

Limits to prediction in a size-resolved pelagic ecosystem model

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A size-resolved pelagic ecosystem model has been developed based on a continuous (with size) set of model equations and using allometric relationships to specify size-dependent physiological rates. Numerical experiments with identical model equations but different initial conditions and size-class distributions are used to investigate inherent limits to prediction of instantaneous state from an initial condition. The simulations have relatively constant physical forcings, such as solar radiation, to emphasize the dynamical properties of the size-resolved model. Initial condition experiments show that perturbations of 1, 0.1, 0.01, 0.001 and 0.0001% of the initial biomass of individual size-classes from a flat size spectrum lead to equal spread of model trajectories. The greatest divergence of trajectories occurs when a 2.7 μm equivalent spherical radius phytoplankton size-class blooms. This divergence has a finite-time Lyapunov exponent of 0.21 day^{-1} and a prediction time of 33 days for a precision of $10^{-3} \text{ mol N m}^{-3}$. Large member ensembles can approximately halve the effect of growth of initial condition perturbations on prediction. Further numerical experiments are undertaken with the mean body weight at which size-classes are solved perturbed randomly with a standard deviation of 0.15, 0.015, 0.0015 and 0.00015 of the unperturbed body weight. The greatest effect, which dominates the $\sigma = 0.15$ and 0.015 ensembles, occurs when the perturbations of the size-class distribution add and/or remove predator–prey links. These results provide a cautionary warning for the prediction of instantaneous states using complex pelagic ecosystems that are displaced from a stable oscillation and for which biological state is not dominated by physical processes.

KEYWORDS: plankton; size; Lyapunov exponent; ensemble spread; initial conditions; prediction

INTRODUCTION

Pelagic ecosystems consist of organisms with volumes spanning 21 orders of magnitude. The distribution of biomass across this size range has general trends throughout the world's oceans (Sheldon *et al.*, 1972). The size-structure of planktonic communities arises from an interaction of size-dependent physiological rates such as maximum growth rates (Tang, 1995) and size-dependent planktonic interactions such as grazing (Platt and Denman, 1977; Hansen *et al.*, 1994; Kerr and

Dickie, 2001). A growing number of numerical modelling studies have set out to predict size-structure using non-linear ecosystem models with size-based formulations.

Prediction of non-linear phenomena has inherent limits due to uncertainties in parameterizations, initial conditions and forcing, among other factors. One method to investigate limits to predictability is to show divergence of simulations with differences that our knowledge of the natural world cannot distinguish.

Famously, Lorenz (Lorenz, 1965) found divergence of model trajectories in a simple model of convection with vanishingly small errors in initial conditions. On the strength of these simulations, Lorenz (Lorenz, 1965) stated that there is “little promise for forecasting instantaneous state [of weather] a month in advance”. One simple experiment had revealed an inherent limit that affects all attempts to predict weather. The rest of the introduction introduces size-based models of pelagic ecosystems, and the rationale for using idealized numerical experiments to investigate limits to prediction.

Size-based modelling of pelagic ecosystems

Size-based modelling generally involves quantifying the biomass of a number of size-classes for a small number of functional groups such as phytoplankton and zooplankton. Following Moloney and Field (Moloney and Field, 1991), size-based models have generally defined one set of parameterizations for each group (Gin *et al.*, 1998; Armstrong, 1999; Baird and Suthers, 2007; Stock *et al.*, 2008). The coefficients for each size-class of these parameterizations are typically obtained from allometric relationships, of which a large number exists in the literature (Moloney and Field, 1989). This approach has allowed the complexity of the models to increase in an objective manner (Gin *et al.*, 1998) providing an attractive method of increasing the sophistication of pelagic ecosystem models. Along with plankton functional type (Le Quere *et al.*, 2005) and plankton trait-based (Bruggeman and Kooijman, 2007) approaches, the size-based framework is presently one of the most active areas of research in plankton modelling.

One limitation to the ability of some size-based models to explore size-based behaviour is the use of food-web constructions that require modification to the model formulation with changes in the number or distribution of size-classes. This may take the form, for example, of an ecosystem structure where the smallest zooplankton class consumes just the smallest phytoplankton class, the second smallest zooplankton class consumes the second smallest phytoplankton class and so on. If the number or distribution of size-classes is altered, the model formulation must be changed, and it will be expected that model behaviour will change.

To overcome this limitation, Baird and Suthers (Baird and Suthers, 2007) developed a pelagic ecosystem model (Fig. 1) that based the diet of a particular sized predator on a size-based prey range. As the number of size-classes increases, new links between predators and prey are created without re-formulating the model. Figure 2A shows the interacting size-classes of the model with 17 size-classes. Figure 2B shows the same interactions for a

62 size-class configuration that has approximately four times more size-classes. As an example, the largest phytoplankton size-class has three predators in the 17 size-class configuration, and 9 in the 62 size-class configuration, but the two configurations are attempting to resolve the same size-dependency. Baird and Suthers (Baird and Suthers, 2007) refer to this approach as size-resolved, to emphasize the independence of model formulation on any particular choice of plankton size in the model integration.

Formally, this approach is written down as a set of continuous (with size) equations (Baird and Suthers, 2007). But to integrate the size-resolved model, the continuous model equations must be discretized, essentially creating a size-based model with a particular choice of plankton size and links. Thus, any one configuration of the size-resolved model could have been developed without using the continuous model equations, and would be indistinguishable from the food-web formulation critiqued above. In the size-resolved approach, however, model configurations with different numbers and distributions of size-classes can be compared with an expectation that the only difference between model behaviour is in the discretization and the links the discretization determines, and not in the model equations or parameter values.

To this end, Baird and Suthers (Baird and Suthers, 2007) created five configurations of the size-resolved model. Each functional group had the same smallest and largest size-class, but the gap between size-class was progressively reduced as the configurations became more resolved. Baird and Suthers (Baird and Suthers, 2007) were able to demonstrate a convergence of model output for increasing model resolution. Or more precisely, from an identical initial state, simulations with higher resolution diverge later (Fig. 3). Divergence from the 489 size-class configuration occurs at approximately 40, 80, 120, 200 and 220 days for the 17, 32, 62, 123 and 245 size-class configurations, respectively. The coarser model configurations diverged from finer resolved ones not because of a different understanding of the ecosystem, as specified by the continuous model equations and allometric relationships, but due to differences in the numerical implementation only. As such, any divergence of model solutions represents inherent limits to the size-based approach that cannot be overcome through improved understanding of the natural ecosystem.

Limits to prediction in pelagic ecosystem modelling

The use of idealized numerical experiments to place limits on the predictability of pelagic ecosystems was

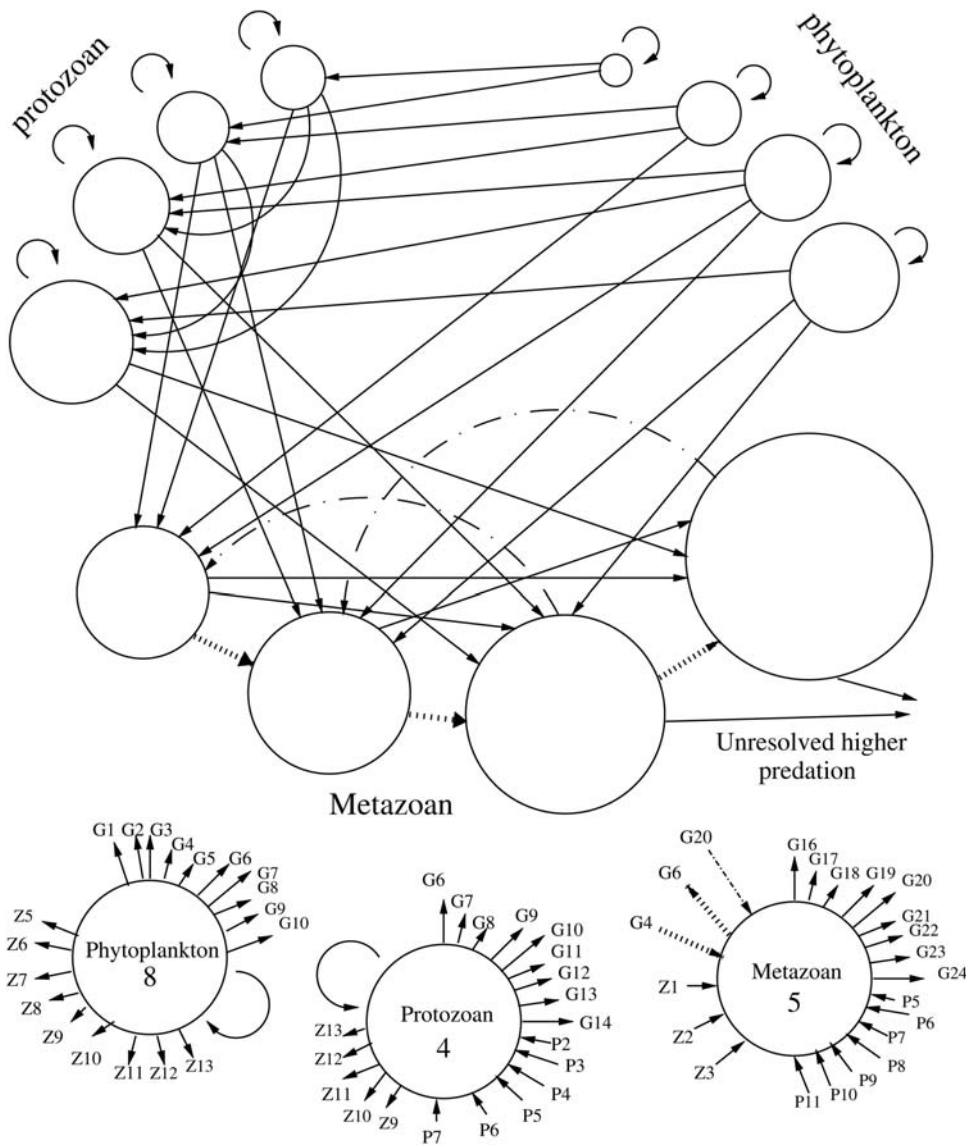


Fig. 1. Schematic of the size-resolved biological model. The phytoplankton and protozoan groups divide, as represented by the arrow turned on itself. Growth of individuals between metazoan size-classes is represented by dashed arrows, while spawning of eggs by metazoa is represented by dot-dashed lines. All other lines are predation terms. In the top schematic, predation is limited to just two size-classes of predators within each functional group, although the 62 size-class configuration typically has 9–11. In the lower schematic, all interactions are given for the 8th phytoplankton class, 4th protozoan class and the 5th metazoan class in the 62 size-class configuration. The largest 15 metazoans have unresolved loss terms which are modelled implicitly using a quadratic loss term that returns nitrogen to the dissolved inorganic nitrogen pool. From Baird and Suthers (2007).

motivated by groundbreaking research in the atmospheric sciences undertaken 45 years ago. Inherent limits to numerical weather forecasting were identified early in the development of the field (Lorenz, 1963), and have strongly influenced progress since. For a simple deterministic non-linear model of thermally forced (convection) rotating flow with small errors in initial conditions, Lorenz (Lorenz, 1965) found divergence of model trajectories. As quoted earlier, Lorenz

(Lorenz, 1965) used these experiments to demonstrate an inherent limit to weather prediction. Lorenz’s quote, which is now known to have been well placed, is remarkable for two reasons. It is unlikely he could have anticipated the enormous advances that have occurred in the intervening 40+ years in the understanding of weather processes, the quality and quantity of observations, as well as in numerical techniques and computational power. Secondly, Lorenz’s model

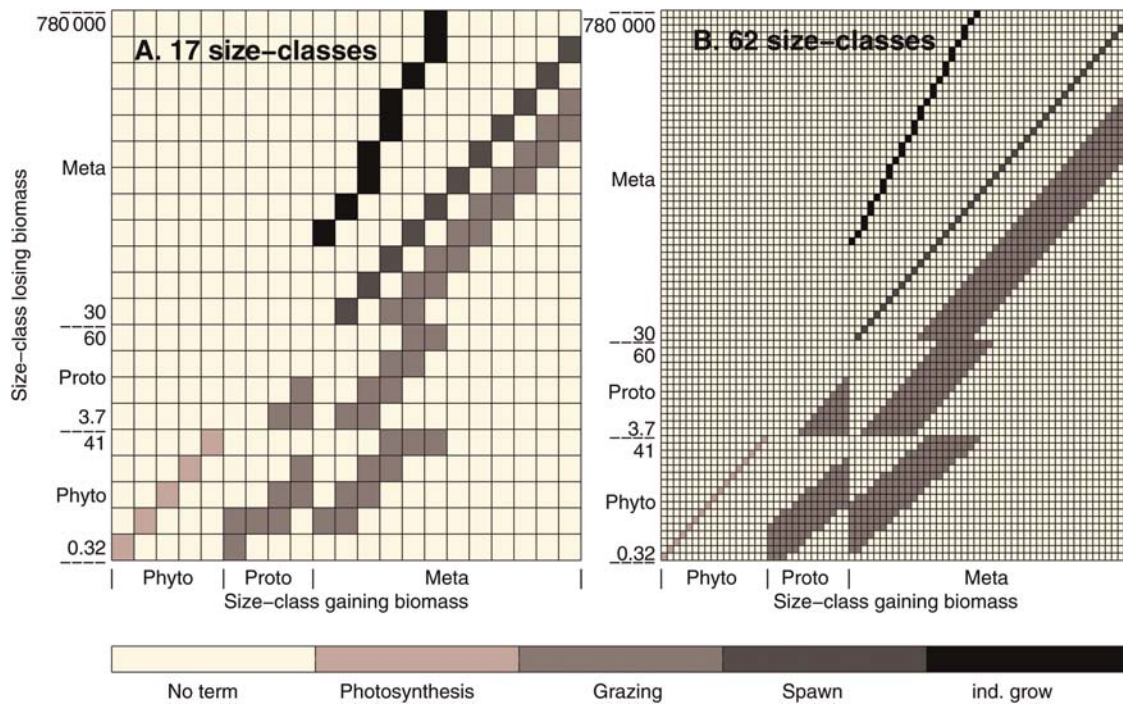


Fig. 2. Schematic of the processes linking size-classes for (A) the 17 size-class configuration and (B) the 62 size-class configuration. The x-axis gives the size-class gaining biomass, and the y-axis (with equivalent spherical radii in μm) the size-class losing biomass. Processes resolved are phytoplankton division (photosynthesis), grazing, individual growth by metazoans and egg spawning by metazoans. White boxes represent no direct link between size-classes. Spawning appears in the top left half of the square as it is a transfer of biomass to smaller size-classes. Photosynthesis (or phytoplankton growth) appears on the 1:1 line, as biomass is not transfer between size-classes. Grazing and individual growth appear in the bottom right half as they move biomass to larger size-classes.

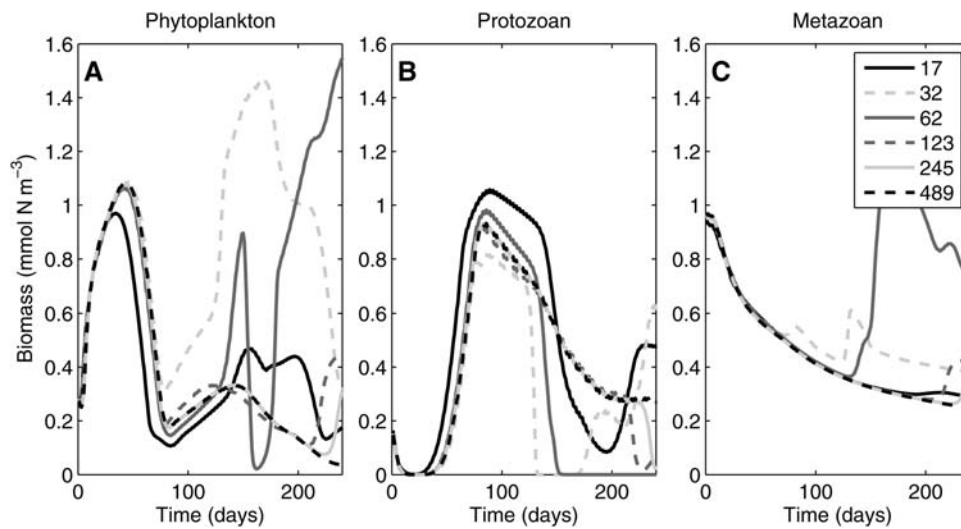


Fig. 3. (A) Total phytoplankton biomass, (B) total protozoan biomass and (C) total metazoan biomass for the 17, 32, 62, 123, 245 and 489 size-class configurations, adapted from Baird and Suthers (2007) and Baird and Suthers (2010).

could not predict the weather. It only considered one process, convection. Numerical experiments with an idealized model alone can provide insights to prediction limits for real world systems if the model captures

the most important non-linear processes with their appropriate time-scales.

The investigation of divergence from an initial state represents one limit to prediction. Perhaps the most

commonly pursued measures of pelagic ecosystem models, and ecological models in general, are steady states (Franks *et al.*, 1986), steady oscillations (Edwards and Brindley, 1996) or, in the case of chaotic systems, attractors (Huisman and Weissing, 2001). The study of divergence from an initial state is uncommon in the ecological literature [an exception being Wilder (2001)], but very common in weather prediction.

The importance of divergence of pelagic ecosystem models from an initial state is likely to become more important in the field of plankton modelling for a number of reasons. First, pelagic ecosystem models are increasingly being used to investigate changes on shorter timescales than a steady state is achieved. This is already true, for example, of models of a week to month long coastal upwelling event (Baird *et al.*, 2006), an open ocean nutrient enrichment experiment (Chai *et al.*, 2007), or fish stock prediction for the coming season (Brander, 2003). However, for complex ecosystem models with long-lived predators, even multi-decadal climate change projections starting at present day initial states may be too short to establish a new steady state.

Secondly, pelagic ecosystem models are routinely coupled to physical models with weather-driven stochastic forcings. These coupled models often assimilate observation of both physical and biological states (Fiechter and Moore, 2009). The physical and even ecosystem states are perturbed by the assimilation procedure in a non-dynamical sense on regular intervals. Such model simulations become a series of short-term forecasts, with sensitivity to initial conditions becoming important. Thus divergence from an initial state is an under-studied phenomenon in ecological modelling and is particularly relevant for complex pelagic ecosystem models.

The limits imposed on prediction of size-based pelagic ecosystem models due to the number of size-classes have already been studied (Baird and Suthers, 2007, 2010). In this paper, two further inherent limits to modelling size-distributions in pelagic ecosystems are investigated. First, initial condition perturbations are investigated, with the approach of applying subtle changes that are beyond our ability to determine which is the more appropriate starting point. Secondly, Baird and Suthers (Baird and Suthers, 2007) used size-classes that increase in an exactly geometrical manner (e.g. doubling of the mean body weight between size-classes). In this paper, experiments are undertaken with a random uniform distribution around the geometric progression. These subtle random changes to the discretization represent an inherent limit to predictability because we have no ability to distinguish which of the subtly different size-distributions should be used.

In order to maximize the generality of the results presented here, the numerical experiments are undertaken for an idealized surface mixed layer with gentle, repetitive physical forcing. This provides an environment to emphasize the dynamical properties of the size-resolved model. Secondly, the initial conditions from which divergence is assessed have a size-distribution equivalent to a slope of the normalized biomass size spectrum (NBSS) of -1 . The NBSS is a histogram-style size-distribution, in which the size axis is divided (normalized) by the width of the size-class, such that the normalized distribution is independent of the width of size-classes (Platt and Denman, 1977). A NBSS of -1 represents equal biomass in geometrically increasing size-classes and is considered a typical value for an oligotrophic surface mixed layer (Sheldon *et al.*, 1972). The results presented may also be considered general because the predator-prey interactions that are the most significant non-linear processes in the pelagic ecosystem are parameterized with coefficients from commonly used allometric relationships (Tang, 1995; Hansen *et al.*, 1997). Thus, while the numerical experiments undertaken might be considered just one instance of one particular model, it is a model with characteristics that are likely to be similar across a broad range of size-based models, and is applied to a generic environment.

In this paper, numerical experiments are undertaken on identical formulations of the 62 size-class configuration of the size-resolved model for a generic surface mixed layer with tiny changes in size-discretization and initial conditions. In both cases, these changes are sufficiently small that it is not possible to distinguish, either through observations of a natural ecosystem or refinement of the size-based understanding, which model configuration should be used for prediction. Thus, the divergence of model trajectories with small perturbations in initial conditions and size-class distributions are used to illustrate inherent limits to prediction of the size-distribution of pelagic ecosystems.

METHOD

Model description

Size-resolved biological model

The size-resolved pelagic ecosystem model contains three functional groups: phytoplankton, protozoans and metazoans, requiring three separately resolved size-distributions. Four features of the size-resolved model are of particular interest to the modelling of

pelagic ecosystems: (i) physical descriptions of planktonic interactions are used to explicitly represent the size-dependencies of limiting physical processes to ecological interactions. Physical descriptions include, for example, calculating the encounter rates of predators and prey based on the physical properties of the fluid and the geometric properties of the organism (Jackson, 1995); (ii) physiological rates are calculated from allometric relationships found in the literature; (iii) a distinction is made in the model between animals that reproduce through division, the protozoa, and those that grow between different life stages, the metazoa (Fig. 1); and (iv) the diet of predators is determined from a size-based prey range rather than an *a priori* trophic structure.

The biological configuration is composed of 62 size-classes doubling in body weight between classes and ranging in volume over 19 orders of magnitude. This ranges from an equivalent spherical radius (ESR) of 0.32 μm , representative of the cyanobacteria *Prochlorococcus* sp., to a metazoan size-class with an ESR of 78.8 cm. The phytoplankton size-classes extend through the first 17 size-classes, protozoan size-classes from the 9th to 21st and metazoan size-classes from the 18th to 62nd. Initially each size-class has an unperturbed biomass of $2.25 \times 10^{-5} \text{ mol N m}^{-3}$. Mass moves between size-classes based on growth of the phytoplankton population (creating organic matter from inorganic constituents), grazing by protozoans and metazoans, growth of individual metazoans from one size-class to another and the spawning of eggs by metazoans (Fig. 2B). Note that of the $75^2 = 5625$ possible interactions between size-classes, only 725 have a process (for more details, see Baird and Suthers, 2007).

Mixed layer model

The size-resolved model is coupled to an idealized one-dimensional mixed layer model that is forced by a sinusoidally oscillating wind with a strength varying between -0.05 and 0.05 Pa over a 3-day period. The vertical profile for vertical diffusivity, turbulent dissipation rate, solar radiation and wind-driven velocity over a 4-day period (200 days after the simulation begins) are given in Fig. 1 of Baird and Suthers (Baird and Suthers, 2007). The wind-driven velocity induces a velocity shear that affects the calculation of the turbulence state variables such as vertical diffusivity and turbulent dissipation rate, but there is no advection in the model. This idealized physical environment is representative of a stable mixed layer in a sub-tropical ocean gyre, and has been used because, with no strong physical

disturbances, the behaviour of the ecosystem is determined primarily by the ecological interactions.

Experimental design

Experiments are undertaken in ensembles. Ensembles are sets of experiments with small but well-defined differences such as in the initial conditions or distribution of size-classes. Other than the defined differences, the model simulations within an ensemble are identical.

Initial condition perturbation experiments

Nine ensembles are undertaken with initial perturbations of 1000, 100, 10, $10^{1/2}$, 1, 0.1, 0.01, 0.001 and 0.0001% of an unperturbed control. Each ensemble consists of 76 members or runs: one member represents an unperturbed control run and the remaining 75 members represent runs in which each phytoplankton, protozoan and metazoan size-class in turn is perturbed. In the perturbed simulations, the initial value of the perturbed state variable is increased. So as to have the same initial mass as the control run, the initial value of the other 74 classes is decreased equally by a 1/74th of the perturbation.

The regular perturbation strategy above allows discussion of the importance of the perturbation of particular size-classes. To ensure that the perturbation experiments produce general results, three further 76-member ensembles were run with all size-classes randomly perturbed in each member of the ensemble. The perturbations in the three additional ensembles fitted a random uniform distribution, and had average initial perturbation magnitudes across all state variables approximately equal to 0.00004, 0.004 and 0.4% of the value of the state variable before perturbation. For comparison with the regular perturbation strategy described earlier, this is equivalent in terms of ensemble spread to perturbing one state variable by 0.0003, 0.03 and 30%.

Size-class distribution perturbation experiments

Four 20-member ensembles are undertaken with the mean body weight at which the size-classes are solved are perturbed using a uniform random distribution from the unperturbed size-class distribution. The magnitude of the random perturbation is quantified as the standard deviation of the unperturbed mean body weight. Ensembles were undertaken with values of $\sigma = 0.15, 0.015, 0.0015$ and 0.00015 . A standard deviation of 0.15 of the unperturbed mean body weight is sufficiently small that the mean body weight of two adjacent perturbed size-classes, $m_{1,\text{pert}}$ and $m_{2,\text{pert}}$ where

$m_{1,\text{unpert}} < m_{2,\text{unpert}}$ will always meet the criterion that $m_{1,\text{pert}} < m_{2,\text{pert}}$.

The sizes of the smallest and largest phytoplankton, protozoan and metazoan groups are unaltered, thus ensuring that the model configurations are representations of the same system, albeit solved with a slightly perturbed grid (size-class distribution). The initial condition for all ensemble members is a NBSS of -1.0 before the random perturbation of the grid is undertaken.

Measures of trajectory divergence

Local Lyapunov exponent

The Lyapunov exponent is a measure of the exponential rate of divergence of adjacent trajectories in a dynamical system (Hilborn, 2000). Positive exponents at a point in time imply there will be a growth of errors in the estimate of the state of the system. If the exponent is on average positive for the region of state space that the system occupies then the system is chaotic. In this paper, the Lyapunov exponent is calculated using the distance, d_j , between the control run and each ensemble member j for each state variable n . The distance d_j is given by:

$$d_j = \sqrt{\sum_{n=1}^N (f_j^n - f_0^n)^2} \quad (1)$$

where f_0^n and f_j^n are the value of state variable n for the control run and ensemble member j , respectively. The Lyapunov exponent over a time period t_1 to t_2 for ensemble member j is given by:

$$\lambda_j = \frac{1}{t_2 - t_1} \ln \frac{d_{j,t_2}}{d_{j,t_1}} \quad (2)$$

In practice λ is found by a least squares fit of the natural logarithm of distance versus time between time t_1 and t_2 . The average Lyapunov exponent for a J -size ensemble is given by:

$$\lambda_{\text{av}} = \frac{1}{J} \sum_{j=1}^J \lambda_j \quad (3)$$

In this paper, where simulations are short relative to the potential time-scales of interactions between state variables, the Lyapunov exponents calculated are local or finite-time exponents and do not consider a sufficient region of the phase space to indicate whether the global behaviour is chaotic.

Ensemble spread

Ensemble spread is a measure of the differences between the members in an ensemble. In this paper, ensemble spread is calculated as the standard deviation of the distance (equation (1)) for all members in the ensemble. To refine the analysis, some calculations of ensemble spread use the distance between a subset of state variables, such as single size-class or all phytoplankton. Such cases are explicitly stated. Otherwise, ensemble spread is for all biological state variables.

Two measures of ensemble spread are used. Ensemble spread from the control run (ESCR) and ensemble spread from the ensemble mean (ESEM), where the spread is calculated relative to the control run and ensemble mean, respectively. These ideas are discussed in the context of the more complex exercise of numerical weather prediction in Buizza (Buizza, 1997) and Buizza and Palmer (Buizza and Palmer, 1998). If ESEM is approximately equal to ESCR, then simulations on average diverge from the ensemble mean as quickly as from a single simulation. Therefore, on average, a single simulation will have the same growth rate of initial condition errors as obtained using the ensemble mean. If ESEM is less than ESCR, then on average simulations diverge less from the ensemble mean. In this case, the use of the ensemble mean reduces the growth of initial condition errors compared with a single simulation, and the ensemble framework reduces the limit to prediction due to the growth of initial condition errors.

RESULTS

The general nature of the size-resolved pelagic ecosystem simulations in this paper are similar to the 62 size-class configuration simulation described in detail in Baird and Suthers (Baird and Suthers, 2007), and shown in Fig. 3 of this paper as a solid grey line. Briefly, the simulations are begun with an equal amount of biomass in each size-class within a functional group. The physical forcing creates an environment similar to the surface mixed layer of a sub-tropical gyre, with a relatively shallow mixed layer and no seasonal cycle. Without strong physical perturbations, the pelagic ecosystem model behaviour is determined primarily by its own dynamical processes rather than environmental perturbations. The dominant oscillation in the model configuration considered is between the phytoplankton size-class with an ESR of $2.7 \mu\text{m}$ and its predators, which causes the period of greatest divergence of trajectories at around Days 120–180.

Sensitivity to initial condition perturbations

Sensitivity to the magnitude of the initial perturbation

Lorenz (Lorenz, 1969) first recognized that in a simple atmospheric model after some finite time, the spread of trajectories becomes independent of the magnitude of initial condition perturbations. Figure 4 plots over time the ESCR of the ensembles with initial perturbations of 1000, 100, 10, $10^{1/2}$, 1, 0.1, 0.01, 0.001 and 0.0001% of an unperturbed control. After 20 days, the 0.1, 0.01, 0.001 and 0.0001% ensembles are within a factor of 2 (after starting three orders of magnitude apart) and are approximately a factor of five greater than the initial spread of the 0.1% ensemble. For a 20-day forecast, it is therefore not possible to improve predictability by refining estimates of the initial conditions below 0.1%. Similarly for a 130-day forecast, only 1% accuracy is required to obtain maximum predictability.

Ensembles with uniform random perturbations of all state variables of magnitudes of 0.0003, 0.03 and 30% show similar behaviour to the regular perturbation strategy (Fig. 4). In particular, randomly distributing a set magnitude of perturbation across all state variables

results in a similar increase in ESCR with time as to allocating the same magnitude perturbation to one variable.

Rates of divergence

To illustrate the divergence of trajectories within an ensemble, the distance between perturbed trajectories and the control run for the 0.0001% perturbation ensemble are given in Fig. 5. The rate of divergence between trajectories varies over time with periods of both growth and contraction, with divergence stabilizing after about 180 days. The average finite-time Lyapunov exponent for 125–140 days, a period of significant trajectory divergence, is 0.210 day^{-1} , corresponding to a prediction time for a precision $P = 10^{-3} \text{ mol N m}^{-3}$ of $1/\lambda_{\text{av}} \ln(1/P) = 33 \text{ day}$.

For the nine ensembles with magnitudes of initial condition perturbations of 1000, 100, 10, $10^{1/2}$, 1, 0.1, 0.01, 0.001 and 0.0001% of the unperturbed control, λ_{av} between 125 and 140 days is 0.210, 0.211, 0.215, 0.217, 0.198, 0.189, 0.169, 0.092 and 0.030 day^{-1} . For the perturbations of 1, $10^{1/2}$, 10, 100 and 1000%, the initial conditions are sufficiently perturbed for the

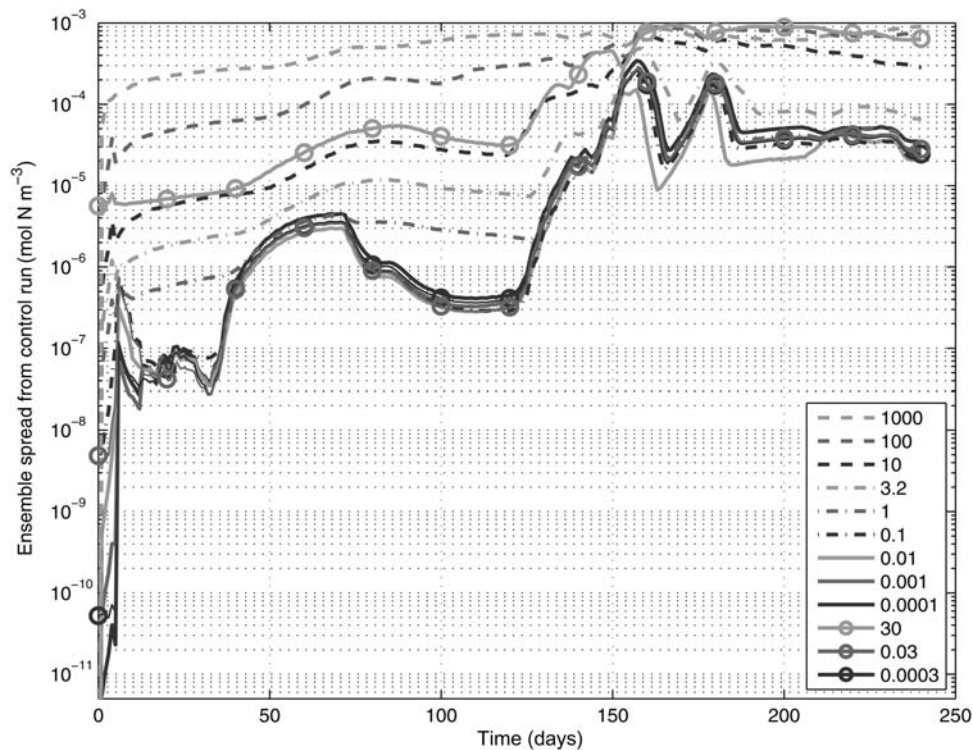


Fig. 4. Ensemble spread from the control run (ESCR) due to a range of magnitudes of initial perturbations in the 76 member ensembles. The magnitude of the initial condition perturbation can be either read from the legend (in percentage change), or from the value at time zero, when the only spread is due the initial perturbation (in mol N m^{-3}). The 1000, 100, 10, $10^{1/2}$, 1, 0.1, 0.01, 0.001 and 0.0001 ensembles have 75 perturbed members with each member containing one perturbed state variable. The 30, 0.03 and 0.0003 ensembles have 75 perturbed members with each member composed of each state variable randomly perturbed.

divergence of trajectories to begin saturating by Day 140. Saturation occurs because of a constraint on the system, in this case, due to mass conservation. In contrast, for perturbations of 0.1% or less the finite-time

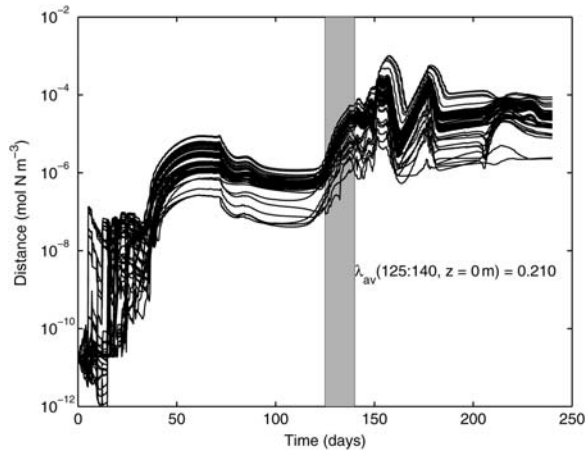


Fig. 5. Calculation of the finite-time Lyapunov exponent (day^{-1}) for members of the ensemble with 0.0001% perturbations in initial conditions. The average finite-time Lyapunov exponent is calculated for the shaded region between Days 125 and 140.

Lyapunov exponents are almost identical. In these cases, the divergence of trajectories has not saturated and the ensembles are indistinguishable because, as seen earlier, the ensemble spread for perturbations of 0.1% or less after 125 days is independent of the magnitude of the initial condition perturbation.

To understand the source of trajectory divergence (and convergence), the contributions to divergence (and, therefore, the Lyapunov exponent) of each state variable can be quantified. Figure 6 gives the result for the ensemble with a 0.1% initial condition perturbation. Figure 6A shows the rate of divergence of diverging size-class for Days 6–10 and 125–140. The size-classes are quantified on the x -axis by their maximum growth rate, as a means of comparing their potential for growth driven divergence with the realized divergence. In the case of large metazoans, divergence is above that which could be achieved through growth. For these large metazoans, the mechanism of divergence is different rates of loss through grazing. Figure 6C shows the rate of convergence of converging size-class.

With an inhomogeneous distribution of mass with size, classes contribute unequally to divergence of the

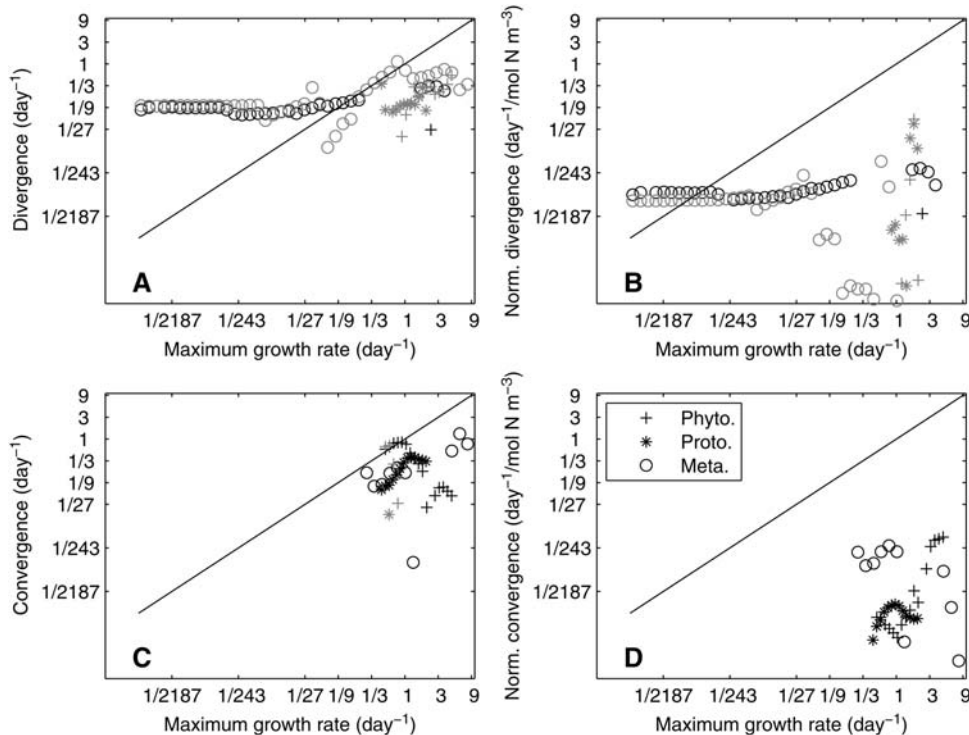


Fig. 6. The contribution to divergence (A and B) and convergence (C and D) of the phytoplankton (+), protozoan (*) and metazoan (o) size-classes during time periods 6–10 days (black symbols) and 125–140 days (grey symbols) for the 0.1% perturbation ensemble. The x -axis is the maximum growth rate of the size-class, and the y -axis is the exponential rate of divergence (or convergence) of the size-class among ensemble members (A and C) or the exponential rate normalized to the biomass of the size-class (B and D). Axes are log–log, with powers of 3 shown for reference. The black line is the 1:1 line for comparison of the maximum growth rate of a class with the realized divergence or convergence. Points on the line have a divergence (or convergence) equal to the maximum growth rate.

whole system. To account for this, Fig. 6B and D display the divergence and convergence multiplied by the mass fraction each size-class contributes to total biomass. In the first time period (6–10 days), biomass is fairly evenly distributed, and the shape of Fig. 6A and C look similar to Fig. 6B and D. For the period 125–140 days, the distribution of biomass is significantly altered. The classes with the highest normalized divergence rates are the 2.7 μm ESR phytoplankton size-class, and the three smallest protozoans. While these size-classes have maximum growth rates of 1.8, 2.0, 1.8 and 1.6 day⁻¹, respectively, the overall divergence of the system, as measured by the Lyapunov exponent, is 0.21 day⁻¹. This is in part because these classes are not reaching their maximum growth (and therefore divergence) rates (Fig. 6A), because they make up only a fraction of the biomass, and because some other size-classes are converging (Fig. 6C and D). A Lyapunov exponent of 0.21 day⁻¹ in a system with individual components that have up to an order of magnitude greater exponential growth rates illustrates the importance of negative feedbacks in pelagic ecosystems.

Comparison of ensemble spread from the control run and ensemble mean

The ESCR and the ESEM between Days 120 to 180 for the nine magnitudes of initial condition perturbations are given in Table I. Both ESCR and ESEM are given for total biomass of phytoplankton, protozoans and metazoans, and additionally for the 2.7 μm ESR phytoplankton size-class and the 242 μm ESR metazoan size-class. ESCR and ESEM are reported as a percentage of the mean biomass of the category (e.g. total phytoplankton biomass) during the same period.

ESCR is generally larger than ESEM for initial perturbations of ≤1%, and approximately equal for ≥10% (Table I). For all ensembles of ≤1%, ESCR is approximately equal, as shown earlier in Fig. 4. The 10^{1/2}% perturbation ensemble is between these two regions: while ESCR is still greater than ESEM, ESCR has become larger than for ensembles of ≤1%.

Table I also shows that ensemble spread (both ESCR and ESEM) of total phytoplankton biomass is generally less than that of the 2.7 μm ESR phytoplankton size-class, and similarly ensemble spread of total metazoan biomass is less than that of 242 μm ESR metazoan size-class for all ensembles. The exception being for phytoplankton in ensembles with initial condition perturbations ≤1%.

Sensitivity of size-class distribution

The sensitivity to small perturbations in the size-class distribution (i.e. the mean body weights at which the model is solved) provides an additional limit on the predictability of the size-resolved model. If model trajectories with small perturbations in the size-class distribution diverge, then a limit exists to prediction based on a single simulation because no single size-class distribution can be said to better match the distribution of any natural system for which the predictions are intended.

Perturbing the grid potentially changes the links between size-classes (because diets are size-based), and the allometrically determined physiological rates of individual size-classes. The unaltered grid has 632 predator–prey links (Fig. 2). In the numerical experiments undertaken, the grid was perturbed with a uniform random distribution with standard deviations of σ = 0.15, 0.015, 0.0015 and 0.00015 of the unperturbed

Table I: Ensemble spread from the control run (ESCR) and the ensemble spread from the ensemble mean (ESEM) from Days 120–180 as a percentage of mean ensemble biomass for different magnitudes of initial condition perturbations of the sum of all phytoplankton, protozoan and metazoan biomass, and for the phytoplankton 2.7 μm ESR size-class and the metazoan 242 μm ESR size-class

Perturbation	Phytoplankton		Protozoans		Metazoans		Phyto. 2.7 μm ESR		Meta. 242 μm ESR	
	ESCR	ESEM	ESCR	ESEM	ESCR	ESEM	ESCR	ESEM	ESCR	ESEM
1000	67.98	58.18	70.77	71.05	48.15	29.76	87.16	74.6	291.85	144.57
100	45.28	45.09	33.43	41.22	23.23	26.23	40.75	44.89	62.23	68.26
10	22.19	22.95	7.86	8.23	6.73	7.58	19.36	22.67	16.02	19.35
10 ^{1/2}	12.95	10	3.67	2.73	3	2.56	9.64	8.11	6.71	5.81
1	10.54	6.5	2.81	1.56	2.19	1.42	7.45	4.71	4.9	3.19
0.1	10.6	4.38	2.87	0.99	2.15	0.99	7.35	3.17	4.8	2.17
0.01	8.62	4.22	2.37	0.96	1.69	0.91	5.93	2.97	3.75	1.97
0.001	9.76	5.06	2.62	1.22	2	1.13	6.85	3.72	4.46	2.49
0.0001	10.08	6.19	2.72	1.55	2.15	1.45	7.22	4.76	4.78	3.24

Examples of ESEM that are <60% of the ESCR are bold.

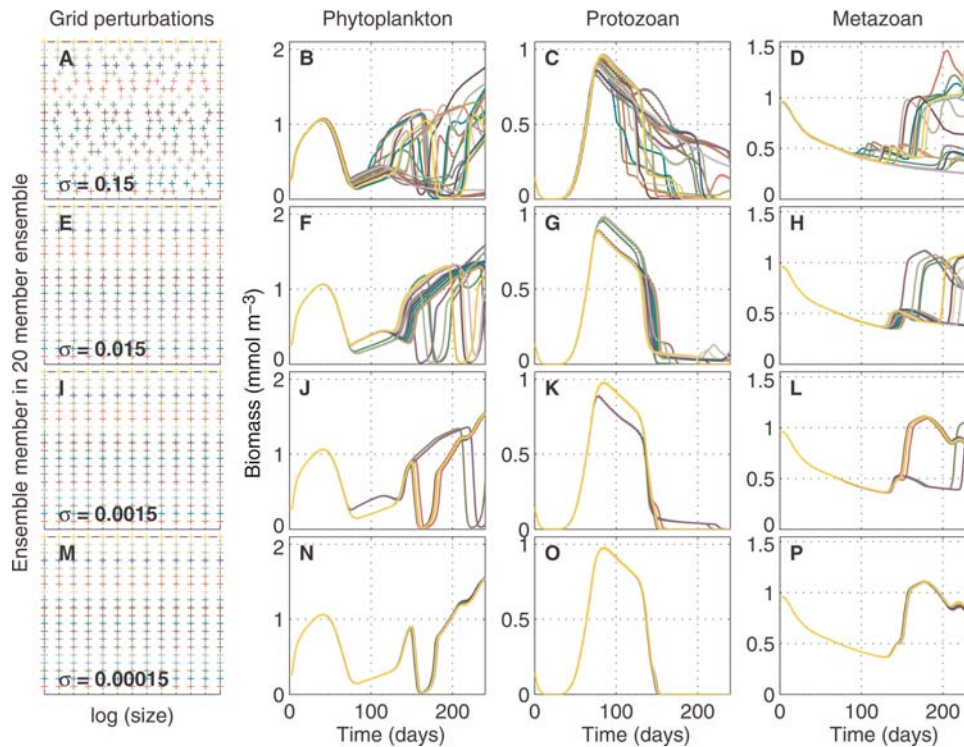


Fig. 7. Sensitivity to size-class distribution. The mean body weight at which size-class are solved is perturbed using a uniform random distribution from the unperturbed size-distribution with a standard deviation of 0.15 (A–D), 0.015 (E–H), 0.0015 (I–L) and 0.00015 (M–P). Panels (A), (E), (I) and (M) show the perturbed grid for protozoans for each of member (a row) of the 20 member ensembles (giving a total of 20 rows per panel). The remaining panels show the sum of biomass of the phytoplankton, protozoan and metazoan groups for each trajectory in the ensemble. A colour version is available in the Supplementary Data.

mean body weight. For the ensembles undertaken, the stagger of the grid can be seen in Fig. 7A, E, I, M, respectively. The stagger of the grid for the 20 ensemble members is obvious for the $\sigma = 0.15$ ensemble (Fig. 7A), and just perceptible for the $\sigma = 0.015$ ensemble (Fig. 7E). The stagger in the $\sigma = 0.0015$ and 0.00015 ensembles is vanishingly small, and not visible in Fig. 7I and M, respectively. For the $\sigma = 0.15$, 0.015 , 0.0015 and 0.00015 ensembles, the mean numbers of changes in predator–prey links are 32 ± 4 , 2.4 ± 1.1 , 0.1 ± 0.3 (i.e. two of the 20 members had one change) and no changes, respectively. As an example of the effect of grid perturbations on physiological rates of individual size-classes, the maximum growth rates of phytoplankton size-classes with an ESR of $2.7 \mu\text{m}$ for $\sigma = 0.15$, 0.015 , 0.0015 and 0.00015 ensembles are on average changed by 0.05 , 0.004 , 0.0005 and 0.00004 day^{-1} , respectively.

For the $\sigma = 0.00015$ ensemble (Fig. 7M–P), divergence is only visible after 200 days. The divergence is a result of changes in physiological and ecological rates of individual size-classes only and is smaller than found for even the smallest initial condition perturbations above. For the 0.0015 ensemble, two members diverge

at around 80 days, while the remainder have only slightly greater divergence than the $\sigma = 0.00015$ ensemble. The two divergent members are the only cases in the 0.0015 ensemble that had random grid perturbations that led to a change in predator–prey links.

The four ensembles show that increasing the grid perturbations causes larger divergence earlier, much in the same way that coarser model configurations diverge earlier. Perturbations with a standard deviation $\sigma = 0.15$ of the mean body weight are less than either the natural variability in size of any particular population of unicellular plankton, or our ability to measure the mean size of a population. The $\sigma = 0.15$ ensemble suggests that single simulations of greater than 80 days of the 62 size-class configuration have limited predictive capabilities.

DISCUSSION

Model simplifications and predictability

As with all numerical ecosystem models, the size-resolved model is an abstraction of the

natural system. Compared with other modelling approaches commonly used, the size-resolved model does not consider functional groups within the phytoplankton and zooplankton (Le Quere *et al.*, 2005), simple behaviours such as vertical migration (Ross and Sharples, 2007), three-dimensional circulation (Baird *et al.*, 2006) or traits within functional groups (Follows *et al.*, 2007). Beyond these considerations, Armstrong (Armstrong, 1999) discussed potentially stabilizing processes that are typically not included in size-based models. Ecological processes Armstrong identified (his list was not meant to be exhaustive) included production of resting stages, mixotrophy and putative killing of diatoms by flagellate bacterivores. As Armstrong (Armstrong, 1999) points out, simple models can have unstable behaviours that, perhaps surprisingly, are damped or eliminated in more complex models.

Another important simplification in the size-resolved modelling approach is the assumption that size-distribution of mean body weight can be dissected into every smaller size-classes, as demonstrated by the 489 size-class configuration. There is evidence to suggest that natural systems are often composed of a small number of discrete size-classes (Schwinghamer, 1981). An enclosed lake with a small number of species is one such example, while the open ocean tends towards less discrete size-classes (Sheldon *et al.*, 1972). This issue is discussed at length in Baird and Suthers (Baird and Suthers, 2010).

For this paper, the most important simplifications are those that affect the divergence of an ecosystem state. The lesson from Lorenz's work is that divergence can be estimated if the most relevant processes are considered. Present weather models contain many complicated atmospheric chemistry processes that were not part of Lorenz's convection model, but Lorenz's conclusions on limits to prediction were nevertheless useful. In the size-resolved model, it is predator–prey interactions that most affect divergence. On this basis, simplifications of the food-web, such as the omission of mixotrophy discussed by Armstrong (Armstrong, 1999), are the most likely to affect the generality of the conclusions of this study. Thus, this study provides cautionary findings for the application of other size-based models, and indeed any complex food-web ecosystem models.

In pelagic ecosystems, the dominant non-linear processes are predator–prey interactions, with size being a first-order determinant of their rates. Thus, as long as the predator–prey equations, allometric coefficients and initial conditions are reasonable representations of the pelagic ecosystems, divergence in the size-resolved model trajectories due to tiny grid and initial condition

perturbations can be used as measures of inherent limits to prediction that are unlikely to be overcome through improved understanding, observations, numerical techniques or computing power.

Sensitivity to magnitude of initial perturbation

Lorenz (Lorenz, 1969) first investigated the sensitivity of an atmospheric model to varying magnitudes of initial condition perturbations. He found at small perturbations, the spread of model trajectories became independent of the magnitude of initial condition perturbation. He concluded that a deterministic system that behaved in this manner would be observationally indistinguishable from a stochastic one. In practice, this behaviour implies there is no accuracy of initial conditions that would increase predictive skill beyond some time. This provides the limit of the predictability of the model given near-perfect initial condition estimates.

The reason that there is similar spread of ensembles with small, but different, magnitudes of initial perturbations was explained by Lorenz (Lorenz, 1969) for the atmosphere and hypothesized to apply to plankton by Platt *et al.* (Platt *et al.*, 1977). Consider the atmosphere. At the smallest temporal and spatial scales, differences between two states may double in 5 min, while large-scale differences may take 5 days to double. Reducing the difference between two almost identical simulations by a factor of 2 reduces the time to get to the original difference by 5 min. Thus, halving an already small initial condition error increases the prediction time by 5 min, not 5 days. In the pelagic ecosystem, the doubling time of large scale differences in state is say 0.21 day^{-1} (the Lyapunov exponent calculated earlier). The fastest growth rates of individual plankton have doubling times of say 2 day^{-1} . Grazing could exceed the fastest rate of growth, and does for larger organisms, but does not for the fastest growing organism (Fig. 6). So a reasonable doubling rate for small differences in model state is 2 day^{-1} . Thus, using a rate of growth of errors of 2 day^{-1} , a reduction in errors of an order of magnitude (as shown in Fig. 4) only increases the prediction time by $(\ln 10)/2 = 1.15$ days, which becomes indiscernible at 50 days.

Figure 4 demonstrates that for an initial spread of less than $10^{-8} \text{ mol N m}^{-3}$, the spread at 40 days is independent of the magnitude of the perturbation of initial conditions. To put this into perspective, for a $2 \text{ km} \times 2 \text{ km} \times 50 \text{ m}$ grid box [typical of a regional ocean application in the oligotrophic ocean such as that off southeast Australia (Baird *et al.*, 2006)], $10^{-8} \text{ mol N m}^{-3}$ represents one additional 1 kg fish (in a total population of

1000 at that size-class), or 10^{15} individuals of the $0.32\ \mu\text{m}$ radius phytoplankton, representative of *Prochlorococcus*. An analog of the butterfly effect (Hilborn, 2004) in the atmospheric sciences can be made: the addition of one *Prochlorococcus* individual in the model will “cause” as large a divergence in the trajectories after 40 days as one less fish caught by an angler.

Ensemble prediction of pelagic ecosystems

Ensemble prediction systems (EPSs) in weather forecasting have been developed to overcome a component of the inherent limits to prediction caused by initial condition errors in single simulation predictions (Palmer and Hagedorn, 2006). The measures of ensemble spread can be used to assess whether such systems will improve predictability of the size-resolved model. Table I showed that for a particular period of the simulation and for initial perturbations of 1% or less, the ESEM of the model was less than the ESCR. That is, the error between a range of feasible model trajectories was less using an ensemble mean than the control run. In these cases, EPSs have advantages over single run simulations. For initial condition perturbations of 10% or more, ESCR and ESEM are of a similar magnitude, suggesting that the ensemble mean is no better at minimizing the effect of initial condition errors than a single control run, and an EPS will not increase predictive skill.

The change in usefulness of EPSs at between 1 and 10% occurs at the same magnitude as the shift between an independence and dependence of trajectory spread on the magnitude of initial condition perturbations. An EPS system is useful in improving skill when it is the inherent non-linearities of the model that determine the spread of trajectories. But when the trajectory divergence is dependent on the magnitude of the initial condition perturbation, an EPS is less useful.

It is unlikely that initial conditions for a size-resolved pelagic ecosystem model will be known to a greater than 1% accuracy, so it is unlikely that an EPS system will in practice overcome an inherent limit to prediction in pelagic ecosystems. However, EPSs have been developed with more sophisticated initial condition perturbation schemes than used in this study, such as the singular vectors used by the European Centre for Medium-Range Weather Forecasts or the bred vectors of the National Centre for Environmental Prediction (Buizza, 2006). Additionally, at different locations in the phase space, the model’s predictive behaviour will change, much like weather being more predictable during stable than unstable conditions. Nonetheless, it is most likely that a month-time scale predictive skill of the size-resolved model will not be improved by an EPS.

While an EPS may not improve the predictive skill of a forecast, it does allow a forecast of the skill of a forecast. In meteorological modelling applications, this often justifies the use of an EPS. In this paper, it has been shown how an ensemble has improved our understanding of model behaviour for the case of a $2.7\ \mu\text{m}$ ESR phytoplankton bloom after 120 days. Regular implementation of an EPS system will allow for similar understanding for whatever system state is simulated.

Effect of long-term steady states and strong physical forcings on predictability

The present study has focused on the short-term behaviour of the size-resolved model with weak forcing beginning from an initial state with equal biomass in all geometrically increasing size-classes (a NBSS of -1); a reasonable but non-steady state for the system. To put these results in context, a further ensemble of the size-resolved model has been run with strong physical forcing for 200 years. The intention is not to exhaustively analyse the new results, but use them to highlight behaviour in the weakly forced short-duration runs.

A 20-member ensemble of the 17 size-class configuration [Baird and Suthers (2007), computing resources requiring the coarser resolution] was run for 200 years, with annual cycles of surface wind, solar forcing and ocean state typical of the Southern Ocean south of Tasmania (Fig. 8). Ensemble members were perturbed using initial conditions described in the Experimental Design.

The 20 members follow similar trajectories for about 10 years before visibly diverging (Fig. 8). For the next 140 years, periods of divergence and convergence occurred. Regime changes are also evident at ~ 100 and ~ 150 years as some size-classes reach vanishingly small biomass, and the longer time-scales of larger size-classes have a top down effect. After 150 years, consistent seasonal oscillations are evident, although the exact oscillation still depends on the initial conditions.

Although this paper has highlighted limits to predictability of instantaneous states in short time periods, there remains oscillatory behaviour that is predictable on longer time scales. Interestingly, divergence and convergence of ensemble members occurs through an annual cycle even though a stable oscillation has been reached. Divergence begins in spring and continues through until autumn. During winter, the ensemble members converge. As with the weather/climate system, it is clear there are different prediction time-scales for instantaneous states and mean conditions.

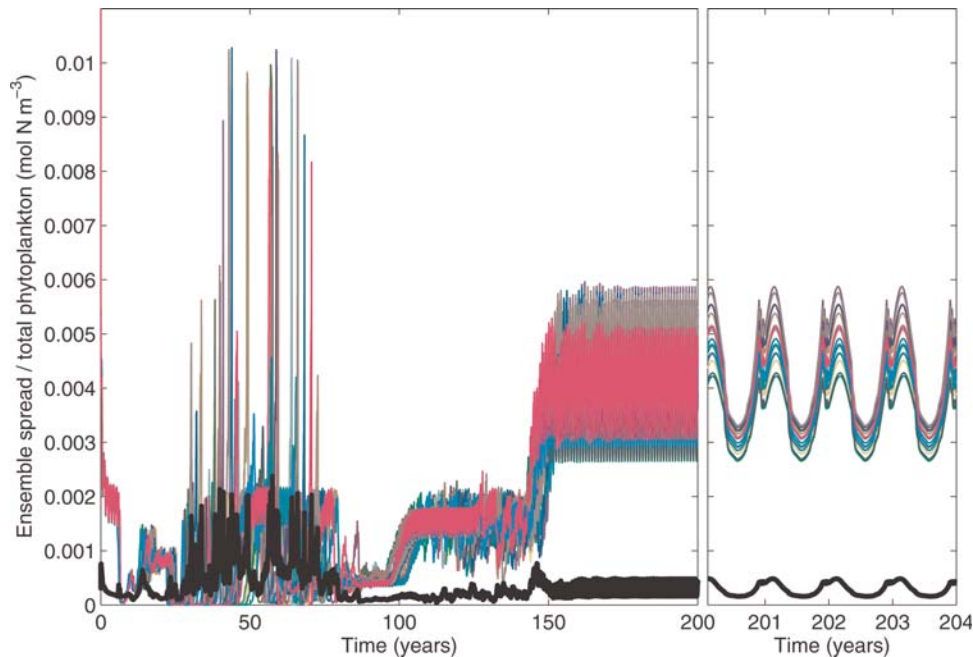


Fig. 8. Ensemble spread and phytoplankton biomass for 20 members of a 200-year ensemble simulation of the 17 size-class configuration with strong seasonal forcing. The 20 members are differentiated by small perturbations in initial conditions. The black line plots ensemble spread calculated from all biological state variables. The grey (colour in the Supplementary Data) lines are total phytoplankton biomass. The right panel focuses on years 200–204 when a stable annual oscillation has been reached.

Other studies of dynamical behaviour of size-based plankton models

The first published comprehensive size-based plankton model (Moloney and Field, 1991) included numerical experiments to investigate the effect of initial conditions on simulations. The study looked for changes in ecosystem behaviour due to significant initial condition perturbations, rather than divergence of simulations with small perturbations. The Moloney and Field (Moloney and Field, 1991) experiments highlighted the importance of seed populations in model simulations. Armstrong (Armstrong, 1999) furthered the work of Moloney and Field (Moloney and Field, 1991) by considering the effects of model structure on the stability of size-based plankton models. Initially Armstrong (Armstrong, 1999) investigated the Moloney and Field (Moloney and Field, 1991) structure of couplets of phytoplankton and grazers, which he found to be relatively unstable. Armstrong (Armstrong, 1999) then considered one herbivore grazing on a number of phytoplankton. The distribution of grazing pressure is a stabilizing influence, allowing realistic size-spectra of phytoplankton to emerge. The size-resolving model presented here has distributed grazing for both phytoplankton and zooplankton and appears to be more stable than the Moloney and Field (Moloney and Field, 1991) model that has very fast predator–prey oscillations.

Although these studies are not directly comparable to the results presented in this paper, they provide a reminder of the range of dynamical phenomena that can be investigated in ecosystem models, from initial condition and model structure sensitivity considered here, to sensitivity to forcing functions, parameter values and functional forms. While this analysis has focused on divergence from an initial state, other analyses could consider changes in steady state, limit cycles or attractors, or the transition between these global behaviours. The focus in this paper has been to identify, through numerical experiments, inherent limits to prediction of instantaneous states. Further work should be undertaken to identify long-term behaviour of the size-resolved model for a range of forcing functions.

Summary

Ensemble simulations of a size-resolved pelagic ecosystem model have been undertaken to better understand model behaviour, and estimate inherent limits to the prediction of instantaneous states of a size-based representation of a pelagic ecosystem. Ensembles have been formulated with identical model equations and parameter values, with tiny perturbations in the discretization of size-classes and the precision of the estimate of

initial conditions. These variations are sufficiently small that no foreseeable improvements in the specification of size-classes or initial conditions could distinguish which ensemble members are a better forecast. Thus divergence in ensemble members is a measure of an inherent limit to prediction. For the size-resolved model, the ensembles with small variations in initial conditions illustrate that after 50 days, no improvements of initial state beyond a 1% error improves model predictions. The ensemble with $\sigma = 0.15$ perturbations in the distribution of size-classes diverges significantly after 80 days, illustrating a second limit to prediction. This work provides a cautionary warning for size-based models of pelagic ecosystems. Propagation of initial condition errors and divergence of configurations with small differences in plankton size suggest that prediction of instantaneous states of the size-distribution of pelagic ecosystem is possible for a month or two, but may not be accurate for longer.

SUPPLEMENTARY DATA

Supplementary data can be found online at <http://plankt.oxfordjournals.org>.

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