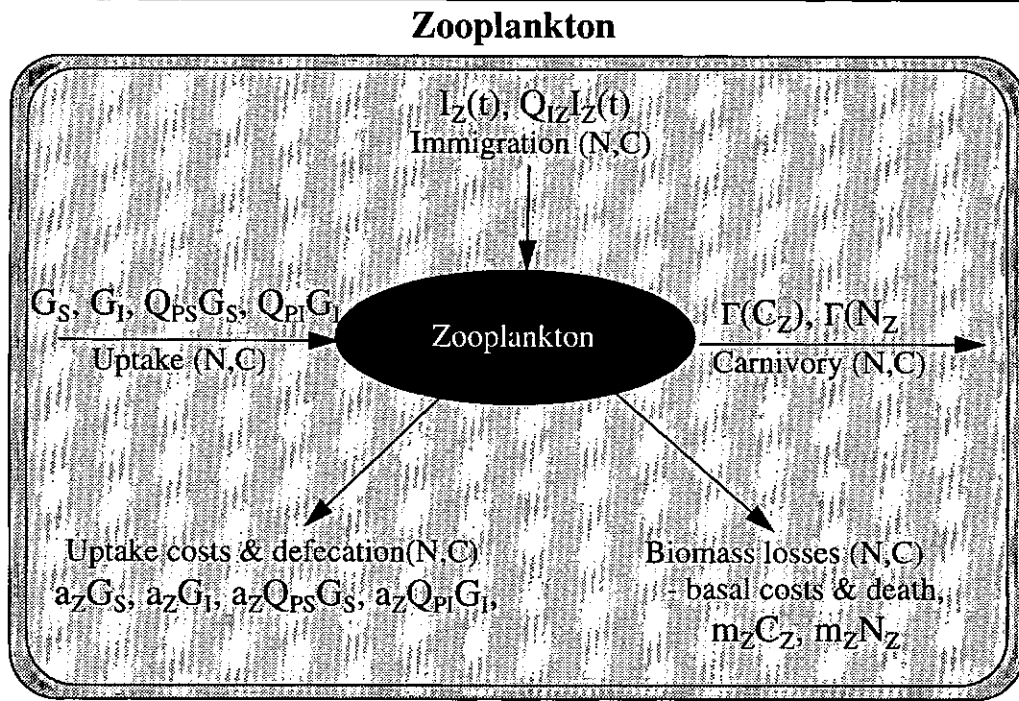
Fig. 1.6 The carbon and nitrogen inputs and outputs of the carnivore trophic level. The symbols are defined in Table 1.2 and the driving functions in Chapter 2.

Carbon:

$$\frac{dC_C}{dt} = \frac{a_C \Gamma - m_C C_C V_S + I_C(t)}{V_S}$$

Nitrogen:

$$\frac{dN_C}{dt} = \frac{a_C Q_Z \Gamma - m_C N_C V_S + Q_{IC} I_C(t)}{V_S}$$



**Fig. 1.7** The carbon and nitrogen inputs and outputs of the zooplankton trophic level. The symbols are defined in Table 1.2 and the driving functions in Chapter 2.

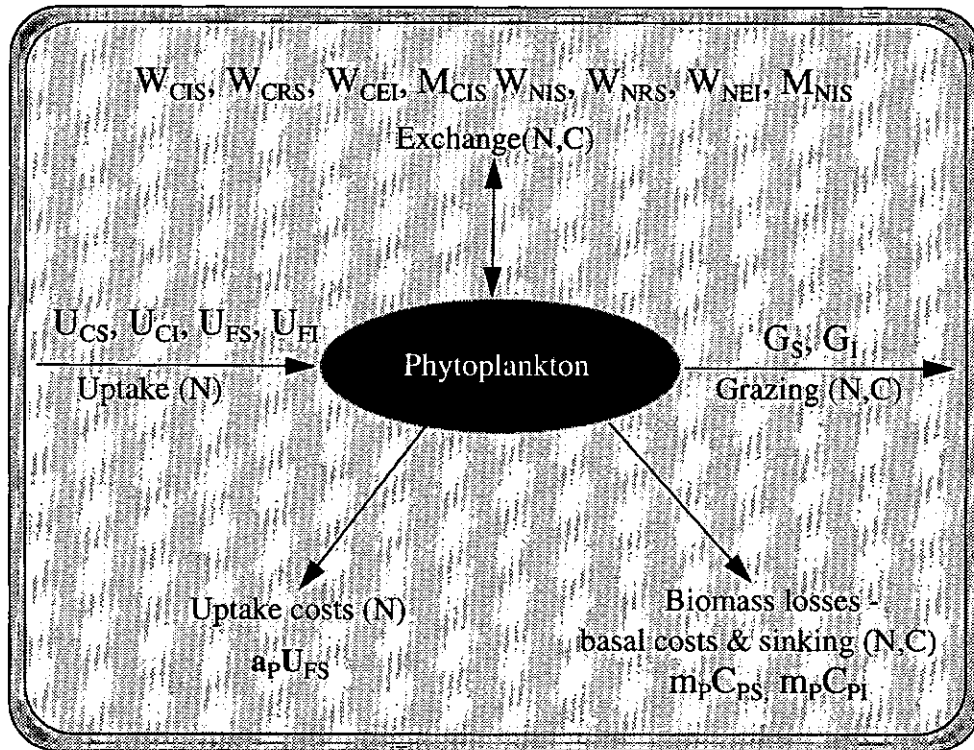
**Zooplankton carbon**

$$\frac{dC_Z}{dt} = \frac{a_Z (G_S + G_I) - m_Z C_Z V_S - \Gamma + I_Z(t)}{V_S}$$

**Zooplankton nitrogen**

$$\frac{dN_Z}{dt} = \frac{a_Z (Q_{PS}G_S + Q_{PI}G_I) - m_Z N_Z V_S - Q_Z \Gamma + Q_{IZ}I_Z(t)}{V_S}$$

**Phytoplankton**



**Fig. 1.8** The model representation of the nitrogen and carbon phytoplankton fluxes. The symbols are defined in Table 1.2 and the driving functions in Chapter 2.

**S-layer phytoplankton carbon**

$$\frac{dC_{PS}}{dt} = \frac{U_{CS} + m_p C_{PS} V_S - G_S + M_{CIS} + W_{CRS} + W_{CIS}}{V_S}$$

**S-layer phytoplankton nitrogen**

$$\frac{dN_{PS}}{dt} = \frac{a_p U_{FS} + m_p N_{PS} V_S - Q_{PS} G_S + M_{NIS} + W_{NRS} + W_{NIS}}{V_S}$$

**I-layer phytoplankton carbon:**

$$\frac{dC_{PI}}{dt} = \frac{U_{CI} + m_p C_{PI} V_I + \delta_P C_{PS} V_S - G_I - M_{CIS} + W_{CEI}}{V_I}$$

**I-layer phytoplankton nitrogen:**

$$\frac{dN_{PI}}{dt} = \frac{a_p U_{FI} + m_p N_{PI} V_I + \delta_P N_{PS} V_S - Q_{PI} G_I - M_{NIS} + W_{NEI}}{V_I}$$

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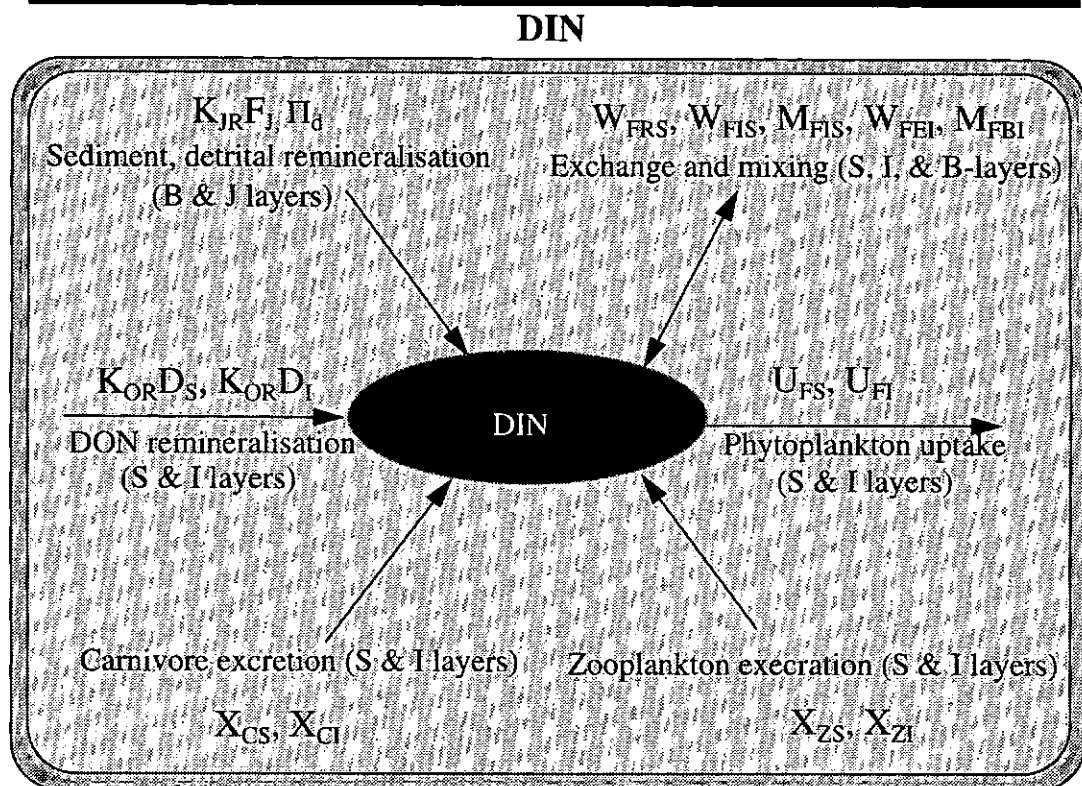


Fig. 1.9 The pathways into and out of the DIN pool. The symbols are defined in Tables 1.1 & 1.2.

**S-layer DIN**

$$\frac{dF_S}{dt} = \frac{X_{CS} + X_{ZS} + k_{OR}D_S V_S - U_{FS} + W_{FRS} + W_{FIS} + M_{FIS}}{V_S}$$

**I-layer DIN**

$$\frac{dF_I}{dt} = \frac{X_{CI} + X_{ZI} + k_{OR}D_I V_I - U_{FI} + W_{FEI} + M_{FBI} - M_{FIS}}{V_I}$$

**B-layer DIN**

$$\frac{dF_B}{dt} = \frac{\alpha \Pi_d + k_{JR}F_J V_J - M_{FBI}}{V_B}$$



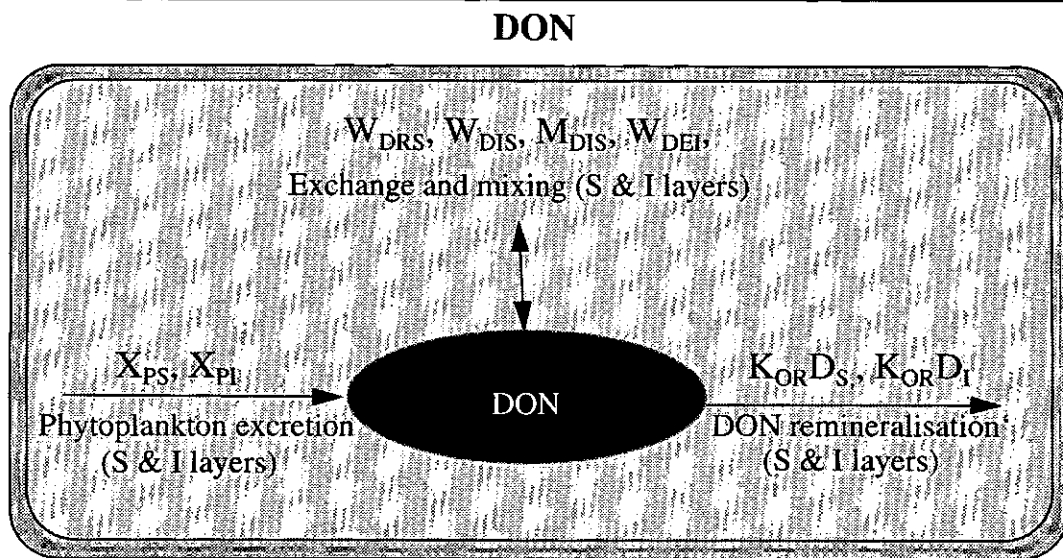


Fig. 1.10 The pathways into and out of the DON pool. The symbols are defined in Tables 1.1 & 1.2.

### S-layer DON

$$\frac{dD_S}{dt} = \frac{X_{PS} - k_{OR} D_S V_S + W_{DRS} + W_{DIS} + M_{DIS}}{V_S}$$

### I-layer DON

$$\frac{dD_I}{dt} = \frac{X_{PI} - k_{OR} D_I V_I + W_{DEI} - M_{DIS}}{V_I}$$

Table 1.2: Intermediate quantities

Description	Equation
Total uptake of zooplankton carbon by carnivores (mgC day <sup>-1</sup> ).	$\Gamma = C_C V_S \Gamma_{\text{Max}} S_C \left[ \frac{C_Z}{C_Z + H_Z} \right]$
Total production rate of corpses and faecal pellets (mgN day <sup>-1</sup> ).	$\Pi_d = d_C Q_Z \Gamma + d_Z (Q_{PS} G_S + Q_{PI} G_I) + ([\delta_C N_C + \delta_Z N_Z] V_S + \delta_P N_{PI} V_I)$
Assimilation rates of carnivores, zooplankton and phytoplankton (dim.less).	$a_C = 1 - d_C - e_{UC}; a_Z = 1 - d_Z - e_{UZ}; a_P = 1 - e_{UP}$
The biomass loss rates of carnivores, zooplankton and phytoplankton (day <sup>-1</sup> ).	$m_C = \delta_C - e_{bC} S_C(t); m_Z = \delta_Z - e_{bZ} S_Z(t); m_P = \delta_P - e_{bP} S_P(t)$
Zooplankton grazing rate in the S-layer (mgC day <sup>-1</sup> ).	$G_S = \mu_Z C_Z V_S G_{\text{Max}} S_Z(t) \left[ \frac{C_{PS}}{C_{PS} + H_P} \right]$
Zooplankton grazing rate in the I-layer (mgC day <sup>-1</sup> ).	$G_I = (1 - \mu_Z) C_Z V_S G_{\text{Max}} S_Z(t) \left[ \frac{C_{PI}}{C_{PI} + H_P} \right]$
Nitrogen quotas of carnivores, zooplankton, S-layer and I-layer phytoplankton (mgN mgC <sup>-1</sup> )	$Q_C = \frac{N_C}{C_C}, Q_Z = \frac{N_Z}{C_Z}, Q_{PS} = \frac{N_{PS}}{C_{PS}}, Q_{PI} = \frac{N_{PI}}{C_{PI}}$
Temperature dependence of carnivore rate processes (dimensionless).	$S_C = 1 - \lambda_C \exp \{ \tau_{CT} \theta(t) \}$
Temperature dependence of zooplankton rate processes (dimensionless).	$S_Z = 1 - \lambda_Z \exp \{ \tau_{ZT} \theta(t) \}$
Temperature dependence of phytoplankton rate processes (dimensionless).	$S_P = 1 - \lambda_P \exp \{ \tau_{PT} \theta(t) \}$
Total uptake of carbon by S-layer phytoplankton (mgC day <sup>-1</sup> ).	$U_{CS} = C_{PS} V_S S_P(t) \text{Min} \left\{ R_{MQ} \left( 1 - \frac{Q_{\text{min}}}{Q_{PS}} \right) + R_{ML} \frac{L_S(t)}{L_S(t) + H_L} \right\}$

Table 1.2: Intermediate quantities

Description	Equation
Total uptake of carbon by I-layer phytoplankton (mgC day <sup>-1</sup> ).	$U_{CI} = C_{PI} V_I S_P(t) \text{Min} \left\{ R_{MQ} \left( 1 - \frac{Q_{\min}}{Q_{PI}} \right) + \frac{L_S(t) \exp \{-\kappa_S \gamma_S\}}{L_S(t) \exp \{-\kappa_S \gamma_S\} + H_L} \right\}$
The total uptake of DIN by S-layer Phytoplankton (mgN day <sup>-1</sup> ).	$U_{FS} = C_{PS} V_S S_P(t) \left[ \frac{U_{\max}}{(1 + \exp \{ \frac{Q_{PS} - Q_{\max}}{Q_{\text{off}}} \})} \right] \left[ \frac{F_S}{F_S + H_F} \right]$
The total uptake of DIN by I-layer Phytoplankton (mgN day <sup>-1</sup> ).	$U_{FI} = C_{PI} V_I S_P(t) \left[ \frac{U_{\max}}{(1 + \exp \{ \frac{Q_{PI} - Q_{\max}}{Q_{\text{off}}} \})} \right] \left[ \frac{F_I}{F_I + H_F} \right]$
Total excretion rate by carnivores into the S-layer (mgN day <sup>-1</sup> ).	$X_{CS} = \mu_C (e_{UC} Q_Z \Gamma + e_{bC} S_C(t) N_C V_S)$
Total excretion rate by zooplankton into the S-layer (mgN day <sup>-1</sup> ).	$X_{ZS} = e_{UZ} Q_{PS} G_S + \mu_Z e_{bZ} S_Z(t) N_Z V_S$
Total excretion rate by carnivores into the I-layer (mgN day <sup>-1</sup> ).	$X_{CI} = (1 - \mu_C) (e_{UC} Q_Z \Gamma + e_{bC} S_C N_C V_S)$
Total excretion rate by zooplankton into the I-layer (mgN day <sup>-1</sup> ).	$X_{ZI} = e_{UZ} Q_{PI} G_I + (1 - \mu_Z) e_{bZ} S_Z(t) N_Z V_S$
Total excretion rate by phytoplankton into the S-layer (mgN day <sup>-1</sup> ).	$X_{PS} = e_{UP} U_{FS} + e_{bP} S_P(t) N_{PS} V_S$
Total excretion rate by phytoplankton into the I-layer (mgN day <sup>-1</sup> ).	$X_{PI} = e_{UP} U_{FI} + e_{bP} S_P(t) N_{PI} V_I$

### 1.3.2 Definitions

We set out in Table 1.2 the definitions of the intermediate quantities used in the balance equations in the previous section. The specific assumptions which underlie these definitions are discussed in this section.

There is overwhelming evidence that zooplanktonic uptake in general, and gelatinous zooplankton in particular (e.g. Reeve 1980) have an uptake rate which is a saturating function of food concentration. We use the simplest form of this function, the type 2 functional response. Thus the total uptake of zooplankton by carnivores is

$$\Gamma = C_C V_S \Gamma_{\text{Max}} S_C(t) \left( \frac{C_Z}{C_Z + H_Z} \right),$$

where  $S_C(t)$ , the temperature dependence of the uptake rate, is defined in Table 1.2.

We assume that the grazing rate, like the carnivore uptake rate, is a simple type 2 functional response. We have previously assumed that separate phytoplankton populations exist in each of the surface and intermediate layers, hence it is necessary to define two functions which represent the total grazing rate in each. We have further assumed that the zooplankton spend a fraction of their time ( $\mu_Z$ ) in the S-layer and the remainder in the I-layer. Thus the total uptake of phytoplankton carbon by zooplankton within the S-layer is defined by:

$$G_S = \mu_Z C_Z V_S G_{\text{Max}} S_Z(t) \frac{C_{\text{PS}}}{C_{\text{PS}} + H_P};$$

and within the I-layer by:

$$G_I = (1 - \mu_Z) C_Z V_S G_{Max} S_Z(t) \frac{C_{PI}}{C_{PI} + H_P},$$

where  $S_Z(t)$ , the temperature dependence, is defined in Table 1.2.

We have chosen to neglect the potential limiting effects of carbon, silicon and phosphorus on the growth of phytoplankton. This leaves nitrogen as the sole limiting nutrient within the model. The availability of light is however a further potential constraint on the growth rate. Most phytoplankton models to date have assumed that the growth rate is the product of a function representing nutrient limitation and a function representing light limitation. There is no logical reason why growth should be limited by two factors at the same time; hence we follow Tett et al. (1986) in choosing a function to represent primary production which is limited by *either* light or nitrogen.

We use the Droop cell quota model to describe the availability of nitrogen for carbon fixation (Droop 1974, Droop et al. 1982), in preference to the more widely used Monod model which depends on ambient nutrient levels (see comparative review by Sommer 1991) - there being considerable evidence that phytoplankton have a significant nutrient storage capacity. The Droop model uses the idea of a minimum phytoplankton quota below which no carbon fixation can occur.

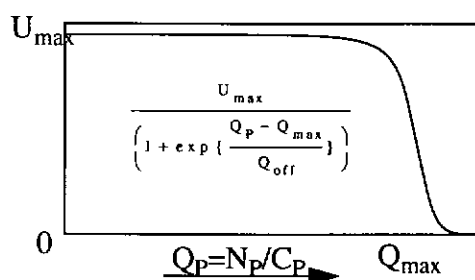
A number of functions of increasing complexity have been used to represent light limitation of nutrient uptake. This must be a saturating function of increasing light level, thus an obvious simple function to use is the type 2 response of predator uptake. This has been found to be a reasonable fit with a wide variety of datasets (e.g. Platt et al. 1977), and we will use it here.

The uptake of carbon within the S-layer is thus given by:

$$U_{CS} = C_{PS} V_S S_P(t) \text{Min} \left\{ R_{MQ} \left( 1 - \frac{Q_{\min}}{Q_{PS}} \right)^+, R_{ML} \frac{L_S(t)}{L_S(t) + H_L} \right\}$$

where  $Q_{\min}$  is the minimum possible phytoplankton nitrogen quota,  $L_S(t)$  is the average S-layer (photosynthetically active) irradiance, and  $H_L$  is the half saturation light level. A similar function for the I-layer is defined in Table 1.2.

To represent the uptake of inorganic nitrogen by phytoplankton we need a function which saturates with increasing nitrogen quota up to the maximum obtainable quota. A suitable function is illustrated in Fig. 1.9.



**Fig. 1.11. The dependence of phytoplankton uptake of nitrogen on the nitrogen quota.**

Like prey uptake for a predator, the uptake of inorganic nutrients is a saturating function of the nutrient concentration. Again a suitable form is the type 2 functional response (Caperon & Meyer 1972b). The total uptake of DIN by phytoplankton within the S-layer is thus:

$$U_{FS} = C_{PS} V_S S_P(t) \left[ \frac{U_{\max}}{(1 + \exp \{ \frac{Q_{PS} - Q_{\max}}{Q_{\text{off}}} \})} \right] \left[ \frac{F_S}{F_S + H_F} \right]$$

A similar function describing the uptake within the I-layer is defined in Table 1.2.

We have illustrated the internal nutrient cycling within the biologically active S & I layers in Fig. 1.5. In addition the faeces and corpses which originate within these layers sink into the bottom layer where we assume a constant fraction ( $\alpha$ ) remineralise, boosting the DIN pool in the B-layer and the remainder sink into the sediment where they remineralise on a longer timescale.

Phytoplankton which take up DIN excrete the nitrogen in organic form. This DON remains in the water for a period before it is decomposed by bacteria to the inorganic state. We represent this as a simple first order process.

#### 1.4 Implementation

The model equations are integrated using a commercially available package (Gurney 1992) based on a fourth-order Runge-Kutta algorithm (Press et al. 1989) with timestep varied automatically, over the range 0.05-0.5 d, in response to estimated numerical error.

## Chapter 2 - Model validation

### 2.0 Introduction

One of our principal aims in this work is to advise on the best strategy for conducting an in depth experimental program on Loch Linnhe. We will thus use the predictions of this model to advise on the optimum use of the available experimental resources.

Since we have not set out to design a full simulation model we cannot expect our model to predict in detail the dynamics of a real system. It should however be sufficiently complete to predict the broad-scale patterns and magnitudes of the major events in the annual cycle. To determine whether this is so, we need to test its performance against data from a real system. We thus require a reasonably spaced time series of data on the spatially averaged abundance of the three trophic levels in the model, as well as free nitrogen inside the system together with reasonable estimates of the external physical and biological influences on the system. In the absence of any published data for Loch Linnhe we choose a system for which there is sufficient data and which is similar enough to Loch Linnhe for the comparison between model and data to be relevant.

The best available data and parameter information we found was for Killary Harbour, a fjordic coastal inlet on the west coast of Ireland. We compile from the literature (McMahon and Patching 1984; Ryan et al. 1986; Roden et al. 1987; Rodhouse and Roden 1987) a dataset for 1981 on this system, to which we can compare some of the model state variables.



Before we do this however we must first parameterise the model.

We need such a large amount of information to determine all these parameters and driving functions that in practise it is impossible to parameterise purely on the available information from Killary Harbour. We thus use information from other systems where needed; preferably from systems which are similar to Killary. In a few instances where no experimental information is available we will need to fit the parameters. We consider three parameter subsets: the biological parameters, the physical parameters and the driving functions.

The physical parameters and driving functions are undoubtedly system specific. Fortunately we can parameterise most of these quantities from information on Killary and related systems. The biological parameters can be considered as system independent provided the plankton communities are similar in each system. We therefore, where possible, ascribe values to these parameters which were measured on species which are commonly found in Killary Harbour.

## **2.1 Biological and nutrient parameters**

We have no information relating to the biological or nutrient rate processes in Killary Harbour. Instead we assume these parameters are system independent. We have obtained from the literature a set of values for these parameters from a large variety of sources. These are discussed below in the context of the trophic level to which they apply.

### **2.1.1 Phytoplankton**

The most common type of coastal phytoplankton on the west coast of the British Isles are diatoms. One species of diatom, *Skeltonema costatum*, is particularly abundant in Killary, at times completely dominating the

phytoplankton assemblage (Roden et al. 1987). Although there is not a great deal of information in the literature on the rate parameters of this species, it is commonly used as a food source in estimating the rate parameters of grazers. We will thus adopt this species as a representative of the phytoplankton trophic level.

It is particularly difficult to assess nitrogen quotas of phytoplankton in the field because of the problems of isolating phytoplankton samples. We must therefore rely on laboratory experiments for estimation of the maximum and minimum nitrogen quotas ( $Q_{\max}$ ,  $Q_{\min}$ ). Tett & Droop (1986), Laws & Bannister (1980) and Caperon & Meyer (1972b) agree on a minimum quota value of 0.05. From Tett & Droop (1986) we estimate the maximum quota to be 0.25 and from Laws & Bannister (1980) a value of 0.22. However the value given by Tett and Droop is more general, covering a number of species hence we will use it here. In the absence of information on the nitrogen quota of phytoplankton in the sea outside Killary Harbour we use the Redfield ratio of 0.15 (average quota of all organic marine material) to represent the quota of immigrant phytoplankton.

An estimate for the maximum growth rate ( $R_{ML}$ ) of the diatom *Thalassiosira pseudonana* under conditions of nitrogen saturation in the laboratory of 1.7-1.9 day<sup>-1</sup> is given by Thompson *et al.* (1989). This compares with values of 1.22 day<sup>-1</sup> for *Thalassiosira fluviatilis* and 2.48 day<sup>-1</sup> for *Chlorrella Pyrenoidosa* found by Laws & Bannister (1980) in the laboratory. We use a central estimate of 1.6 day<sup>-1</sup>.

There are more estimates of the light saturated growth ( $R_{MQ}$ ). Caperon & Meyer (1972) give maximum growth rates of 0.076, 0.087, & 0.090 hour<sup>-1</sup> for *Coccochloris stagnina*, *Cyclotella nana*, & *Dunaliella tertiolecta* respectively (Oceanic species); which, assuming 12 hours light per day, corresponds to 0.91, 1.04, & 1.08 day<sup>-1</sup> respectively. Tett et al. (1986) and

Woods (1991) use a value of  $1.2 \text{ day}^{-1}$  for the maximum growth rates in their cell quota model of phytoplankton growth applied to the Sound of Jura and the North Sea respectively. Holligan *et al.* (1984) recorded a maximum value of  $1.17 \text{ day}^{-1}$  in the field (mixed diatom assemblage in the western English Channel). We also choose a value of  $1.2 \text{ day}^{-1}$ .

The value of the half saturation light constant for photosynthesis ( $H_L$ ) is determined by a central estimate from data of: Keller & Riebbessel (1989) of  $\sim 80 \mu\text{Einst. m}^{-2} \text{ s}^{-1}$ ; Laws & Bannister (1980) of  $\sim 60 \mu\text{Einst. m}^{-2} \text{ s}^{-1}$ ; and Thompson *et al.* (1989) of  $\sim 40 \mu\text{Einst. m}^{-2} \text{ s}^{-1}$ . We choose a value of  $60 \mu\text{Einst. m}^{-2} \text{ s}^{-1}$ .

Caperon & Meyer (1972) found maximum DIN (nitrate or ammonia) uptake rates ( $U_{\text{max}}$ ) for a number of different species in the range  $0.2 - 2.64 \text{ mg N mg C}^{-1} \text{ d}^{-1}$ , with a mean of 1.2. In addition they found the mean of the half saturation for nitrate uptake ( $H_F$ ) was  $4.2 \text{ mgN m}^{-3}$ . We use both of these mean values here. We use a value of 5% for the percentage of phytoplankton nitrogen uptake excreted ( $e_{\text{UP}}$ ) which is within the range of 2-8% found by Zlotnik & Dubinsky (1989) for normal light conditions.

The storage switch transition width ( $Q_{\text{off}}$  - Fig. 1.11) is the range of nitrogen quota over which the nitrogen uptake converges on zero. As such it is not an easily estimated parameter. It is assigned a large enough value (0.01) such that there are no computational difficulties, associated with near discontinuities.

The sinking rate ( $\delta_p$ ) is another difficult parameter to estimate because it is determined both by biological factors and the vertical density structure of the system. Bearing this in mind we estimate this parameter from the data of Bienfang 1977 to be  $0.1 \text{ day}^{-1}$  (assuming a layer depth of 8m and a

sinking rate of  $2\text{m day}^{-1}$ ). The parameter which represents the retained fraction of phytoplankton in water transport across the layer boundary ( $\Omega$ ) is even less well defined. At this stage we simply assign a value of 0.5.

The basal costs ( $e_{BP}$ ) are normally measured as carbon losses in the dark. The values reported for this quantity by Laws & Bannister (1980) for *Thalassiosira fluviatilis*, are in the range of 0.04-0.35. We choose a value of 0.25 which is not significantly different from the mean value of 0.24 obtained by Keller and Riebesell (1989) during the spring bloom (mainly *Skeltonema costatum* and *Thalassiosira* spp.) in an enclosed mesocosm.

We have little information on how the phytoplankton rate parameters vary with temperature. The temperature parameters  $\tau_{PS}$ ,  $\lambda_{PS}$ , are hence considered to be fitting parameters. We assign tentative values of 0.1 & 1 respectively which allows the parameters to vary by a factor of  $\sim 1.5$  over the temperature range found in Killary (8-16C). A summary of the phytoplankton parameters is given in Table 2.1., together with the values used, the sources of these values and the species for which the value is measured.

### 2.1.2 Zooplankton parameters

The most abundant of the herbivorous zooplankters in Killary are copepods, particularly *Acartia*, *Oithonia*, and *Calanus* species (Ryan *et al.* 1986, Rodhouse *et al.* 1987).

Kjørboe *et al.* (1985) measured the maximum grazing rate of *Acartia tonsa* feeding on a mixed culture of *Isochrysis galbana* and *Rhodomanas baltica* to be  $1.8\text{ mgC mgC}^{-1}\text{ day}^{-1}$ . This compares with a measured range of 0.21-0.32 for *Acartia tonsa* fed small diatoms by Libourel Houde & Roman (1987). Deason (1980) found a range of 0.65 - 6.0 for *Acartia clausi*

Table 2.1 Phytoplankton parameters

	Description	value	Units	Source	Species
$\delta_p$	Phytoplankton death (sinking) rate.	0.1	d <sup>-1</sup>	Bienfang 1977	Mixed
$\lambda_p$	Coefficient in phytoplankton temperature equation.	1.0	dimensionless	Fitted	
$\tau_p$	Coefficient in phytoplankton temperature equation.	0.1	°C <sup>-1</sup>	Fitted	
W	Phytoplankton washout retention factor.	0.5	dimensionless	Fitted	
$e_{BP}$	Fraction of phytoplankton biomass respired/excreted per day	0.25	d <sup>-1</sup>	Keller & Riebesell 1989 Laws & Bannister 1980	Various <i>Thalassiosira Fluviatis</i>
$e_{UP}$	Fraction of phytoplankton uptake excreted.	0.05	dimensionless	Zlotnik & Dubinsky 1989	<i>Chlorrella, Isochrysis</i>
H <sub>F</sub>	Half-saturation dissolved nitrogen concentration.	4.2	mg N m <sup>-3</sup>	Caperon & Meyer 1972b	Mixed
H <sub>L</sub>	Half-saturation irradiance.	60	μEinst. m <sup>-2</sup> s <sup>-1</sup>	Keller & Riebesell 1989 Laws & Bannister 1980 Thompson <i>et al.</i> 1989	Mixed <i>Thalassiosira Fluviatis</i> <i>Thalassiosira pseudonana</i>
Q <sub>IP</sub>	Nitrogen quota of immigrant phytoplankton.	0.15	mg N mg C <sup>-1</sup>	Redfield ratio	General
Q <sub>max</sub>	Maximum phytoplankton nitrogen quota.	0.25	mg N mg C <sup>-1</sup>	Tett & Droop 1986 Laws & Bannister 1980	General <i>Thalassiosira Fluviatis</i>
Q <sub>min</sub>	Minimum phytoplankton nitrogen quota.	0.05	mg N mg C <sup>-1</sup>	Tett & Droop 1986 Caperon & Meyer 1972a Laws & Bannister 1980	General Various <i>Thalassiosira Fluviatis</i>
Q <sub>off</sub>	Storage switch transition width.	0.01	mg N mg C <sup>-1</sup>	Fitted	
RMQ	Maximum phytoplankton growth rate (light saturated).	1.2	d <sup>-1</sup>	Caperon & Meyer 1972a Tett <i>et al.</i> 1986 Jones <i>et al.</i> 1978 Holligan <i>et al.</i> 1984	<i>Thalassiosira Fluviatis</i> Unspecified <i>Monochrysis</i> Mixed diatoms.
RML	Maximum phytoplankton growth rate (N saturated).	1.6	d <sup>-1</sup>	Laws & Bannister 1980 Thompson <i>et al.</i> 1989	<i>Thalassiosira Fluviatis</i> <i>Chlorrella pyrenoidosa</i> <i>Thalassiosira pseudonana</i>
U <sub>max</sub>	Max. phytoplankton N uptake rate per unit biomass.	1.2	mg N mg C <sup>-1</sup> d <sup>-1</sup>	Caperon & Meyer 1972b	Various

feeding on *Skeletonema costatum*; and Checkley (1980) found a value of 3.6 for *Paracalanus parvus* feeding on *Thalassiosira weissflogii*. We use a value for the maximum Grazing rate ( $G_{\max}$ ) of  $2.0 \text{ mgC mgC}^{-1} \text{ day}^{-1}$ .

We estimate the half-saturation constant for zooplankton uptake of phytoplankton to be  $150 \text{ mgC m}^{-3}$ , which is in agreement with data presented by Deason (1980) for *Acartia clausi* feeding on *Skeletonema Costatum*. Estimates of  $\sim 200$  and  $\sim 100\text{-}200$  for *Acartia tonsa* based on the data of Kiørboe *et al.* (1985) and Libourel Houde & Roman (1987) respectively, are not significantly different from our chosen value.

The fraction of zooplankton uptake defaecated ( $d_Z$ ) is estimated by Kiørboe *et al.* (1985) to be in the range: 0.19-0.49 for *Acartia tonsa* and by Daro (1980) to be 0.36 for *Calanus finmarchicus*. We choose this latter value. From the data of Kiørboe *et al.* (1985) we estimate the zooplankton uptake costs (fraction of uptake excreted -  $e_{UZ}$ ) to be 0.15 and the basal costs ( $e_{BZ}$ ) to be 0.05; in both cases for *Acartia tonsa*. Corkett and McLaren (1979) estimate copepod death rates ( $\delta_C$ ) to be approximately  $0.05 \text{ day}^{-1}$ .

In the absence of any better estimate we assume that zooplankton spend half their time in the S-layer and the other half in the I-layer (i.e.  $\lambda_Z = 0.5$ ) - not an unreasonable assumption in Killary since the S&I layers are of similar size.

In the same way we dealt with the phytoplankton response to temperature, we assign notional values of 0.1 & 1 to the zooplankton temperature parameters  $\tau_Z$  and  $\lambda_Z$  respectively. We also set the nitrogen quota of immigrant zooplankton to the Redfield ratio. A summary of the parameters specific to the zooplankton trophic level is given in Table 2.2.

Table 2.2 Zooplankton parameters

	Description	value	Units	Source	Species
$\delta_Z$	Zooplankton death rate.	0.05	d <sup>-1</sup>	Corkett & Maclaren 1979	<i>Pseudocalanus</i>
$d_Z$	Fraction of zooplankton uptake defecated.	0.36	dimensionless	Kjørboe <i>et al.</i> 1985 Daro 1980	<i>Acartia tonsa</i> <i>Calanus</i> spp.
$\mu_Z$	Fraction of zooplankton time spent in surface layer.	0.5		Fitted	
$e_{bZ}$	Fraction of zooplankton biomass excreted per day	0.05	d <sup>-1</sup>	Kjørboe <i>et al.</i> 1985	<i>Acartia tonsa</i>
$e_{uZ}$	Fraction of zooplankton uptake excreted.	0.15	dimensionless	Kjørboe <i>et al.</i> 1985	<i>Acartia tonsa</i>
$G_{max}$	Maximum zooplankton grazing rate.	2.0	mgN m <sup>-3</sup>	Kjørboe <i>et al.</i> 1985 Deason 1980 Libourel Houde & Roman 1987	<i>Acartia tonsa</i> <i>Acartia hudsonica</i> ( <i>A. clausi</i> ) <i>Acartia tonsa</i>
				Checkley 1980 Corner <i>et al.</i> 1967	<i>Paracalanus parvus</i> <i>Calanus finmarchicus</i>
$H_P$	Half-saturation phytoplankton carbon concentration.	150	mgC m <sup>-3</sup>	Kjørboe <i>et al.</i> 1985 Deason 1980 Libourel Houde & Roman 1987	<i>Acartia tonsa</i>
$\lambda_Z$	Coefficient in zooplankton temperature equation.	1.0	dimensionless	Fitted	
$Q_Z$	Nitrogen quota of immigrant zooplankton.	0.15	mg N mg C <sup>-1</sup>	Redfield ratio	General
$\tau_Z$	Coefficient in zooplankton temperature equation.	0.1	°C <sup>-1</sup>	Fitted	

### 2.1.3 Carnivore parameters

There is a wide range of organisms which are eligible for a carnivore trophic level - from large pelagic fish through to very small omnivorous copepods. The most abundant carnivorous organisms in Killary Harbour however are gelatinous zooplankton. There are two blooms of gelatinous zooplankton in this system: a spring bloom dominated by medusae (mainly the scyphomedusae *Aurelia aurita*) and a smaller autumn bloom dominated by the ctenophore *Pleurobrachia pileus* (Ryan *et al.* 1986, Rodhouse *et al.* 1987). We thus parameterise this class under the assumption that it is comprised entirely of gelatinous zooplankton.

Because it is larger than the 'bloom' of *Pleurobrachia* bloom in Killary, we would ideally like to parameterise our carnivore trophic level for medusae. However the dearth of quantitative work on medusae leaves us with no other option but to consider other types of gelatinous zooplankton. For the purposes of parameterisation we will consider only those gelatinous zooplankton which have a chemical composition close to that of *A. aurita* (from Schneider 1988 we find that dry weight is 1.8% of wet weight, nitrogen is 1.4% of dry weight, and carbon is 5.0% of dry weight). The ctenophores *Pleurobrachia*, *Bolinopsis*, and *Mnemiopsis* spp. fall into this category (carbon is 1.5% & 1.4% 1.9% of dry weight respectively - Reeve 1980). This carbon to dry weight ratio is more than an order of magnitude less than that of their copepod food source.

This difference in ratio points to the difficulty in measuring the true costs of these organisms. A copepod has a much larger organic structure to maintain relative to its total weight, hence its resting costs must be much closer to its active costs than can be the case for the largely silicon based (almost neutrally buoyant) gelatinous zooplankton. Hence although the assumption that the searching costs of copepods are reflected in its basal or



Table 2.3 Carnivore parameters

	Description	Value	Units	Source	Species
$\Gamma_{\max}$	Maximum carnivore predation rate	15	mgC mgC <sup>-1</sup> day <sup>-1</sup>	Reeve 1980	Mnemiopsis leydi, Bolinopsis, Pleurobrachis pileus
$\delta_C$	Carnivore death rate.	0.05	day <sup>-1</sup>	Fitted	
$\mu_C$	Fraction of carnivore time spent in surface layer.	0.5	dimensionless	Fitted	
$d_C$	Fraction of carnivore uptake defecated.	0.5	dimensionless	Reeve et al 1978	Mnemiopsis leydi
$e_{bC}$	Fraction of carnivore biomass excreted per day	0.75	days <sup>-1</sup>	Reeve et al 1978	Pleurobrachis pileus
$e_{UC}$	Fraction of carnivore uptake excreted.	0.2	dimensionless	Reeve et al 1978	Pleurobrachis pileus
$H_Z$	Half-saturation zooplankton carbon concentration.	500	mgC m <sup>-3</sup>	Reeve 1980	Mnemiopsis leydi, Bolinopsis, Pleurobrachis pileus, Sagitta elegans
$\lambda_C$	Coefficient in carnivore temperature equation.	1.0	dimensionless	Fitted	
$Q_{TC}$	Nitrogen quota of immigrant carnivore.	0.15	mg N mg C <sup>-1</sup>	Redfield ratio	General
$\tau_C$	Coefficient in carnivore temperature equation.	0.1	°C <sup>-1</sup>	Fitted	

uptake costs is not unreasonable, this is unlikely to be the case for many gelatinous zooplankton.

Unfortunately most of the estimates of respiration or excretion of gelatinous zooplankton have been done whilst the animal is resting, and hence resulted in low estimates of respiration (e.g. Kremer 1977 found respiration rates of 5-20% for resting, unfed, *Mnemiopsis leydi*). The exception to this is the estimate made by Reeve *et al.* (1978) for *Pleurobrachia* actively feeding on *Acartia tonsa* in the aquarium. From this (fairly sparse) data we estimate a value for  $e_{BC}$  of  $0.75 \text{ day}^{-1}$ .

Clearly if the biomass specific basal costs of gelatinous zooplankton are that much greater than that of their prey, the maximum ingestion rate must also be significantly higher if they are to persist for any length of time. This seems to be confirmed by the measurements of Reeve *et al.* 1978 who found a value of  $\Gamma_{\max}$  for *M. leydi* of  $20 \text{ day}^{-1}$  although Reeve (1980) also observed lower values for *P. pileus* of  $2 \text{ day}^{-1}$  and *Bolinopsis* of  $3 \text{ day}^{-1}$ , values which are much closer to our chosen value of the maximum grazing rate,  $G_{\max}$ , of  $2 \text{ day}^{-1}$ . We chose a value of  $\Gamma_{\max} = 15$ , partly on the basis of the above, and partly because we need a large enough value for the carnivore class to persist, at least in a biomass model of this type. Particularly since the data of Reeve (1980) suggest a value for the half saturation of zooplankton uptake by carnivores ( $H_C$ ) of about:  $400 \text{ mgC m}^{-3}$  for *Pleurobrachia*;  $450 \text{ mgC m}^{-3}$  for *Bolinopsis*; and greater than  $1000 \text{ mgC m}^{-3}$  for *Mnemiopsis*, all values well above the chosen value of  $H_Z$  (the half saturation for phytoplankton uptake by zooplankton). We choose the value of  $H_C$  to be  $500 \text{ mgC m}^{-3}$ .

We estimate the feeding costs ( $e_{UC}$ ) to be 0.2 from data of Reeve *et al.* (1978) on *Pleurobrachia*; and the fraction defaecated ( $d_C$ ) to be very approximately 50%.

**Table 2.4 Nutrient parameters**

	Description	Value	Units	Source
$\alpha$	Labile fraction of corpses and faecal pellets	0.2	dimensionless	Fitted
$K_{JR}$	Rate constant for sediment to bottom remineralisation	0.01*	day <sup>-1</sup>	Davis 1978, Edwards & Grantham 1978, Harrison 1978
$K_{QR}$	Rate constant for DON remineralisation	0.2	day <sup>-1</sup>	Harrison 1978

\*This is a compound parameter in the normal sense of sediment remineralisation.

The uncertainty in all of these parameters means they cannot readily be described as known; instead we consider them to be semi-fitted (i.e. fitted, with some guidance from the literature). Those parameters ( $\mu_C$ ,  $\tau_C$ ,  $\lambda_C$ ) for which we have no information, like their counterparts in the zooplankton group, we fit. A summary of the carnivore parameters is given in Table 2.3.

#### 2.1.4 Nutrient parameters

We estimate that the average remineralisation period for organic material falling into the sediment to be 100 days (from the measurements of: Davis 1978 in Loch Ewe; Edwards & Grantham, 1986, in Loch Etive; and Harrison, 1978, in southern California and the CEPEX mesocosms in Sanich Inlet). Thus the sediment remineralisation rate ( $K_{JR}$ ) is  $0.01\text{day}^{-1}$ . The DON remineralisation rate we estimate from a review given by Harrison (1978) to be  $0.2\text{day}^{-1}$ . We assign a value of 0.1 to the proportion ( $\alpha$ ) of faeces and corpses which is remineralised within the water column.

### 2.2 Physical parameters and driving functions

Killary Harbour is a long, shallow, inlet on the west coast of Ireland, with a restricted entrance at the mouth. It has a mean depth of about 14m, a maximum depth of 45 m and a total volume of  $\sim 1.1 \times 10^8\text{ m}^3$  (Roden *et al.* 1987). According to Booth (1975), the outflowing surface layer in this inlet varies in depth between 5 and 10 m, while Roden *et al.* (1987) report brackish layer depths of 1-3 m from three samples in spring and summer in the inner loch, but suggest that this structure is broken down quite quickly. We therefore assume a surface layer depth of 7.5 m.

Given the shallow overall depth of this loch, no lower pycnocline is formed and the intermediate layer extends right down to the sediment. Since our model, for generality, also includes a bottom layer, we make this

very small and well mixed with the I-layer - an assumption which excludes any possibility of turnover events. Because the balance equations contain only the ratios of the layer volumes, we choose to use the surface layer ( $V_S$ ) as the unit of volume. Taking into account the surface area and under-water shape of the fjord we calculate that the I-layer volume is  $\sim 95\%$  of that of the surface layer ( $V_S$ ) and set the notional B-layer volume to  $0.1V_S$ .

**Table 2.5 Catchment features**

Feature	Value*
Catchment area (Km <sup>2</sup> )	11
Catchment type	Bog, Heathland
Maximum rainfall (mm month <sup>-1</sup> )	433 (September)
Minimum rainfall (mm month <sup>-1</sup> )	48 (April)
Mean rainfall (mm month <sup>-1</sup> )	225

\*Data from Roden et al.1987. Rainfall figures are the average of two stations in Killary Harbour during 1981.

The Killary region has very high rainfall (Table 2.5), with the inlet itself surrounded largely by bog and heathland. We obtain monthly freshwater input data from McMahon and Patching (1984). Since there is no significant seasonal trend in freshwater runoff, we treat it as constant and choose the mean monthly value to calculate an input volume of  $0.036 V_S d^{-1}$ . We calculate total tidal exchange to be  $0.8V_S d^{-1}$ . We estimate from the data of McMahon and Patching's (1984) that a quarter of this volume is entrained within the surface layer, assuming a notional value for the mixing rate between S & I layers of  $0.05 day^{-1}$ , with no evident seasonal pattern.

**Table 2.6 Physical parameters**

	Description	Units	Value
$V_B/V_S$	Volume of bottom (B) layer / volume of surface (S) layer.	dimensionless	0.1
$V_I/V_S$	Volume of intermediate (I) layer / volume of S-layer.	dimensionless	0.95
$V_J/V_S$	Volume of sediment (J) layer / volume of S-layer.	dimensionless	0.06
b	Proportion of tide entrained into S-layer.	dimensionless	0.25
$T_{BI}/V_S$	Volume exchange rate for mixing between B & I layers / Volume of S-layer.	days <sup>-1</sup>	0.02*
$T_E/V_S$	Volume exchange rate for tide into I-layer / Volume of S-layer.	days <sup>-1</sup>	0.8

**Table 2.6 Physical parameters**

	Description	Units	Value
$T_{IS}/V_S$	Volume exchange rate for mixing between I & S layers / Volume of S-layer.	days <sup>-1</sup>	0.05*
$T_R/V_S$	Volume exchange rate for run-off into S-layer / Volume of S-layer.	days <sup>-1</sup>	0.036

\*These are compound parameters in the normal sense of turbulent diffusion.

The tidal flushing in Killary Harbour is thus large enough that the influence of the external system may be critical to the internal dynamics. It is therefore essential that for those model variables which are subject to the physical transport processes, we have a reasonable idea of the equivalent time-varying values in the external system.

Although there are no direct measurements of DIN or phytoplankton concentrations at the mouth of Killary Harbour, Roden (1984) gives some rather sparse data for these quantities for the coastal waters off Connemara, a few kilometres to the south, during 1980-1981. From these data we make rough estimates of the appropriate driving functions using sinusoidal representations. For each quantity we assessed how many seasonal maxima are normally observed and estimated when the minimum and maximum values are likely to occur.

The concentrations of phytoplankton and DIN in the incoming seawater are assumed to have two peaks per year, since in the coastal waters off the west coast, there is typically a spring bloom followed by a smaller autumn bloom (Colebrook 1984, Roden 1984). From this data we have estimated the autumn bloom to be half the magnitude of the spring bloom. We assume that remnants of oceanic and coastal zooplankton blooms find their way into the fjord considerably later than their occurrence and hence the peak is in the autumn.

From the data of McMahon and Patching (1984) we calculate the monthly DIN concentration in run-off from their data on concentrations of particulate organic carbon in the freshwater input, using their quoted median C:N ratio of 13, and assuming a 10% inorganic content for the particulate material. This DIN concentration, which has two large peaks (spring and fall), we treat as a driving function. Dissolved organic nutrient (DON) input is assumed to be 10% of DIN input. We assume that phytoplankton concentration in the runoff is zero.

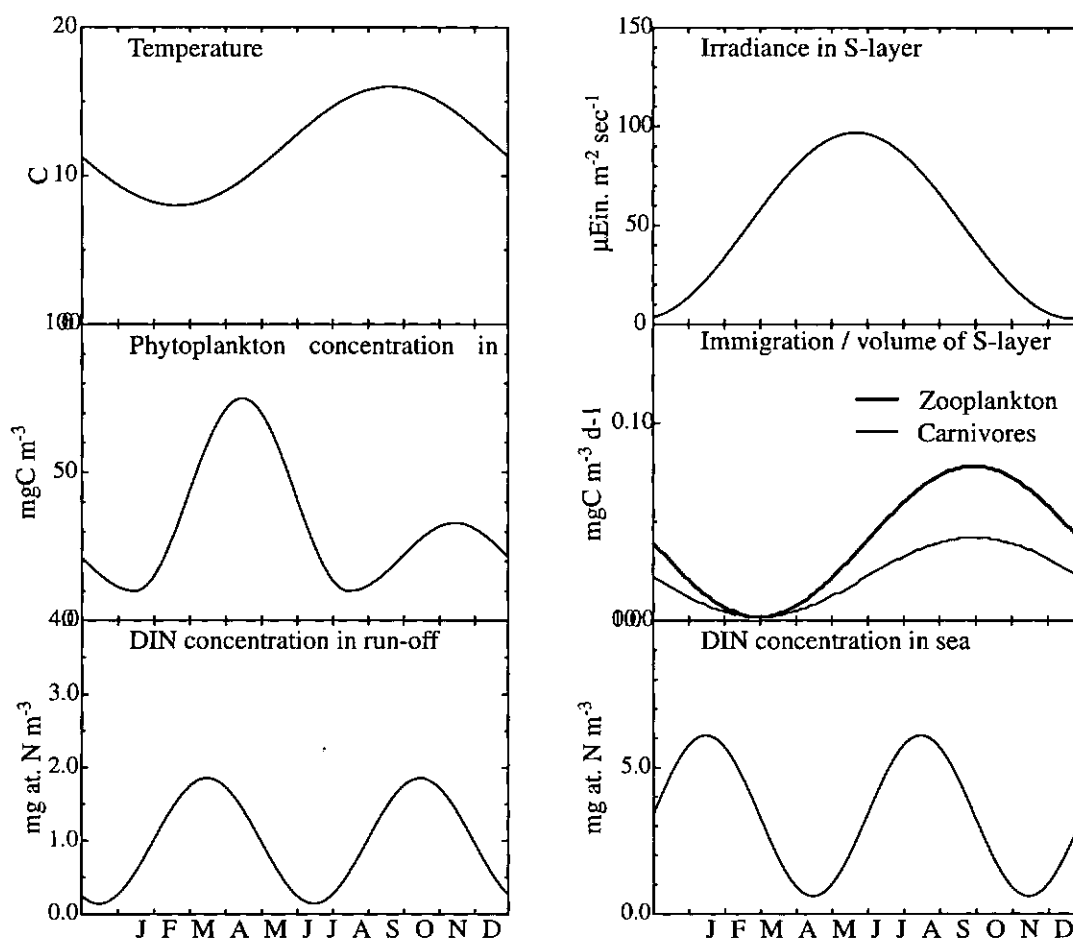


Fig. 2.1. The major driving functions of the model.

We consider that temperature is a sinusoidal function with a minimum in spring of  $\sim 8^{\circ}\text{C}$  and a maximum in autumn of  $\sim 16^{\circ}\text{C}$  (Roden *et al.* 1987). We have no irradiance data for Killary; instead we have assumed the attenuated irradiance in the surface layer follows seasonal day-length pattern, with average values inferred from a preliminary cruise on Loch Linnhe. We estimate the attenuated irradiance in the intermediate layer to be  $\sim 10\%$  of that in the surface, using the PAR attenuation coefficient of  $\sim 0.23\text{ m}^{-1}$  obtained by M.R. Heath during August 1990 for Loch Linnhe.

**Table 2.7 Driving functions.**

Symbol	Description	Units
$C_{PE}$	Phytoplankton carbon concentration in the sea.*	$\text{mg C m}^{-3}$
$C_{PR}$	Phytoplankton carbon concentration in the run-off.*	$\text{mg C m}^{-3}$
$D_E$	DON concentration in the sea.*	$\text{mg N m}^{-3}$
$D_R$	DON concentration in the run-off.*	$\text{mg N m}^{-3}$
$F_E$	DIN concentration in the sea.*	$\text{mg N m}^{-3}$
$F_R$	DIN concentration in the run-off.*	$\text{mg N m}^{-3}$
$I_C$	Total immigration rate of carnivore carbon.*	$\text{mg C day}^{-1}$
$I_Z$	Total immigration rate of zooplankton carbon.*	$\text{mg C day}^{-1}$
$L_I$	Irradiance in intermediate layer.*	$\mu\text{Einst. m}^{-2}\text{ s}^{-1}$
$L_S$	Irradiance in surface layer.*	$\mu\text{Einst. m}^{-2}\text{ s}^{-1}$
$N_{PE}$	Phytoplankton nitrogen concentration in the sea.	$\text{mg N m}^{-3}$
$N_P$	Phytoplankton nitrogen concentration in the run-off.	$\text{mg N m}^{-3}$
$Q$	Sea temperature.*	$^{\circ}\text{C}$

\*See Fig 2.1 for the values of these driving functions.

## 2.3 Validation against data.

### 2.3.1 Data sources

The phytoplankton concentrations within the system are estimated from the mean of several subsamples of chlorophyll concentration given by Roden *et al.* (1987), using a C:Chl ratio of 20:1. Although the authors specify data from both brackish and non-brackish water, the incompleteness of data from the brackish water combined with the high variability in the ex-



tent of this brackish layer and the incompatibility of brackish layer depth and depth of outflowing surface water, does not justify specifying concentrations in surface and intermediate layers. We thus combine all samples from each sampling occasion. The number of such samples varies from 4 to 19 with a mean of  $\sim 9$ .

Data on the species and numbers of herbivorous and gelatinous zooplankton are given by Ryan et al (1986) and converted to carbon concentration by Rodhouse et al. (1987). We differ from these authors in using a carbon to dry weight conversion factor of 0.1 (rather than 0.2) for gelatinous zooplankton a value more appropriate to the gelatinous zooplankton species found in Killary.

### **2.3.2 Comparison of model and data**

The model output is shown on the right hand column of Fig. 2.2. We plot the equivalent biomass and nutrient data on the left hand side of the same figure (the nutrient data does not include ammonium or nitrate, which may comprise a significant proportion of the DIN concentration). In the first half of the year, through the spring bloom and into early summer, the model predicts both the general pattern and magnitude of the data at least as well as can be expected from a simplified model such as this - particularly pleasing is the strong similarity between model and data in the succession of phytoplankton, zooplankton and carnivore spring blooms. The one exception to this success is the underprediction of summer DIN concentrations which is probably due to the relatively poor information available on nutrients in the external system. It is encouraging to note however that this quality of fit is obtained by simply applying the independently measured parameter set. No fitting of any kind has been performed.

In the second half of the year however, the predictions shown by the light line deviate quite significantly from the pattern shown by the data.

This is apparently caused by our failure to predict the late summer phytoplankton bloom. A comparison of the predicted and observed zooplankton trajectories reveals the probable reason for this discrepancy: the model fails to predict the summer zooplankton crash which is in turn responsible for the August phytoplankton bloom. This suggests that we have underestimated zooplankton summer losses.

One obvious explanation for this is that our death rate is too low. Given the available food resources however no reasonable estimate of the basal losses or natural mortality provides an explanation for this sudden fall off in biomass. The absence of any significant biomass in the carnivore (gelatinous zooplankton) trophic level rules this out as a potential explanation. We note however that in late summer, sea lochs on the west coast of Scotland typically experience a substantial immigration of late larval and juvenile fish (Cooper 1980) which are known to be voracious predators upon zooplankton.

We therefore hypothesize that during July and early August Killary Harbour experiences a similar influx, which is not reflected in the census of gelatinous predators upon which the estimates of carnivore numbers are based. To explore this hypothesis we performed a second model run with parameters identical to the first, except that during the late summer period we introduced a substantial immigration of the generic carnivores, intended to mimic (albeit crudely) the influx of fish larvae. The results of this run are shown by the heavy line in Fig 2.2, which now exhibits good qualitative agreement with the observations over the whole of the observation period.

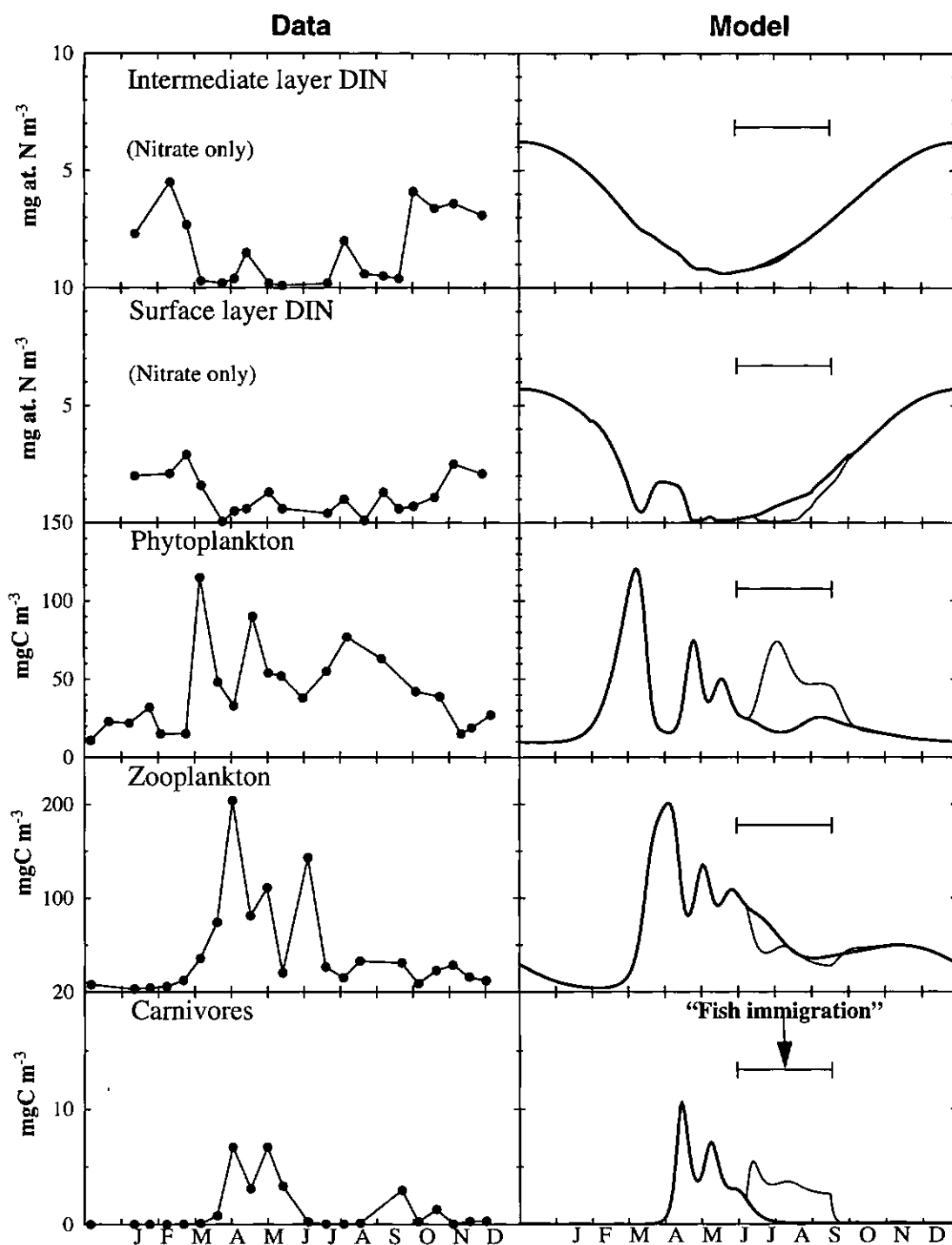


Fig. 2.2 Comparison of a model run with the default biological and nutrient parameters (Tables 2.1-2.4) and site-specific physical parameters with a dataset for Killary Harbour from 1981 (sources given in Chapter 2- the first zooplankton and carnivore data points are from 1982 and the last three phytoplankton data points are from 1980). The two top plots show data for nitrate only whereas the model comparison is the total predicted DIN. The thick line illustrates the effects of a summer immigration of larval and juvenile fish. Note: to facilitate comparison with experimental observations the predicted concentrations of DIN are displayed in units of mg-atoms  $N m^{-3}$ .

## Chapter 3 - Model behaviour

### 3.0 Introduction

We have established in the previous chapter the relevance of our model to a fjordic inlet on the west coast of Ireland. Whereas that system has much in common with sea-lochs on the west coast of Scotland (similar climate cf. Tables 2.5 & 3.1, and species composition), some aspects of the physical system, notably the shallowness and consequent rapid tidal flushing, may have a considerable influence on the nutrient and plankton dynamics. In order to explore the dynamics and underlying mechanisms of the model we will therefore consider in this chapter a physical system which is more typical of the west coast of Scotland.

**Table 3.1: Catchment features**

	Loch Linnhe - inner basin <sup>†</sup>
Catchment area (Km <sup>2</sup> )	20
Catchment type	Heathland, mountain, coniferous forest
Maximum rainfall (mm month <sup>-1</sup> )	307 (November)
Minimum rainfall (mm month <sup>-1</sup> )	83 (April)
Mean rainfall (mm month <sup>-1</sup> )	173

<sup>†</sup>Rainfall figures are for Fort William at the head of the inner basin (Meteorological Office data: 1976-1986).

### 3.1 A generic Scottish sea-loch

We assume that the species composition of the three trophic levels is similar to that of Killary (an assumption supported by the observations of Tett *et al.* 1978, Marshall & Orr 1934, and M.R. Heath pers. comm.) and hence that the biological and nutrient parameters which we used in the previous chapter are applicable to this generic system. We have no further information on some of the physical parameters, such as the entrained fraction of tidal exchange and the turbulent diffusion between S & I layers, hence we use the same values as we used for Killary Harbour.

We have estimated the layer structure of Loch Linnhe from data obtained during a preliminary cruise (M. Heath). This structure showed a well developed upper pycnocline at 10 m and a marked lower pycnocline at 40 m, with the average overall depth in the upper basin being 110 m. and inferred volumes for the intermediate and bottom layers of  $1.5V_s$  and  $1.9V_s$  respectively.

According to Tett *et al.* 1986b, the tidal exchange calculated from salt balance equations in Loch Creran is approximately equal to the maximum tidal exchange at mean neap tide. This loch, like Loch Linnhe opens out to the Firth of Lorne, and has been described by Landless & Edwards (1976 p30): "in its dimensions, run-off and tides, Creran is close to the unrealised typical Scottish fjord." We thus estimate the tidal exchange volume of the system to be  $0.4V_s \text{ d}^{-1}$ . This is well within the range calculated by Tett (1986) from salt balance equations, for a number of west coast lochs, of 0.08-0.6 of total loch volume. Freshwater runoff was calculated from rainfall data obtained from the Meteorological Office, which averaged over the catchment area, yielded an input of some  $0.035V_s \text{ d}^{-1}$  which is considerably lower than tidal flushing, hence for simplicity this is kept constant. Finally, guided by the observations of Edwards and Sharples (1986), and Tett (1986) on flushing times in west coast fjords, we estimated that turbulent diffusion exchanges  $0.05V_s \text{ d}^{-1}$  between the

intermediate and surface layers and  $0.02V_S \text{ d}^{-1}$  between bottom and intermediate layers.

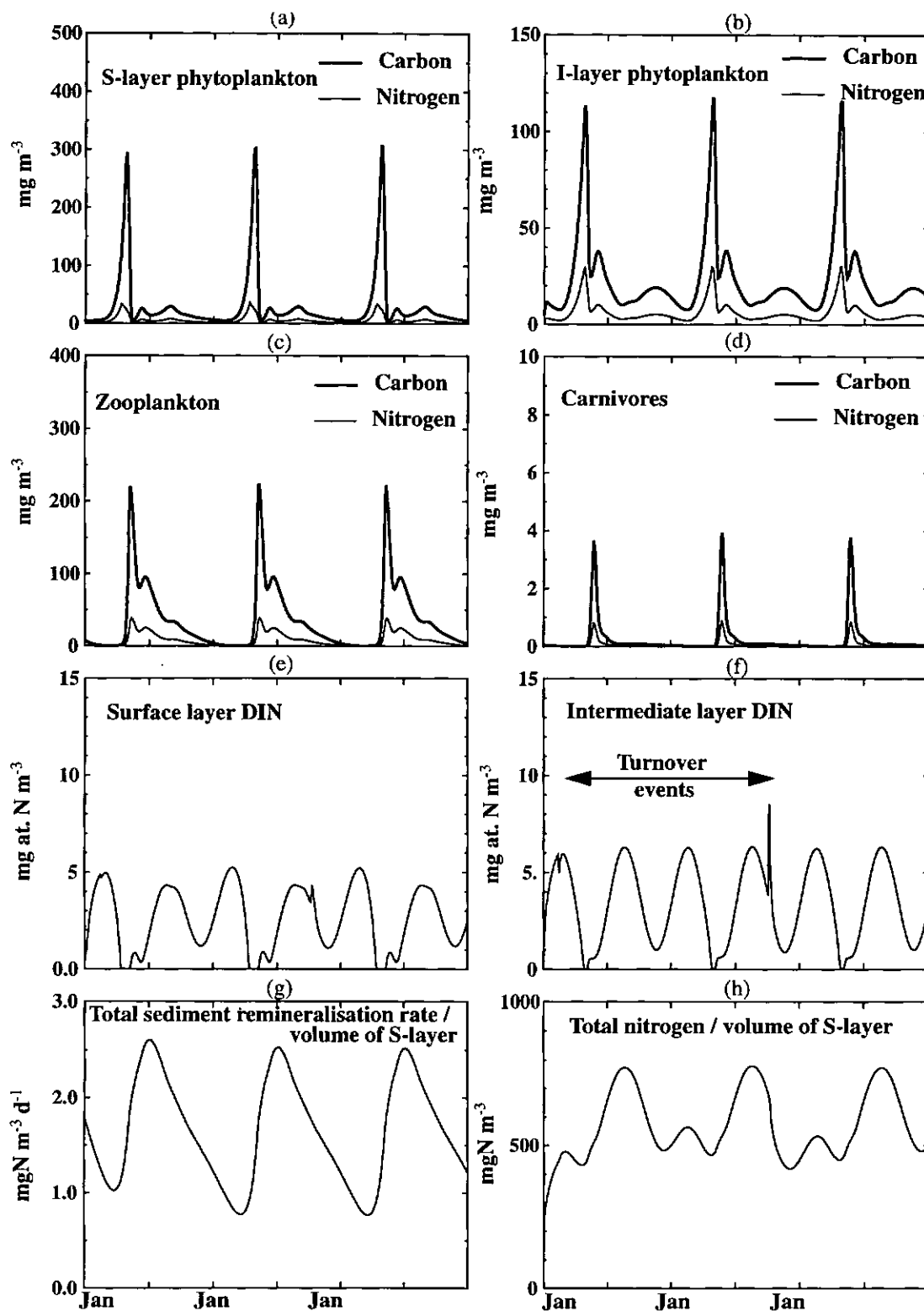
**Table 3.2: Physical parameters**

	Description	Units	Value
$V_B/V_S$	Volume of bottom (B) layer / volume of surface (S) layer.	dimensionless	1.9
$V_I/V_S$	Volume of intermediate (I) layer / volume of S-layer.	dimensionless	1.5
$V_J/V_S$	Volume of sediment (J) layer / volume of S-layer.	dimensionless	0.06
$\beta$	Proportion of tide entrained into S-layer.	dimensionless	0.25
$T_{BI}/V_S$	Volume exchange rate for mixing between B & I layers / Volume of S-layer.	days <sup>-1</sup>	0.02*
$T_E/V_S$	Volume exchange rate for tide into I-layer / Volume of S-layer.g	days <sup>-1</sup>	0.4
$T_{IS}/V_S$	Volume exchange rate for mixing between I & S layers / Volume of S-layer.	days <sup>-1</sup>	0.05*
$T_R/V_S$	Volume exchange rate for run-off into S-layer / Volume of S-layer.	days <sup>-1</sup>	0.035

\*These are compound parameters in the normal sense of turbulent diffusion.

### 3.2 The dynamic behaviour of the model

We will use the default parameter set for the generic system discussed above as a benchmark to assess the effects of parameter changes on the model behaviour. The results of a model run with this default set over a period of three years are shown in Fig 3.1. With the initial conditions we have chosen, the system settles into a stable pattern of fluctuation within the first year. A spring phytoplankton bloom, triggered by increasing temperature and irradiance, is followed first by a zooplankton bloom which reduces the phytoplankton to a relatively low concentration, and then by a carnivore bloom which similarly grazes down the zooplankton. The phytoplankton then recover producing a weak second bloom. This is accompanied by an even weaker recovery of the zooplankton, before the system is shut down by the onset of winter.



**Fig. 3.1** The results of the model with the default parameter set (Tables 2.1-2.5, Table 3.2) over a 3-year period. For ease of comparison between systems the units used for DIN concentration are  $\text{mg-atoms N m}^{-3}$ .

Our representation of phytoplankton nitrogen storage is reflected in the low levels of DIN in the S-layer (Fig. 3.1e) when the primary production is high. In winter when the lack of light prevents photosynthesis, the levels of DIN reach an annual maximum. The total nitrogen in the system (inorganic, organic, alive, and dead - Fig 3.1h) also shows a marked seasonal cycle. High primary production during spring effects a high nitrogen import rate causing a doubling in the total nitrogen within the system; followed by a decline during the post-bloom period to winter levels. A similar, but much weaker cycle, occurs during the autumn bloom. It would thus appear that the nitrogen dynamics are mainly influenced by the balance with the external system.

The perceived wisdom (e.g. Edwards & Grantham 1986) is that turnover events are enriching. This is not the case with the two turnover events in our model (indicated by the arrows in Fig. 3.1f) since nutrient cycling is not critical. In a fjord whose upper layers are continuously and rapidly flushed, the only result of a turnover event is to load the upper layers with more nutrient than the phytoplankton can immediately absorb. The surplus is then washed out of the fjord mouth and lost in the sea. In this system therefore, turnover events act to reduce the total nitrogen in the system and hence to impoverish it.

Although there is a substantial loss of nutrient arising out of a turnover event, there is little consequent effect on primary production, and hence on the biota in general. We illustrated this in Fig. 3.2, by showing the annual cycle of carbon concentrations for phytoplankton and zooplankton: a) with two turnover events (one in spring and the other in late summer), and b) without turnover events. The trajectories in both cases are almost identical. This is explained by the net import rates for organic and inorganic nitrogen shown in Fig. 3.2. A large pulse of nitrogen is



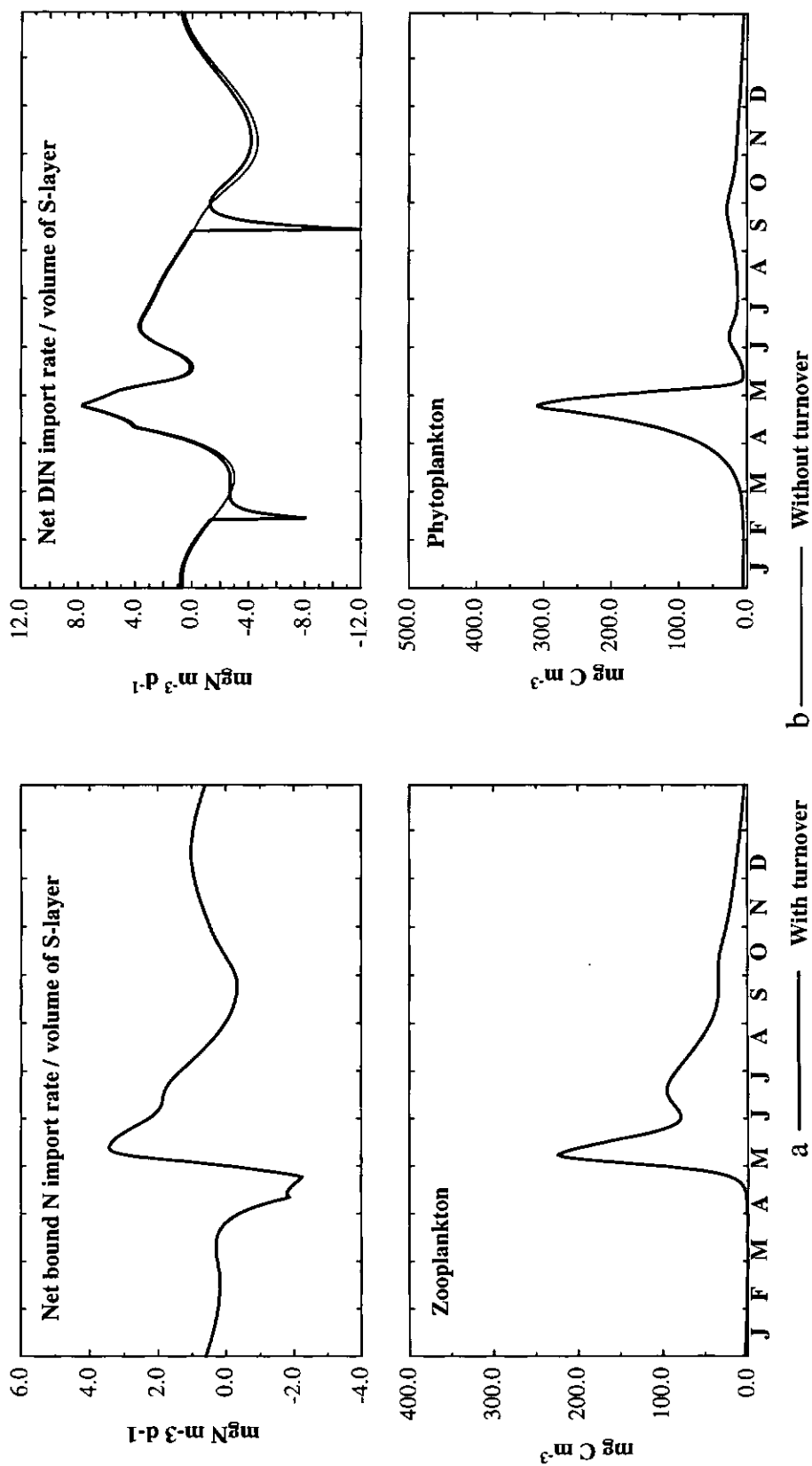
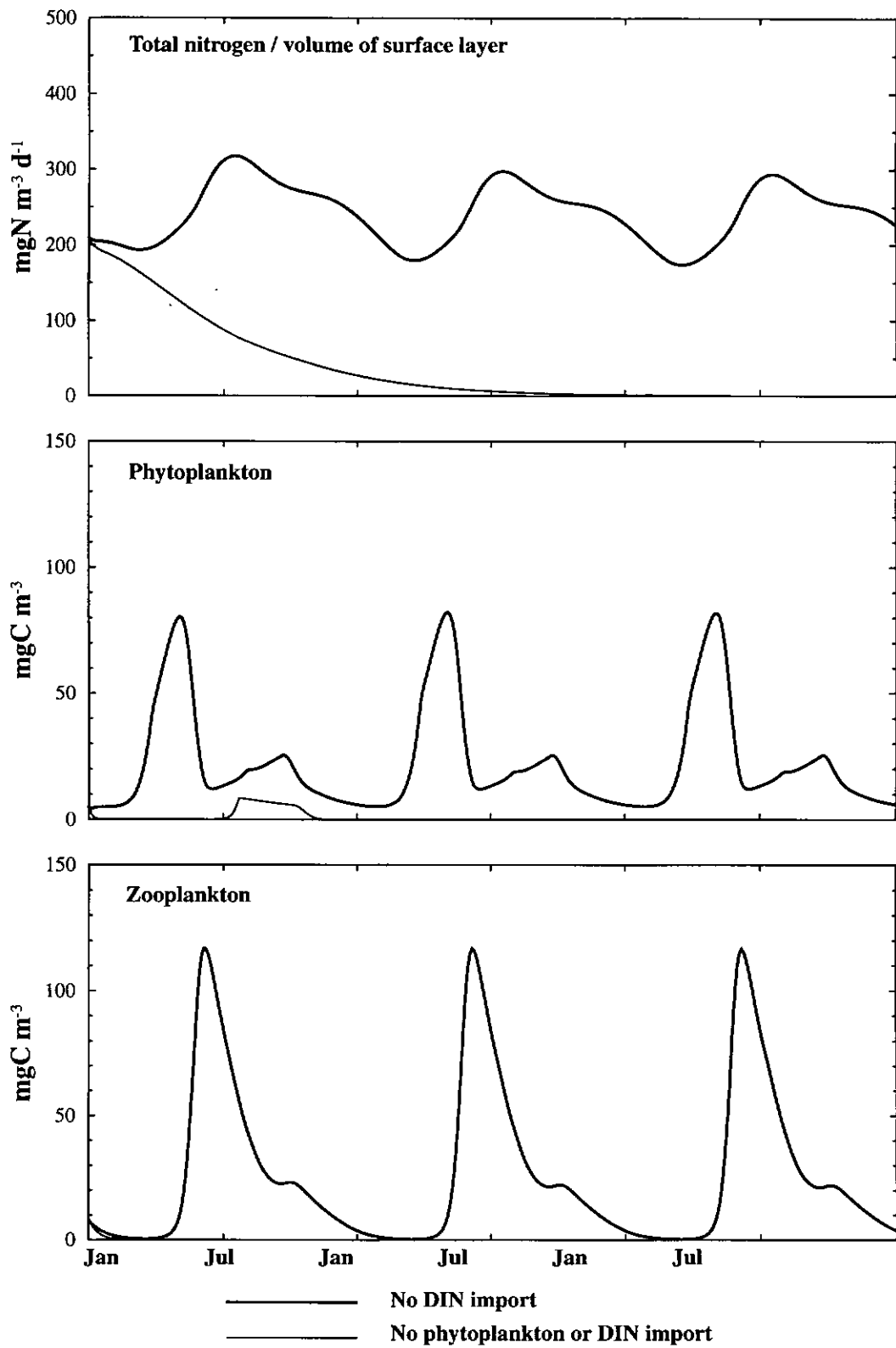


Fig. 3.2 An illustration of the effects of turnover events. The run with the turnover absent is shown as a thin line while the run with the two turnover events is displayed as a heavy line. For both phytoplankton and zooplankton the two are almost indistinguishable.

exported from the system immediately following a turnover event. Thereafter the dominant influence of the external system ensures that the fjord returns to its unperturbed state within a short period. Even in the case of the late summer turnover, which produces almost a 25% reduction in total system nitrogen, a small increase in the nitrogen import rate during the late summer restores the original balance.

The key influence on the dynamics of these systems is thus the large fluxes of nutrient being imported and exported. The system behaviour must ultimately be dictated by the balance of these fluxes. To understand these processes more fully we consider the fluxes of free (inorganic) and bound (organic) nitrogen separately. Figure 3.2 shows that in the default run these two processes are of comparable magnitude. To investigate their relative importance to the system dynamics we show in Fig. 3.3, two runs performed with the default parameter set, but with modified nitrogen import. The thick line, shows the effect of turning off inorganic nitrogen import both through freshwater runoff and tidal inflow. As we might expect, this produces a reduction in the average nitrogen content of the system and hence in primary production. The dominant influence of external factors on system behaviour is confirmed by the thin line in this figure, which shows the further change in behaviour which results from the assumption that the sea outside the fjord mouth is now not only barren of DIN, but is also empty of phytoplankton. In this case the system, deprived of all nutrient import, becomes totally impoverished over a period of about a year. After a minor burst of primary production (too small to trigger an accompanying zooplankton bloom) in the first year, the system is effectively dead.

Having determined that the system, with the default parameters, is ultimately controlled by the external supply of nutrient (in free and bound forms); we will now try and quantify this control. To do this we plot in Fig. 3.4 the maximum concentrations of phytoplankton and zooplankton



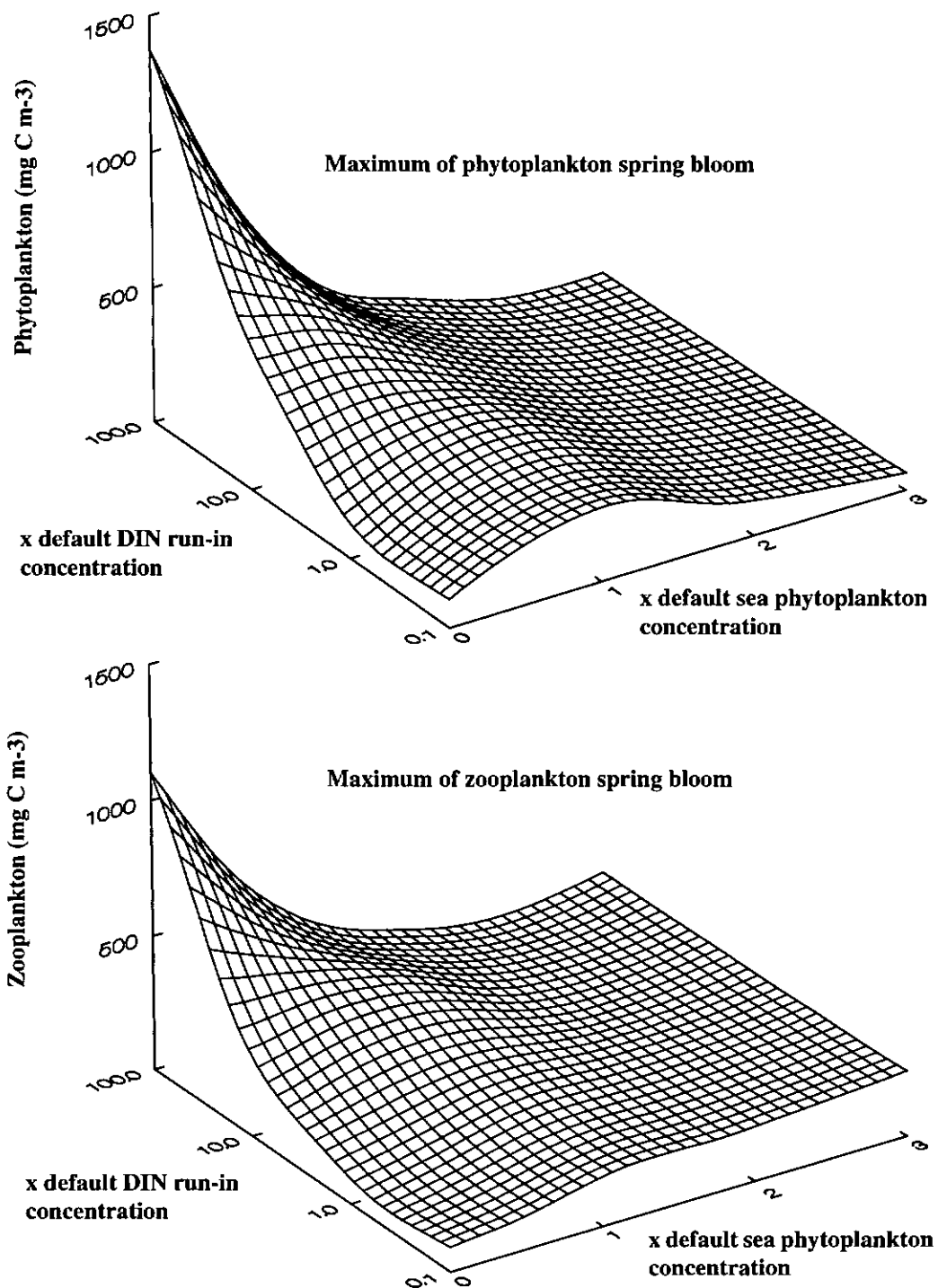
**Fig. 3.3** The effects of restricting imports on the persistence of plankton and total nitrogen in the fjord.

carbon in the spring bloom as a function of both inorganic nitrogen concentration in the runoff water and phytoplankton concentration in the external seawater. The variation of these quantities is given as the ratio of the value used to the default value, and the values used are varied over three orders of magnitude in the case of inorganic nitrogen, and a factor of 20 in the case of phytoplankton concentration.

At very low sea phytoplankton concentrations, the bloom size increases monotonically with increasing inorganic nitrogen import; although we note that the increase is slow until concentrations are above the default value. When both the inorganic nitrogen import and sea phytoplankton concentrations are low, the phytoplankton and zooplankton bloom sizes increase as a result of increased import of either bound or unbound nitrogen. This is consistent with the common perception of how a nutrient limited system should behave.

Under conditions of increasing nutrient supply and low sea phytoplankton concentrations however, the bloom sizes decrease with increasing sea phytoplankton concentration. The reason for this is that, in accordance with observations (Roden et al. 1987), the import of phytoplankton is assumed to continue at significant levels throughout the winter. In contrast to DIN imports, which cannot affect zooplankton in winter because lack of light shuts off primary production, imports of phytoplankton directly increase overwinter survival of the zooplankton. This increased survival gives the zooplankton a higher platform from which to respond to the spring increase in phytoplankton population, and thus enables them to reduce the magnitude of the phytoplankton bloom.

When sea phytoplankton concentrations are already high, further increases produce a larger zooplankton bloom, but result in a decreased standing crop of phytoplankton. This reflects the combined effect of pre-

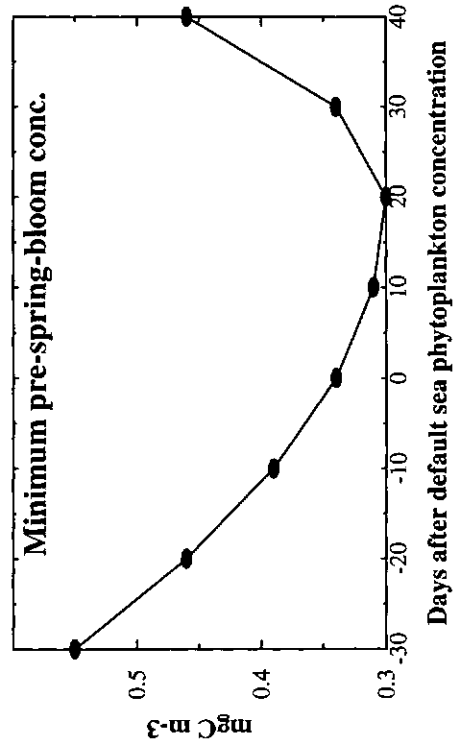
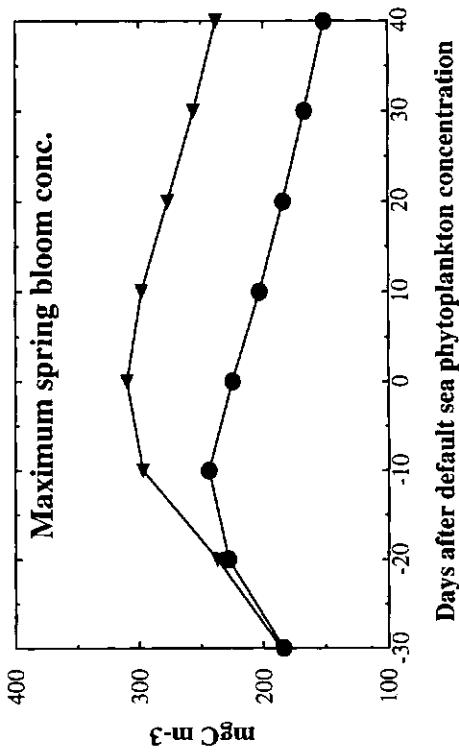
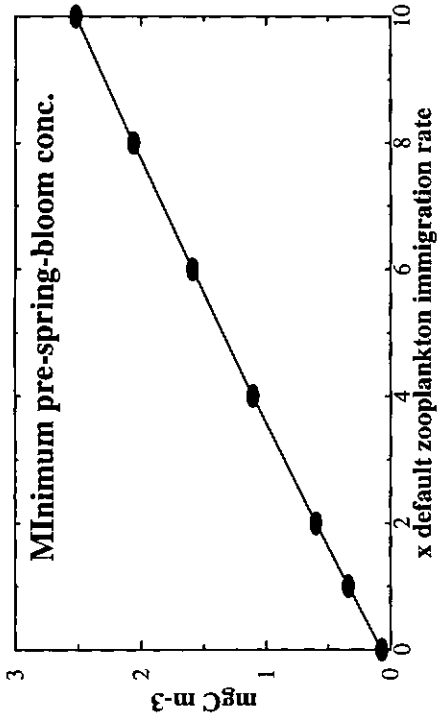
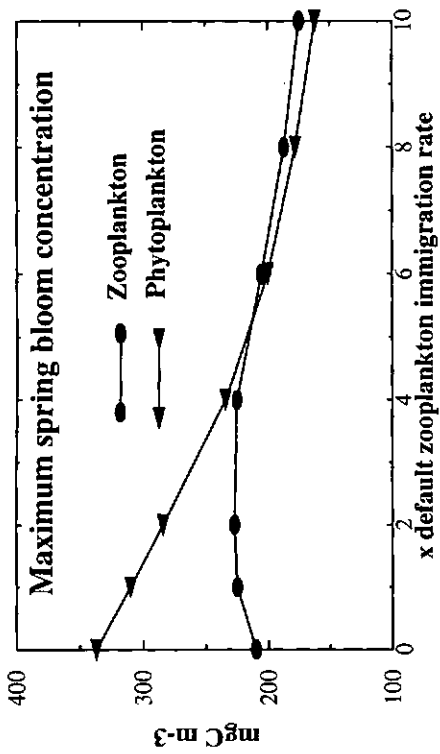


**Fig. 3.4.** The differing effects of varying DIN import (three orders of magnitude) and phytoplankton import (factor of twenty) on maximum phytoplankton and zooplankton spring bloom size.

bloom conditions and increased uptake of primary production by higher trophic levels during the bloom.

If increasing the amount of imported phytoplankton can reduce the phytoplankton bloom size by increasing the uptake of zooplankton, it follows that an increase in the zooplankton immigration rate will have a similar effect. This is confirmed by the upper two sections of Fig. 3.5; changing the zooplankton immigration rate from 0 to 10 times the default level results in a steady increase in the pre-spring bloom zooplankton level, and a consequent decrease in the size of the spring phytoplankton bloom.

A related, if somewhat more subtle, effect is demonstrated in the lower two sections of Fig. 3.5 where the driving function describing phytoplankton concentration in the external system is shifted over a range of 70 days. In the default run, the spring peak in sea phytoplankton population (and hence phytoplankton imports) occurs ~20 d after the peak of the phytoplankton bloom inside the loch - cf. Figs. 2.1 and 3.2. A change in the position of this peak (and the minimum that precedes it) affects the pre-bloom zooplankton levels, and hence the bloom size in two ways. Firstly, moving the sea phytoplankton driving function to a later time relative to the default, increases the phytoplankton import rate around the turn of the year, thus decreasing zooplankton death rates during this period. However, the same change in the driving function also delays the start of zooplankton population growth, which takes place as the phytoplankton import rate begins to increase from its early spring minimum. Delaying the driving function thus decreases the zooplankton loss rate but increases the period over which it is applied. Close to the default value these two effects almost balance out. When the driving function is heavily delayed the decrease in loss rate is the dominant effect, while if the driving function is significantly earlier than the default, the change in decay period overwhelms the rather small change in loss rate. Thus with



**Fig. 3.5** The effects of zooplankton immigration and the phase of phytoplankton immigration on minimum pre-bloom zooplankton concentration and resultant maximum phytoplankton and zooplankton spring bloom sizes.

the default sea phytoplankton driving function there is a minimum in pre-spring bloom zooplankton concentration and a consequent maximum in spring bloom size. Deviating from the default in either direction results in increasing pre-bloom zooplankton populations, and hence in decreasing bloom sizes.

As a second illustration of the dynamic subtlety of this system, we now re-examine the effects of changes in inorganic nitrogen import rates; looking now at a whole season (Fig. 3.6) rather than focusing only on the spring bloom. As expected from our earlier work, increasing (decreasing) the DIN import rate increases (decreases) the size of the spring phytoplankton bloom. However, over the rest of the year the imposed changes (two orders of magnitude) in inorganic nitrogen imports, produce no significant shift in the concentrations of phytoplankton, zooplankton, or carnivores. The reason for this is evident in the plot of phytoplankton nitrogen quota (N:C ratio) compared to the level above which specific growth rates are controlled by available light. Both the default run and the low DIN import run show a cell nitrogen quota dipping below the critical level at the height of the spring bloom, so that the spring bloom is nutrient limited. For the major part of the year however, irradiance rather than nutrient supply, determines primary production and hence controls the entire biological system.



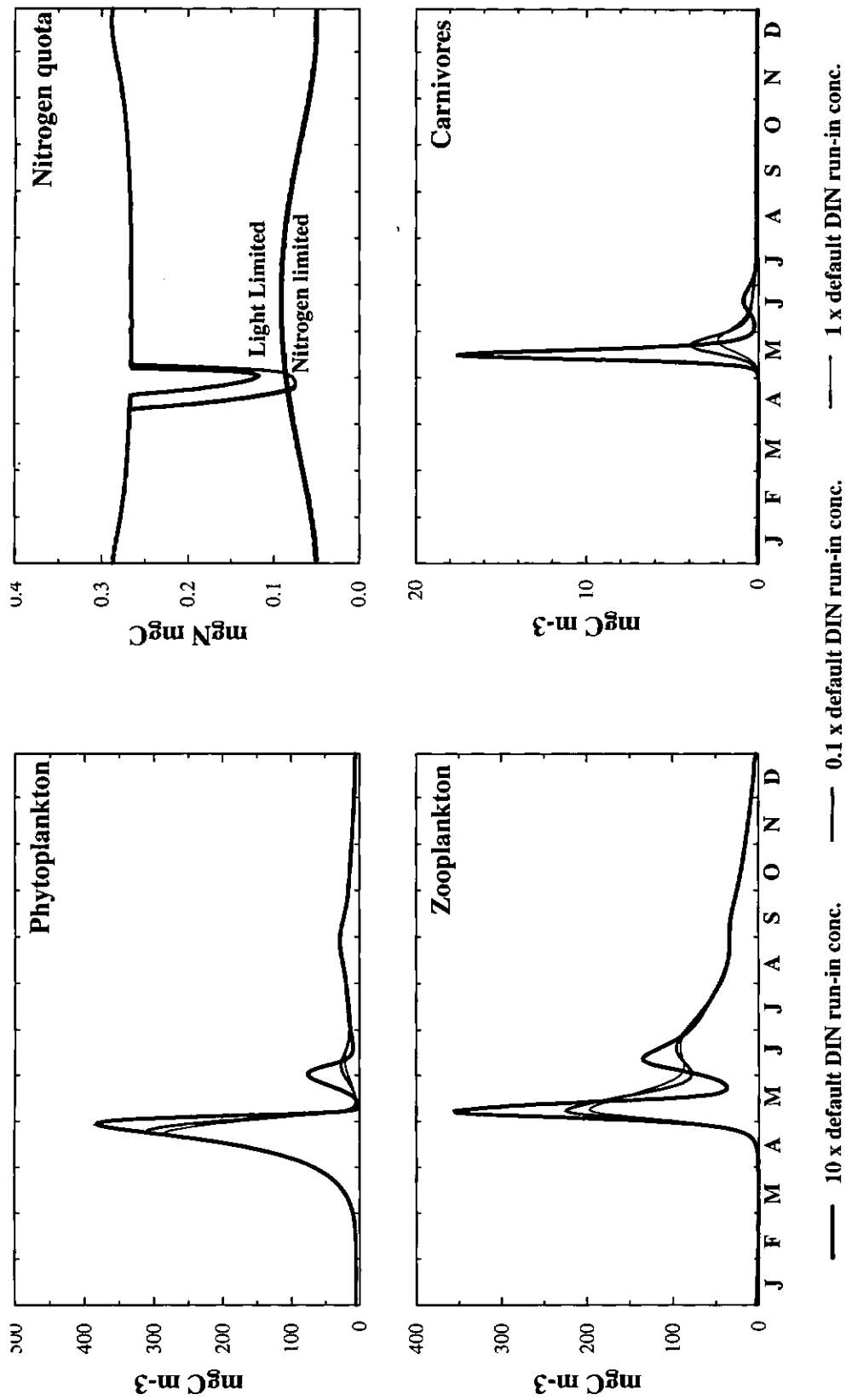


Fig. 3.6 The effects of varying DIN import rate on whole-year dynamics. The DIN run-in variation is equivalent to a transect of Fig. 3.5 with sea phytoplankton concentration held to its default value.

## **Chapter4 - Conclusions from the strategic simulation model**

### **4.1 Summary**

In constructing a strategic simulation model of a fjord ecosystem, we have been careful to avoid gross inconsistency in spatial and temporal scales. This has resulted in a model of sufficient structural simplicity to allow considerable insight into the mechanisms underlying its predictions. Despite this simplicity it is capable of semi-quantitative agreement with the observed behaviour of the Killary Harbour ecosystem during 1981. This agreement was obtained using a parameter set determined almost entirely from measurements unconnected with the test data set.

The key conclusion from our analysis of the behaviour of the model with a parameter set chosen to represent a typical Scottish west coast sea loch, is that the behaviour of the system is ultimately determined by the balance between nutrient import and export. This behaviour results primarily from the combination of a large tidal range with an underwater topography which promotes upwelling of the tidal inflow into the surface layer. When further combined with the large, nutrient rich, freshwater inputs common in Scottish conditions, this produces nutrient dynamics which closely resemble those of a laboratory chemostat. This is in contrast with the behaviour of inland lakes and slowly flushed, non-stratified, inlets, which are often sufficient approximations to closed systems to be dominated by nutrient recycling (e.g. Smith et al. 1989).

As in a chemostat, sea-loch equilibrium nutrient levels are determined by the balance between nutrient inflows accompanying the influx of water from outside the system, nutrient outflows resulting from water containing unabsorbed nutrient being expelled from the system, and nutrient uptake by primary producers. Unlike in a chemostat however, in a sea loch, the release of stored nutrient into the rapidly flushed upper layers (by a turnover event for example) can temporarily induce nutrient concentrations in these layers which are much higher than those in the sea outside; resulting in large (but short-lived) net outward fluxes.

Although the inorganic nutrient dynamics of a sea loch resemble those one might expect in a chemostat, the analogy is weaker for phytoplankton dynamics. The concentration of phytoplankton near the pycnocline, where seaward velocities are low, implies that they are washed out less quickly than dissolved nutrients. Moreover, the seawater flowing into the system contains viable phytoplankton as well as inorganic nutrient. This influx of phytoplankton not only represents an important source of imported nitrogen, but also affects the biological dynamics, both by changing the pre-spring bloom zooplankton levels and by prolonging the spring phytoplankton bloom and hence enhancing the following zooplankton bloom.

Another significant conclusion from the model analysis is that primary production in our generic Scottish west coast sea loch is nutrient limited only very briefly during the spring bloom. It is controlled by irradiance at all other times of the year. This control is due to the combination of low irradiance caused by the turbid conditions found in such systems; the continuous supply of inorganic nutrient resulting from chemostat-like nutrient dynamics; and (in summer) limitation of the phytoplankton population by grazing. The low standing crop of nutrient during the sum-

mer period reflects the high uptake rate of inorganic nitrogen rather than nutrient limitation. The cell nitrogen quota remains above the level at which nutrient limitation replaces light limitation as the determinant of cell division rate.

Although the *persistence* of a fjordic system is ultimately determined by imports of both organic and inorganic nutrient, the within-year dynamics are strongly influenced by predator-prey interactions. In common with all models lacking direct density dependence at intermediate trophic levels this model predicts that increases in productivity do not result in lasting changes in the standing crop of primary producers. Instead the increased production flows up the food chain to increase the numbers of the highest trophic level which lacks direct density dependence. This emphasizes the critical influence of carnivory on the within-year dynamics displayed by this model. A particularly notable example of this influence is provided by the improvement in fit to the Killary Harbour data produced by assuming episodic immigration of juvenile and larval fish at a time in late summer when the spring carnivore "bloom" had died away.

In view of the poor performance of nutrient cycling models when applied to closed aquatic ecosystems (e.g. Nisbet *et al.* 1990) it is reasonable to ask why the model developed here performs well in matching the behaviour of the Killary Harbour ecosystem. The answer seems to be that most key aspects of the dynamics of a fjordic ecosystem are determined by extrinsic factors which are incorporated reasonably accurately into this model. Adequate nutrient concentrations are maintained by the chemostat action of tidal and freshwater flushing, the spring phytoplankton bloom is triggered by temperature and irradiance, and primary productivity is irradiance controlled for most of the year. The details of within year dynamics following the spring bloom are primarily determined by the biological interactions which (on the evidence of closed system studies) this model probably oversimplifies. However these interactions are heavily stabi-

lized both by the extrinsic control of primary productivity and by the immigration of phytoplankton from the outside sea. This model system thus displays realistically damped predator-prey cycles instead of the highly divergent oscillations so easily generated by the related family of closed system models.

#### **4.2 Application to the field program.**

The major purpose in formulating this model was to develop a quantitative understanding of the processes within the Loch Linnhe system, and to utilize this understanding in the design of the forthcoming SOAFD experimental program. We have therefore performed a number of model runs with parameters chosen to resemble each of the two main basins of Loch Linnhe. These runs emphasize the conclusions set out above. The long term behaviour depends on the balance of imports and exports of nutrient, with the system ultimately coming to an equilibrium cycle in which yearly average imports exactly balance yearly average exports.

Since the within-year dynamics are strongly influenced by the variation of these fluxes, the most critical measurements concern the physical exchange of all categories of organic and inorganic nutrients (including phosphorus). These measurements must be done at both the seaward end of the lower basin and at the sill separating the upper and lower basins. Continuous recording instruments measuring temperature, salinity, current, and nitrogen concentration at hourly intervals have therefore been deployed as near as practicable to the Corran narrows (the boundary between upper and lower basins) and at the surface front between the Isle of Mull and Lismore Isle which marks the effective outer boundary of the loch.

Flushing times due to freshwater input are longer than those due to tidal action, and the within-year dynamics appear to be less sensitive to

DIN imports than to changes in phytoplankton influx. Thus the routine monitoring data available from the Highland River Purification Board on riverine inflows and inorganic nitrogen concentration should supply adequate detail concerning freshwater inputs to the system. The restricted influence of the (nutrient controlled) spring bloom on the behaviour of the system over the bulk of the year, and the key importance of higher trophic levels in determining phytoplankton concentrations (and hence gross primary production) over most of the year, imply that at least as much field and experimental effort should go into observations of zooplankton and carnivores as into direct estimation of primary production.

The SOAFD program will therefore entail frequent cruises covering the length of the loch from Lismore to the head of the inner basin, during which spatially resolved samples of both primary and secondary producers will be obtained, together with measurements of hydrographic and nutrient parameters. Taken together with the temporally highly resolved hydrographic and biological data which will be obtained from a single set of moored instruments deployed in each basin, these observations should form the basis of a comprehensive test of this sea-loch model.

### **4.3 Conclusions.**

This modelling study has shown that the dynamics of a sea-loch ecosystem are critically influenced by the balance between inward and outward fluxes of nutrients and phytoplankton. Phytoplankton imports are particularly important since they are both a significant source of nitrogen input into the system, and exert a central influence on the outcome of the predator-prey interactions which largely determine within-season dynamics. They do this by increasing over-winter survival of zooplankton and also by extending the period of rapid zooplankton growth beyond that directly attributable to the internally generated phytoplankton bloom.

In the conditions applying on the west coasts of both Scotland and Ireland the supply of inorganic nutrient appears to comfortably exceed demand except at the peak of the spring bloom. Thus for the majority of the year, primary production is controlled by irradiance and the activities of higher trophic levels. These controls on primary production imply that immigration of both zooplankton and carnivores, although insignificant in nutrient terms, can have a significant impact on the within-season dynamics of the system. Zooplankton immigration early in the year tends to increase pre-spring bloom zooplankton levels and hence suppress the spring phytoplankton bloom. Carnivore immigration tends to cut back zooplankton levels, and thus increase production, particularly in late season. The sensitivity of these systems to effects of this kind is particularly evident in the study of the Killary Harbour dataset.

## **Part 2**

### **Comparison of dynamics between systems**



## Chapter 5 - Model development

### 5.1 Introduction

In Part 1, we developed, tested, and analysed an ecosystem model of a fjordic inlet. This model is sufficiently simple in terms of both its biology and hydrography to allow an intuitive understanding of its mechanisms; and yet sufficiently complete to be capable of semi-quantitative agreement with observations of the seasonal cycle of an inlet on the west coast of Ireland - perhaps in part due to the simple nature of the system. Some further analysis has underlined the insensitivity of the model to anything but large parameter changes.

That model was mainly designed to advise on the optimal design of a field program on Loch Linnhe during 1991. Although the field program has now been completed, we do not at this stage have the data available to test the model for this system. Instead we return to the literature to obtain further datasets against which we can test the model.

Using this new data we shall attempt to develop a fully testable model capable of quantitative agreement with data on four contrasting sea-loch systems: Loch Airdbhair - a small, very rapidly flushed inlet, Killary Harbour - a narrow, well flushed fjordic inlet; Loch Creran - of similar size but more slowly flushed than Killary; and Loch Etive - a large, two basin

system with a slowly flushed inner basin.

We hypothesize that the observed differences in the annual cycle of nutrients and plankton in these systems result from differences in their environment and hydrography. We thus hope to show quantitative agreement between model and data for inorganic nitrogen, phytoplankton, and (where available) higher trophic levels; whilst applying the same set of biological parameters to all systems.

## 5.2 Four sea lochs

We have assembled four data-sets from the literature for four physically distinct sea-loch systems:

**Loch Airdhair** is a small unstratified loch on the north-west coast of Scotland. It has a mean depth of about 8m and a flushing time to the open sea of about one day (Gowen *et al.* 1983). The available data comprise a time-series of near-surface phytoplankton chlorophyll measurements made over the whole 1981 annual cycle, and a sparse series of depth-averaged nitrate concentration measurements for the same period.

**Killary Harbour** is a long, shallow, inlet on the west coast of Ireland, with a mean depth of about 14m and a somewhat constricted entrance. It is normally well stratified due to a high fresh-water input, and is flushed to the open sea with a time constant of between two and three days. In part 1 we collated a data-set for this system comprising seasonal measurements of chlorophyll and nitrate (Roden *et al.* 1987), together with holozooplankton and gelatinous zooplankton biomass (Ryan *et al.* 1986, Rodhouse & Roden 1987).

**Loch Creran**, which opens onto the Lynn of Lorne on the west coast of Scotland, has a similar total volume to that of Killary Harbour, and is also well stratified. Its relatively shallow and obstructed mouth however, gives it a noticeably longer flushing time - Tett (1986), using salt balance calculations, estimated the whole loch to be flushed in 6-7 days. Although it is divided into several subsidiary basins, temperature and density data suggest that these are reasonably well coupled (Tyler 1983), and that the horizontal structure plays little part in the dynamics. We have assembled data on the annual cycles of: chlorophyll for the six years 1970-76 (Tett & Wallis 1978, Jones 1979); dissolved organic and inorganic nitrogen data for 1971 (Solarzano & Ehrlich 1979); and DON and DIN data for 1974-75 (Jones 1979). This loch has been characterised by Landless and Edwards (1976) as "the typical Scottish sea-loch".

**Loch Etive** is a fjordic inlet extending from the Lynn of Lorn at its mouth, some 28km into mountainous terrain at its head. It is internally divided into two distinct basins which are relatively weakly coupled because of tidal attenuation at the shallow, restricted mouth. The outer basin is of similar conformation to Loch Creran, while the inner basin has a maximum depth of some 150m. According to Tett (1986) the whole system is flushed in approximately 12 days - a result which is heavily influenced by the depth of the upper inner basin. We estimate that the lower basin is flushed in approximately 3-4 days and the inner basin in approximately 10-14 days. The available data for this system comprise measurements on the annual cycles of: chlorophyll in the lower basin during 1971 (Wood *et al.* 1973, Solarzano & Ehrlich 1977a); and DON and DIN measurements for the upper and lower basins during the same period (Solarzano & Ehrlich 1977a,b).

The annual cycles of these four systems show significant variations which appear to be correlated with either their environment or their hydrological characteristics. Loch Airdbhair, the most open of the four systems, does not have a well marked spring bloom, but instead shows a broad period of enhanced phytoplankton standing crop (about  $40 \text{ mgC m}^{-3}$ ) between March and July. For the rest of the year, the standing crop shows only small variability about a mean level of about  $5 \text{ mgC m}^{-3}$ . Killary Harbour shows a sharp increase in phytoplankton abundance, to over  $100 \text{ mgC m}^{-3}$ , in late March with an almost equally sharp fall a few weeks later. It then exhibits a smaller peak in early June, with a third, slower, rise to over  $50 \text{ mgC m}^{-3}$  during August. Lochs Creran and Etive, which are more slowly flushed than the first two and share a common external environment, show sharp blooms to over  $200 \text{ mgC m}^{-3}$  in mid-March, falling to a more or less constant summer level of around  $50 \text{ mgC m}^{-3}$  some three to four weeks later.

The diatom *Skeletonema costatum* is the most abundant primary producer in the three systems for which we have information on species composition. We thus speculate that all four systems may (at the level of aggregation dealt with here) have essentially similar biota. This taken together with the clear correlation between annual cycle and some combination of environment and physical characteristics, suggests that it should be possible to predict all four annual cycles with a single model, using system-specific parameters only for hydrographical and environmental quantities.

### 5.3 The new model

The model we develop here is a close relation of the strategic simulation model described in Chapter 1. As a result of detailed testing of this model against data from a variety of sea-lochs, we have introduced a number of changes. Some, such as the introduction of a single storage pool to represent both sediment and stable bottom waters, reflect the removal of

extraneous detail which has been shown not to have a significant influence on model behaviour. Most, however, have been motivated by the inability of previous model versions to reproduce significant features of observed dynamics. These latter changes have focused particularly on the influence of light on primary production, and on several features of zooplankton dynamics.

The structure of the simplified physical part of the model is shown schematically in Fig. 5.1. The schematic representation of the biological and nutrient models is identical to that shown in Chapter 1 (Figs 1.4 & 1.5). The equations, driving functions and parameters of the new model are reproduced in Appendix A.

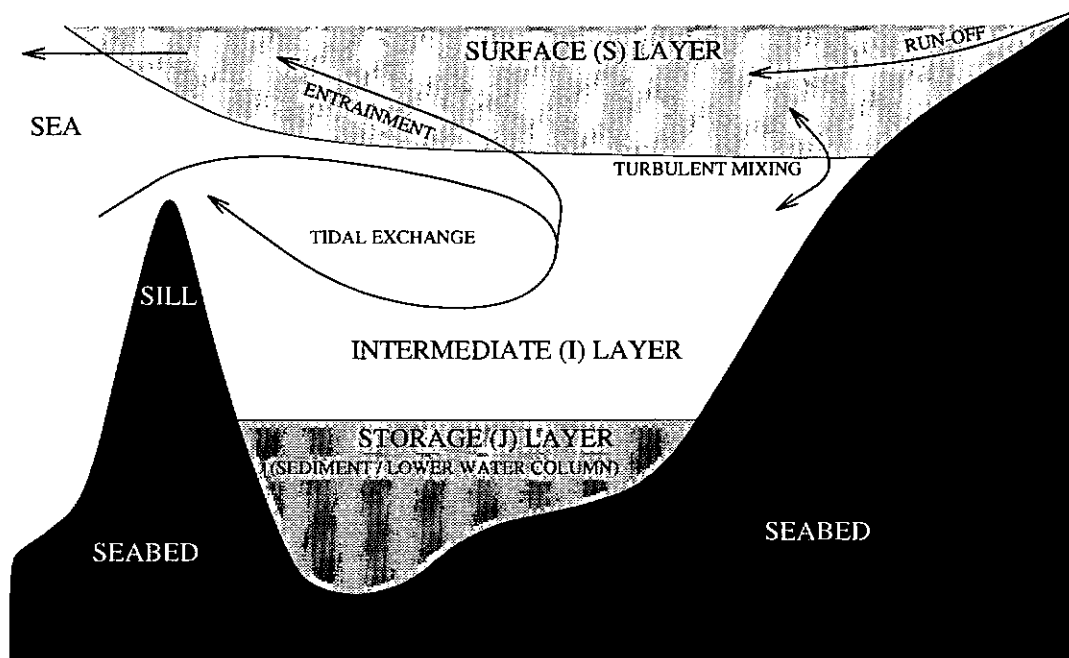


Fig. 5.1. The modified model of the physical system with a combined sediment and bottom layer which is now termed the storage layer.

### 5.3.1 Primary Production.

Our representation of the factors limiting primary production relies on the assumption that the surface and intermediate layers are well mixed vertically and horizontally. This implies that the vertical distribution of phytoplankton is uniform within each layer, as are inorganic nutrient concentration and phytoplankton nitrogen quota. Under these assumptions, a simple box-model ecosystem description can readily be extended to achieve an exact treatment of depth dependent primary production. We discuss here only the surface layer in detail, but we have also made a similar calculation for the intermediate layer; the results of which are summarised, along with those for the S-layer, in Appendix A (Table A.2).

Within the surface layer the light intensity at depth  $\gamma$ ,  $L(\gamma)$ , is related to the surface irradiance,  $L_S$ , by the Lambert-Beer Law

$$L(t, \gamma) = L_S(t) e^{-\kappa\gamma} \quad \text{Eqn.: 5.1}$$

We assume that the depth dependent attenuation coefficient,  $\kappa$ , is given by the linear combination of a background value  $\kappa_0$ , with a self-shading term proportional to the phytoplankton concentration  $C_{PS}$ ,

$$\kappa = \kappa_0 + \rho C_{PS} \quad \text{Eqn.: 5.2}$$

For the sake of compactness, we define two functions:

$$\Psi_L(\gamma) = R_{ML} \frac{L(\gamma)}{L(\gamma) + H_L} \quad \text{Eqn.: 5.3}$$

and

$$\Psi_Q = R_{MQ} \left(1 - \frac{Q_{\min}}{Q_{PS}}\right)^+ \quad \text{Eqn.: 5.4}$$

which represent the potential limiting effects of light and nutrient quota respectively. Following our formulation in Chapter 1, we assume that rate of carbon uptake by the phytoplankton is determined by the most limiting of these two factors, so the specific rate of carbon fixation at depth  $\gamma$  is

$$u(\gamma) = C_{PS} S_P(t) \text{Min}[\Psi_L(\gamma), \Psi_Q], \quad \text{Eqn.: 5.5}$$

where  $S_p(t)$  represents the seasonally varying effects of temperature.

Since the light intensity declines monotonically with increasing depth, equating the limiting factors defined in equations 5.3 & 5.4 yields a depth,  $\gamma_L$ , below which primary production is light limited. Recognising that the meaningful range of results for this calculation is from 0 (the surface) to  $\gamma_S$  (the depth of the surface layer) we find that

$$\gamma_L = \text{Min} \left[ \gamma_S, \left[ \frac{1}{\kappa} \ln \left\{ \frac{L_S}{H_L} \left( \frac{R_{ML}}{\Psi_Q} - 1 \right) \right\} \right]^+ \right]. \quad \text{Eqn.: 5.6}$$

The total nutrient fixation rate in the surface layer,  $U_{CS}$ , is now determined by integrating  $u(\gamma)$  over volume of the surface layer, taking the nutrient limited and light limited regions separately. This finally gives

$$U_{CS} = V_S C_{PS} S_P(t) \left[ \frac{\gamma_L}{\gamma_S} \Psi_Q + \frac{R_{ML}}{\gamma_S \kappa} \ln \left\{ \frac{L_S e^{-\kappa \gamma_L} + H_L}{L_S e^{-\kappa \gamma_S} + H_L} \right\} \right], \quad \text{Eqn.: 5.7}$$

where  $V_S$  is the total volume of the surface layer.

### 5.3.2 Zooplankton Dynamics.

Uye (1982) gives data for a population of *Acartia clausi* in Onagawa Bay, which shows that resource partitioning between growth and reproduction is highly dependent on water temperature, and hence on season. Low temperatures were correlated with low per-capita fecundity and high maximum carapace length, with the inverse situation being seen at low temperatures; suggesting a temperature dependent shift in the proportional allocation of resources.

The dynamics of this process are complex, and are closely connected with the production of resting eggs. Uye observed that during winter the major source of recruitment to the population came from resting eggs hatching from the sediment, while during the rest of the year most of them hatched directly in the water column. Maximal deposition of resting eggs to the sediment was observed to take place during July and August.

Since Onagawa Bay somewhat resembles Killary Harbour in both hydrography and temperature profile, and because *Acartia clausi* is prevalent in both systems, we might expect the processes observed by Uye to be present in our systems. This may have a significant impact in two ways. Firstly the shift away from growth and towards the production of resting eggs (many of which will subsequently be lost) constitutes a significant increase in immediate losses from the zooplankton population. Secondly the survival of a small proportion of the resting eggs over winter will affect the pre-bloom zooplankton abundance the following year, and



may hence exert an influence on dynamics of that year's bloom (see Chapter 3).

A proper representation of overwintering effects is a complex modelling task which we shall not attempt here. However, in the context of our biomass model, the immediate effect can be represented as a time dependent addition to the zooplankton loss rate. In view of Uye's observation of a correlation between fecundity and temperature we postulate that this loss term is directly dependent on temperature through a simple "activated process". We thus write the total zooplankton loss rate as

$$m_Z = \delta_Z + e_{bZ} S_Z(t) + \Delta \exp\left(-\frac{T_{ZE}}{T}\right) \quad \text{Eqn.: 5.8}$$

where  $\delta_Z$  is the background per capita mortality, and  $e_{bZ} S_Z(t)$  is the (temperature dependent) basal metabolic rate.

The model described in Part 1 assumed that the zooplankton spent a fixed proportion of their time feeding in each of the two surface layers, independent of the relative phytoplankton abundance. A more plausible supposition is that the zooplankton are to some degree capable of modifying their behaviour in response to phytoplankton density. It is not possible to model such effects exactly in the context of a simple box-model, but we can simulate the "refuge" effect which would be produced by aggregation of the zooplankton onto regions of high phytoplankton density by assuming that the zooplankton feed solely in whichever of the two upper layers has the higher phytoplankton population. To avoid the numerical difficulties posed by such a discontinuous switch of activity, we make the change a little more progressive by writing the proportion of time spent feeding in the surface layer ( $\mu_Z$ ) as

$$\mu_Z = \text{Min} \left[ \left\{ \frac{1}{2} + \omega_a \left( \frac{C_{PS}}{C_{PI}} - 1 \right) \right\}^+, 1 \right] \quad \text{Eqn.: 5.9}$$

### 5.3.3 Biological Parameters.

The four sea-lochs which are the subject of this study have different locations and characteristics. On the scales at which this model was designed however, it is reasonable to regard their biota as identical, and to seek to explain the differences in their behaviour solely as the outcome of their hydrography and the external sea conditions. Hence, we have a single set of biological parameters (Appendix A - Table A.4) which are largely the same as those used in Part 1. We have however made some structural modifications, which taken together with the results of the testing discussed above, has resulted in a number of parameter changes which we will discuss in detail here.

The most significant structural changes relate to depth dependent primary production and the amalgamation of the sediment and the bottom layer into a single storage compartment. We have determined both the background attenuation and the self-shading parameter required by the primary production model from Tyler's (1983) observations of irradiance in Loch Creran. The change to a single storage compartment was made primarily for reasons of simplicity, since our previous analysis has shown the behaviour of the model is very weakly influenced by this part. We have thus chosen the return rate parameter for this compartment so as to produce the same flux of inorganic nitrogen into the intermediate layer as that implied by our more hydrodynamically realistic first generation model.

The parameters describing the new features of zooplankton biology (preferential feeding in regions of high phytoplankton concentration and temperature dependent loss rates) cannot readily be obtained from the

literature. We thus treated them as free parameters in the sense that we optimised them to yield an acceptable fit to the Killary Harbour data, and then assumed unchanged values for comparison with the other systems in our data-set.

Two further parameters (the carnivore half saturation zooplankton concentration and the DON remineralisation rate) have been changed as a result of the model tests to be described later. Our original estimate of the DON remineralisation rate was made from data (Harrison 1978) on California waters, and proved to be considerably too high. The most appropriate value for Scottish waters was determined by optimising our model fit to the DIN and DON data available for Loch Creran (Solorzano & Ehrlich 1977a & b).

#### **5.3.4 Hydrological Parameters.**

The basic hydrological parameters required by the model are the volumes and depths of the two active layers, a (nominal) volume for the storage layer, and the proportions of the active layers exchanged per unit time with each other and with the external environment. The values used for the four systems examined in this study are given in Appendix A (Table A.5) For Killary Harbour, we derived the necessary values from our earlier study (Part 1). For the three Scottish systems we obtained the physical conformation of the system from Admiralty Charts, and took data on layer depths and tidal exchanges from Gowen *et al.* (1981 - L. Airdbhair), Edwards & Sharples (1986 - L. Etive), Wood *et al.* (1973 - L. Etive), Tett & Wallis (1978 - L. Creran), Tett *et al.* (1986 - L. Creran), and Tyler (1983 - L. Creran).

#### **5.3.5 Driving Functions.**

The external environment of the system is modelled by driving functions for:

temperature,  
surface irradiance,  
sea concentrations of DIN, DON, and phytoplankton,  
immigration rates of zooplankton and carnivores  
fresh-water run-in rate.

In view of their importance to the observed dynamics we have taken care to obtain the best possible values for these quantities, but inevitably we have more complete information for some systems than for others. Details of all driving functions are given in Appendix A (Table A.6), and the seasonal variation of the most significant of them are illustrated in Fig A.1.

Tyler (1983) gives a detailed time-series of surface irradiance values at Dunstaffnage Marine Laboratory during the year 1975. In view of the quality of this data, and the fact that all the systems are at essentially the same latitude, we have used this data as the surface irradiance driving function for all our model systems. However, for Killary Harbour and Loch Airdhair, which are some distance from Dunstaffnage, we smoothed out variability with a period of less than 1 week. For similar reasons we assumed the same seasonal variation of temperature for all four systems and used the pattern of an early spring minimum and a fall maximum described in Chapter 2.

Tett (1973) gives detailed data for the seasonal variation of the phytoplankton concentration in the Lynn of Lorne during 1971, which forms an appropriate driving function for both Loch Creran and Loch Etive (Appendix A - Fig A.1). For the sea off Killary Harbour we have less detailed data in Roden (1984) and Colebrook (1979), and in the absence of any appropriate data for the vicinity of Loch Airdhair we choose the

same driving function for this system on the grounds that it, too, faces more or less directly into open shelf waters.

Unpublished field data show that the sea-DIN concentrations appropriate to Lochs Creran and Etive are similar to those derived in Chapter 2 (from the data of Roden 1984) for the sea off Killary Harbour. In the absence of any detailed information about DIN concentrations in Eadrachilles Bay, we also used this driving function for the Loch Airdbhair simulation.

In Chapter 2 we, perhaps controversially, regarded run-in volume as constant and took the concentration of DON and DIN in that water as varying seasonally. We here adopt the more conventional viewpoint that run-in volume varies and nutrient concentrations remain constant. Detailed rainfall records are available for the nearby Fort William area (Meteorological Office). We have assumed that the seasonal pattern of run-in to all our systems is the same as the seasonal pattern at Fort William. Where we have mean run-in data we simply adjusted the mean value of the standard time-series to accord with the known value, where we did not have direct run-in information, we assumed that the rainfall amount was the same as at Fort William and calculated run-in on the basis of the catchment area of the system concerned.

### **5.1. A Two-Basin extension.**

Loch Etive, is composed of two linked basins separated by an inner sill. The tidal velocities at such points are normally high, leading to potentially complex hydrodynamics. In the interests of model simplicity we assume that the two subsystems are coupled only by exchanges between their surface and intermediate layers, and have incorporated the additional mixing implied by turbulence and entrainment at the inner sill into the existing parameters. We assume that the phytoplankton populations are coupled by the same physical processes as nutrient exchange, and that

each basin has independent zooplankton and carnivore populations. The equations governing the physical exchange processes for the two-basin version of our model are shown in Appendix B.

## 5.4 Testing and refining the model

### 5.4.1 Methodology.

In the work reported here we are concerned with obtaining an accurate representation of the annual cycle of the systems under consideration. Carefully constructed diagrams, with data and predictions shown on the same axes with helpfully chosen aspect ratios, are an indispensable part of such an exercise, and are probably the most effective way of pinpointing serious errors in prediction. However, as the model fit becomes more accurate, small changes to structure or parameters often produce improvements to the fit in some variables at the expense of a reduction in the accuracy of others. In such situations, eye-ball methods are prone to mislead and a quantitative measure of accuracy is required, which can be compared across a number of quantities whose sizes may be very different. After some experimentation we chose as our test statistic the normalised mean absolute error, defined for a variable  $x$  as:

$$E_{\text{abs}} \equiv \frac{\sum_{i=1}^N |P_i(x) - O_i(x)|}{\sum_{i=1}^N O_i(x)}; \quad \text{Eqn.: 5.10}$$

where  $P_i(x)$  is the  $i$ th predicted value of the quantity  $x$ , and  $O_i(x)$  is the equivalent observed value. We chose this statistic rather than the

coefficient of variation, which it somewhat resembles, because it is easier to interpret in a situation where neither the observed values nor the deviations seem likely to be characterised by a stationary probability distribution.

To provide a quantitative guide to the quality of individual fits, we calculate  $E_{\text{abs}}\{.\}$  separately for each state variable for which data exists. We compile an overall score for the model by averaging the normalised mean absolute error over all tested state variables.

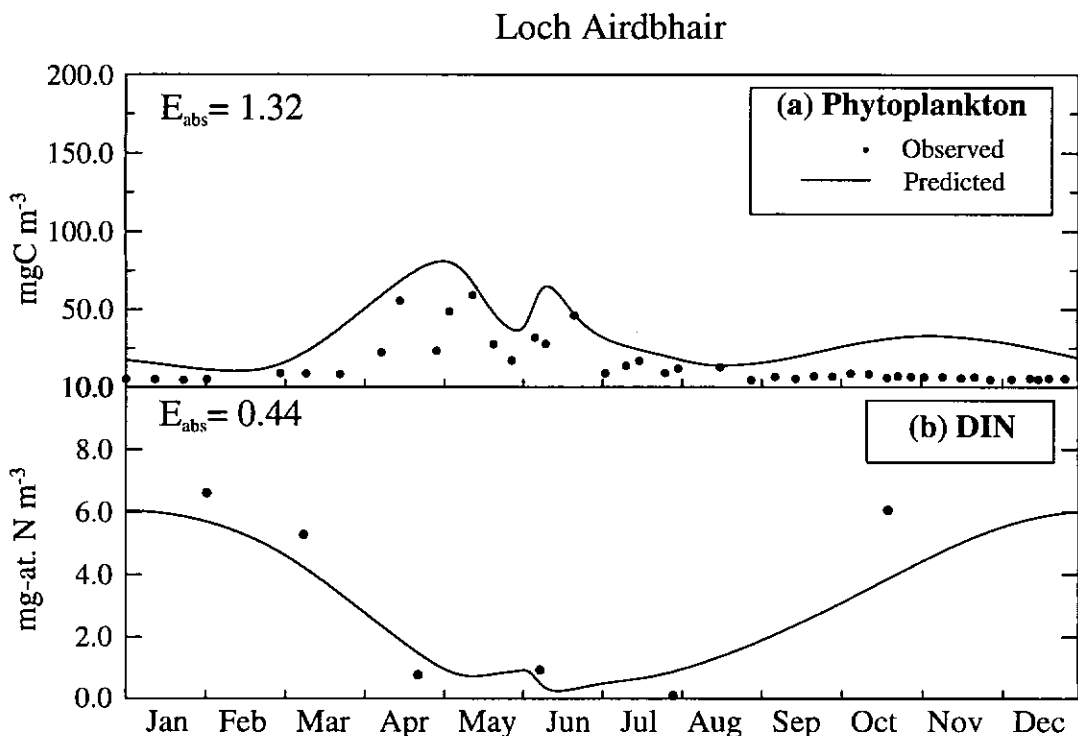
#### **5.4.2 Baseline Model Results**

We now consider to what extent the baseline model, defined in Appendix A (Tables A.1 and A.2), can successfully postdict the data-sets we have collated for four contrasting sea-loch systems. We use the single set of biological parameters given in Appendix A (Table A.4) together with the well defined (and reasonably well known) site-specific hydrological parameters given in Table A.5, and our best estimates of the appropriate driving functions (Table A.6).

The annual cycles predicted by the baseline model are illustrated in Figs 5.2-5.5. There is a good quantitative agreement, both visually and between the predicted and observed values. This is backed up by the uniformly low values of normalised mean absolute error. As a standard of comparison, the overall normalised mean absolute error calculated from this fit to the Killary Harbour data is 0.65, whereas the equivalent value for the semi-qualitative fit obtained in Chapter 2 to the same data is 0.88. The improvement in this agreement is mostly in the areas of nutrient and carnivore abundance.

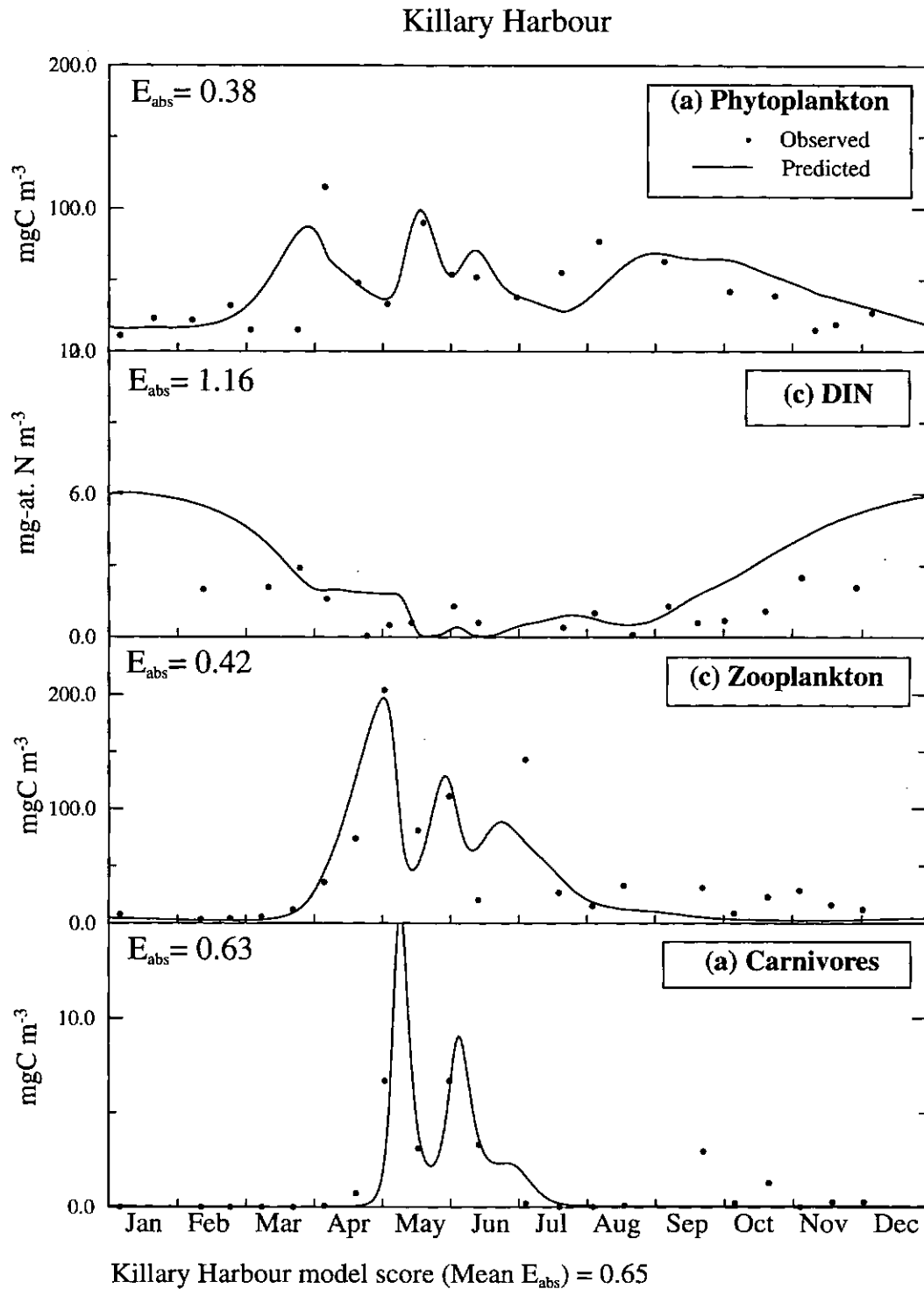
Closer examination of Figs 5.2-5.5, shows good agreement of maximum

spring phytoplankton abundance over a range from about 50 mgC m<sup>-3</sup> in Loch Airdbhair to over 200 mgC m<sup>-3</sup> in Loch Etive. Moreover the site-specific shape of the spring bloom has been correctly captured - very wide and blurred in Loch Airdbhair, multiple-peaked in Killary Harbour, and short and intense in Lochs Creran and Etive. The general pattern of summer and autumn phytoplankton abundance has also been quite accurately reproduced - a strong autumn bloom in Killary Harbour, and weaker (but noticeable) increases in late summer standing crop in Lochs Creran and Etive.



**Fig. 5.2** The baseline model, using a common set of biological parameters and system specific physical parameters and driving functions, compared with data from Loch Airdbhair on the north west coast of Scotland.





**Fig. 5.3** The model compared with data from Killary Harbour. NB. In this version of the model we compare a mean of the S & I layer DIN with the mean of the data from two stations in Killary Harbour - one station is at in the inner fjord at 3m, the other station is at the entrance to the fjord at 20m.

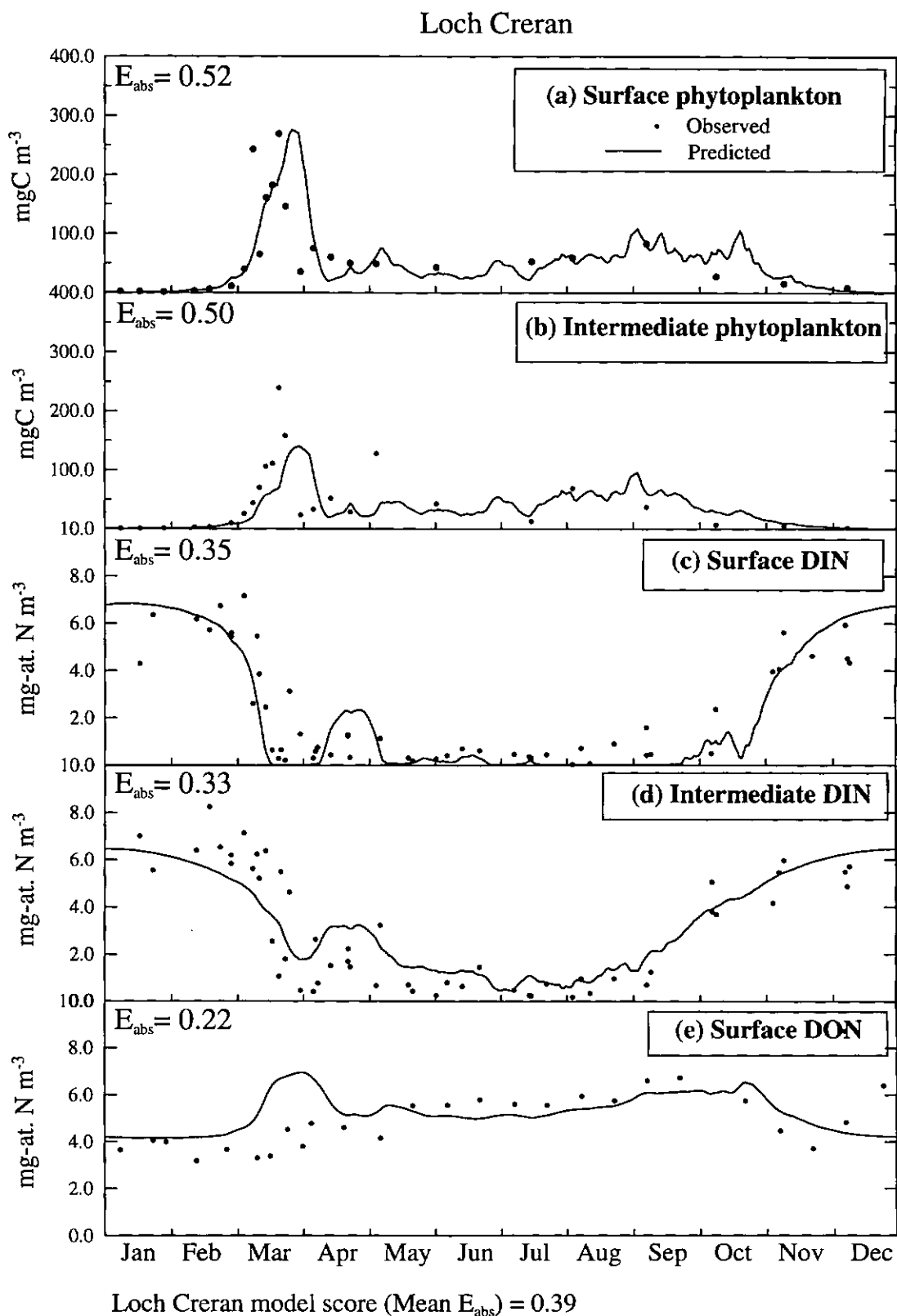


Fig. 5.4 The model compared to data from Loch Creran.

## Loch Etive - outer basin

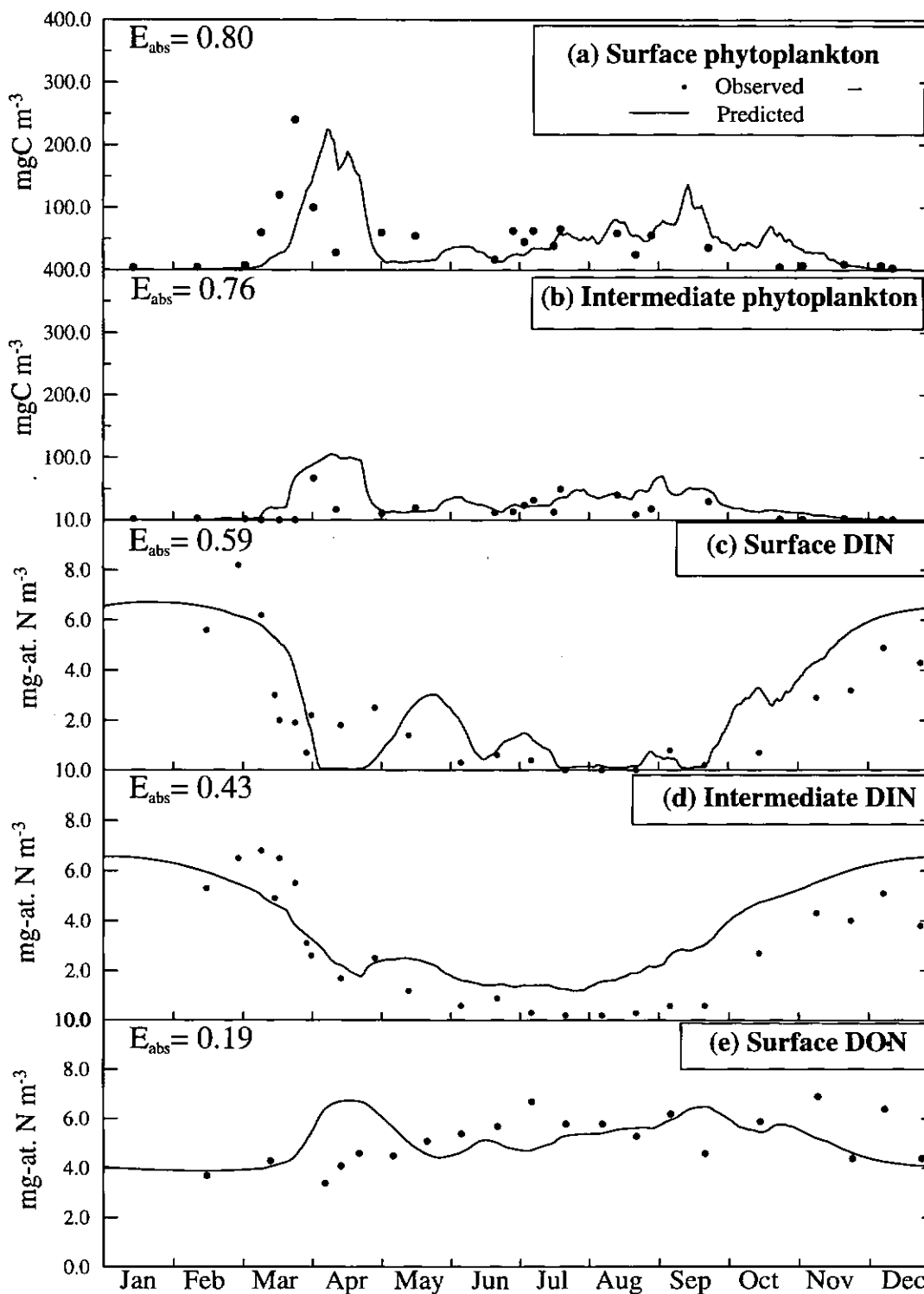


Fig. 5.5a The model compared to data from Loch Etive Outer basin.

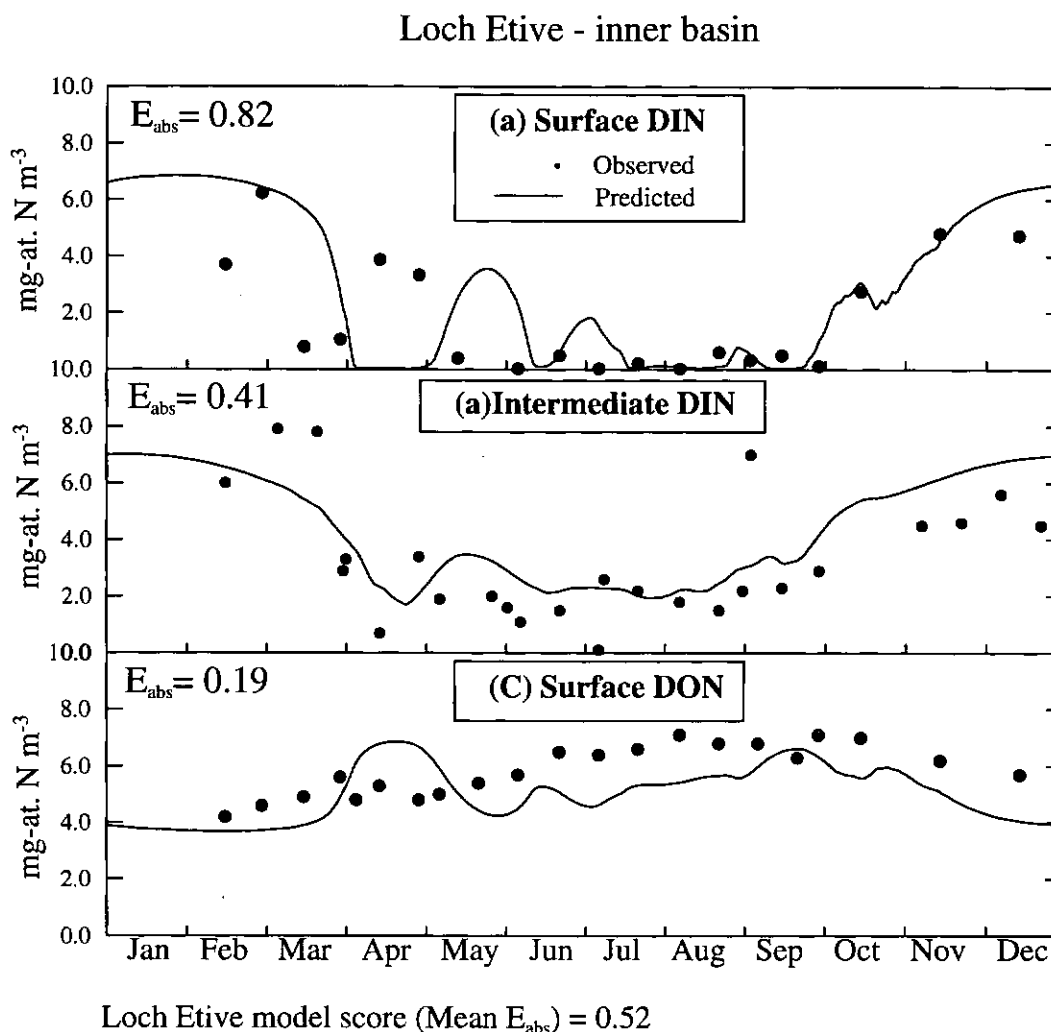


Fig. 5.5b The model compared to data from Loch Etive inner basin.

In both Lochs Creran and Etive however, the model systematically fails to predict the timing of the spring bloom accurately. We have investigated the possibility that physical parameters or driving functions may be responsible for this error, and after considerable numerical exploration concluded that no plausible alteration of either group of quantities results in either uniformly improved model scores, or in visually better trajectories. This leads us to suspect a structural error in the formulation of

our model.

### **5.4.3 A Modified Primary Production Model**

We have a clue in the Loch Etive data as to the cause of this structural error. Although we have no phytoplankton data for the upper basin, we can identify the leading edge of the spring bloom from the rapid fall in DIN levels in early spring. We thus see that the upper basin blooms approximately two weeks earlier than the lower basin, whereas the model predicts that they should bloom at the same time. The mechanism underlying these predictions is simply that both basins have surface layers of the same depth with the same background turbidity. Thus at a given level of surface irradiance the average irradiance delivered to the S-layer phytoplankton is exactly the same in the two basins and their (irradiance controlled) blooms occur at the same time.

It is clearly necessary to re-examine our hypothesis that the surface layer is vertically well-mixed. Solarzano and Ehrlich's (1977a) data show vertical profiles of chlorophyll density during the development of the spring bloom. During the later part of the bloom the phytoplankton distribution is seen to be vertically uniform, or even biased towards the pycnocline. During the early stages of the bloom however, they observe a strong accumulation of phytoplankton in the vicinity of the surface.

Near-surface accumulation of primary producers early in the year is clearly responsible for the initiation of net phytoplankton growth. What then is responsible for the relatively uniform vertical distributions observed later? It seems unlikely that the intensity of vertical mixing increases rapidly because of, or coincidentally with, the development of the bloom, although we cannot positively rule this out. An alternative hypothesis is that zooplankton aggregate to and hence feed preferentially upon, high phytoplankton densities. The effect of such behaviour would

clearly be to equalise phytoplankton densities over the surface layer.

We can now formulate a hypothesis potentially capable of explaining the pattern of bloom timing observed in our test systems. Early in the year the phytoplankton vertical distribution is heavily biased towards the surface; with the depth to which a substantial phytoplankton density penetrates being controlled by the vertical mixing rate. As the zooplankton density increases the vertical phytoplankton density becomes more uniform.

Although the box-model format restricts the amount of mechanistic detail of this process we can practically represent, we can capture its essence by assuming that while nutrients are well mixed over the whole of the S-layer, its phytoplankton and zooplankton populations are confined to a notional, well mixed, upper layer of depth  $\gamma_p$ . We hypothesise that the depth of this layer is dependent on the zooplankton density thus

$$\gamma_p = \gamma_{p0} + [\gamma_s - \gamma_{p0}] \left[ 1 - \exp \left\{ -\frac{G_s}{G_0} \right\} \right] \quad \text{Eqn.: 5.11}$$

where  $\gamma_{p0}$  is the minimum depth of the phytoplankton layer in zooplankton free (winter) conditions,  $G_s$  is the surface layer zooplankton grazing rate (defined in Table 1b) and  $G_0$  is a parameter.

The typical winter zooplankton grazing rate in these systems is very close to zero, so we choose a value of  $G_0$  (=10) comfortably above this value but well below the normal summer grazing rate. We expect the minimum phytoplankton layer depth,  $\gamma_{p0}$ , to depend on the rate of vertical mixing, which should itself be correlated with the system flushing time. However, since we have no information which might guide us as to the form of either of these dependencies we regard  $\gamma_{p0}$  as a system dependent parameter

whose value is chosen to achieve an acceptable fit to the data.

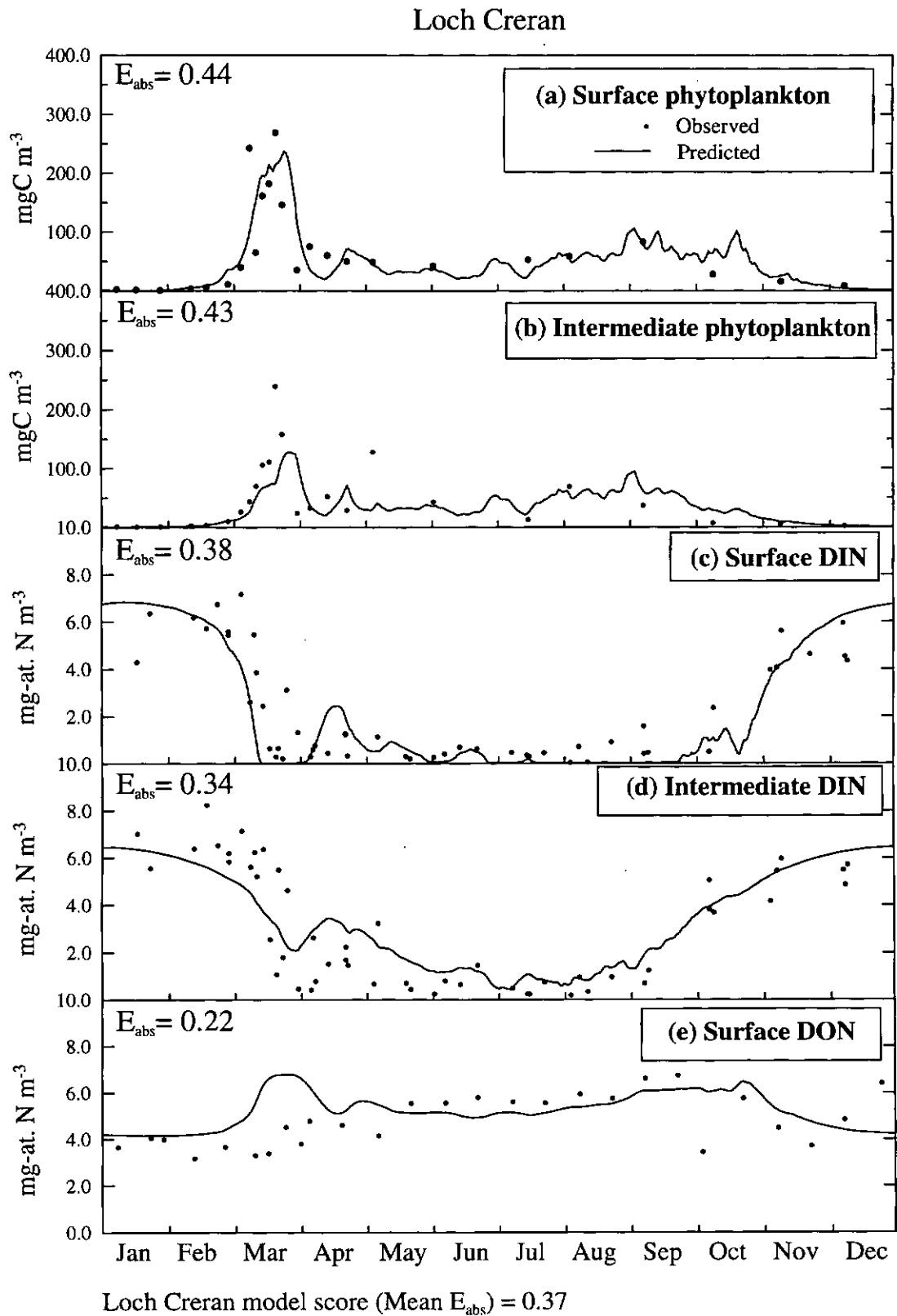
The relationship of this modified model to the baseline model is fully described in Appendix A (Table A.7). Because Loch Airdbhair and Killary Harbour are so rapidly flushed that  $\gamma_{p0}$  is comparable with the depth of the pycnocline, the modified model makes entirely unchanged predictions of the annual cycle in these systems. As Figs 5.6-5.7 show however, it significantly changes the predictions for Lochs Creran and Etive. The difference is seen most clearly in the correct prediction of the bloom initiation in all three basins under consideration, but is also clear in the improvement of the overall model scores, for example 0.52 to 0.45 for L. Etive. In Table 5.1 we show the values of  $\gamma_{p0}$  used to achieve the levels of fit shown for each of our test systems, and demonstrate that these values correlate well with the overall flushing time of the system concerned.

Although in the absence of further test data we cannot regard the details of the proposed mechanism as established, the closer correspondence produced between data and predictions by the modified model, suggests we use it as a basis for further development and testing.

**Table 5.1**

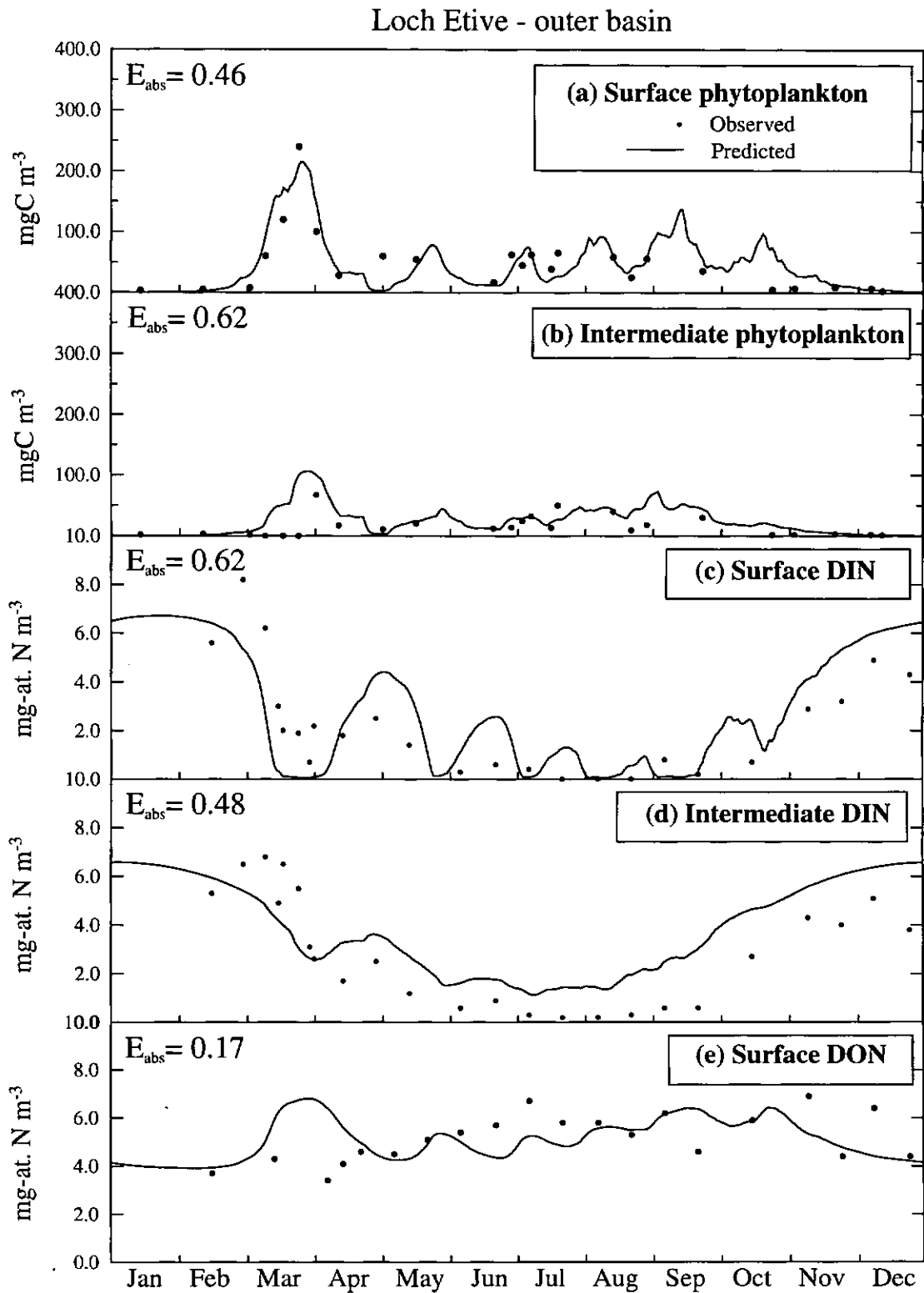
System	Flushing rate <sup>a</sup> ( $V_s$ / day)	$\gamma_s$ (m)	$\gamma_{p0}$ (m)
L. Airdbhair	1	8	layer depth
Killary Harbour	0.83	7.5	layer depth
L. Etive (outer)	0.64	10	layer depth
L. Creran	0.37	8	7
L. Etive (inner)	0.26	10	5

a. Calculated from tidal exchange and freshwater run-in.

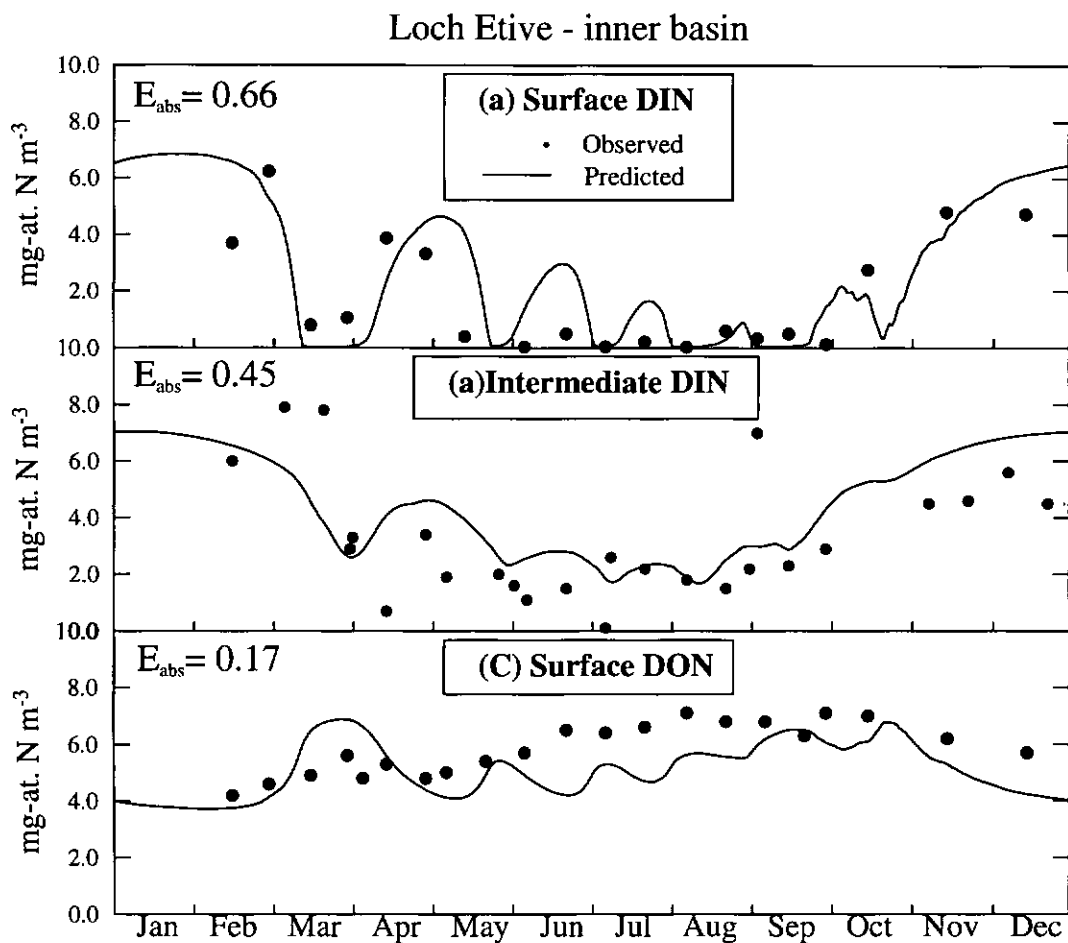


**Fig. 5.6** The modified primary production model compared with data from Loch Creran.





**Fig. 5.7a** The modified primary production model compared with data from Loch Etive outer basin.



Loch Etive model score (Mean  $E_{abs}$ ) = 0.45

**Fig. 5.7b** The modified primary production model compared with data from Loch Etive inner basin.

## Chapter 6 - Model structure and complexity

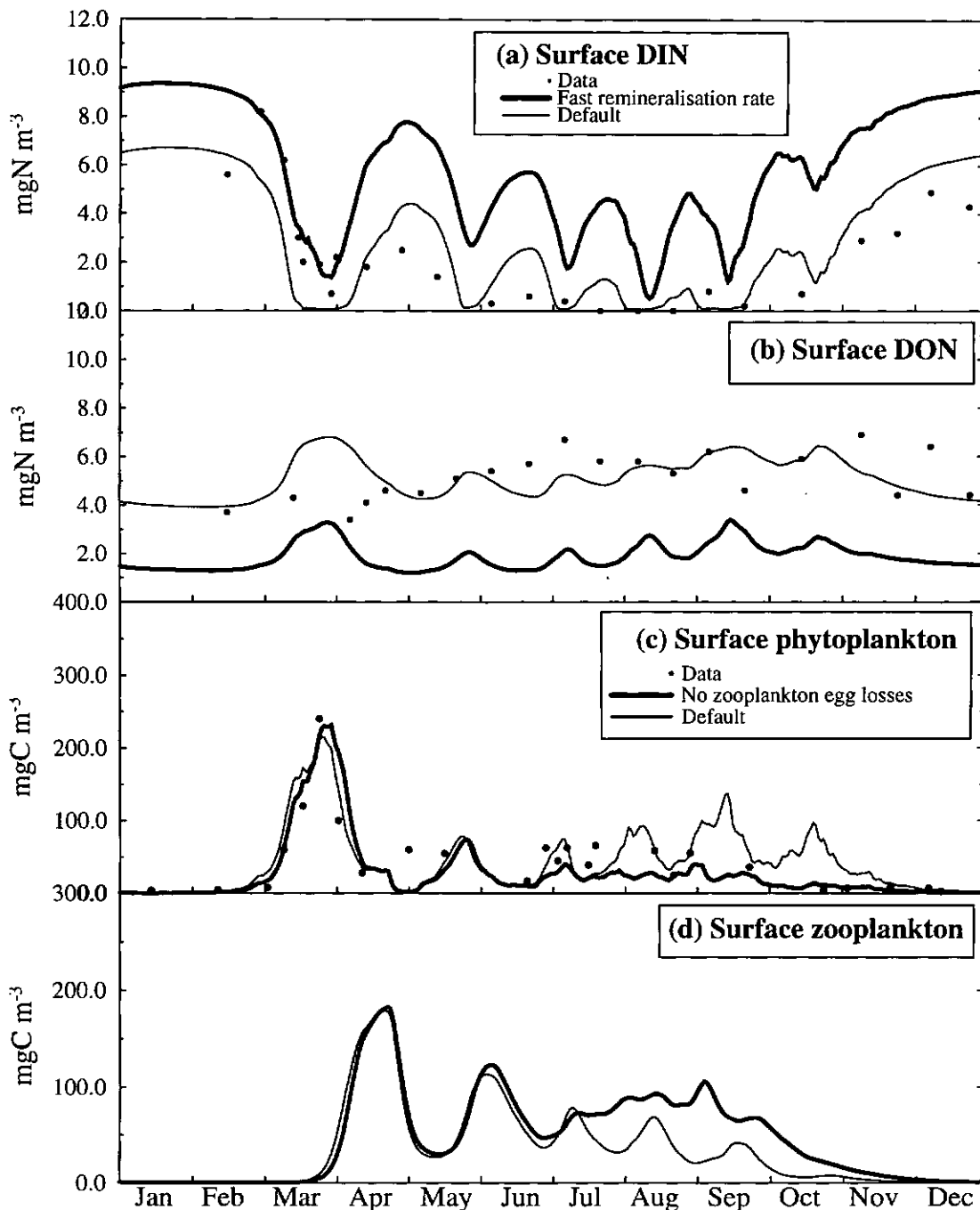
### Introduction

In the previous chapter we introduced some additional biological features into the model to explain inconsistencies between the model and some of the data. In this chapter we will take an *a posteriori* look at why these complications are necessary. We will do this by assessing the performance of the model when these features are removed.

One of the major conclusions arising out of Chapters three and five is that these sea loch systems are light and not nutrient limited. As a consequence of this it should be possible to define a very much simpler, biomass only, model which contains no nutrient recycling. We will therefore assess, in the latter part of this chapter, the requirements of a minimal model of a sea loch ecosystem which is capable of good quantitative agreement with the observed biomass data.

### 6.1 Structural Sensitivity.

In Fig. 6.1a and 6.1b we plot the model predictions (DIN and DON respectively) for the outer basin of Loch Etive using two different DON remineralisation rates: the value used in Chapter 5 (0.02) is the thin line

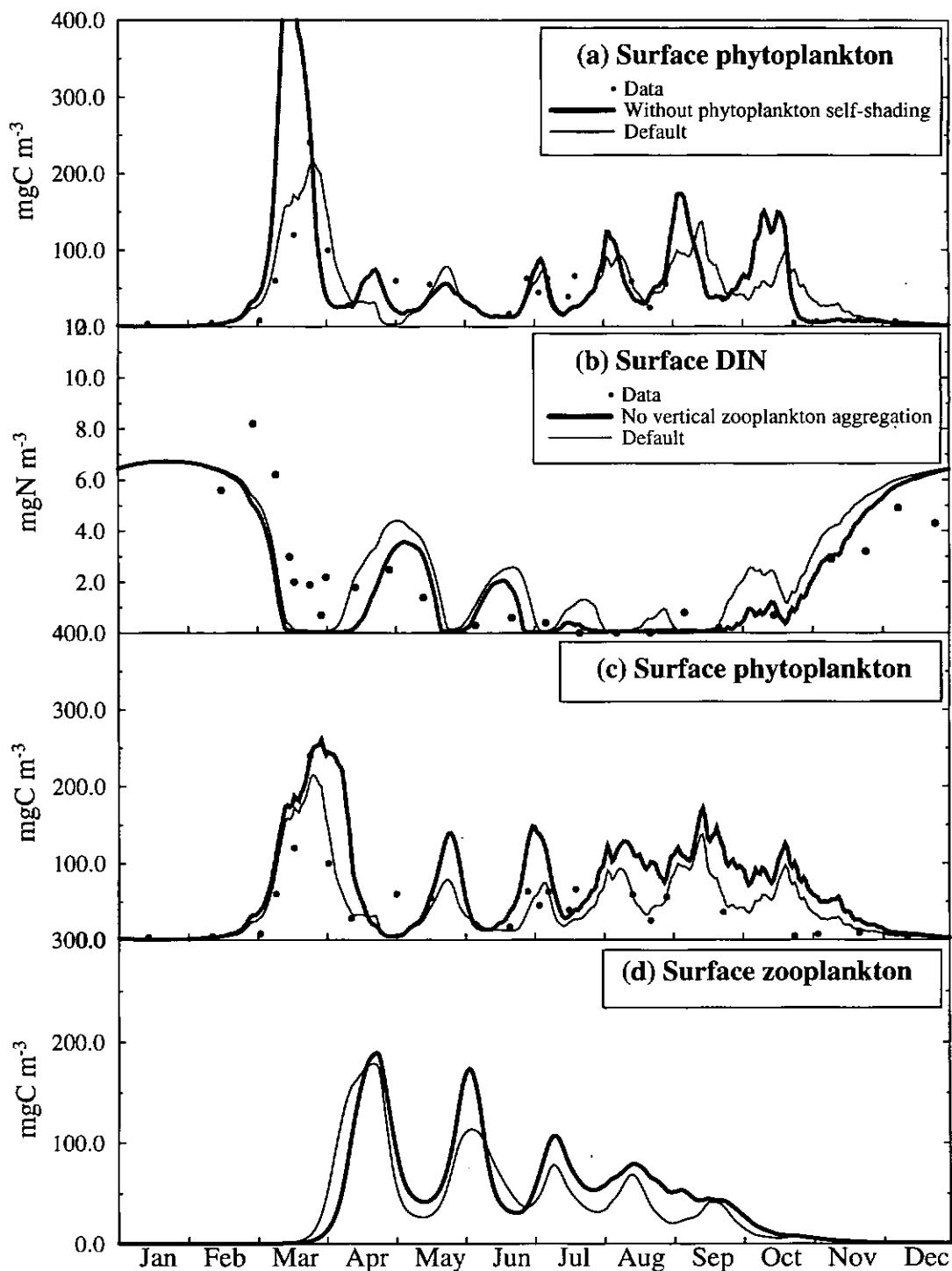


**Fig. 6.1** Alterations in the modified model's performance produced by changes in: DON remineralisation rate - a) shows DIN, b) shows DON, dotted curve shows behaviour with default value ( $0.02 \text{ days}^{-1}$ ), continuous curve shows behaviour with fast remineralisation ( $0.2 \text{ days}^{-1}$ ); Zooplankton egg losses - c) shows phytoplankton, d) shows zooplankton density, dotted curve is default behaviour, continuous curves are result of removing egg losses.

and the value used in Part 1 (0.2) is the thicker line. Using the value for the DON remineralisation rate from Part 1 clearly results in a predicted DON/DIN ratio which is considerably lower than that observed, whereas the modified value yields predictions which match the data in all important respects. This parameter change results in very little change in the annual cycle other than those shown - in particular the effect on the biota is virtually undetectable.

The effect of the temperature dependent zooplankton loss rate introduced to mimic the resource allocation shifts suggested by the data of Uye (1982) is shown in Figs 6.1c and 6.1d. There is no effect on either zooplankton or phytoplankton trajectories during the early part of the year. The additional losses implied by the modification however, produce a noticeable reduction in grazing in late summer and early autumn. This mechanism thus allows a relatively high autumn phytoplankton abundance which would not occur in its absence. We note that the additional losses also produce a noticeable reduction in system stability in late autumn, resulting in unrealistic high frequency predator-prey oscillations.

One of the most significant changes introduced into the revised model, was the introduction of self-shading. Fig 6.2a shows the effect of this mechanism on the predicted annual cycle of phytoplankton abundance in the outer basin of Loch Etive. The most dramatic effects are observed during the spring bloom, where in the absence of self-shading, there is a considerable (almost a factor of two) overprediction of the peak abundance. A further important consequence of the introduction of self-shading is an increase in stability of the model predictions, in the sense that in its absence, the mild predator-prey oscillations in the default predictions become unrealistically large.



**Fig. 6.2** Alterations in the modified model's performance produced by changes in:  
**phytoplankton self-shading** - a) shows phytoplankton density, dotted curve is default, continuous curve is without self shading;  
**vertical zooplankton aggregation** - b) shows DIN, c) shows phytoplankton, d) shows zooplankton, dotted curve is default, continuous curve is without vertical aggregation.

A further stabilising mechanism is the vertical aggregation of zooplankton onto high concentrations of phytoplankton. There are two separate aspects to this vertical aggregation: firstly, the division of time between surface and intermediate layers is sensitive to the relative phytoplankton concentrations in these layers; secondly, the near-surface concentration of phytoplankton observed early in the year is forced into a uniform vertical distribution by grazing pressure. Fig. 6.2b-d illustrates the result of removing this effect on the DIN, phytoplankton and zooplankton respectively.

Not surprisingly there is no effect at all on the initial rise phase of the spring bloom since the zooplankton biomass is still insufficient to affect the phytoplankton vertical distribution. As the bloom develops however, and the zooplankton biomass accumulates, the absence of zooplankton aggregation reduces the grazing rate and as a consequence the bloom is larger and more prolonged. As a result of the limiting effect of self-shading however, this increase in peak spring abundance is not particularly marked.

Indeed, simply judged on a comparison with the nutrient and phytoplankton data available for Loch Etive, this prediction is little more convincing than the default. The major consequence however is an increase in stability; in particular the zooplankton trajectory shown in Fig. 6.2d shows that the removal of aggregation has a major impact on the stability of the zooplankton population in the latter part of the year - inducing large predator prey oscillations between the zooplankton and carnivore populations.

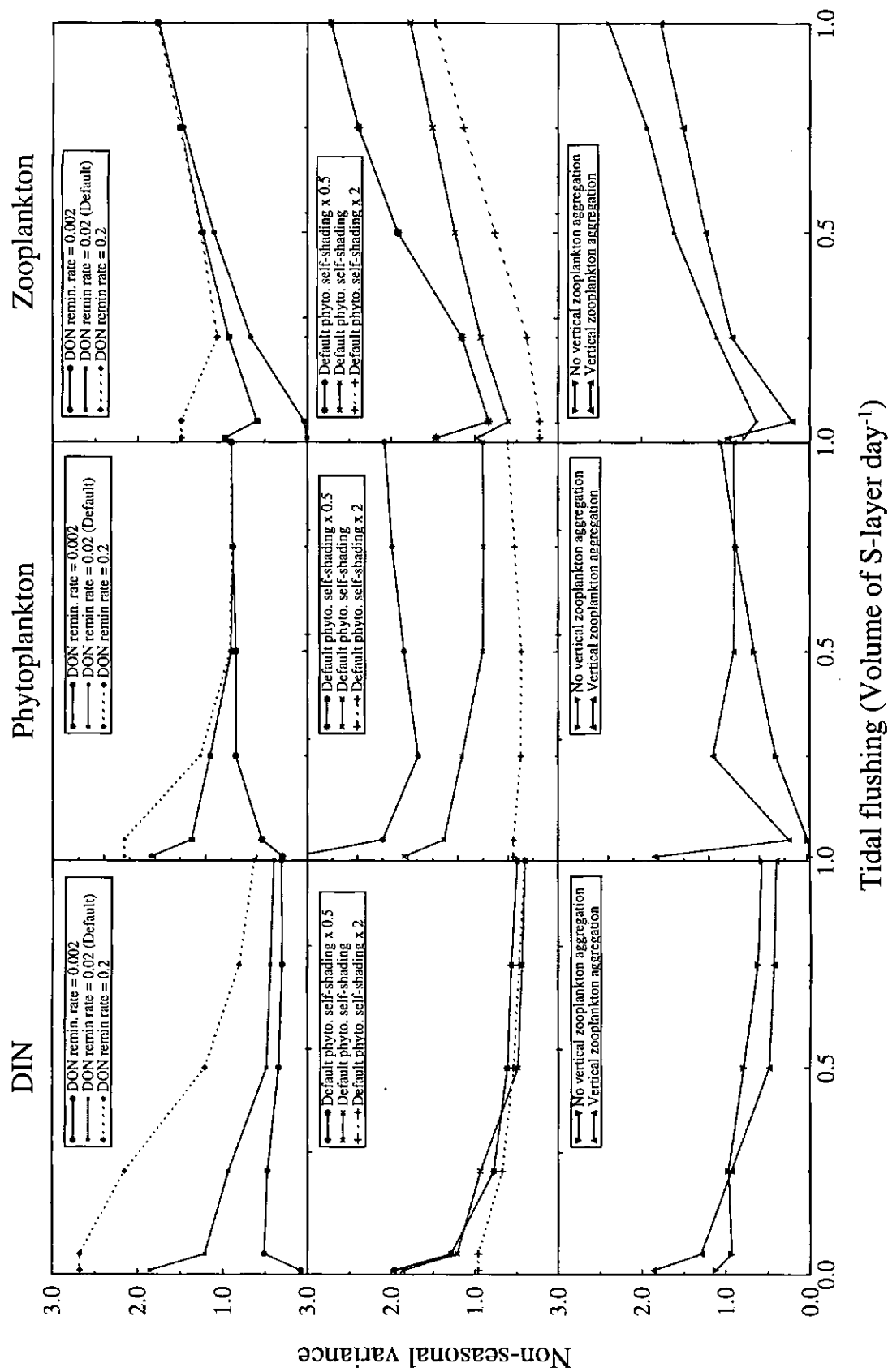


Fig. 6.3 Model stability. Variation of non-seasonal variance in DIN, phytoplankton, and zooplankton as the flushing rate of the system is varied: (a) for different DON remineralisation rates; (b) for different self-shading levels; and (c) with and without zooplankton vertical aggregation.



## 6.2 System stability

It is clear from Figs 6.1 and 6.2 that changes to either the structure or the parameters of the model can result in changes both to the broad trend of the annual cycle, and the occurrence of rapid predator-prey oscillations on top of that trend. Although the detail of these oscillations is of doubtful significance, it can be argued that they are diagnostic of system stability. Thus, in this section, we shall investigate the factors which control the propensity of the model to exhibit such oscillations.

We require a quantitative measure of the intensity of high-frequency oscillation which is as nearly as possible independent of accompanying changes in the annual cycle. We first smooth the predictions, using locally linear smoothing (the "lowess" method - Cleveland 1979) with a window width of 73 days (20% of a year) and then calculate the variance of the difference between the actual and smoothed annual cycles.

Fig. 6.3 shows how this non-seasonal variance changes with flushing rate for the three key components of the Loch Creran ecosystem; nutrient (DIN), phytoplankton, and zooplankton. The figure contains three such triplets in each of which the behaviour of the final default model is compared with that of variants with different DON remineralisation (sequence a), different self-shading (sequence b) or different zooplankton aggregation (sequence c).

The default model shows the expected decrease in non-seasonal variance of nutrient concentration as flushing rate, and hence connectivity with the outside sea is increased. Neither zooplankton aggregation nor self-shading have any significant effect on the stability of this level of the system, except at very low flushing rates. Increasing the DON remineralisation

rate significantly increases the non-seasonal variance, particularly for systems with low flushing rates.

In contrast, both phytoplankton and zooplankton show enhanced non-seasonal variability as flushing rates increase. This effect, which is more marked for zooplankton than for phytoplankton, is the result of the productivity increase which accompanies the increased nutrient imports facilitated by high flushing rates. This effect is only dependent on DON remineralisation rate when the system is relatively closed (low flushing rate). However, both self-shading and zooplankton aggregation are strongly stabilising. In the case of vertical aggregation, this effect is again most marked at high flushing rates, and hence high productivity. In contrast, aggregation, which both provides a phytoplankton "refuge" and facilitates rapid zooplankton build-up during the spring bloom, proves strongly stabilising at all flushing rates.

### **6.3 A Minimal Model.**

Although this model was designed to be as simple as possible, it is still a complex structure. We now seek a minimal representation capable of yielding the same quality of fit to the data.

The study in Part 1 showed that although the persistence of fjordic systems is ultimately dependent on the balance of nutrient export and import, their primary productivity is almost always determined by irradiance. The nutrient concentration is thus determined from the top down and its dynamics are irrelevant to the behaviour of the biotic system. To illustrate this, we have constructed a sea-loch ecosystem model with only three state variables - the carbon concentrations in phytoplankton, zooplankton and carnivores.

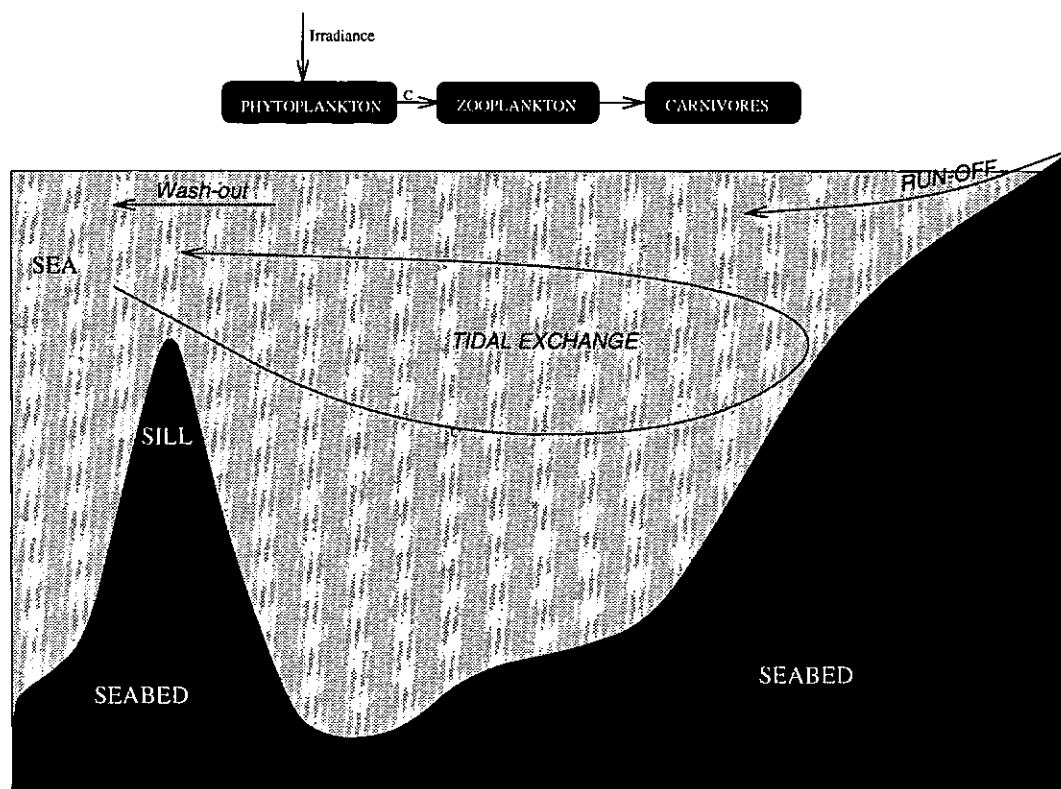
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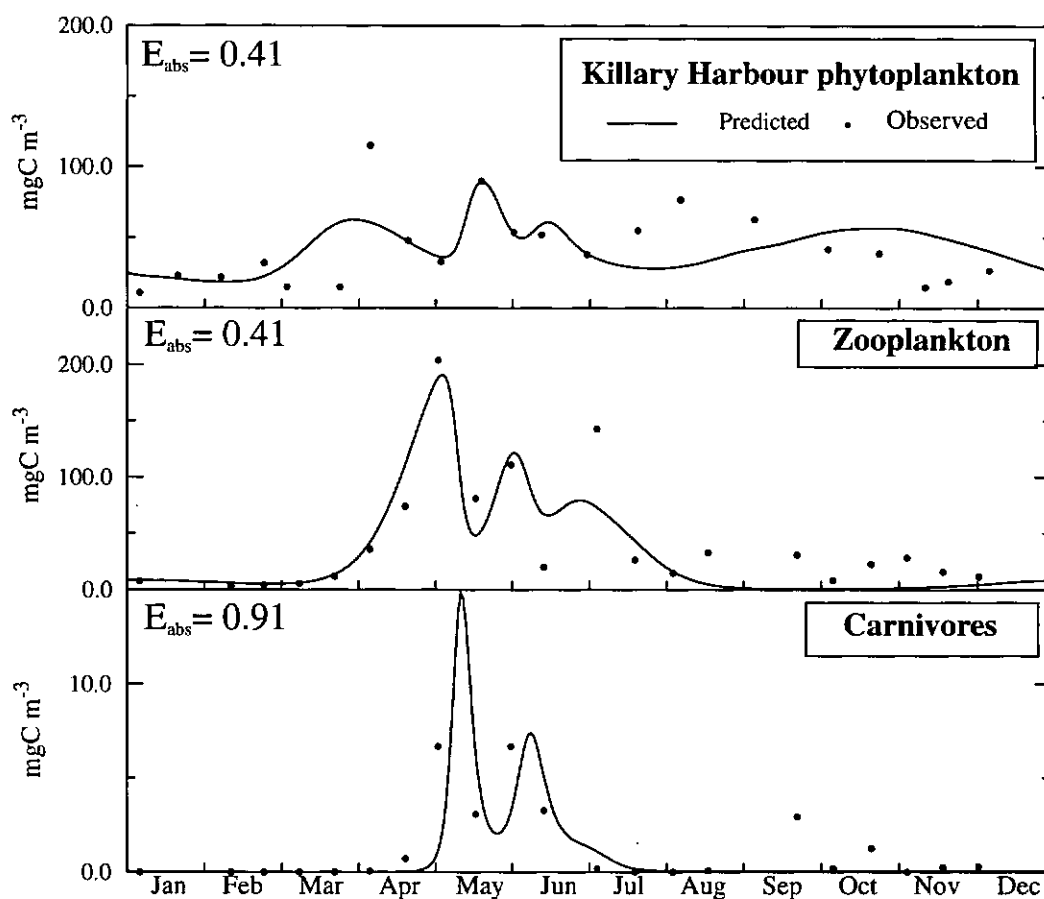
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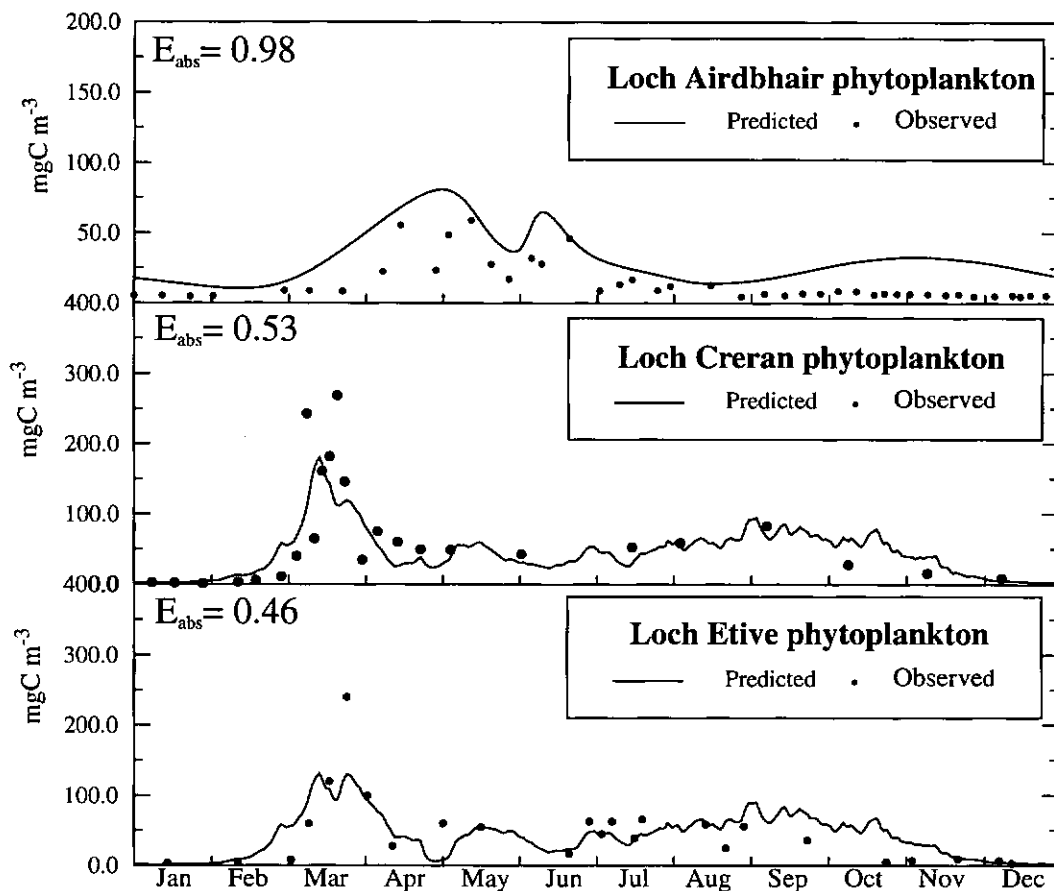
**Fig. 6.4** The food web and the physical system in the simple model

This model, which is illustrated in Fig. 6.4 and set out in detail in Appendix C (Tables C.1-C.3), is simply a single layer version of the model described in Chapter 5, shorn of all elements relating to nutrient concentrations. The phytoplankton description remains exactly as before, including the zooplankton driven changes in vertical distribution. However, we assume that the phytoplankton nutrient quota remains permanently set at its maximum permitted value. System specific factors are now the system depth, the flushing rate as it affects phytoplankton exports, the external concentration of phytoplankton, and the immigration rates for zooplankton and carnivores. Figures 6.5 & 6.6 show that this model yields a fit to the biotic data for our four test systems which is essentially indistinguishable from that produced by the more complex

model.

Model score (Mean  $E_{\text{abs}}$ ) = 0.58

**Fig. 6.5.** The simplified model applied to Killary phytoplankton, zooplankton and carnivore data.



**Fig. 6.6.** The simplified model applied to phytoplankton data for Lochs Airdbhair, Creran and Etive.

## 6.4 Conclusions

In this study, the strategic simulation model developed in Part 1 has been further developed to the point where it is capable of showing quantitative agreement with all available data on nitrogen, primary producers, and secondary producers from four hydrodynamically distinct sea-loch systems. This agreement is achieved with a single set of biological

parameters; the system specificity coming from (mainly) well-known hydrological and environmental parameters.

The main conclusions are that the nutrient dynamics of the sea-loch resemble a laboratory chemostat, in the sense that the major fluxes of nutrient in these systems are imports or exports across the sill rather than recycling through the sediments. We find that the primary productivity is controlled almost exclusively by irradiance, and thus that the nutrient standing crop is (in essence) set by the requirements of gross balance between import and uptake rates. The total primary production is thus controlled for most of the year by grazing pressure, which is in turn modified by carnivory.

We have confirmed this view of almost total "top-down" control, by constructing a single-layer model of almost strategic simplicity, which describes only the carbon dynamics of the three functional groups of biota and yet yields a fit to the primary and secondary producer data which is almost indistinguishable from our more complex model. The key features of this model are self-shading of primary producers, variation in the vertical distribution of phytoplankton driven by grazing pressure, phytoplankton imports from the outside sea, and temperature dependent energy allocation by zooplankton (represented by a temperature dependent loss term).

## **Chapter 7 - Disturbance**

### **7.1 Introduction**

In developing management strategies for marine ecosystems there is a need to develop methods for assessing the impact of disturbance. Because of their quantitative basis, ecosystem models are potentially powerful tools for this purpose. Before any such model can be utilised as a practical tool however, it must first demonstrate its applicability to the systems under consideration i.e. it must be quantitatively tested.

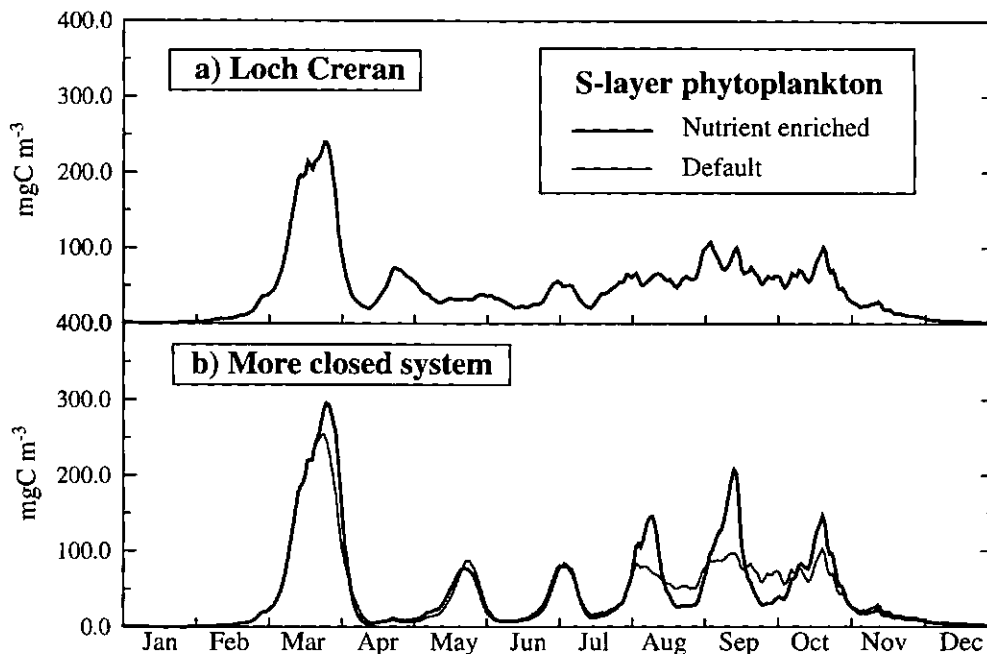
Given that the model we have developed has demonstrated its applicability to a number of real systems, we are now in a position to explore the possible effects of certain types of disturbance on these systems. For the purposes of this exploration, we use model parameters appropriate to Loch Creran, a sea-loch on the west coast of Scotland. This was one of the group of systems we used for model testing in Chapter 5.

### **7.2 Effects of disturbance**

An issue of significant concern to environmental managers is the effect of nutrient enrichment on primary production. In our model the only nutrient which is potentially limiting in this context is nitrogen. However, for all the systems for which our model has been parameterised, primary productivity is limited by light rather than nitrogen (Chapter 5). We thus expect nitrogen enrichment to have little or no effect in these systems - a

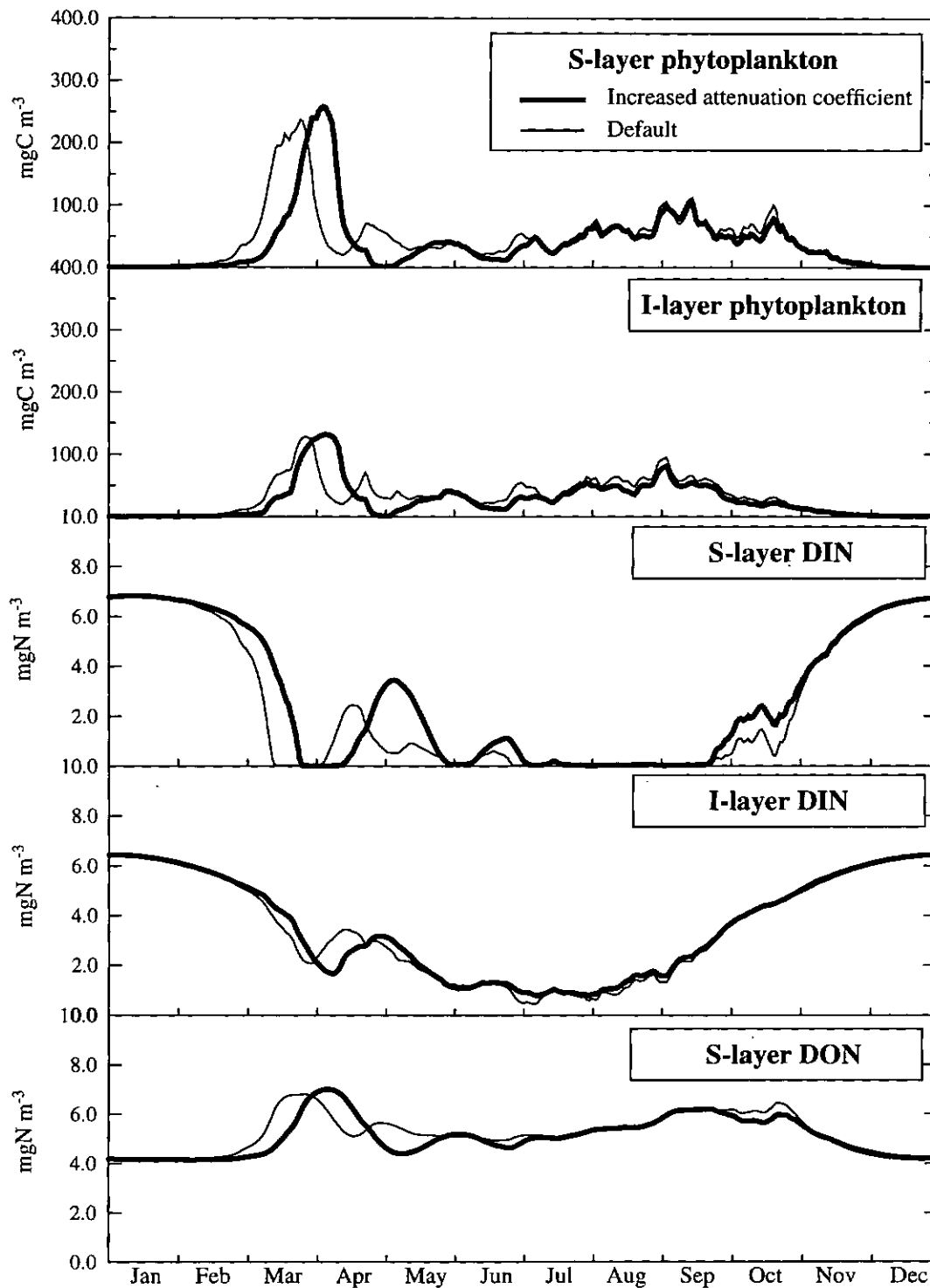


conclusion which Fig 7.1a illustrates by examining a ten-fold increase in DIN concentration in the fresh-water input to Loch Creran<sup>1</sup>.



**Fig. 7.1** The effects of nutrient enrichment: (a) In Loch Creran - there are two lines plotted in this graph - a thick line represents the nutrient enriched system (DIN concentration in run-off is 10 times the default); the thin line represents the default - these lines are indistinguishable; and (b) The same as in (a) but for a hypothetical system, identical to Loch Creran, in which the tidal exchange rate is a factor of ten lower.

1. To illustrate the relative importance of anthropogenic nutrient inputs we estimate the nutrient enrichment from a hypothetical fish farm in Loch Creran containing 500,000 fish weighing 2 kg each. Assuming that 3% of the wet weight to be nitrogen (A. Bryant pers. comm.) and assuming a typical value of the ration of 2% of body nitrogen per day of which 25% is unassimilated (N. Broekhuizen pers comm.), the nutrient added to the water column will be  $1.85 \cdot 10^8 \text{ mgN day}^{-1}$ . This is 50, 100 and 225% respectively of the mean predicted fluxes of DIN, DON and phytoplankton nitrogen between the loch and the external system. DIN imports from the river are estimated to be  $6.4 \cdot 10^7 \text{ mgN day}^{-1}$  i.e. a third of that estimated for the hypothetical fish farm.

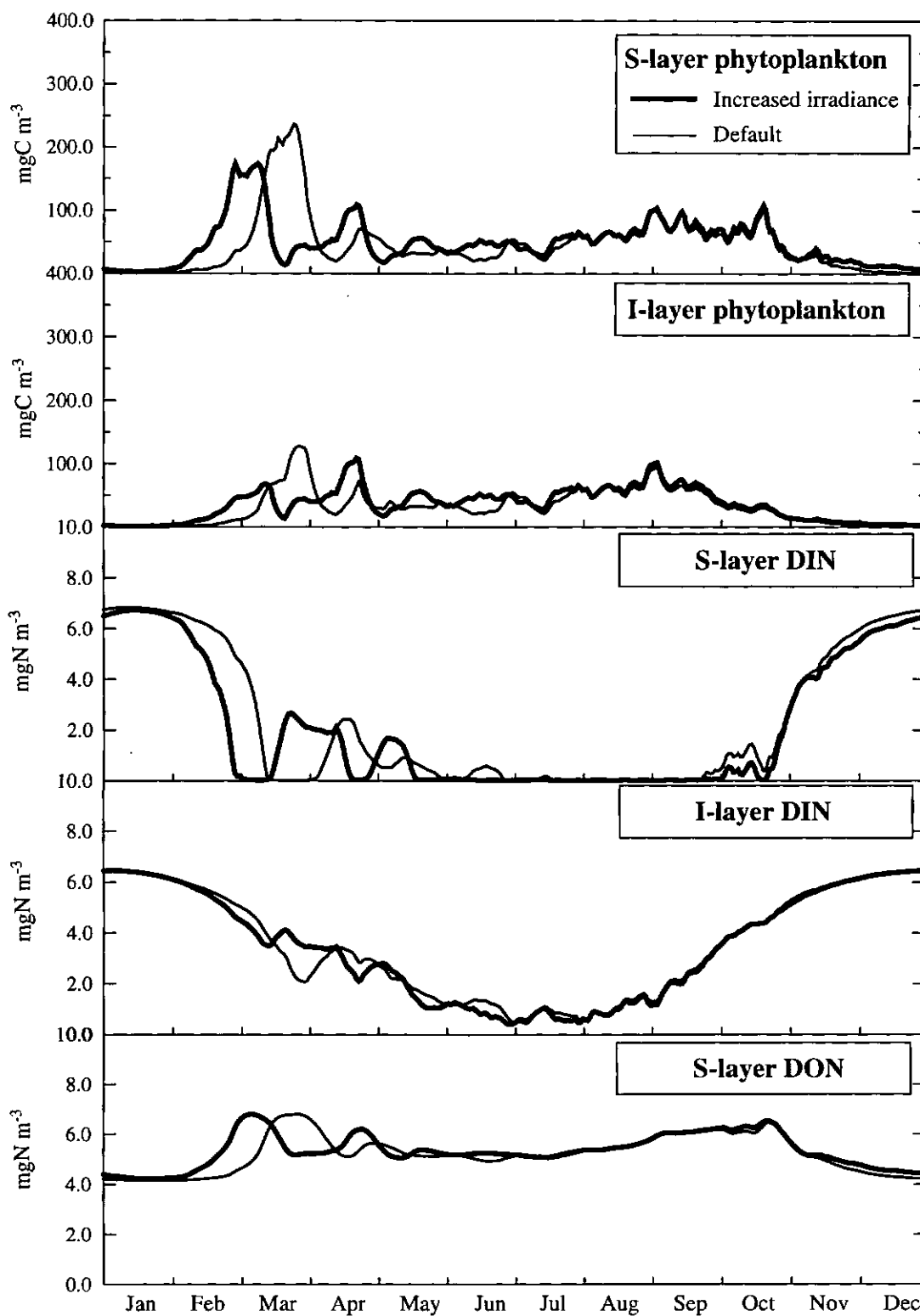


**Fig. 7.2** The result of an increase in the attenuation coefficient ( $\times 1.5$ ) caused by an increased particulate load. The thick line represents the perturbed system; the thin line is the default. The major affect is a phase shift in the spring bloom.

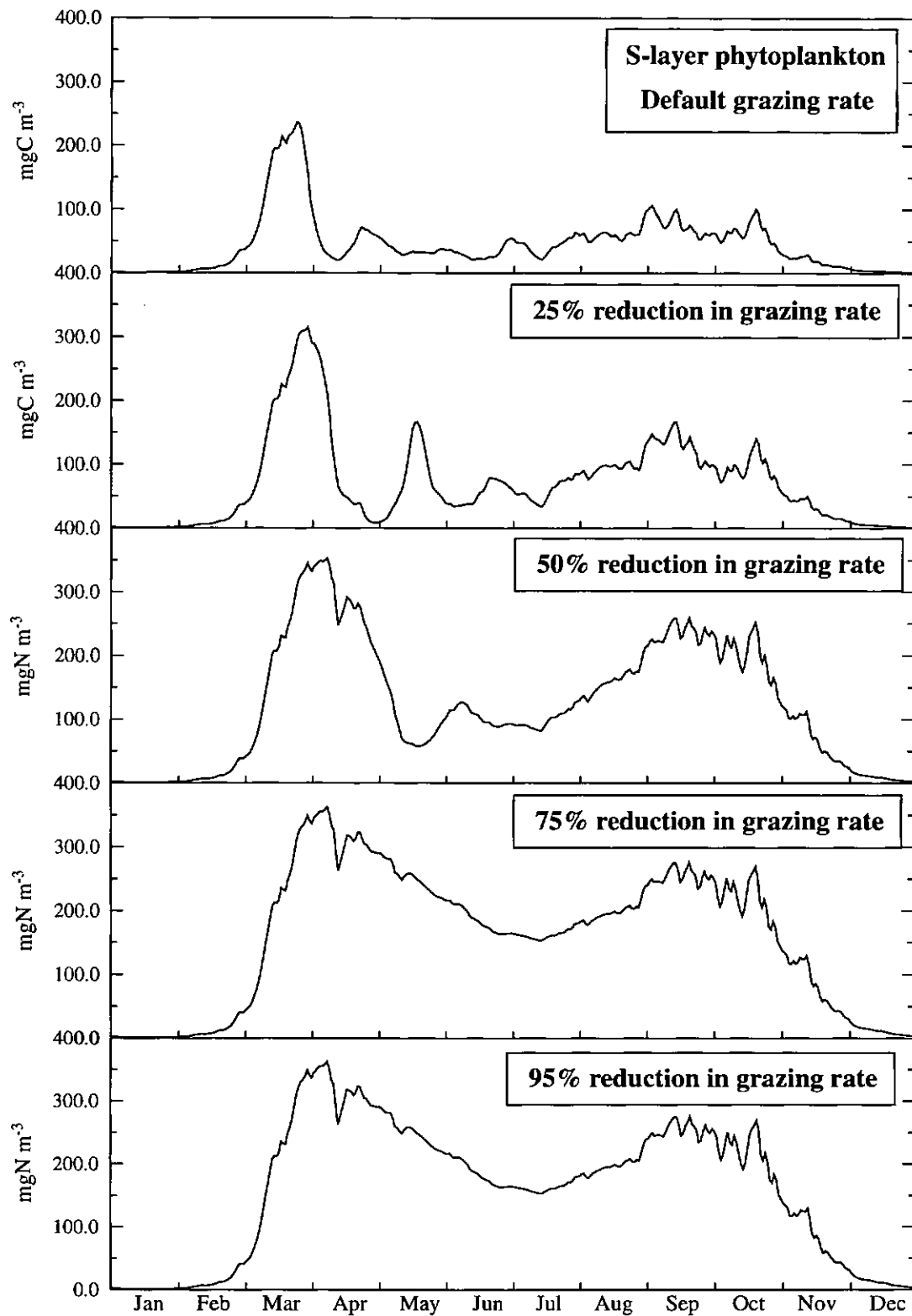
The main reason why the systems we have modelled are so insensitive to nitrogen enrichment is that the chemostat-like nature of their nutrient dynamics implies a continuous supply of nitrogen from the external sea during the spring and summer. To explore the question of how weak the connection with the sea must become before nitrogen limitation becomes important, and enrichment can pose a potential threat, we examine a hypothetical system which resembles Loch Creran, except that it has a much (one order of magnitude) smaller tidal exchange rate. Fig. 7.1b shows that for this system, a strong enrichment of the fresh-water run-in has a small but detectable effect on the yearly cycle.

In the systems we have modelled, primary productivity (i.e. specific phytoplankton growth rate) is generally light limited, so we might expect a decrease in the background attenuation coefficient, caused for example by an increased particulate load, to produce a significant reduction in total primary production. In Fig. 7.2 we illustrate the effects on the annual cycle in Loch Creran of a 50% increase in background attenuation coefficient: the heavy line shows the perturbed annual cycle; the thin line is the default as shown in Fig. 7.1. Surprisingly, there is little reduction in the total standing crop of any of the compared variables. The major effect is a phase shift in the standing crops in the first half of the year caused by a delay in the spring phytoplankton bloom.

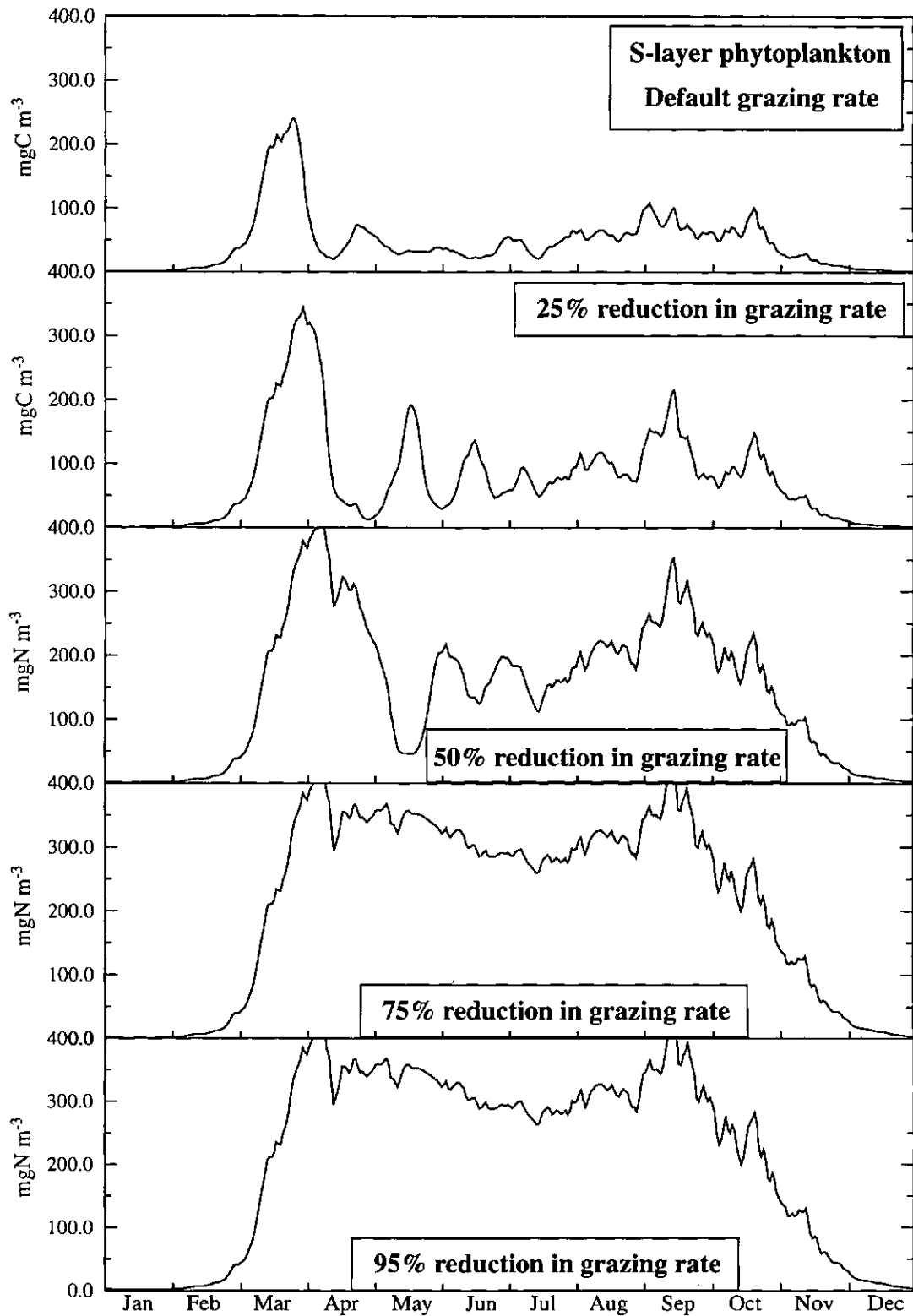
This emphasises the need to distinguish primary productivity, which in this case depends only on light availability, from total primary production, which is the product of the primary productivity and the standing crop of primary producers. To reinforce this point, we show in Fig. 7.3 the consequences of a 50% increase in incident irradiance. Here again, because the post-bloom standing crop of primary producers is controlled



**Fig. 7.3** The result of an increase in the incident irradiance (x 1.5). The results are similar to Fig.6.2 but the phase shift is in the opposite direction.



**Fig. 7.4** The effects of successive reductions in the maximum grazing rate i.e. successive increases in the handling time.



**Fig. 7.5** The results of a successive reduction in the maximum grazing rate when combined with nutrient enrichment (DIN concentration in run-off is 10 times the default).

by grazing, the increase in light availability produces a noticeable change in the timing of the bloom, but little effect on standing crop. Indeed, we observe a slight reduction in the peak phytoplankton levels during the spring bloom, caused by an increase in the grazing rate consequent upon either a higher pre-bloom zooplankton population or increased primary productivity during the early part of the bloom (see Part 1).

To further illustrate importance of grazing in determining phytoplankton standing crops, we plot in Fig. 7.4 the S-layer phytoplankton standing crop for a set of model runs where the maximum grazing rate is successively reduced. We see two highly significant effects. Firstly, small reductions in grazing permit the peak height of the spring bloom to rise, although the extent of this change is limited by nutrient availability, and further reductions below 50% of the default level yield no consequent change. Secondly, although a small decrease in grazing has no very marked effect on the annual cycle after the end of the spring bloom, a reduction of 50%-75% in grazing pressure produces a largely nutrient limited annual cycle in which phytoplankton standing crops remain at or above 200 mgC m<sup>-3</sup> for most of the productive year.

We have seen that under the circumstance of drastically reduced grazing, the system can become nutrient limited for much of the year. This implies that under such a regime, nutrient enrichment may become important. To explore this possibility we plot in Fig. 7.5 a similar set of runs to that of Fig. 7.4 except the DIN concentration in the run-off has been increased by a factor of ten. We see that there is now some effect of nutrient enrichment, particularly where the grazing rate has been reduced by 75% or more. We note however, that both because the run-in is a relatively small part of the total nitrogen supply to the system, and because of self-shading effects, the

change in annual cycle, even at 95% grazing reduction, is relatively small.

### 7.3 Conclusions

In this chapter we have used a model which has demonstrated its applicability to a number of real systems (Chapter 5), to assess the effects (at the whole-loch scale) of possible disturbances of sea-loch ecosystems.

We find that the physical characteristics of a typical Scottish sea-loch imply that, averaged over the whole system, nutrient enrichment of either the fresh-water run in or of the external sea, has little effect. For very closed systems, with relatively high incident irradiance and/or low light attenuation, there may be a detectable effect if substantial nutrient enrichment is involved. Such conditions are unlikely to apply to whole sea-lochs but may result from substantial local nutrient input to a shallow subsidiary embayment.

A more common disturbance to these systems is likely to be an increased particulate load, from quarrying activity for example, resulting in increased attenuation of incident irradiance. We have found the consequences of such a disturbance to be significant only when grazing is not the major control on the phytoplankton growth rate - a condition which normally obtains only during the development of the spring bloom. The most likely effect of increasing particulate loads is thus a delay in the development of the spring bloom. Following the same argument the major consequence of an increased level of incident irradiance, for example by a reduction in cloud cover, would be early occurrence of the spring bloom.



We find that the only type of disturbance which poses a significant threat at the whole-loch scale, is a reduction in the grazing rate. Potential causes of such an effect, are, for example, an artificially introduced toxic source, grazing inhibitory substances produced by toxic dinoflagelletes, or anoxic conditions.

The effects on the Loch Creran model system of a significant reduction in the maximum grazing rate are substantial, with phytoplankton levels throughout the spring, summer and autumn at or near levels obtained during the spring bloom in the unperturbed system.

A significant consequence of the increased phytoplankton standing crop is enhanced total nutrient demand, which in turn implies that for a significant period during the summer, primary productivity is nitrogen limited. This has the clear implication that nutrient additions occurring when grazing is reduced will act to increase phytoplankton standing crop. We note however that because freshwater run-in is a small contributor to total nitrogen import in these systems, a large percentage increase in nitrogen concentration in the run-in results in only a small percentage increase in standing crop. We also note that increases in phytoplankton standing crop are often likely to be limited by self-shading effects, thus ameliorating the effects of large increases in nutrient availability.

We thus conclude that, on the scale of the whole system, the disturbances which have the greatest effect are those which result in a large reduction in the zooplankton grazing rate. Particularly when such a disturbance is combined with nutrient enrichment, there is potential for a serious environmental problem, with the possibility of positive feedback through the development of anoxic conditions. This scenario is perhaps less likely

to occur in conditions on the west coast of Scotland because of the low incident irradiance and consequent early onset of self-shading limitation. Even here however, shallow slowly flushed systems, may be at risk.

## Chapter 8 - Conclusions

### 8.1 Summary

Our principal aim in this work has been to understand enough about the general pattern of nutrient flow in a sea loch to enable us to advise on the best use of resources for a field program on Loch Linnhe. The strategy has been to build a model that is sufficiently detailed to permit a realistic chance of quantitative comparison with real systems; whilst being sufficiently simple to allow us to understand its predictions. In this we have largely succeeded, obtaining good quantitative comparison with data from four real systems, together with a good understanding of both the flow of nutrients and the trophic dynamics.

We have found the major flow of nutrient (both bound and dissolved) to be between the loch and the external coastal water. As a consequence of the high tidal exchange rate found in sea lochs and the relatively high level of nutrient standing crop in the external system, this flux is large enough to dwarf the two other major fluxes into the water column - the freshwater run-in and sedimentary remineralisation. Indeed it is large enough to relegate the internal nutrient cycling to a subordinate role. With respect to inorganic nutrients this system resembles a laboratory chemostat in so much as the uptake of nutrient is subject to the external supply.

In relation to these findings it is not surprising that from the autumn through to spring the phytoplankton growth is limited by light rather

nutrient. Particularly so when we consider the relatively low incident irradiance and high attenuation coefficients which are typical of these systems. The chemostatic flushing always maintains a sufficient quantity of nutrient to meet photosynthetic requirements. What is surprising however, is that this situation prevails throughout the summer months. This in spite of the fact that the nutrient concentration in the external system is at annual minimum during this period; that the incident irradiance is at a maxima; and that the background attenuation coefficient is also at an annual minima (due to low rainfall).

As the zooplankton biomass develops in the spring and persists at high levels through to the autumn months, grazing exerts a severe constraint on the phytoplankton standing crop and hence on the primary production. We thus determine the cause of the summer light limitation of phytoplankton growth to be this reduction in primary production. It is worth emphasising here the divergence that occurs between primary production (population growth) and primary productivity (individual growth) during this period.

The zooplankton in fact exert a large influence on the trophic dynamics. We find that the magnitude and timing of the spring bloom is particularly sensitive to the pre-bloom zooplankton concentrations (Chapter 3). We also find the post-bloom concentrations to be markedly affected, in that in the absence of grazing the bloom continues at more or less spring levels right through to the onset of winter (Chapter 7). Although carnivores also exert some influence on the trophic dynamic, due to their high uptake rate and consequent high costs, this only matters during the late spring to early summer when the zooplankton biomass is at a high enough level to support growth.

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## 8.2 Discussion

In developing this model we were aware of the need for simplicity in the model design, both to allow us to understand the mechanisms behind what the model predicts; but also because our knowledge about (and the available information on) these system was limited. This led us to represent the system on the whole loch scale, incorporating only the most obvious spatial structure - the vertical layers. This clearly has paid dividends in allowing us to understand the system at this scale. Our conclusions however do not necessarily hold on much smaller scales. It is certainly possible that nutrient limitation occurs: at the very top of the water column; in shallow embayments off the main system or in persistent eddies - particularly so in the more closed and sheltered systems.

In using just three trophic categories we have not addressed the dynamical importance of different resource pathways between various functional groups on different trophic levels. Two such pathways which are often considered to be of some importance, are the loss of nutrient from phytoplankton caused by bacteria; and the source of food that bacteria provide for micro-zooplankton. However the low remineralisation rate of the dissolved organic nitrogen evident from Lochs Creran and Etive is symptomatic of low bacterial levels, which suggests we are justified in omitting a direct representation of bacteria in this model.

Our parameterisation of the three trophic categories is necessarily non specific. This raises the possibility that our model will entirely fail to represent some functional groups or individual species if their rate parameters are significantly different from those we have chosen. The late autumn 'bloom' of *Pleurobrachia* in Killary is an illustration of this. The parameterisation of our carnivore class has been a particularly difficult business, with much uncertainty remaining in the choice of parameter values. This emphasizes the need for a more quantitative understanding of the physiology of gelatinous zooplankton.

Describing the transport of the different trophic groups has been perhaps the most difficult modelling judgement. We have taken the view that the zooplankton and carnivores are sufficiently in control of their movements as not to be greatly affected by the physical conditions typical of a sea-loch. Hence we have assumed single populations of each. We recognize however the discrepancy that exists between this assumption and our supposition that there is no dynamic exchange with external populations in the coastal sea. We simply do not, at present, have sufficient information to begin to describe such processes.

Of the phytoplankton, only the larger flagellates can be considered to have much independent control. Flagellates however are less numerous in sea lochs than diatoms. This taken together with the observations of Tett (1986) that there is retention of phytoplankton in the loch over what bulk water movements imply; suggested an intermediate description between complete control and complete passivity. Again because of the limited available information, we chose the simplest representation, incorporating a retention factor.

In Fig. 8.1 we illustrate the vertical structure of the phytoplankton spring bloom in Loch Creran during 1975. The graph on the left hand side is a smoothed surface of data on phytoplankton concentration (Jones 1979) over five different depths (0,2,4,7,11, & 16m). The right hand graph is an equivalently smoothed surface of the model predictions on the same days of the year as the data were collected. Because of the model assumptions with respect to the vertical structure the prediction is in fact a smoothed surface of a step structure. The upper part of this step is either the S-layer or the 'thin-layer' (see Chapter 5); the lower step is either zero (in the presence of a thin-layer) or the I-layer.

Smoothed surface of the spring bloom over a depth of 0-16 m in Loch Creran during 1975

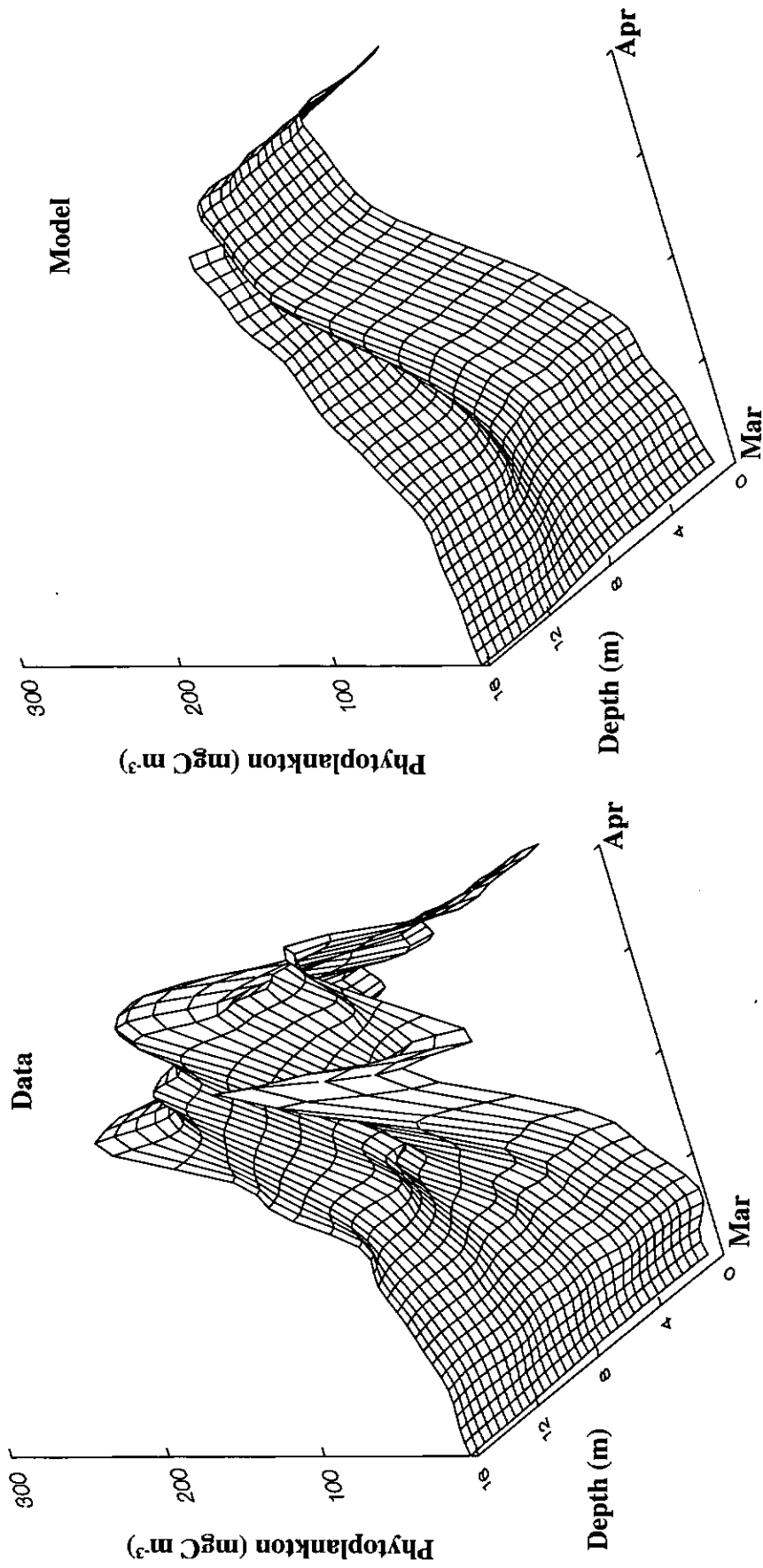


Fig 8.1 The developing bloom over depths from 0-16m. The surface represents



The developing bloom is clearly initiated near the surface, propagating further down the S-layer into the I-layer within 1-2 weeks. Thus it would appear we are justified in incorporating the additional vertical structure in order to predict the timing of the spring bloom. Solarzano & Ehrlich (1977a) present sparser data from Loch Etive during 1971 which demonstrates similar vertical behaviour of the spring bloom). Both sets of data show increased phytoplankton concentrations near the pycnocline during the latter part of the bloom. This may well be due to the sinking of phytoplankton into the slower moving water near the pycnocline, resulting in a build up of phytoplankton there.

Our enhanced representation of the vertical processes (Chapter 5) relies heavily on the assumption that zooplankton aggregate vertically to regions of high phytoplankton concentration - an assumption supported by the observations of Bainbridge (1953). Clearly for a build up of phytoplankton to occur near the pycnocline, such aggregation would need to involve some delay - probably more so than our representation implies.

Simple models of predator-prey systems have a tendency to exhibit oscillatory behaviour. There are a number of stabilising mechanisms in our model which reduce such instability. The connectivity of the system to the coastal sea results in an increased import rate of phytoplankton when the phytoplankton standing crop within the system is lower than outside, and vice-versa when the standing crop is higher. In addition we have included a small immigration rate of zooplankton and carnivores to compensate for the lack of a representation of overwintering in this model. (immigration is only a significant proportion of the total zooplankton and carnivore flux over the winter period).

Generally however the stabilising mechanisms in this model are those which provide resource limitation. In typical, non nutrient limited sea-

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Generally however the stabilising mechanisms in this model are those which provide resource limitation. In typical, non nutrient limited sea-

lochs, factors that inhibit phytoplankton growth at high densities are self-shading and vertical zooplankton aggregation. In less open, nutrient limited systems, slowing the DON remineralisation rate is very stabilising (Fig. 8.3).

Our model does however still have a tendency to exhibit some oscillatory behaviour which is probably unrealistic (e.g. Loch Etive 5.6b, Fig. 6.3). One likely reason for this is our simplistic representation of the spatial structure; e.g. the tendency of phytoplankton to accumulate near the pycnocline (as discussed above) may well provide further stability by reducing mean primary productivity during the post-bloom period. Other, more complex features, such as age-structure within the zooplankton and carnivore population, could also affect the stability within the model. It is clear however that no one factor contributes towards trophic stability - a whole range of biological and physical factors are involved.

Apart from our simple representation of the vertical processes, our model largely ignores spatial inhomogeneities within the loch. That this does not seem to unduly affect the model's performance when compared with data is probably to do with the interaction of various types of processes restricting the extent of patchiness.

The interaction of physical processes is one reason e.g. the ameliorating influence of mixing on run-off induced patchiness. Another reason is the action of physical processes on biologically induced aggregations, e.g. turbulent diffusion can restrict the extent of predation induced patchiness. On the other hand some of the biological processes tend to restrict physically induced spatial structure, e.g. grazing may act to reduce vertical structure caused by light, sinking etc. (Chapter 5).

It would appear that in systems of this scale, these various processes, acting in consort, limit the extent and persistence of spatial structure. This allows us to model the system fairly well whilst representing only the most obvious aspects of the spatial structure.

If it is the size of sea-lochs that allows us to represent their water column ecosystems with very little spatial representation; then larger systems, such as regional sea or indeed oceans, would seem to be outside the scope of this model. Not necessarily our representation of the biota or nutrients however - if it is possible to achieve a reasonably simple description of the spatial processes on the timescales we use here (days to weeks) then much of the biological and nutrient parts of the model could be used as here.

A somewhat different set of problems arises in applying this model to more closed water bodies such as very slowly flushed inlets and freshwater systems. In such systems many of the physical processes are significantly weaker than they are in the sea and consequently biologically induced spatial structure is more persistent. In this respect our representation of the biological and nutrient processes is perhaps too unsophisticated. Closed systems present additional problems to the modeller such as how to represent internal recruitment (overwintering) effectively. In addition, the limited number of species which are present in such systems may restrict the applicability of an unstructured biomass model. Nevertheless a model of this type may well be a good starting point in examining such systems particularly if applied to a series of progressively more closed systems. The reward for examining these systems is clearly a better understanding of the biological mechanisms than can be achieved in more open systems.

### **8.3 Further development**

The program of research reported in this thesis was initiated to advise on the strategy for a field program on Loch Linnhe during 1991. This field programme is now complete and at the time of writing the data is being processed. A large amount of spatially resolved data covering all the variables and driving functions in our model has been collected.

As well as providing a stringent test of the model, it is hoped that this data will provide further insight into some of the problems that we have discussed above e.g.: vertical processes; seasonal zooplankton egg production etc.

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