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Simulating plankton ecosystems by the Lagrangian Ensemble method

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SUMMARY

Understanding the plankton ecosystem in the ocean requires detailed demographic analysis. It is impossible to sample the ocean adequately for such analysis, but progress can be made by analysing data sets generated by mathematical models provided they realistically simulate the ecosystem. The Lagrangian Ensemble method is well suited to demographic studies because it generates large data sets containing complete information on all the families living in the simulated ecosystem. It provides audit trails of individual families for unambiguous analysis of mechanisms responsible for the simulated changes in community and environment. Recent papers based on the Lagrangian Ensemble method are reviewed.

1. INTRODUCTION

Biological production in the open ocean starts with tiny planktonic plants with densities so close to seawater the Archimedes force nearly balances their weight. Primary production per unit mass is high because phytoplankton do not need to invest in structures to raise them into the sunlight. Buoyancy allows the possibility of floating freely rather than being fixed to the seabed; they sink so slowly through the water, that they can be kept in the photic zone by turbulence or, in some species, by buoyancy control or modest swimming. But even the faster phytoplankton swim at only a few metres per day, so they are unable to change their environment significantly in one year by swimming horizontally, because the horizontal correlation scale of environmental gradients is seldom less than one kilometre for fluid dynamical reasons (Woods 1988). The vertical correlation scale of environmental variables is much shorter (metres to tens of metres) so a plankton experiences great changes in its ambient environment[†] when it moves vertically. That difference between the horizontal and vertical defines the concept of plankton. One-dimensional models capture the key processes of plankton ecology.

Being planktonic offers substantial benefits, not

least being the freedom to spread out from the narrow coastal strip where sunlight reaches the sea floor to populate the surface waters of the deep ocean, exploit sunlight falling on two thirds of the planet, and to support abyssal life with detritus from that euphotic zone. But there are costs: survival is tricky in the open ocean, many phytoplankton die when they sink into the dark abyss. Plankton have evolved functions that allow them to maintain a significant population in the seasonal boundary layer[‡]. The theorist must identify those functions and explain how they operate in the changing physical and chemical environment, in an interacting community of many plankton species.

The first scientific problem is to explain how phytoplankton survive in the open ocean, despite the fact that they sink slowly through the water. The solution must lie in the turbulence of the surface mixing layer, which can keep a viable population of phytoplankton in the euphotic zone provided their reproduction is sufficient to compensate for losses to grazing and gravity. Converting that paradigm into a quantitative theory requires demographic analysis of plankton populations. Sampling the ocean does not provide a sufficient data base for such quantitative analysis[§], so the literature is vague about the key ecological issues of survival, natural selection and adaptation.

Today we have a new tool to unblock that barrier to progress: realistic mathematical simulation of plankton ecosystems by the Lagrangian Ensemble (LE) method, which provides a consistent approach to plankton demography. The LE method is still relatively new and subject to continual refinement, but it has already made significant contributions to plankton ecology. This brief progress report will indicate the scope of the method by summarizing some recent

[†] The ambient environment of an organism is the set of values that the environmental fields have at its position at each moment in time.

[‡] The seasonal boundary layer extends from the sea surface down to the annual maximum depth of the mixed layer, which occurs at the end of the winter cooling season. The average depth of the SBL is about 100 m, but it varies from less than half in the tropics to more than 1 km in parts of the northeast Atlantic.

[§] The environment is so unrealistic in artificial enclosures in the sea or in the laboratory that they cannot address the demographic problems of plankton survival in the open ocean.

Table 1. *Variables in the LE'93 model*

environment	variable
physical	
water	light (27 spectral bands), turbulence, temperature
air	atmospheric pCO ₂ , temperature, monthly climate, ozone, dust
sunlight	solar elevation
chemical	
dissolved	nitrate, ammonium, inorganic carbon, pCO ₂
particulate	detritus (dead plankton), faecal pellets
biological	
explicit	phytoplankton (diatoms), herbivores (copepods)
implicit	carnivores, bacteria

results reported in scientific papers, including simulation of interaction between plankton and the changing field of turbulence; the seasonal cycle; interaction with the greenhouse effect; and diatom demography in winter.

2. THE LAGRANGIAN ENSEMBLE METHOD

All plankton ecology models are based on a set of variables (table 1) which describe the state of the ecosystem at each time step of the integration, and a set of equations that relate their values at consecutive time steps (listed in Woods & Barkmann 1993*a*). The special feature of the Lagrangian Ensemble method lies in the method of integrating those equations. The model is structured in terms of families^{||} of plankton, which follow trajectories through the environment, which is described in terms of values at each of an array of locations fixed in space (normally one metre cubes).

The physiological equations are integrated separately for each family describing its growth in response to its ambient environment. The location of each family is changed at each time step by behavioural equations based on the ambient fluid motion and the motion through the water of one of the many plankters present in the family. Because each family follows a unique trajectory through the simulated ocean, it samples the environmental fields differently from its neighbours. The biological equations include terms for adaptation to the environment, so families arriving at the same location by different routes are differently adapted and respond differently to the same ambient environment. This adaptative diversity

^{||} The computational cost depends on the number of independent trajectories used to represent the diversity in plankton growth and behaviour. It is too costly to allocate a separate trajectory to every plankter, so they are grouped into families, each with a unique trajectory. Each family comprises a set of identical plankters, which (because they follow the same trajectory and therefore sample the environment identically) grow identically and experience simultaneous cell division. All plankters in one family have the same dates of birth and death. When they reproduce, their family separates into two families with independent trajectories.

has important demographic consequences (Woods & Barkmann 1993*b*).

The environmental variables are updated at each time step according to equations based on the current state of the physical, chemical and biological environment. The biological environment is computed statistically from the ensemble of plankton families present in each one metre cube. This allows explicit treatment of the biological feedback to the physical, chemical and biological environment. In its present configuration the LE method does not feature Lagrangian interactions, i.e. predator-prey encounters between individual families.

As in all ecological models, the progress of an integration is sensitive to the values chosen for adjustable parameters incorporated in the model equations. The selection of physical parameters is based on measurements made at sea and in the laboratory as reported in the scientific literature (e.g. Kirk (1983) for solar radiation and Federov & Ginsburg (1992) for turbulence). The choice of biological parameters can be made in the same way (e.g. from sources cited in monographs by: Morris 1980; Corner & O'Hara 1986; Jumars 1993). Fasham (1993) has considered the validity of a single set of biological parameters over a wide geographical range of environments, and Sommer (1989) has considered how best to design parameter sets to simulate seasonal succession. Although the state of the art features fixed parameter sets (and they are used in all the LE papers cited here) steps are being taken to address this restriction to the credibility of plankton ecology models, either by initializing a model integration with several plankton guilds, each defined by its own parameter set, or by including the possibility of evolution through mutation of parameter values and natural selection. It is too early to decide which of the various approaches to this central problem will prove most effective. However, discrimination between alternative methods will depend on the ability to diagnose demographic differences, which the LE method permits for the first time.

Demographic analysis

Demographic diagnosis of the ecosystems simulated by the LE method is based on data sets recording the states of the environment and of every family of plankton every half hour for several years. Such a data set typically contains a few billion words of data per simulated year. The first step towards demographic analysis is taken by generating a new data set (called the Parish Register) with chronological entries for each event that changed the population of plankton in every family. For diatoms they include: births (cell division), deaths by natural mortality (which kills the whole family) or by predation (which thins down the number of plankton in the family), also the break up of a family to pursue independent trajectories, and the marriage of two families to follow the same trajectory. This Parish Register is complete, so demographic analysis does not require assumptions about the form of statistical distributions. Lythgoe (1993) has analysed a Parish Register to reveal the longevity of

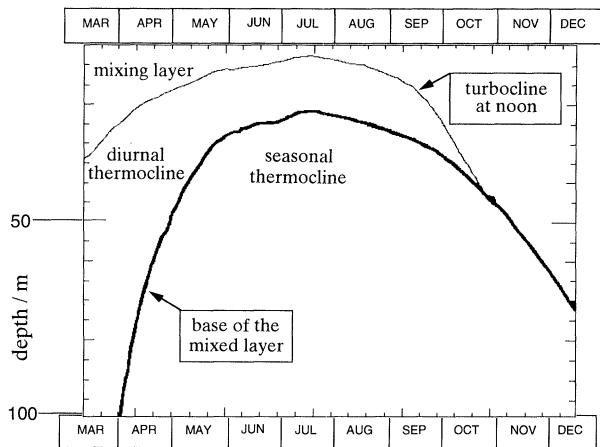


Figure 1. Seasonal variation of the daily maximum and minimum depths of the turbocline at the base of the mixed layer.

individual families and the seasonally varying life expectancy of individual diatoms. These products will be used to discriminate between different schemes for incorporating variable parameter sets into the biological equations.

3. RESULTS

The LE method is under continual development, but each year one version of the code serves as the basis for a series of models. The results presented in this symposium used the LE'93 version, which contains the variables in table 1 and the equations and fixed parameters in Woods & Barkmann (1993a). Within those constraints it has proved possible to simulate the gross features of the upper ocean plankton environment, including diurnal and seasonal changes in the vertical distribution of phytoplankton and zooplankton, and to relate those to changes in the depth of the mixed layer and the concentration of nutrients and other environmental fields.

(a) Audit trails

The Langarian Ensemble method makes it possible to go beyond diagnosing the simulated ecosystem in terms of mere correlations between changes in the biological, physical and chemical fields. It allows detailed analysis in terms of the audit trails of individual families of plankton, whose trajectories pass through critical locations in space and time as the ecosystem evolves. Audit trail diagnosis is a powerful tool for resolving uncertainty in the cause of ecological events. For example, Woods & Barkmann (1993b) have used it to re-interpret the classical concepts of 'critical depth' and 'compensation depth' used by Sverdrup (1953) to predict the spring bloom. They showed how the seasonal variation of compensation depth is controlled by a statistical difference between the photo-adaptation of phytoplankton in the mixed layer and the seasonal thermocline.

Earlier, Woods & Onken (1953) had shown that the rate of primary production is influenced by the changes in trajectory during the day when turbulence

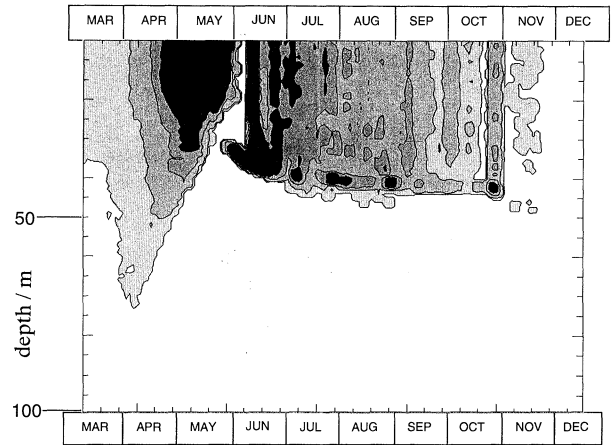


Figure 2. Seasonal variation of phytoplankton growth rate. Contours at 0.01, 0.1, 0.5, 1, 2, 5 $\text{mg C m}^{-3} \text{d}^{-1}$.

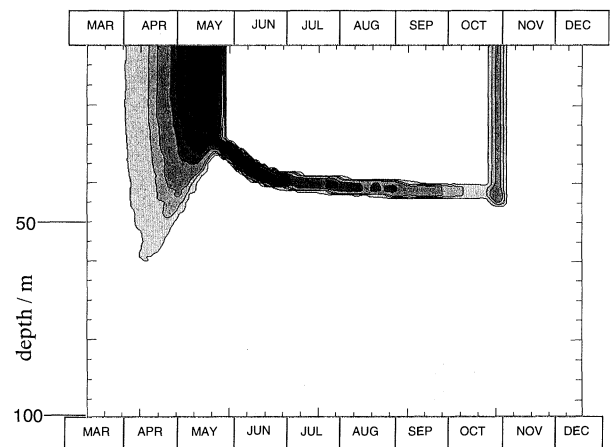


Figure 3. Seasonal variation of nitrate uptake by phytoplankton. Contours at 1, 5, 10, 30, 50 $\text{mm N m}^{-3} \text{d}^{-1}$.

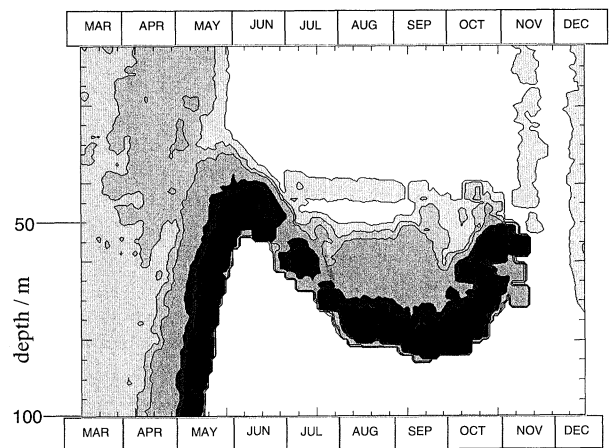


Figure 4. Seasonal variation of natural mortality in phytoplankton. Contours at 1, 5, 10, 30, 50, 100% per day.

is suppressed by solar heating. This diurnal effect, which leads to much of the phytoplankton population passing the hours of daylight in laminar flow at a fixed depth, has important consequences for the demography of diatoms in winter. Woods & Barkmann (1993b) showed that the population begins to grow in February because the diurnal thermocline has already shoaled to 50 m, even though the mixed layer is still deepening.

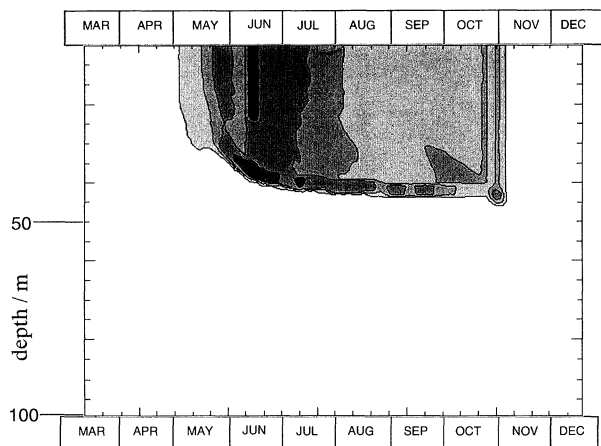


Figure 5. Seasonal variation of ammonium uptake. Contours at 1, 5, 10, 30, 50, 100 $\mu\text{M N m}^{-3} \text{d}^{-1}$.

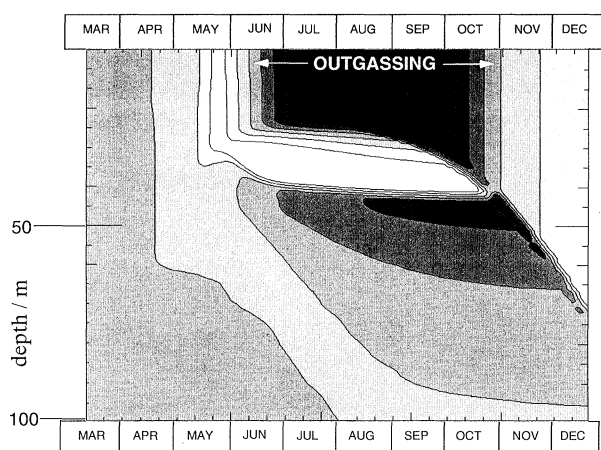


Figure 6. Seasonal variation of carbon dioxide partial pressure. Contours at 0.32, 0.33, 0.34, 0.35, 0.36, 0.37 millibar.

(b) *The seasonal cycle*

One of the essential capabilities of any plankton ecology model is its ability to simulate realistically the seasonal cycle of the upper ocean environment, including the biomass in each plankton guild. The best documented features are the spring bloom and the subsequent exhaustion of nitrogen in the mixed layer (summer oligotrophy), leading to the deep chlorophyll maximum. The ability of the LE'93 model to simulate the seasonal cycle off the Azores is illustrated in figures 1–6[†]. Earlier, Wolf & Woods (1991) had used LE'89 to analyse the onset of summer oligotrophy and the formation of the deep chlorophyll maximum. They investigated the impact of upwelling on the spring bloom and showed that when upwelling is slower than the sinking speed of the phytoplankton (1 m d^{-1} in the model) the rate of primary production increases in the deep chlorophyll maximum (as observed by Strass (1992)), but when it is faster, upwelling drives the nutricline up into the mixed layer producing a summer bloom.

[†] We plan to publish a report on LE'93 including a CD-ROM containing all fifty of the colour figures used to illustrate our talk at the Discussion Meeting.

(c) *Climate change*

Woods & Barkmann (1993a) used LE'93 to investigate the sensitivity of the flux of detritus into the deep ocean (the biological pump) to an increasing atmospheric IR flux. They concluded that raising the IR by 5 W m^{-2} reduces the biological pump by 10%, reducing the influx of carbon dioxide from the atmosphere by a corresponding amount, and accelerating global climate change due to the greenhouse effect.

4. THE FUTURE

The Lagrangian Ensemble method has now been developed to the point where it has a stable code capable of serving all aspects of theoretical plankton ecology and offers significant advantages over classical methods which do not resolve the trajectories of individual plankton families (Platt *et al.* 1994). Integrations of LE'93 take a few hours per simulated year on a Sun Sparc2 workstation. It is now being incorporated into a user-friendly plankton modeller's workbench, which will make available the full capability of the LE method without the need for computer programming.

Work has started on the LE'94 version of the model which will feature several guilds of plankton (defined by parameter sets), and mutation of biological parameters on cell division. The aim will be to develop a capability to address seasonal succession of guilds and biogeography.

5. CONCLUSION

The Lagrangian Ensemble method has been demonstrated to simulate the gross features of the upper ocean plankton quite realistically. It has sufficient sensitivity to reveal subtle but important responses to climate change. It supports audit trails of individual families of plankton, which allow unambiguous diagnosis of diurnal, seasonal and other changes in the simulated ecosystem in terms of mechanisms involving turbulence and other environmental variables. The large data set (gigawords per year) generated by an integration of an LE'93 model permit complete demographic diagnosis, an essential tool for investigating the inherent chaotic nature of the ecosystem, and seasonal succession and geographical distributions.

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