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The Use of Optimization Techniques to Model Marine Ecosystem Dynamics at the JGOFS Station at 47 degrees N 20 degrees W [and Discussion]

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The use of optimization techniques to model marine ecosystem dynamics at the JGOFS station at 47° N 20° W

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SUMMARY

A seven-compartment model of the mixed layer ecosystem was used to fit a time series of observations derived from data obtained during the 1989 JGOFS North Atlantic Bloom Experiment. A nonlinear optimization technique was used to obtain the best fit to the combined observation set. It was discovered that a solution which gave a good fit to primary production gave a bad fit to zooplankton and vice versa. The solution which fitted primary production also showed good agreement with a number of other independent data sets, but overestimated bacterial production. Further development is necessary to create a model capable of reproducing all the important features of the nitrogen flows within the mixed layer.

1. INTRODUCTION

The goals of the JGOFS programme can be summarized as: understanding the carbon cycle within the ocean; and predicting how this cycle might change under the forcing of global climate change. It is impossible to sample the ocean with sufficient temporal and spatial resolution to quantify all the biogeochemical cycles on a global scale, and so the observational programme must be focused on providing the information necessary for developing good mathematical models of the key processes (SCOR 1990). This is the justification for the rolling programme of worldwide JGOFS process studies which began in 1989 with the North Atlantic Bloom Experiment (NABE). It is now important that we begin to assess the explanatory power of our models; here we describe an attempt to do just this using the observation set obtained at 47° N 20° W.

Simple ecosystem models have been developed to model the annual cycle of biological concentrations and production in the ocean mixed layer (Evans & Parslow 1985; Frost 1987; Steele & Henderson 1992). Despite their simplicity, such models have been reasonably successful in simulating the seasonal observations from time series stations such as Bermuda Station 'S' (Fasham *et al.* 1990; Steele & Henderson 1993), Ocean Weather Stations I (Fasham 1993) and P (Frost 1993) and the 47° N NABE site (Marra & Ho 1993; Taylor *et al.* 1993). All these models require a large number of parameters to specify the ecological interactions, but estimating their values is difficult. Some parameters, such as phytoplankton and bacterial growth rates or zooplankton grazing and excretion rates, can be measured experimentally at sea. Others, including phytoplankton natural mortality rate or detrital remineralization rate are, at present, almost impossible to measure accurately.

The approach of most modellers to this problem has been to use experimentally determined parameter values where available, and then adjust the remaining parameters until the model shows a good agreement with the observation set. However, with a large parameter set it is often difficult to achieve a good fit to all the observation set using such hit-and-miss methods. One cannot tell if a bad fit is due to inadequacies of the model or whether the best area of parameter space has been missed. A more rational approach is obviously needed and, with the power of modern computers, this is now possible using techniques of nonlinear optimization. Here we will report on our experience of using such a method to test the ability of a marine ecosystem model to fit the NABE data at 47° N 20° W.

2. THE ECOSYSTEM MODEL

The model used for the optimization experiments was the mixed layer nitrogen-based model of Fasham, Ducklow & McKelvie (1990) (FDM). As nitrogen is considered to be the limiting nutrient in most of the world ocean, understanding the nitrogen cycle is a necessary prerequisite to modelling the carbon cycle. FDM considered that the simplest model capable of capturing the essence of the nitrogen cycle required seven compartments (see figure 1) namely phytoplankton, zooplankton, bacteria, nitrate, ammonium, labile dissolved organic nitrogen (LDON) and detritus. The basic equations governing the model and the underlying rationale are given in FDM and so only a brief description of the structure and parameters will be given here. There are 28 parameters (see table 1 for a full list).

The seasonal changes in mixed layer depth are specified in advance based on climatic mixed layer depths (Levitus 1982) supplemented by NABE observations for the period of the spring shoaling of the

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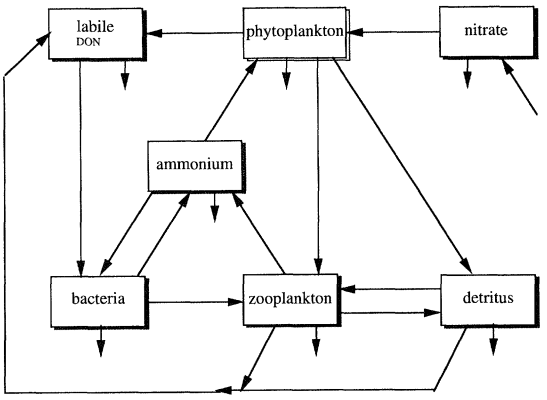

Figure 1. Ecosystem model structure.

pycnocline (Chipman *et al.* 1993). Mixed layer deepening throughout the late autumn and winter entrains nitrate from below the mixed layer. The amount of nitrate entrained depends on the vertical nitrate gradient below the mixed layer and this is specified using the equation $N = N_s + N_g z$ (where z is depth and N_s, N_g are model parameters). Mixing of entities across the pycnocline is parameterized using a constant mixing rate m . The other physical forcing function is solar radiation; this is parameterized using standard astronomical formulae (Brock 1981) and a model of cloud transmittance (Evans & Parslow 1985) assuming a constant fractional cloudiness C. Light transmittance through the water column is modelled using a water attenuation coefficient k_w and phytoplankton self-shading coefficient k_c.

Primary production is determined by two parameters V_p, the maximum growth rate and α, the growth rate per unit light at low irradiance. The nutrient-saturated phytoplankton growth rate, averaged over the day and the mixed layer, is calculated using the equation of Evans & Parslow (1985). Dissolved inorganic nitrogen (DIN) exists as both nitrate or ammonium. Nitrate uptake in many algae is inhibited by fairly low concentrations of ammonium (Dortch 1990) and this was modelled by multiplying the Michaelis–Menten term for nitrate limitation by a negative exponential function of the ammonium concentration (Wroblewski 1977). The effect of DIN limitation is therefore specified by three parameters, the half-saturation constants for nitrate (k_1) and ammonium (k_2) uptake and the inhibition constant ψ. Phytoplankton exude a fraction (γ) of their production as LDON and the natural mortality is assumed to be a linear function of biomass with parameter μ_1.

Zooplankton feed on phytoplankton, bacteria and detritus, so the zooplankton grazing model is defined by four parameters: (i) the maximum specific grazing rate g; (ii) the half-saturation constant for grazing k_3; (iii) the feeding preferences of zooplankton for phytoplankton (p_1); and (iv) the feeding preferences of zooplankton for bacteria (p_2), when these resources

Table 1. *Model parameter set: definitions, and the values obtained from the two optimization solutions*

parameter	symbol	units	solution 1 $T_{obs} = 7.8$	solution 2 $T_{obs} = 8.2$
fractional cloudiness	C	—	0.85	0.53
cross-thermocline mixing rate	m	m d^{-1}	0.16	0.13
surface nitrate concentration	N_s	mmol m^{-3}	4.46	4.46
nitrate depth gradient	N_g	mmol m^{-4}	0.025	0.022
water attenuation coefficient	k_w	m^{-1}	0.034	0.033
phytoplankton self-shading coefficient	k_c	m^2 (mmol N)$^{-1}$	0.11	0.23
phytoplankton maximum growth rate	V_p	d^{-1}	1.51	1.17
initial slope of P-I curve	α	(W m^{-2})$^{-1}$ d^{-1}	0.103	0.068
half-saturation constant for nitrate uptake	k_1	mmol m^{-3}	0.82	0.85
half-saturation constant for ammonium uptake	k_2	mmol m^{-3}	0.69	0.81
nitrate uptake ammonium inhibition parameter	ψ	(mmol N m^{-3})$^{-1}$	2.91	3.03
phytoplankton specific mortality rate	μ_1	d^{-1}	0.050	0.037
phytoplankton LDON exudation fraction	γ	—	0.015	0.016
zooplankton maximum ingestion rate	g	d^{-1}	0.98	1.00
zooplankton ingestion half-saturation constant	k_3	mmol m^{-3}	1.02	0.86
zooplankton assimilation efficiency	β		0.76	0.46
zooplankton excretion rate	μ_2	d^{-1}	0.11	0.09
fraction of zooplankton excretion going to ammonium	ϵ	—	0.32	0.89
zooplankton mortality parameter	μ_5	(mmol m^{-3} d)$^{-1}$	0.27	0.28
fraction of zooplankton losses going export	Ω	—	0.19	0.19
zooplankton feeding preference for phytoplankton	p_1	—	0.23	0.12
zooplankton feeding preference for bacteria	p_2	—	0.36	0.04
bacterial maximum uptake rate	V_b	d^{-1}	2.58	0.78
bacterial excretion rate	μ_3	d^{-1}	0.20	0.03
bacterial half-saturation constant for uptake	k_4	mmol m^{-3}	0.37	1.06
ratio of ammonium uptake:LDON uptake for bacteria	η	—	0.27	1.50
detrital sinking rate	V	m d^{-1}	3.89	6.43
detrital breakdown rate	μ_4	d^{-1}	0.01	0.06

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have equal concentrations (the feeding preference for detritus (p_3) is fixed by the equation $p_3 = 1 - p_1 - p_2$ and so is not a free parameter). The grazing model used allows for positive switching between resources depending on their relative concentrations (FDM). A constant assimilation efficiency (β) is assumed and excretion is proportional to biomass at a rate μ_2. A fraction ϵ of the excretion is ammonium, the remainder is LDOM. Zooplankton mortality is a quadratic function of zooplankton biomass (Fasham 1995) with parameter μ_5, and it is assumed that a fraction Ω of this mortality flux is exported as fast-sinking detritus while the remainder is recycled to ammonium within the mixed layer (FDM).

Bacteria require DOM for their carbon supply but they can also take up and excrete ammonium (Goldman et al. 1987). The bacterial growth is parameterized by means of the maximum growth rate, V_b, the half-saturation constant, k_4, for the uptake of LDON, a constant η that defines the ratio of LDON to ammonium uptake, and the excretion rate μ_3.

Detritus sinks out of the mixed layer at a rate V. Detritus can also be recycled within the mixed layer through reingestion by zooplankton (Poulet 1983) or breakdown into DOM and subsequent uptake by bacteria. The latter process is parameterized by a breakdown rate μ_4.

3. OPTIMIZATION

We wish to choose parameters which minimize the sum of squared deviations between model predictions and observed values. However, it is not clear whether absolute or relative errors should be minimized; this is dependent on the form of the variation and how it changes with mean value. We have chosen (more or less arbitrarily) to assume that variance increases as the square root of the actual value; a compromise between constant absolute and constant relative error. The misfit measure T_{obs} is therefore defined as

$$T_{obs} = \Sigma\Sigma\,(\sqrt{x_{obs}} - \sqrt{x_{pred}})^2,$$

where x_{obs} and x_{pred} are the observed and predicted values, and the summation is over all variables and all observation times.

Before this, we had ideas of what the parameter values should be: both intrinsic bounds on parameters (fractions lie between 0 and 1; grazing rates are not negative) and a target value which we would select in the absence of data, but ignore if the data strongly suggest another value. These ideas are incorporated in a penalty function depending on three terms: T, the suggested or target value of the parameter, and U and L, its upper and lower bounds. If p is a trial parameter value with estimated variance v, then a term

$$P(p) = (T-p)/(p-L)v \quad L < p \leqslant T,$$
$$(p-T)/(U-p)v \quad T < p \leqslant U,$$

is appended to T_{obs} to give a combined penalty function for minimization. If the variance v is large (a value of 10 was used), then the penalty is small except very near the bounds where it grows without bound. This means that the majority of the misfit would come from data rather than from parameters.

Regardless of the technique (we used Powell's conjugate direction method, see Press *et al.* 1992) used to iteratively seek the best fit, we can assume that this is a parameter set which fits the data and has no parameter values which can be regarded as implausible. We found no other parameter set that gave a better fit without offsetting moves in parameter directions which are outside the specified parameter range.

The definition of 'a good fit' is somewhat pragmatic; a 'correct' definition weights misfits to quantities that are intrinsically less variable, more highly, both in the intrinsic variation of the quantity and the accuracy of the measurements. Intrinsic variation itself depends on how we use the model: if we want to fit a particular observation set then it does not include expected interannual variation; if we want to describe an overall average carbon cycle then it does.

4. OBSERVATIONS

The observation set was obtained from measurements made during the 1989 JGOFS North Atlantic Bloom Experiment at 47° 20° W (Ducklow & Harris 1993; Lochte *et al.* 1993). The bulk of the data covered the period from 24 April to 31 May obtained on two U.S. cruises (*Atlantis II* 119–4 and 119–5) and one German cruise (*Meteor* 10/2). The *Meteor* cruise covered the period during which *Atlantis II* was in port, ensuring a complete coverage of the spring bloom period. Some data were also obtained during July from British cruises (*Discovery* 183 and 184), and during August from the Dutch cruise on *Tyro*. Despite the almost unprecedented amount of ship time, data are only available for about a third of the year.

To provide data for comparison with the model, values within the top 30 m were averaged and multiple observations for a given day were averaged to give one value per day. Phytoplankton chlorophyll values were converted to mmol N m^{-3} using a N:chlorophyll ratio of 14 (Ducklow *et al.* 1993), whereas ^{14}C primary production estimates were converted to mmol N m^{-3} d^{-1} using the Redfield ratio of 6.625. Bacterial cell counts were converted to mol N using a value of 2×10^{-14} g C $cell^{-1}$ (Ducklow *et al.* 1993) and a bacterial C/N ratio of 5 mol C/mol N.

The resulting data set (see figure 2) represents a combination of temporal changes and the effects of horizontal spatial variability. The spatial distribution of the eddies in the region was well mapped (Robinson *et al.* 1993) and biological variability associated with these eddies was observed (Lochte *et al.* 1993; McGillicuddy *et al.* 1994). However, for the purposes of this analysis any effect of spatial variability was regarded as noise superimposed on a strong seasonal cycle representing the average seasonal change in the ecosystem dynamics.

During the spring bloom the nitrate concentration declined from 7 mmol m^{-3} to < 0.5 mmol m^{-3}, whereas the phytoplankton concentrations increased

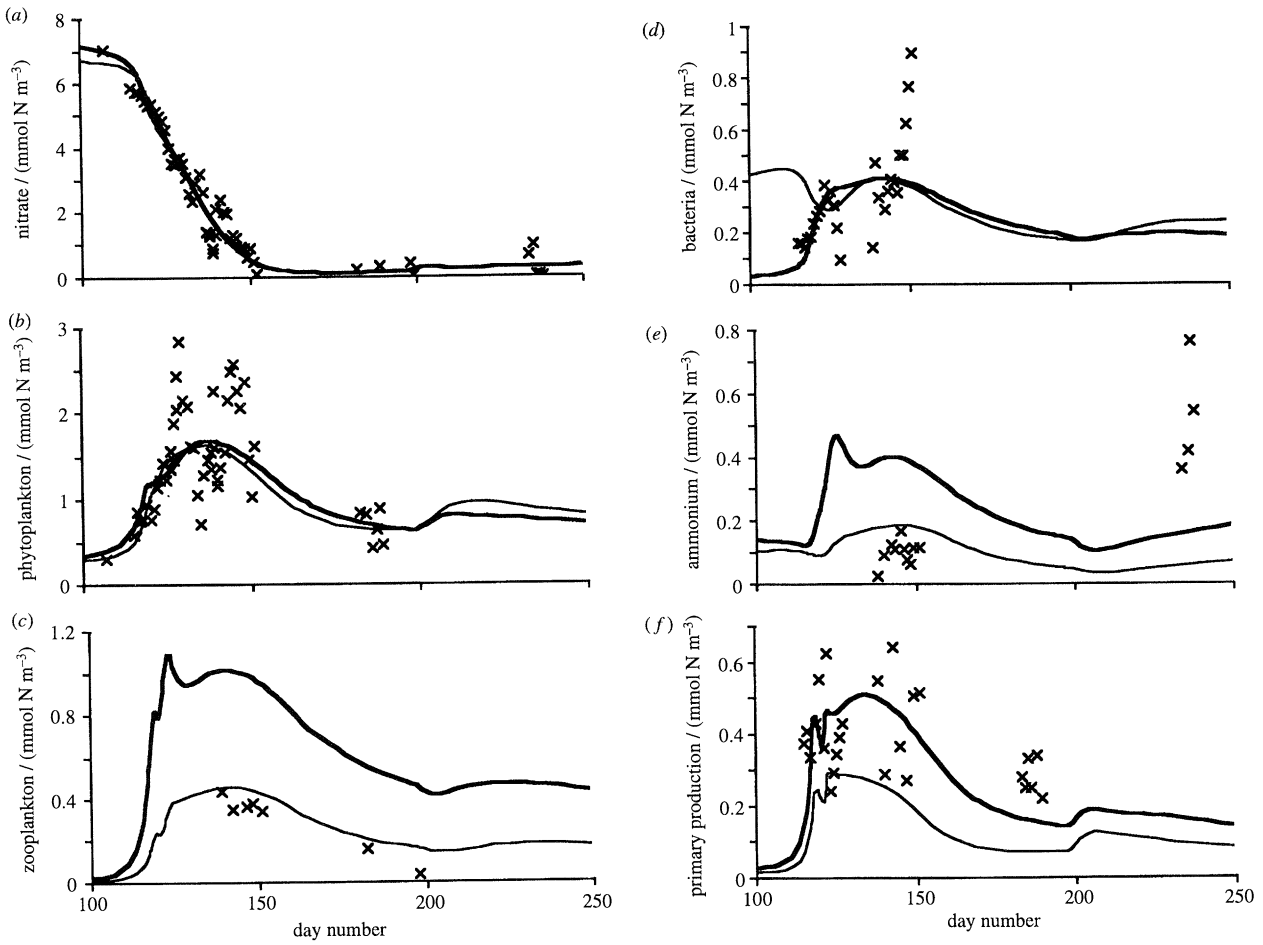

Figure 2. Comparison of observations (crosses) with model predictions from optimizations 1 (thick line) and 2 (fine line): (*a*) nitrate (*b*) phytoplankton (*c*) zooplankton (*d*) bacteria (*e*) ammonium and (*f*) primary production.

from < 0.5 mmol m^{-3} to peak values of ~ 3 mmol m^{-3} (see figures 2*a*, *b*). During July and August nitrate concentrations remained low and phytoplankton concentrations continued to decline, reaching values < 0.5 mmol m^{-3}. The data set for primary production was more limited (see figure 2*f*). Lochte *et al.* (1993) suggested that the U.K. and German ^{14}C incubations during the spring bloom period may to some extent have been affected by metal contamination and so only the U.S. data have been used for this period. For the July–August period only the ^{14}C measurement made on *Discovery* 183 were available.

A good set of bacterial count data was obtained on the two Atlantis cruises (see figure 2*d*) and showed a strong increase in biomass associated with the spring bloom. Very few ammonium measurements were made and we have been restricted to observations made on *Atlantis* 119–5 and the *Tyro* cruise (see figure 2*e*). A similar lack of data affects estimates of zooplankton biomass (see figure 2*c*). Most of the grazing of phytoplankton, at least during the spring bloom, was due to microzooplankton (Burkill *et al.* 1993; Verity *et al.* 1993). Unfortunately, obtaining good estimates of microzooplankton biomass is time-consuming and only five estimates were available from *Atlantis* 119–5 (Verity *et al.* 1993) and one each from *Discovery* 183 and 184 (Burkill *et al.* 1993).

A closer analysis of the spring bloom shows that it consists of two separate peaks. As the *Meteor* and *Atlantis* were not occupying exactly the same position during their sampling, this double peak could perhaps be attributed to spatial variability. However, the nitrate data showed a good continuity between all three cruises; the silicate was almost totally utilized during the period of the first peak suggesting that this bloom consisted mainly of diatoms. This is supported by phytoplankton species counts made on the *Meteor* cruise (Lochte *et al.* 1993). The main contribution to the second chlorophyll peak came from small flagellates (Sieracki *et al.* 1993; Taylor *et al.* 1993).

5. RESULTS

The parameter target values and ranges were mostly chosen to be as broad as possible consistent with the values used in FDM. It was found that the choice of some target values can have a large effect on the optimization and solutions were obtained that gave similar overall fits to the total data set but varied in the degree of fit to individual variables. This will be discussed in more detail in a later paper, and we will restrict ourselves here to discussing the results obtained using just two of these parameter sets.

For the first optimization all of the observations were given an equal weight and the resulting parameter values are shown in table 1. The simulated changes between days 100 and 250 for five of the state variables and for primary production are shown in figure 2

(thick line). The nitrate observations are fitted very well; this is hardly surprising given that the spring nitrate decline was so well-defined by the observations and that nitrate has the largest concentrations. The initial spring increase in phytoplankton is also modelled well but the peak and the double peak structure are not. This latter failing is not surprising bearing in mind that the model has only one class of phytoplankton (for a model with three functional groups of phytoplankton, see Taylor *et al.* 1993). The initial spring-time increase in bacterial biomass is modelled well but the large increase in bacterial biomass occurring after day 146 is not reproduced.

The predicted primary production values are within the range of observations during the spring bloom (see figure 2*f*), although they are still less than the observed values in July. It should be remembered that the model assumed a constant cloudiness throughout the year, whereas Martin *et al.* (1993) demonstrated that a large amount of the day-to-day variability in primary production was due to daily variations in cloud cover. It might, therefore, be best to compare the model results with the average primary production over the whole period of the US observations. Martin *et al.* (1993) estimated that the average primary production in the top 35 m between 24 April and 1 June was 86 mmol C m^{-2} d^{-1}, or 0.37 mmol N m^{-3} d^{-1}. For the same period the model estimate was 0.44 mmol N m^{-3} d^{-1}, an overestimate of only 20%.

A failing of optimization 1 is that it predicts zooplankton concentrations that are more than twice the observed values; overestimating the ammonium observations in spring and underestimating them in the late summer. One of the problems with this data set is the considerable discrepancy between the numbers of observations of zooplankton concentration compared to the other state variables. One possible way of countering this is to give the zooplankton observations a higher weighting, and for the second optimization a weighting of 10 was used. The resulting zooplankton simulation was in good agreement with the observations and showed a closer agreement with the spring ammonium values (see figure 2, fine lines). However, this was achieved at the expense of a worse fit to the bacteria data and considerable underestimation of the primary production (see figure 2*f*).

6. DISCUSSION

(*a*) *Comparisons of model results with other observations*

An independent check on the model results can be made by comparing various stock and flux estimates obtained during NABE with equivalent values derived from the model. As the first optimization gave the best fit to the primary production observations attention will be focused on these results.

A comparison of modelled and observed particulate organic nitrogen concentration (PON) has particular value as it does not depend on any assumptions about conversion factors from chlorophyll or bacterial cell numbers to nitrogen units. Two methods were used to calculate model PON. The first summed phytoplankton,

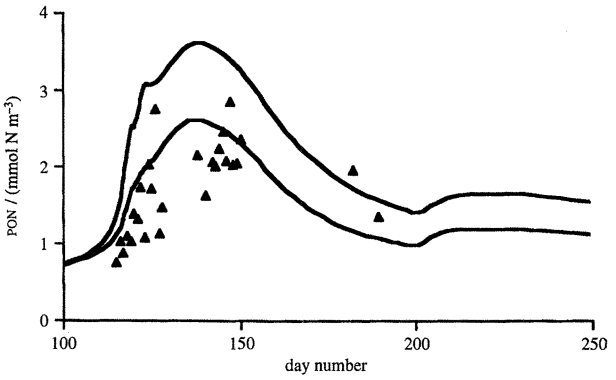

Figure 3. Comparison of modelled and observed PON (triangles) for the first optimization. The two solid lines represent modelled PON including and excluding zooplankton biomass.

bacteria and detritus concentrations and the second also included zooplankton, thereby giving lower and upper bounds for PON. The observed PON values (see figure 3) mainly fall below the lower modelled PON values during the spring bloom, but the predicted concentrations of organic matter are within 20–25% of the observed values.

The annual total and new primary production were 1.54 and 0.82 mol N m^{-2} a^{-1} respectively, giving an annual *f* ratio (defined as the ratio of new to total primary production) of 0.53. No long time-series of primary production observations have been obtained at 47° N 20° W and so it is difficult to know whether these estimates are realistic or not. Berger (1989) produced a compilation map of primary production observations and the estimate of primary production at 47° N 20° W was 35–60 gC m^{-2} a^{-1} (0.44–0.75 mol N m^{-2} a^{-1}), which is much less than the model estimates. However, it is generally considered that the new clean techniques for measuring ^{14}C production are giving production estimates that are about twice the historical values (J. Marra, personal communication). This is supported by the fact that the estimate of average primary production obtained by Martin *et al.* (1993) during NABE (86 mmol C m^{-2} a^{-1}) was 6 times the higher estimate from the Berger map. Martin *et al.* (1993) estimated the average *f* ratio between days 114–151 as 0.45; the equivalent modelled value is 0.43. However, the Martin *et al.* (1993) value was not a true *f* ratio but the ratio of the export particle flux to primary production and the modelled estimate of this quantity was 0.30. The observed and predicted particle fluxes out of the mixed layer can be compared directly for the spring bloom period. Martin *et al.* (1993) used free-floating sediment traps at a number of depths to derive a particle-flux depth relation for the period between days 114–151. This was used to extrapolate to a depth a 35 m to give an average PON flux of 6.8 mol N m^{-2} d^{-1}, i.e. an average over the 35 m depth of 0.19 mol N m^{-3} d^{-1}. The equivalent model estimate was 0.15 mol N m^{-3} d^{-1}.

We have seen that the model predicts a much higher zooplankton biomass than is suggested by the limited observation set. Another independent check on the validity of the zooplankton component may be to

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compare modelled and observed zooplankton grazing rates. Microzooplankton grazing rates were measured during *Atlantis II* leg 2 using the dilution technique and fractionation experiments by Verity *et al.* (1993), and using the dilution technique alone by Burkill *et al.* (1993) on *Discovery* 183. Such experiments gave estimates of the phytoplankton specific growth and grazing rates, but it is difficult to compare these values with the models because the experiments apparently overestimate the natural *in situ* phytoplankton growth rates. For example, the average phytoplankton growth rate between days 138–149 calculated from the experiments of Verity *et al.* (1993) was 0.69 ± 0.20 d^{-1}, whereas the growth calculated by dividing primary production by phytoplankton biomass was 0.26 ± 0.10 d^{-1}. The average modelled growth rate over the same period was 0.26 d^{-1}. It may, therefore, be better to compare the observed and modelled estimates of the fraction of phytoplankton production grazed by the zooplankton. The average experimentally measured values of this quantity was 79% between days 138–149 (Verity *et al.* 1993) and ~ 100% between days 182–189 (Burkill *et al.* 1993). The predicted values were 82% for the first period and 76% for the second. Using this criteria the model grazing rates are not unreasonable, although more observations will be needed before we can feel confident with the model predictions, especially bearing in mind the discrepancy between modelled and observed biomass values.

During the period that bacterial production estimates were made (*Atlantis II* leg 2), the simulated bacterial production was about $\frac{1}{4}$–$\frac{1}{2}$ the observed values. However, to convert the observations to nitrogen units various average conversion factors had to be assumed (Ducklow *et al.* 1993); the observations could be brought into better agreement with the model results by using the lowest measured value of the ratio of cells produced to the uptake of tritiated Thymidine, rather than the average value. This again is an area that needs further careful analysis before we can feel confident that the models are reproducing the pattern of nitrogen flows observed in the mixed layer during the NABE period.

(*b*) *General conclusions*

This study has demonstrated that nonlinear optimization techniques can be used to good effect in fitting ecosystem models to observations of the seasonal cycle of production. However, it was found that despite the large number of parameters defining the model, we were not able to determine a parameter set that would give a good fit to the whole observation set simultaneously. The optimization that gave the best fit to the primary production results also gave a good fit to the estimated spring-time particle flux out of the mixed layer but underestimated the bacterial production. Considering that the biological components of the ecosystem are modelled by just three compartments this is perhaps not surprising, although some of the problems may arise from the difficulty of reliably estimating microzooplankton biomass and bacterial production.

The next stage in the research will be to apply the technique to other JGOFS time series observations, and to investigate whether improved explanatory power can be provided by more complex models (see, for example, Ducklow & Fasham 1992; Taylor *et al.* 1993) or models involving other nutrients such as silicate. The long-term aim is to develop geographically robust models capable of explaining the whole JGOFS observation set and reliably predicting the flux of carbon from the atmosphere to the deep ocean.

We would like to thank the many JGOFS scientists whose hard work at sea contributed to the observations used in this paper, and Roy Lowry and George Heimerdinger whose development of database systems has made these data easily accessible to modellers.

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Discussion

D. A. Kiefer (*Department of Biological Sciences, USC, Los Angeles, U.S.A.*). Has Dr Fasham explored his model by comparing parameter values of his plankton model obtained by turning to different state variables or different combinations of state variables?

M. J. R. Fasham. I have tried optimizations using subsets of the total number of variables (e.g. chlorophyll and nitrate). The result was similar to the full optimization, although the misfit to the whole observation set was increased.

M. Creasey (*Department of Oceanography, University of Southampton, U.K.*). Regarding choice of suitable starting parameters for Dr Fasham's optimization technique, may I suggest he starts by optimizing a substantially reduced data set, say for only a few days around the peak of the bloom, and then with the resulting estimates for the parameters, as starting parameters, repeat the optimization process for successively larger data sets (adding a few days at a time) until he has optimized the complete data set. Has he considered this approach?

M. J. R. Fasham. No I have not, but I will certainly try it out in the future.

H. Leach (*University of Liverpool, U.K.*). How much vertical structure is there in the model?

M. J. R. Fasham. Only a mixed-layer (and thermocline).

H. Leach. So it is only a two-layer model?

M. J. R. Fasham. Yes.

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