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Stability and predictability of a virtual plankton ecosystem created with an individual-based model

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Abstract

This paper establishes the predictability of a one-dimensional virtual plankton ecosystem created by Lagrangian Ensemble integration of an individual-based model. It is based on numerical experiments for a scenario, in which the surface fluxes have stationary annual cycles, and the annual surface heat budget is in balance, i.e. solar heating equals cooling to the atmosphere. Under these conditions, the virtual ecosystem also followed a stationary annual cycle. We investigate the stability of this ecosystem by studying the statistics of multi-year simulations of the ecosystem in a virtual mesocosm moored off the Azores. The integrations were initialised by a first guess at the state of the ecosystem at the end of the cooling season, when the mixed layer was approaching the annual maximum depth. The virtual ecosystem quickly adjusted to a stable attractor, in which the inter-annual variation was only a few percent of the multi-year mean. This inter-annual variation was due to random displacement of individual plankters by turbulence in the mixed layer. The inter-annual variance is nearly, but not exactly ergodic; the deviation is due to inheritance of zooplankton weight through lineages.

The virtual ecosystem is independent of initial conditions: that is the proof of stability. The legacy of initialisation error decays within three years. The form of the attractor depends on three factors: the specification of the ecosystem model, the resource level (nutrients), and the annual cycle of external forcing. Sensitivity studies spanning the full range of model parameters and resource levels demonstrate that the virtual ecosystem is globally stable. In extreme cases the zooplankton becomes extinct during the simulation; the attractor adjusts gracefully to this new regime, without the emergence of vacillation or a strange attractor that would signal instability. At high resource levels, some of the zooplankton produce two generations per year (as was observed by Marshall and Orr [Marshall, S. M., and Orr, A. P. (1955). *The biology of a marine copepod*. Edinburgh: Oliver and Boyd. 188 pp.]; again the attractor adjusts gracefully to the new regime. Ocean circulation does not disrupt the stability of the virtual ecosystem. This is demonstrated by a

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numerical experiment in which the virtual ecosystem drifts with the mean circulation on a five-year cycle, following a track in the Sargasso Sea that penetrates deep into the zones of annual heating and cooling. The legacy of initialisation error decays within three cycles of the external forcing. Thereafter the ecosystem lies on a five-year geographically-lagrangian attractor. The stability of virtual ecosystems offers useful predictability with a good sign-to-noise ratio.

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1. Introduction

There has been speculation in the biological oceanography community about the inherent stability of the plankton ecosystem (Berryman & Millstein, 1989). Understanding the stability is important because it determines the limits to predictability. Prediction is needed for designing procedures to deal with a wide variety of problems in which plankton play a role. They include pollution, eutrophication, toxic algal blooms, fisheries, climate and human diseases from plankton. Predictability is normally established by mapping the boundary between stability and instability in mathematical simulations. To be useful, the methods used to create those simulations must not themselves introduce instability that does not occur in nature. The aim of our investigation was to learn more about the stability of plankton populations in models designed for such applications. We hoped to throw some light on whether the plankton ecosystem in the sea is inherently predictable on the time scales of those applications.

It is important to define what is meant by stability. Consider a simulated ecosystem with a small set of species and nutrients. If it is stable that ecosystem will always respond in the same way to external forcing. If it is unstable the response will exhibit fluctuations. The former is like a classical newtonian mechanism with clockwork reproducibility. The latter owes more to Poincaré's world, in which minute differences in the initial conditions produce large differences in the future state, with the result that the system has limited predictability. Originally it was assumed that such unpredictable variability was an attribute of complex systems, such as the weather. Later it was shown that instability can also arise in very simple models when their equations are non-linear. Theoretical ecologists noted that the simple Lotka–Volterra models used to describe predator–prey interactions contain non-linear equations. It was shown that when such models are integrated they describe populations that may be stable, or oscillate, or fluctuate irregularly, depending on the values of the model parameters. There is now a rich literature on such chaotic behaviour in simple models of ecosystems.

These discoveries have influenced expectations about the inherent predictability of the plankton ecosystem. The plankton ecosystem is “computationally complex”, a term used in information theory for an intrinsic property which does not depend on the algorithms used to compute the changing state of the system (Traub & Werschulz, 1998). Simple models of the plankton ecosystems use non-linear equations, making their simulated populations prone to instability. Another consideration is the analogy with fluid systems, which are inherently unstable, producing chaotic fluctuations called turbulence. Fluid instability can be simulated in models by the Navier–Stokes equation; it is caused by the non-linear advection terms. The suspicion that the natural plankton ecosystem may be inherently unstable rests on those arguments. We shall see later that they may be misleading.

Substantial variability does exist; indeed it is a hallmark of the plankton ecosystem. It produces inter-annual variation in time series such as those collected at Bermuda and Hawaii (Michaels & Knap, 1996) and in the Continuous Plankton Recorder (Godfray & Blythe, 1990). And it is seen as spatial patchiness in satellite images of ocean colour. That patchiness has a larger amplitude in biomass than can be attributed to redistribution by the mesoscale turbulence, so it must involve amplification by biological processes.

However, that does not mean the ecosystem is inherently unstable: it might be responding stably to chaotic forcing. The ecosystem is driven by surface fluxes, which are characterised by regular astronomical cycles modulated irregularly by weather in the atmosphere and its equivalent in the ocean, mesoscale turbulence comprising transient eddies and meandering mesoscale jets (Allen, Smeed, Nurser, Zhang, & Rixen, 2001; Rhines, 1979; Woods, 1988). Even if the wind were steady it would produce irregular fluctuations in the Ekman current profile (Woods, 2001). There exists no statistical test that can be applied to observations to reject the hypothesis that the ecosystem is intrinsically stable (Sugihara, Grenfell, & May, 1990; Taylor, Allen, & Clark, 2002). Nor do we know the signatures of a stable plankton ecosystem responding to chaotic forcing. The need to gain such knowledge motivated our analysis of a Virtual Ecosystem that is demonstrably stable.

1.1. Evidence from models

The notion that plankton populations are unstable, like turbulence in fluid flow, is reinforced by stability analysis of mathematical models. May (1976) discovered that simple predator–prey models are unstable under some circumstances, for example when the model parameters have certain values. This phenomenon has been studied extensively, and it now appears in textbooks of population ecology (e.g. Cushing, Costantino, Dennis, Desharnais, & Henson, 2003; Kot, 2001; McGlade, 1999; Mueller & Joshi, 2000). The mathematics of instability, which arises from non-linearity in the model equations, has also been extensively studied and features in undergraduate textbooks (e.g. Glendinning, 1994). The generic form of such models is as follows:

$$dx/dt = x(a + a_1x + b_1y), \quad dy/dt = y(b + b_2x + a_2y),$$

where x and y are the biomass concentrations of the predator and prey populations. Integrating these simple Lotka–Volterra models can produce populations that are stable, or vacillating or chaotic, depending on the values of the model parameters. In the unstable regimes, simulations are sensitive to initial conditions.

The simplest model of the plankton ecosystem is the classical food chain (Cushing, 1995), which features one dissolved nutrient (N , usually nitrogen), one phytoplankton population (P , usually diatoms), one herbivorous zooplankton population (Z , usually calanoid copepods) that graze on the phytoplankton, and detritus (D , for dead plankton and faecal pellets). The model includes a trophic closure term in which zooplankton mortality often varies as Z^2 (Steele & Henderson, 1995). Diatoms and copepods are the most common plankton in the sea. Simple NPZD models exhibit instability of the kind discovered by May (1976); see, for example, Ascioti, Beltrami, Carroll, & Wirick (1993), Edwards & Brindley (1996, 1999), Truscott & Brindley (1994). The simulated plankton populations are stable for some values of the predation parameters, while for others they vacillate or become chaotic. On this evidence Scheffer (1991) suggested that the natural plankton ecosystem is inherently unstable.

Such models are described as simple because they describe changes in the populations without biofeedback to the environment. They do not contain sufficient information to serve as a basis for useful prediction. They may have heuristic value, unless their lack of realism leads to misleading demographic behaviour. Complexity science provides a warning. The emergent properties of a complex system are often counterintuitive, especially when intuition has been honed on much simpler models (Casti, 1997; Johnson, 2001). Is this the case for simulations of the plankton ecosystem? We shall discuss this important question after presenting the results of our investigation.

To be useful the simulation must describe the changing spatial distribution of the ecosystem, and it must be based on a credible description of the biology. We can specify what should be featured in a NPZD model to make it yield simulations that satisfy most of the criteria for realism.²

² The main omission is lack of competition, so NPZD models cannot be used to model biodiversity.

1.2. What is needed to make an NPZD model realistic?

To be useful for such testing, the model equations should be consistent with the results of reproducible laboratory experiments; ideally they will be “primitive” equations. The method of integration must realistically mimic nature by treating the plankton as individual organisms with their growth, reproduction and behaviour. It must accurately calculate the biofeedback processes that are the quintessence of ecology. And it must be sufficiently realistic to justify verification by comparison with observations using the Ecological Turing Test (Woods, 2002, Chapt. 18), and to serve as a basis for prediction of some practical problem. Table 1 lists the main features that must be included in a NPZD model to make it useful. Progress has been made in recent years in developing models that incorporate many of these essential features (Totterdel, 1993; JGOFS; GLOBEC). In practice, however, limited available computer power has often meant that some features had to be omitted, the choice depending on the particular application.

1.3. Metamodels

The scientific literature contains many examples of one-dimensional NPZD modelling. They can be divided into three groups, based on the choice of metamodel, which determines the form of the equations used in the model and the method of integration. The specification for the *model* may be identical in simulations that use different metamodels. It may describe the same functions for the physical environment, for the chemicals (nutrients and pigments), and for the plankton, and the same biofeedback processes that bind them together. It may describe a limited plankton community comprising a few species or functional groups. And it may use the same scenario for exogenous properties, such as the ocean circulation, insolation and weather, which control the ecosystem. But choosing the metamodel constrains the form of the equations used to describe those functions, and the method of integration used to create the simulation. The resulting simulation will have a character that strongly reflects the metamodel. We shall see later (in the Discussion) that the stability of a virtual ecosystem may depend more on the choice of metamodel than on the specification of the model and scenario.

We identify three classes of metamodels: (1) Box, (2) Field, and (3) Lagrangian Ensemble. The Box metamodel has been used for many investigations of plankton ecosystem stability, but it does not concern us here because models based on the box do not satisfy the conditions for useful prediction listed in Table 1.

The Field metamodel can be used for prediction. It is distinguished by a simplifying assumption, namely that the biomass in each plankton population can be treated as a continuum field, rather than as a cloud of discrete organisms. This may seem reasonable, given the large number of plankters per millilitre. The spatial distribution of plankton biomass is described by values in each layer of a one-dimensional mesh. The biological equations describe how the biomass in each layer changes in response to the other ecosystem properties in that layer, including the biomasses of other species, which may be competitors, predators or prey. This is known as population-based modelling. The field metamodel uses eulerian integration to describe the changing state of the environment from one time step to the next. That is computationally much cheaper than the LE modelling described below. And it builds on the experience of eulerian modelling in physical oceanography. It is the metamodel used by most plankton ecologists.

Our investigation is based on the newer, Lagrangian Ensemble metamodel. It uses the technique of agent-based computation, which lies at the heart of complexity science (Casti, 1997), to compute the life histories of individual plankters. It is therefore an example of individual-based modelling (*ibm*), which has traditionally been heuristic. The LE metamodel goes further: it has been designed to satisfy

Table 1
Features needed for realistic simulation of the plankton ecosystem

Feature	Phenomenon	Effect
<i>I. External forcing</i>		
Astronomy	Solar radiation spectrum	Diurnal and seasonal variation
Atmosphere	Clouds, dust, gases (water, ozone, carbon dioxide)	Short-wave radiation; greenhouse effect
Sea surface	Wind waves and wind stress, air–sea fluxes of heat, water, gases	Light scattering; Ekman currents, turbulence buoyant convection carbon cycle
Ocean circulation	Large scale advection	Changing ambient climate ^a
Ocean mesoscale turbulence	Meandering jets with vortex stretching	Mesoscale patchiness
<i>II. Marine physics</i>		
Solar radiation spectrum	Seawater and plankton absorption and scattering (wavelength dependent)	Buoyant convection, mixed layer depth photosynthesis, vision,
Turbulence	Surface mixing layer (diurnal and annual cycles; response to weather)	Turbulent diffusion of seawater properties; random displacement of particles
Laminar flow	In the thermocline	Molecular diffusivities; plankton behaviour
Temperature	Plankton respiration	Response to ambient climate and bio-optical feedback; diurnal and seasonal environment
	Air–sea heat flux	
<i>III. Biology</i>		
Phytoplankton physiology	Photosynthesis, photo-adaptation, nutrient uptake, respiration	Natural mortality; cell division; C and N content of plankters
Behaviour	Sinking and swimming	Migration and foraging
Zooplankton predation	Growth, starvation, cannibalism	Reproduction, mortality
Structured growth and reproduction	Body weight, gestation	Breeding success, inheritance, behaviour
Biofeedback	Seawater turbidity; excretion and egestion	Solar radiation profile, nutrient regeneration
Microbial action	Extraction of nutrients from dead plankton and faecal pellets	Concentrations of dissolved inorganic carbon and nitrogen

^a “Ambient” means at the location of the object; in this case, the water column containing the ecosystem.

the requirements of Table 1 and therefore become a candidate for operational prediction. In order to do so it diagnoses the demography of whole populations and their biofeedback to the environment as emergent properties of the life histories of the individuals. The LE metamodel is documented in the accompanying paper (Woods, 2005), which illustrates emergent phenomena discussed in this paper.

1.4. *Previous investigations of stability*

Popova, Fasham, Osipov, & Ryabchenko (1997; hereafter abbreviated to PFOR) undertook a detailed stability analysis of simulations derived from the Field metamodel. They used an NPZD model that has a specification similar to ours. The vertical structure of the environment included a surface mixed layer the depth of which followed a prescribed stationary seasonal cycle. They found that the plankton populations exhibited inter-annual oscillations or chaotic fluctuations under certain circumstances, especially when the nutrient concentration was high. They drew attention to the implications of their results for the (lack of) predictability of such models. Their results echoed the instability found in NPZD Box models. They reinforced the expectation that the natural plankton ecosystem may be intrinsically unstable; especially in upwelling regions, where the nutrients are abundant. Such regions account for most of the pelagic production in the ocean (Longhurst, 1998).

1.5. *Hypothesis*

We start with the hypothesis that the natural plankton ecosystem is intrinsically stable. If that were true then the complex variability observed in space and time would be the rational response of the ecosystem to chaotic forcing by turbulence in the atmosphere and ocean. We believe that the view held by many biological oceanographers that the natural ecosystem is intrinsically unstable arose from false analogies with (a) continuum dynamics and (b) simple models of predator–prey interaction.

Modelling the plankton as though it were a continuum field can lead to instability. We suspect that this may be an artefact of the Field metamodel. Possible causes include excessive non-linearity of population-based predation equations (Caswell & Neubert, 1998), inability to simulate migration and foraging, unrealistic displacement of plankton by turbulence, neglect of structured reproduction, and the absence of intra-population variability (Lomnicki, 1988, 1999). We shall postpone consideration of these shortcomings until we have presented the results of our numerical experiments. They can be avoided by using the LE metamodel. Our hypothesis was that such individual-based modelling would be stable. This paper reports the results of numerical experiments designed to test that hypothesis.

1.6. *This paper*

The next section (Method) describes the particular conditions used to create Virtual Ecosystems (VEs) for our investigation of stability. It also introduces our research strategy and the criteria used to define stability. The following section (Results) assesses the stability of the VE in terms of those criteria. Those results are interpreted in terms of ecological processes revealed by the emergent properties of the VE. We show how the stability varies with model parameters, ambient climate and ocean circulation. Finally we show how the stability of the VE translates into predictability in a 50-year simulation of climate change. The next section (Discussion) is devoted to understanding the results, in particular why individual-based modelling produces simulations that are more stable than population-based modelling. The Conclusion looks forward to the application of LE modelling in operational oceanography. The accompanying paper (Woods, 2005) documents the procedures and products of Virtual Plankton Ecology.

2. Method

2.1. Strategy

We decided to test our hypothesis by examining the stability of a virtual ecosystem created by the LE metamodel, an NPZD model and a scenario in which the exogenous forcing had a stationary annual cycle. We expected that the plankton populations in this VE would also exhibit stationary annual cycles. If the VE were stable, those cycles would be independent of initial conditions. If it were not stable, then the plankton populations [$P(d, y)$, $Z(d, y)$] on a particular day of the year ($1 < d < 365$) would vary from year to year (y) outside narrow stochastic limits.

Stability is all or nothing in Virtual Ecosystems. All or none of the emergent properties, whether environmental or plankton variables, must have stable annual cycles. They are linked by biofeedback, which influences the environment in two ways: (1) through the optical properties of the water, which affect the solar heating profile and therefore the depth and temperature of the mixed layer; and (2) through the fluxes of particulate carbon and nitrogen into the seasonal thermocline, where they are remineralised by bacteria to affect the dissolved chemical environment of the euphotic zone later.

If the environment exhibits stationary annual cycles, then so must the plankton demography. Our aim was to create a scenario in which the physical environment was forced by a stationary annual cycle of exogenous variables.

2.2. Criteria for stability

There are two criteria for stability: (1) the inter-annual variances of $P(d, y)$ and $Z(d, y)$ are no larger than the demographic noise inherent in the simulation, and (2) after a period of adjustment, the populations settle to an attractor [$P_A(d)$, $Z_A(d)$], which is independent of the initial conditions [$P(60, 0)$, $Z(60, 0)$]. The time taken to adjust to the attractor provides a measure of the strength of the ecological stability.

2.3. Geographical location

Our numerical experiments required the emergent environment to follow a stationary annual cycle. We chose to simulate the environment found at a real location as closely as possible, given the design constraints of our NPZD model. For reasons that will soon become clear, we started with a site [41°N, 27°W], which lies just north of the Azores in the Atlantic Ocean (Fig. 1). This site offers a number of advantages over the rival site, Bermuda, used for monitoring the plankton ecosystem (Siegel, Karl, & Michaels, 2001). The greatest advantage for the present investigation is that it lies on the trans-Atlantic line where the annual surface heat budget (B) is in balance (i.e. solar heating equals heat loss to the atmosphere) according to climatologies based on ship observations (Bunker data analysed by Isemer & Hasse, 1987) or on global meteorological analysis (ERA data analysed by Garnier, Barnier, Siefridt, & Beranger (2000)). The Bunker and ERA lines for $B = 0$ pass the Azores within 100 km of each other. The contour of annual surface water balance also lies nearby (Wijffels, 2001). So, the net annual advective flux divergences of heat and fresh water (and therefore of seawater density) in the seasonal boundary layer are negligible at our chosen site (Large & Nurser, 2001). Furthermore, annual upwelling due to the divergence of Ekman transport is small (Isemer & Hasse, 1987). So, too, are the permanent geostrophic current, and the eddy kinetic energy (Fu, 2001). In summary, advection and geostrophic turbulence play a much smaller part in the environment of the euphotic zone at the Azores than they do at Bermuda, where they strongly influence the ecosystem (McGillicuddy & Robinson, 1997). For the purpose of our model we assume they are both zero at all depths in the seasonal boundary layer at our chosen a site. The seasonal boundary layer extends from the sea surface to the annual maximum depth of the mixed layer ($0 < z < H_{\max}$).

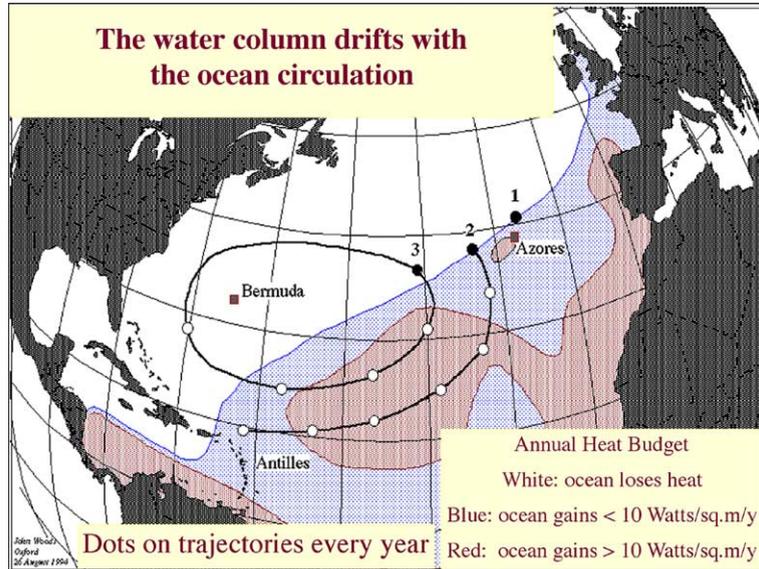


Fig. 1. Map showing the locations of Virtual Ecosystems used in this investigation: (1) water column fixed at 41°N, 27°W; (2) drifting from Azores to Antilles; (3) drifting around a closed five-year circuit.

Previous investigations (Woods & Barkmann, 1994) had provided a general knowledge of the diurnal and annual cycles in this Azores VE. The simulated ecosystem is contained in a virtual mesocosm, nominally one square kilometre cross-section and extending vertically from the sea surface to a depth of 500 m. This water column is either moored at a fixed location (Fig. 2) or allowed to drift barotropically with the mean flow derived from a circulation model (New et al., 1995). The VE in this mesocosm is controlled by initial conditions derived from the ambient ocean climate (from the NOAA world ocean atlas, Levitus, 1998), and boundary conditions from the ambient atmospheric climate (Garnier et al., 2000; Isemer & Hasse, 1987). The ambient climate comprises monthly mean values at intervals of one degree of latitude and longitude. The boundary condition file was created before each integration, by interpolating the climate to the geographical location of the water column at each half-hour time step of the planned simulation. The boundary conditions were used to compute sea surface fluxes of momentum, heat, water and carbon dioxide and solar radiation (from an astronomical model for solar elevation, and cloud cover).

2.4. Achieving a stationary emergent environment

As we mentioned above, biological processes in the simulated ecosystem influence the emergent annual cycles of the physical and chemical environment. So it is not expected that these cycles would be precisely stationary in the Azores VE (even though $B = 0$) if it settles to an attractor with an annual cycle of surface temperature that is slightly different from the climate value used to compute B . At the site where $B = 0$ in the climate data the attractor had a non-zero emergent B_A , with the result that the depth and temperature of the mixed layer drifted slowly. To eliminate that drift we introduced a correction ΔB to the surface heat flux at every time step, and a temperature correction ΔT on the 1st March each year to return the mixed layer temperature to its initial value. The physical environment exhibited a stable annual cycle with $\Delta B = +4 \text{ W/m}^2$ and $\Delta T = -0.1 \text{ K/y}$.

Each year in the Azores VE, the downward fluxes of dead plankton and faecal pellets transport nitrogen below the annual maximum depth of the mixed layer. This haemorrhage of nitrogen from the seasonal

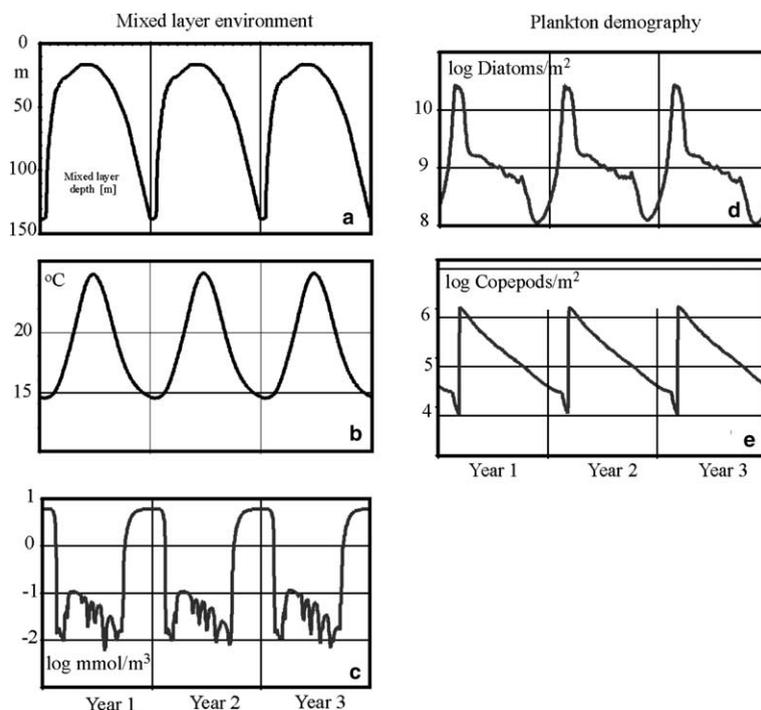


Fig. 2. Stationary annual cycles in the balanced Virtual Ecosystem at the Azores site: (a) mixed layer depth, (b) mixed layer temperature, (c) mixed layer nitrogen concentration, (d) phytoplankton population, (e) zooplankton concentration.

boundary layer causes a slow drift in the supply of nitrogen for the growing season in successive years, with a corresponding decline in annual primary production. To eliminate this drift we replaced the lost nitrogen by adding ΔN into the mixed layer on 1st March each year, thus ensuring that the supply of limiting nutrient was the same at the start of each growing season, year after year. The chemical environment exhibited a stable annual cycle with $\Delta N = 0.1 \text{ mmol N/m}^3$. These three corrections (ΔB , ΔT , ΔN) are much smaller than the uncertainties in climatological data at the Azores site.

We call the resulting simulation the “balanced Azores VE”. The annual cycle was qualitatively like that in the unbalanced Azores VE ($\Delta B = \Delta T = \Delta N = 0$) described by Woods and Barkmann (1994). However, there were quantitative differences in several features. For example, the annual maximum depth of the mixed layer was 137 m in the balanced version and 152 m in the unbalanced version. And the date of the annual maximum phytoplankton biomass was 22 April, compared with 16 May in the unbalanced version. We note in passing that the balanced version better simulates observations of SeaWiFS observations, which had a maximum phytoplankton biomass on 29 March \pm one month at our site (Liu & Woods, 2004a, 2004b). Such comparisons with observations will be the subject of another publication. The present numerical experiments do not require us to tune the model parameters to match observations (Fasham, Sarmiento, Slater, Ducklow, & Williams, 1993).

2.5. Numerical experiments

The numerical experiments involved more than 100 VEs each lasting 34 years or longer. The reference simulation was initialised with balanced phytoplankton and zooplankton numbers and weights, found by trial and error correction. The test of stability involved an experiment with four VE initialised with different

initial conditions, the phytoplankton and zooplankton numbers being set to twice and/or half the balanced values. Then we performed a series of experiments to explore the sensitivity of the results to the values of four key parameters in the model equations: (1) carnivorous predation, (2) grazing threshold, (3) grazing saturation, and (4) epidemiological respiration in diatoms. Next we studied the response of the plankton populations to changes in nitrogen concentration, temperature and ocean circulation. The final numerical experiment was designed to show how stability permits useful predictability under climate change.

3. Results

3.1. The annual cycle in the balanced Azores VE

The principal result of our investigation is already clear from the fact that we were able to create a stationary environment. This implies that the plankton populations also followed a stationary annual cycle once the simulation had achieved a balanced state. This is illustrated in Fig. 2, which shows time series of the mixed layer environment and plankton populations during the last sixteen years of the 34-year simulation.

3.2. Inter-annual variation

There is a little inter-annual variation in the plankton populations, which induces inter-annual variation in the physical and chemical environment (Fig. 3). What causes this variation? There are two possibilities. The first is that inter-annual variation is a rational response of the plankton to chaotic forcing. The second is that it is due to mathematical instability in the modelling of predator–prey as seen in simple models (May, 1973). Understanding the stability of Virtual Ecosystems depends on being able to discriminate between those two causes. Our strategy for resolving this issue is based on two critical tests. If the cause is stochastic forcing the VE should be ergodic: if it is chaos the VE should be sensitive to initial conditions.

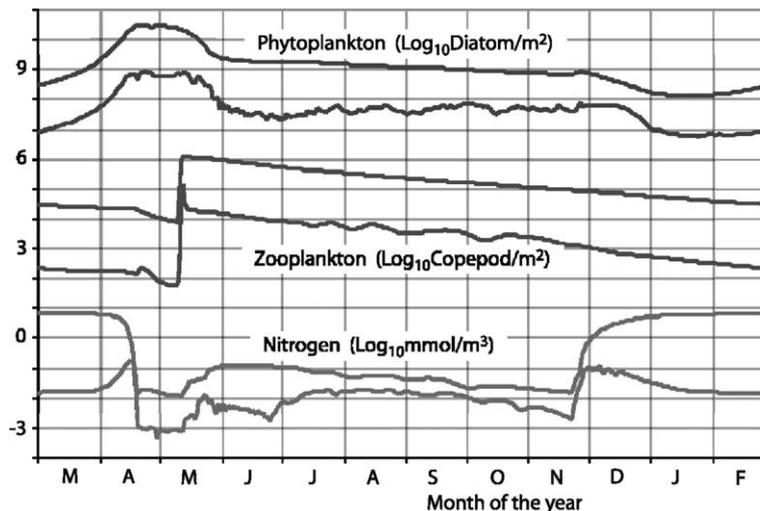


Fig. 3. Inter-annual variation during the last 16 years of the 34-year simulation shown by values on 1st March each year: (a) phytoplankton population, (b) zooplankton population, (c) nitrogen in the mixed layer. In each case, the upper curve is the 16-year mean for each day of the year, and the lower curve is the inter-annual standard deviation for that day of the year.

3.3. Demographic noise due to turbulence

The only stochastic element of the WB model is the turbulent displacement of particles in the mixing layer (Fig. 4). A pseudo-random sequence of numbers is used to compute these displacements. Different instances of the VE are created with different seed values used to initialize the random number generator. The demographic noise of the VE is defined by the standard deviations of the inter-instance differences in plankton populations on each day of the year. Using more computer agents to represent the plankton reduces the demographic noise (Al-Batran, Field, Wiley, & Woods, 1998). Time series of ensemble mean and demographic noise for 1st March each year (Fig. 5) confirm that the demographic noise is stationary in both phytoplankton and zooplankton. The 1st March was chosen because it occurs at the start of the growing season each year. The full annual cycle of demographic noise is shown in Fig. 6.

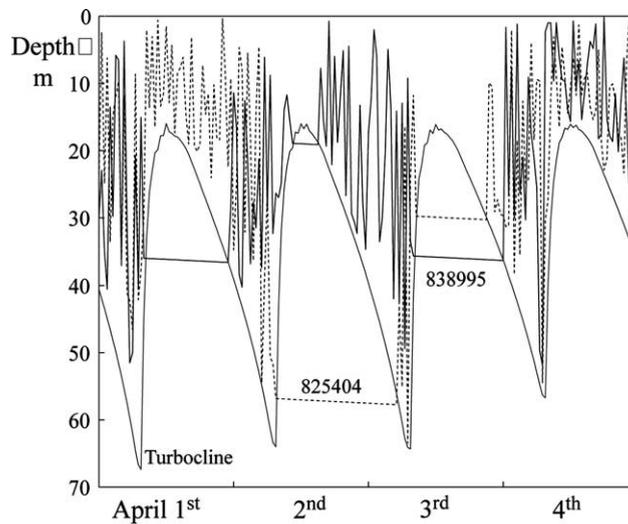


Fig. 4. The trajectory of two diatom showing random vertical displacement in the turbulent mixing layer (above the turbocline) and steady sinking in the laminar flow thermocline at 1 m/d (approximately 2 cm per half-hour time step).

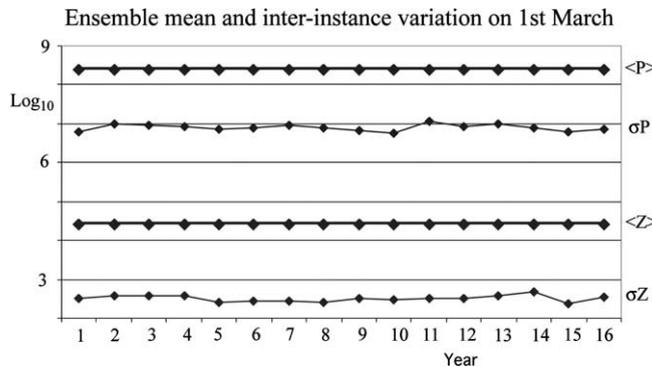


Fig. 5. A 16-year time series derived from an ensemble of 16 instances of the Azores VE on the 1st March. Ensemble mean populations for phytoplankton $\langle P(60, y) \rangle$ and zooplankton $\langle Z(60, y) \rangle$ and inter-instance standard deviations $\sigma_P(60, 24)$ and $\sigma_Z(60, 24)$. (Units: number of plankters per square metre.)

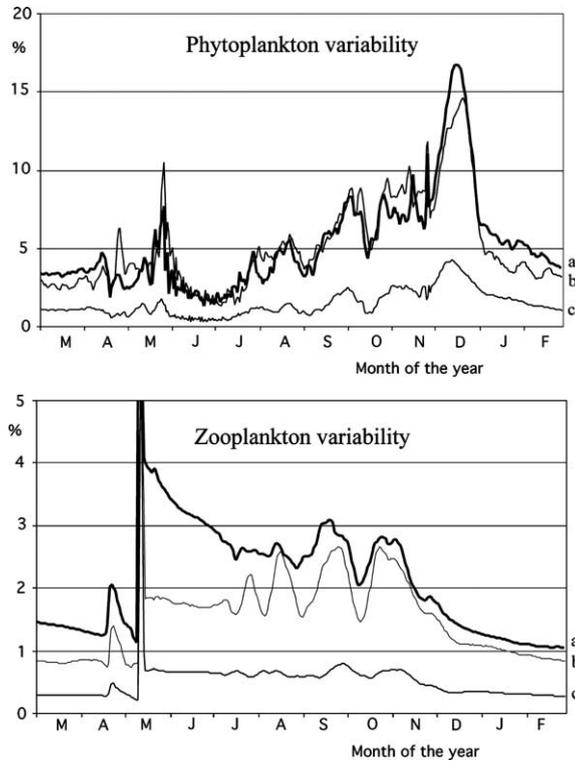


Fig. 6. The test for ergodicity in the phytoplankton and zooplankton populations: (a) inter-annual variation over 16 years in one instance, (b) inter-instance variation in one year ($y = 24$) from an ensemble of 16 instances, (c) inter-instance variation over 16 years.

3.4. Emergent ergodicity

Is the inter-annual variation seen in a single instance (Fig. 3) due solely to turbulence? Is it the same as the demographic noise? The test is to show that the difference between inter-annual variation and inter-instance variation is not statistically significant, given the (identical) degrees of freedom of the two time series. If that were true the virtual ecosystem would be ergodic. The results of this test are shown in Fig. 6, which compares (a) the inter-annual variation in the last 16 years of one instance, with (b) the inter-instance variation of 16 instances in the 24th year, and then (c) over the last 16 years. We conclude that the non-ergodicity is not detectable in the phytoplankton, but it is significant in the zooplankton. It peaks at the start of each new zooplankton generation and declines as the numbers fall as the result of predation. In both phytoplankton and zooplankton, the demographic noise over 16 years is one quarter ($\sqrt{16}$) of that in one year, confirming that it is random.

The cause of the small non-ergodicity in the zooplankton population is revealed by analysing the audit trails of two zooplankton lineages (Fig. 7). Some of the inter-annual variance is due to intra-population variation in the zooplankton population, which is inherited through lineages and therefore not random and non-ergodic. Copepods inherit breeding success through lineages from year to year. Breeding success ranks with winter weight, which is also inherited through lineages. The two properties are correlated through the date of hatching. Copepods with higher winter weight breed earlier. Their offspring are more numerous because the food concentration (diatoms) has been less depleted during gestation; they feed better for the same reason; and they end the growing season with a higher body weight. During the period of

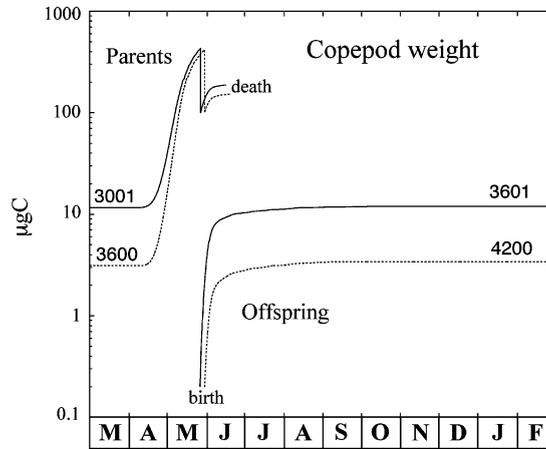


Fig. 7. Changing body weight of copepods in two zooplankton sub-populations with different winter weights, and in their offspring, showing inheritance of winter weight through lineages.

the year when they are starving, potential weight loss is compensated by cannibalism, which reduces numbers faster in lineages with low-weight copepods. The maximum biological non-ergodicity occurs at the time of reproduction, when inter-lineage variation in the number of copepods is greatest. It declines as carnivores using visual predation preferentially consume the smaller, less agile (and therefore more visible) copepods, which hatched later than average. That is the mechanism by which inheritance through lineages produces the non-ergodic component of inter-annual variation in zooplankton seen in Fig. 6.

3.5. Testing for instability

The critical test for stability is that the annual cycles of the plankton populations should be insensitive to initial conditions. The simulation is initialised with assumed values for all the state variables. That initial state is seldom in balance with the model and the scenario. The difference is the initialisation error. If the virtual ecosystem is stable, the legacy of that initialisation error decays with time. After that period of adjustment the VE settles to an attractor, which is independent of the initial conditions. The inter-annual variation will be no larger than the demographic noise. The properties of the attractor can be displayed in Poincaré maps in which one emergent property of the VE is plotted against another on the same day of each year. For example, we might plot the values of $Z(d):P(d)$, $N(d):P(d)$ for all years. If, on the other hand, the VE were unstable, the annual cycle in each population would vacillate or exhibit chaotic fluctuations. A Poincaré map reveals the latter to have a strange attractor with inter-annual variation much greater than the demographic noise.

We test for stability in three stages: (1) the initial transition to a balanced state, (2) the sensitivity of the demographic attractor to initial conditions, and (3) the annual demographic attractor.

3.5.1. The initial transition to a balanced state

We focus on one day of the year, the 1st March ($d = 60$). That date lies between the start of the phytoplankton growing season (21 January), and the start of the heating season (3 March) when the mixed layer begins to shoal. Those two events coincide in Sverdrup's (1953) famous model of the onset of the spring bloom. They are separated in our VE because it includes the diurnal thermocline (Woods & Barkmann, 1993). Nevertheless, the 1st March is a relatively quiet time of year in the plankton ecosystem, and therefore suitable for initialisation.

Fig. 8 shows time series of the environment and plankton populations on the 1st March year for 34 years. The mixed layer depth is the daily maximum depth of the turbocline. The other panels show daily mean values computed from the half-hour time steps used in the integration. We see the transition from an unbalanced initial condition to the attractor. The transition is dominated by the slow progress of the

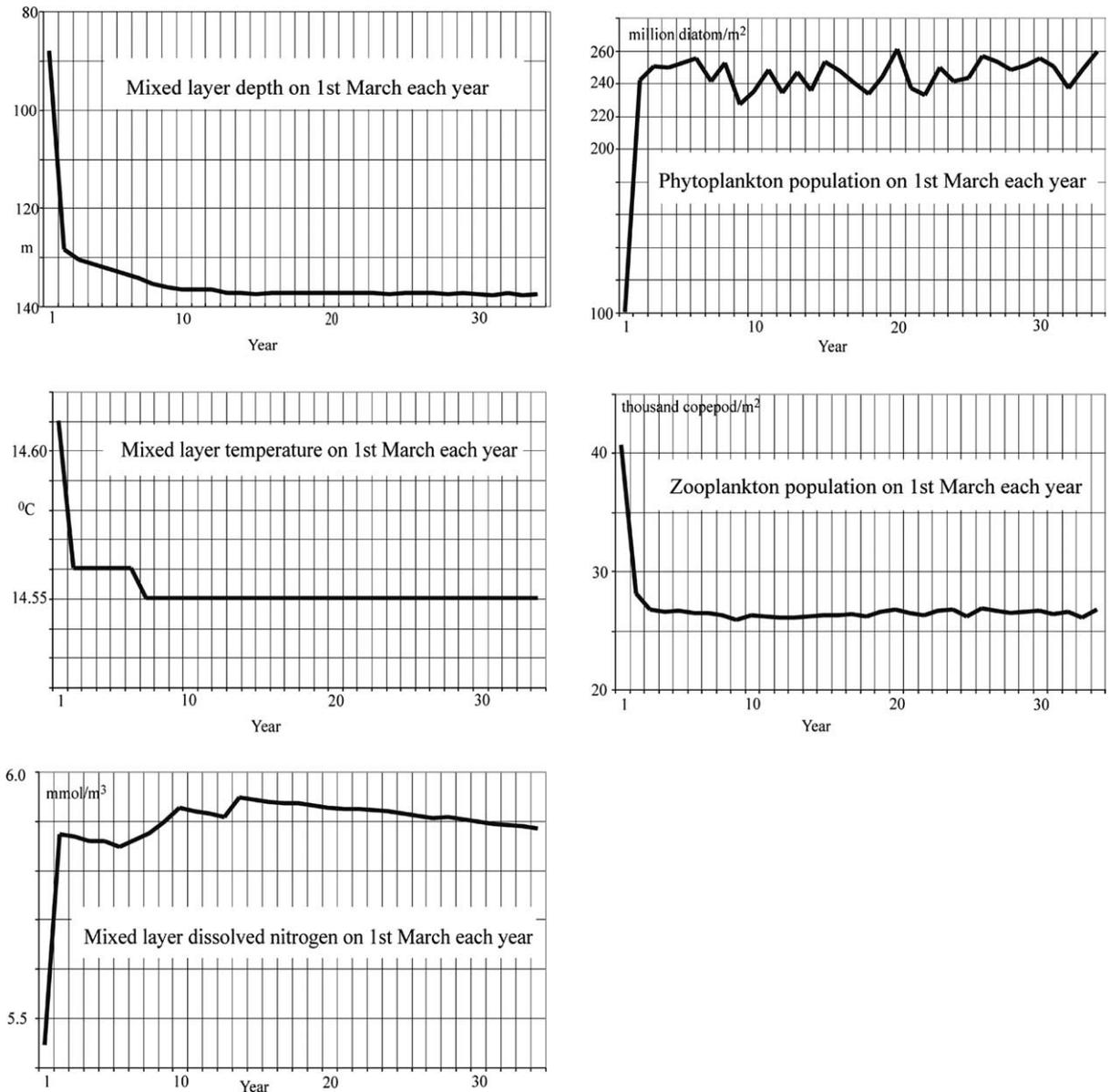


Fig. 8. The adjustment of the ecosystem from unbalanced initial conditions to stationary annual cycles is shown by 34-year time series of the values on 1st March each year: (a) mixed layer depth, (b) mixed layer temperature, (c) nitrogen concentration, (d) phytoplankton population, (e) zooplankton population.

mixed layer to its balanced state, which is artificially slowed by the annual temperature correction (ΔT) introduced to eliminate multi-year drift in mixed layer temperature. Despite the relatively slow adjustment of the mixed layer depth to its balanced state, which provokes transient fluctuations in nitrogen concentration, the plankton populations adjust to their balanced state within three years. The three-year timescale for demographic adjustment to the stationary environment is controlled by the fact that WB (Woods & Barkmann model) copepods reproduce only once and then die. In essence the predator–prey interaction is so heavily damped that the initialisation error provokes only one oscillation before becoming lost in the demographic noise. Later we shall show what happens when there is sufficient resource (nitrogen) for copepod lineages to produce two generations in the same year (Fig. 19).

3.6. Sensitivity to initial conditions

Fig. 9 is a Poincaré map for $[P(60, y):Z(60, y)]$ for $y = 1–34$. The data came from the same VE initialised with four different values of $P(60, y = 0)$, $Z(60, y = 0)$. We see that inter-version differences are lost in the same demographic noise within three years. We conclude that the versions are not significantly different. Regardless of initial condition, they all quickly converge on the same demographic attractor $[P_A(60), Z_A(60)]$. This insensitivity to initial conditions proves that the VE is stable.

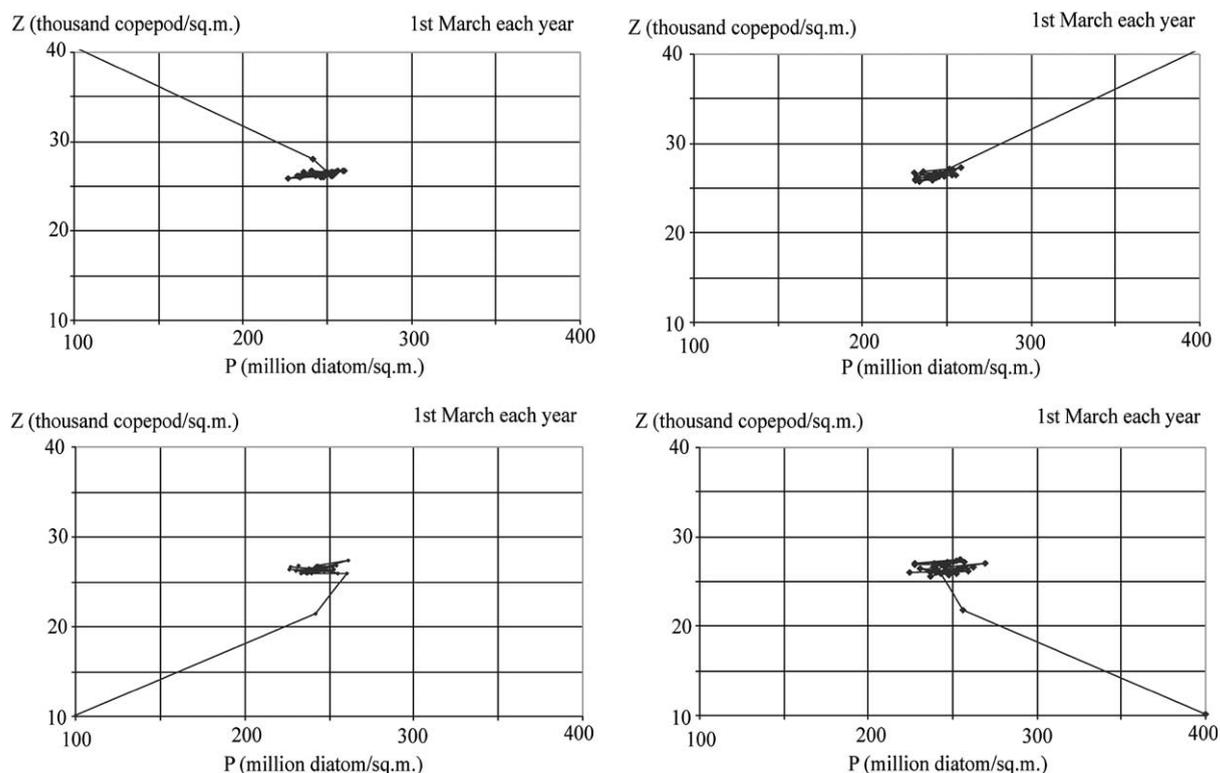


Fig. 9. The transition from unbalanced initial conditions to the demographic attractor $[P_A(60), Z_A(60)]$, revealed by 34-year time series of the demographic state on 1st March ($d = 60$) each year. The four examples started with the following initial conditions: (a) $[0.5P_A(60), 0.5Z_A(60)]$, (b) $[0.5P_A(60), 2Z_A(60)]$, (c) $[2P_A(60), 2Z_A(60)]$, (d) $[2P_A(60), 0.5Z_A(60)]$.

3.7. The annual demographic attractor

Having established that the plankton follow stationary annual cycles, with very small inter-annual variation, we can plot their daily mean values together in a Poincaré map for the whole year (Fig. 10). Given that the ergodicity error is small (Fig. 6), we can use either ensemble or multi-year mean values. This is the annual demographic attractor for the virtual ecosystem specified by the WB model and Azores scenario.

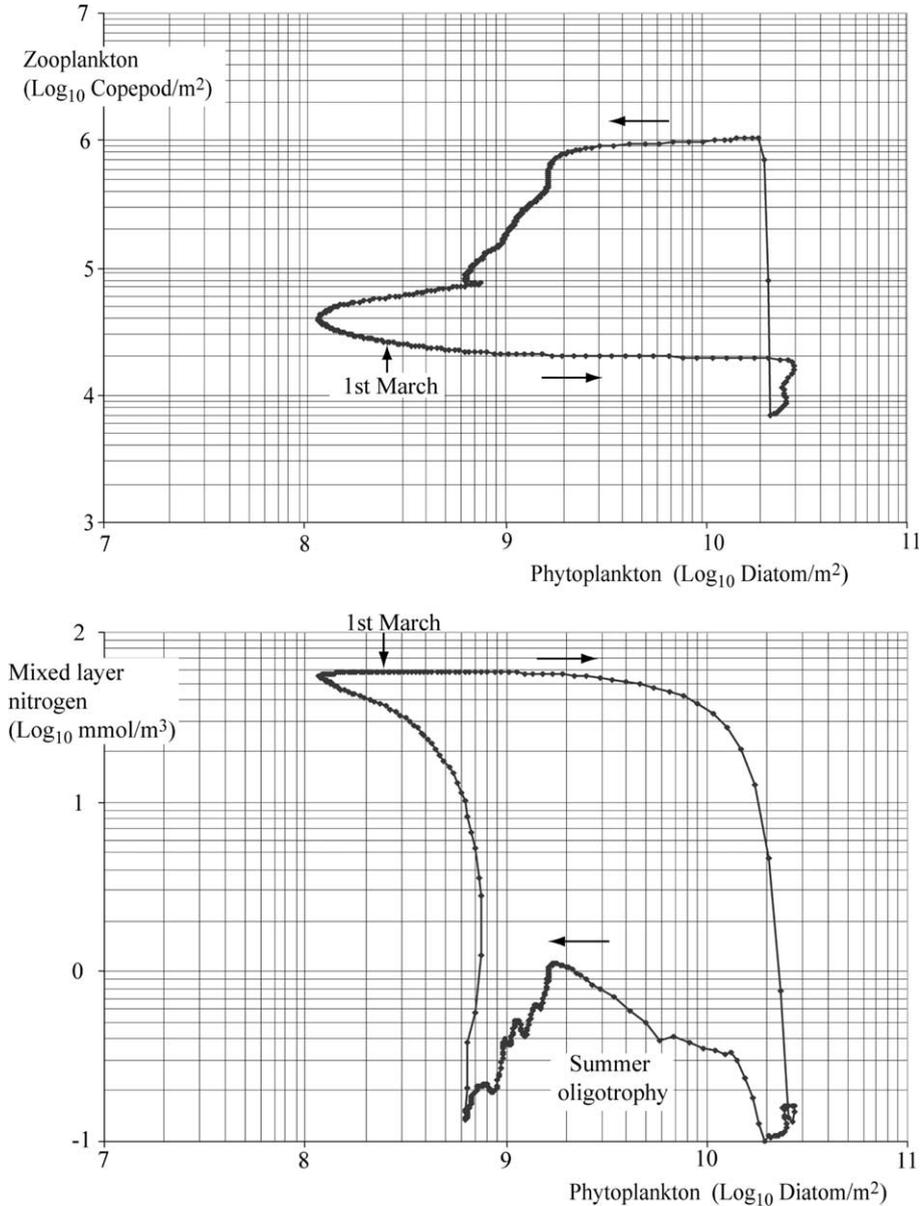


Fig. 10. The annual demographic attractor $[P_A(d):Z_A(d)]$ and the annual nutrient attractor $[P_A(d):N_A(d)]$, based on mean values for the last 16 years of a 34-year simulation of the Virtual Ecosystem at the Azores. Each point marks the attractor for one day of the year.

Fig. 10 also shows the annual nutrient attractor, the Poincaré map of $[P_A(d):N_A(d)]$ in which the year proceeds in a clockwise direction.

Inspecting these Poincaré maps of the attractor, we recognize familiar features of the annual cycle in the ecosystem. They are illustrated in the accompanying paper (Woods, 2005). The light-limited spring bloom occurs between P_{\min} and P_{\max} . The increasing space between daily markers shows the accelerating growth in biomass. The maximum value, P_{\max} is attained when the nitrogen concentration in the mixed layer sharply declines, marking the onset of summer oligotrophy. Thereafter cell division continues more slowly, as a combination of new production below the nutricline (located at a depth of 30 metres) and regenerated production in the mixed layer and seasonal thermocline. Losses to the phytoplankton population are dominated by grazing (natural mortality by energy starvation is negligible in the summer euphotic zone). Gains and losses are finely balanced during the week after $P = P_{\max}$. First the population declines, then it rises again to a secondary maximum. A few days later the zooplankton start to reproduce, and their number rises sharply from Z_{\min} to Z_{\max} in four days. The phytoplankton population declines noticeably while the zooplankton reproduce, which explains why the last to hatch grow less well (Fig. 7).

Secondary production is measured by the number in the new generation ($Z_{\max} - Z_{\min} = 10^6/\text{m}^2$) multiplied by their birth weight ($0.2 \mu\text{g C}$). So in this case it is $200 \text{ mg C}/\text{m}^2 \text{ y}$. For the first three weeks after reproduction the number of zooplankton declines as mothers die by prescribed senility. During that period their food supply falls by a factor of 10. The decline in zooplankton population then proceeds more rapidly by a combination of carnivorous predation and cannibalism. The food supply declines by a factor of 4 in this summer period.

The autumn bloom occurs when the deepening mixed layer reaches the nutricline, and turbulence entrains nutrients into the surface waters. This produces a short-lived increase in phytoplankton numbers peaking on 20 September. But within one week the phytoplankton population resumes its decline as the mixed layer continues to deepen and the day length decreases. This light-limited decline in P during autumn and early winter ends on 21st January, when the cell division rate again becomes greater than the losses to grazing and natural mortality. During that period the number of copepods halves, and copepod ingestion declines with decreasing food supply, so grazing becomes less important. The next growing season (defined by P_{\min}) begins on 21st January, while the mixed layer continues to deepen during late winter, so that the nutrient continues still to increase by entrainment from the seasonal thermocline.

4. Sensitivity studies

The annual demographic attractor is the icon of stability in Virtual Ecosystems. It provides a touchstone for assessing the response of the ecosystem to changes in values of model parameters or of external forcing. Complex non-linear systems are often stable under some conditions, but unstable under others. The conditions include values of external forcing and model parameters. For example, PFOR showed that their simulation is stable when the resource level (nitrogen content) was low, but became progressively more unstable (first oscillations and then chaotic fluctuations in the plankton populations) as nitrogen content was increased. Others have found that instability in simple predator–prey systems depends on the value of predation parameters in the model equations. We now present the results of numerical experiments designed to discover whether there are conditions under which the Azores VE becomes unstable.

4.1. Sensitivity to model parameters

There are four biological processes that affect the demographic stability of NPZD models: (a) natural mortality due to starvation, (b) the survival of plankton in winter, when there is no reproduction, (c) grazing by copepods on diatoms, and (d) predation by carnivores on copepods. In Box and Field models,

instability depends on the values of parameters used in the equations for these processes. We performed numerical experiments to discover how the stability of the Azores VE is affected by changing the values of the corresponding parameters in the WB model.

4.1.1. The epidemiological parameter

It is believed (Lack, 1954) that natural mortality in plankton depends on two factors: starvation and disease. Two of our students, Tim Barrell & Reza Adams (unpublished dissertations 2000), modified the WB model to simulate the spreading of infectious disease through the phytoplankton population. They parametrized the physiological consequences of infection by increasing respiration rate. That reduces the reproduction rate and increases natural mortality by energy starvation. The incidence of infection increases with the density of the population P , and is therefore lowest at P_{\min} in winter. Barrell & Adams established that the population mean respiration rate R and the population density P are related by the classical epidemiological equation $R/R_0 = P/(P + P_0)$. This equation was introduced into the WB model to parametrize mortality due to infectious disease. It is the only population-based equation; all other biological equations apply to the ambient environment of an individual plankter. We call P_0 the epidemiological parameter. The WB model has a default value of $P_0 = 80$ million diatoms per square metre. When $P = P_0$ the respiration of every diatom is reduced by 50%. The default value yields 50 mg C/m² of phytoplankton biomass near the Azores in winter. This is consistent with observations (Longhurst, 1998), assuming that it comprises diatoms with identical mass (460 pg C).

We performed a numerical experiment to establish the sensitivity of the annual demographic attractor to the value of the epidemiological parameter P_0 . The result of reducing P_0 by a factor of 10 is shown in Fig. 11. The VE still has a stable attractor. P_{\min} is reduced by 60%, and occurs three days later. On that day, the epidemiological factor reduces respiration by 80%, so disease contributes slightly less to natural mortality in winter. Despite the lower winter biomass the peak of the spring bloom P_{\max} is unchanged. This catch-up is equivalent to one extra (light-limited) reproduction event in winter, while the mixed layer is

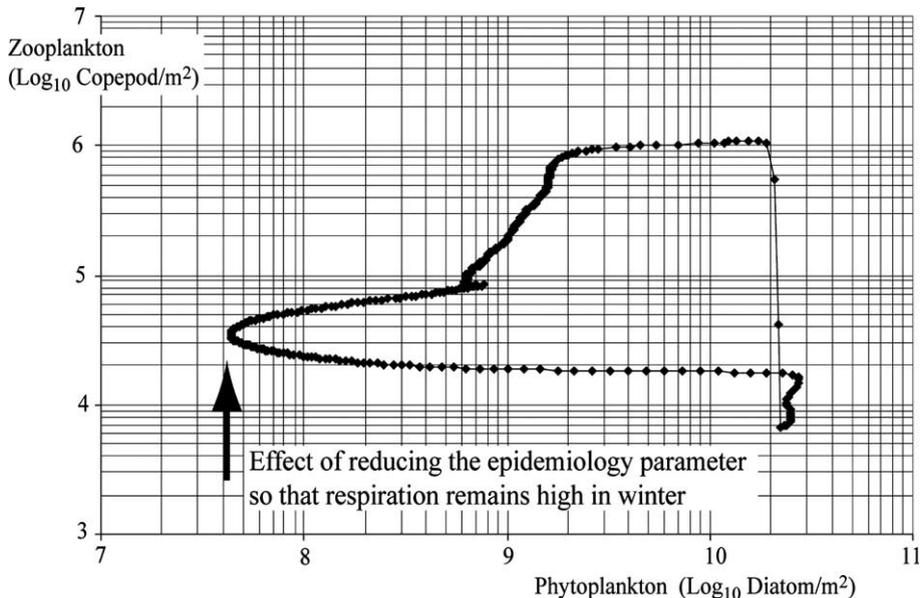


Fig. 11. The annual demographic attractor for the Azores Virtual Ecosystem when the epidemiological parameter P_0 is reduced by a factor of 10.

deepening (i.e. as nitrogen is still being entrained from the seasonal thermocline). The change of P_0 does not affect the comparison of the peak of the spring bloom with SeaWiFS data (Liu & Woods, 2004b; Woods, 2002, Chapt. 18). The annual new primary production (approximately P_{\max} because $P_{\max} \gg P_{\min}$) is controlled by the nutrient supply N_0 , and is therefore unchanged. The annual secondary production (approximately Z_{\max}) is decreased by 3% and Z_{\min} is decreased by 2.5%. This small reduction is due to poorer grazing during the early stages of the spring bloom, when the concentration of food is slightly lower, which delays copepod reproduction. That delay allows more time for carnivorous predation on mature (pregnant) adults, so fewer of them survive to reproduce.

These changes in the attractor are emergent properties of the Azores VE. The changes are too small to be observed at sea, given the problem of sampling patchiness. They are the rational response to a different assumption about the incidence of disease in winter. Modulating respiration by the population-based epidemiological factor in the WB model does not affect stability. The inclusion of a parameter like P_0 is common practice in plankton ecosystem modelling (Evans & Fasham, 1993). It is designed to prevent the total number of phytoplankton becoming unrealistically low in winter when the mixed layer is deep. We conclude that this traditional concern is unnecessary because P_{\max} is insensitive to P_{\min} . Late reproduction (i.e. just before P_{\max}) takes only a few hours to make up for any error in P_{\min} . So excluding P_0 does not significantly affect the model estimation of P_{\max} and annual new primary production.

4.2. The grazing parameters

Classical studies of the stability of ecosystems focus on the interaction between predator and prey populations, in our case between zooplankton (copepods) and phytoplankton (diatoms). In Box models, time series of predators and prey biomasses may have three characteristic forms: they may be (1) stable, (2) vacillate, or (3) fluctuate chaotically. Transitions between these three conditions depend on the value of parameters in the predation equations. We investigated the stability of the Azores VE to variation in predation parameters.

WB predation is described by n_j the number of diatoms ingested per time step by one of the copepods in sub-population j (which all have the same weight W_j) when the ambient food concentration is p diatom/m³:

$$n_j = \text{constant} \times W_j^{2/3} pE,$$

where the grazing efficiency factor $E = (p - p_0)/(p + p_1)$.

The default values for the two parameters are $p_0 = 100,000$ diatom/m³ and $p_1 = 4,000,000$ diatom/m³. The annual variation of p in the mixed layer is shown in Fig. 12(1). The grazing efficiency factor E is illustrated in Fig. 12(2) for various values of the parameters p_0 and p_1 used in the sensitivity study described below.

4.2.1. The threshold parameter p_0

At its annual minimum the phytoplankton population in the mixed layer is 0.5 million diatom/m³, which is five times the default value for p_0 so grazing efficiency is reduced by 20% in winter. Reducing p_0 to zero eliminates this reduction. The attractor adjusts so that P_{\min} is halved, but that does not significantly change the inter-annual variation (Fig. 13). In other respects the annual cycle is virtually unchanged: the changes in P_{\max} , Z_{\min} and Z_{\max} are less than 1%. So, while removing the grazing threshold dilutes the phytoplankton in winter, it does not significantly change secondary production. The remaining sensitivity studies all used $p_0 = 0$.

4.2.2. The grazing saturation factor p_1

We see that in the default model ($p_1 = 4$ million diatom/m³) the phytoplankton population rises high enough significantly to increase the denominator of E in spring and summer, but not in autumn and winter.

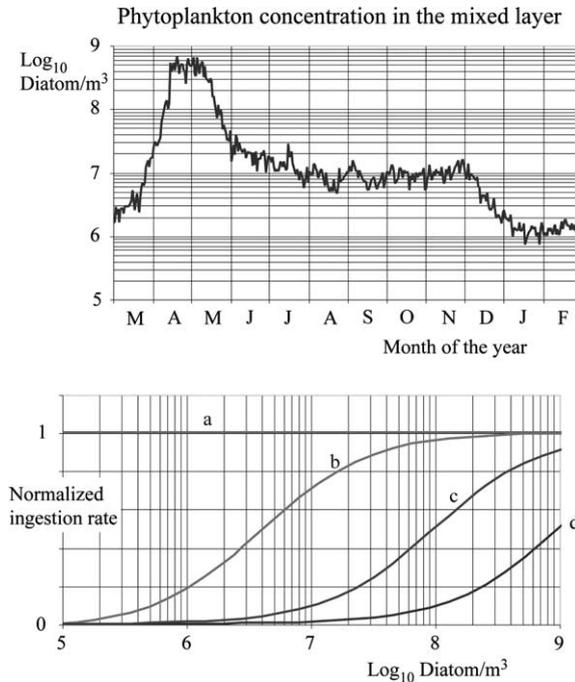


Fig. 12. The grazing parameters. (1) The annual variation of phytoplankton concentration in the mixed layer. The high frequency variation is the single layer equivalent of demographic noise. (2) Ingestion efficiency for the four cases used in the sensitivity study: (a) $p_0 = 0, p_1 = 0$; (b) $p_0 = 10^5, p_1 = 4 \times 10^6$ (default values); (c) $p_0 = 0, p_1 = 10^8$; (d) $p_0 = 0, p_1 = 10^9$.

Setting $p_1 = 0$ linearises the ingestion equation, so that the grazing rate n is proportional to p . Grazing rises compared with the default model. Fig. 13 shows that the stability of the ecosystem is unaffected. P_{\min} is halved, but P_{\max} , Z_{\min} and Z_{\max} are unchanged. So the grazing-induced decline in the winter population of phytoplankton does not affect annual secondary production.

Increasing p_1 reduces grazing rate, except when $p \gg p_1$. In the default case ($p_1 = 4$ million diatom/ m^3), this reduction occurs during spring and periodically in summer. Raising p_1 to 100 million diatom/ m^3 extends this period of reduced grazing to all but the spring bloom (Fig. 12(2)). The ecosystem continues to have a stable attractor (Fig. 13). P_{\min} is reduced by a factor of 4 to 250 million diatoms/ m^2 . P_{\max} and Z_{\min} are virtually unchanged, but Z_{\max} is reduced from 1.2 to 0.85 million copepods/ m^2 . So secondary production is one third lower than in the default simulation. As annual primary production remains unchanged, there is a corresponding increase in natural mortality. Which means that the fall-out of dead phytoplankton (the biological pump) will also be higher. The VEs shown in Fig. 13 exhibit a stable attractor with no significant increase in inter-annual noise.

4.2.3. Extinction

Increasing p_1 to 10^9 diatom/ m^3 reduces grazing substantially at all times of year (Fig. 14). The zooplankton become extinct on 1st October of the first year after one feeble reproduction event, which produces a second generation of only 170,000 copepods/ m^2 , i.e. a reduction of 83% compared with the default model (Fig. 10). The population of second-generation copepods is not large enough to survive losses to carnivorous predation and cannibalism. None survives to reproduce in the second year.

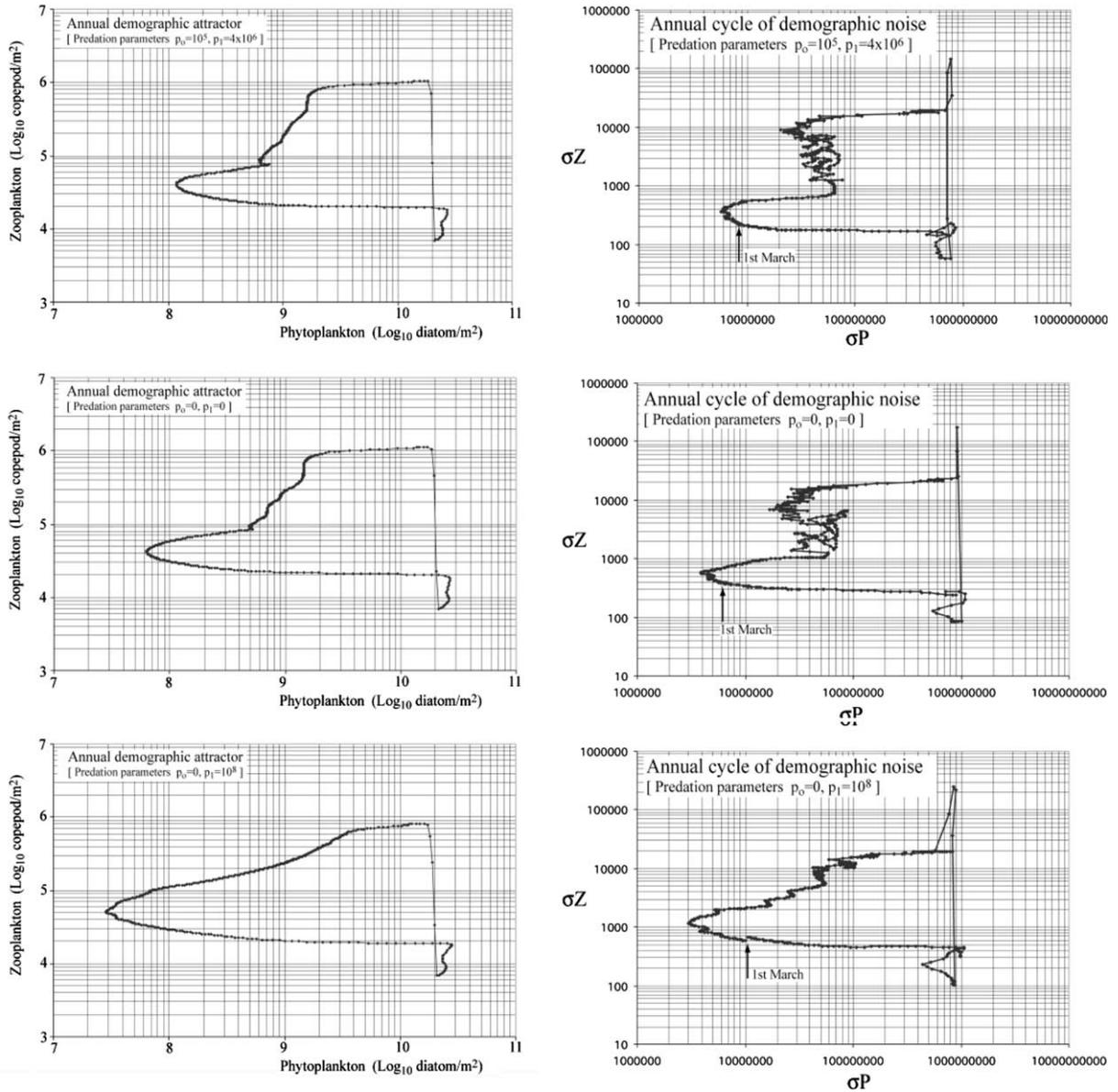


Fig. 13. Poincaré maps for the three parameter sets (a)–(c) in Fig. 12. Demographic attractor (left) and demographic noise (right).

4.2.4. Transition to extinction

To clarify the transition from stability to extinction we made a set of simulations in which the saturation parameter has ten values in the range $10^8 < p_1 < 10^9$. Grazing efficiency declines as p_1 increases (Fig. 15). This affects the integrated ingestion of every copepod during the growing season, and therefore the number of offspring it produces. Reproduction success, measured by the number of offspring per breeding copepod (N_i), depends on three variables: the over-wintering weight $W_i(0)$, the integrated ingestion (G_i) minus respiration (R_i) during spring up to the moment of reproduction; and four model parameters: the weight

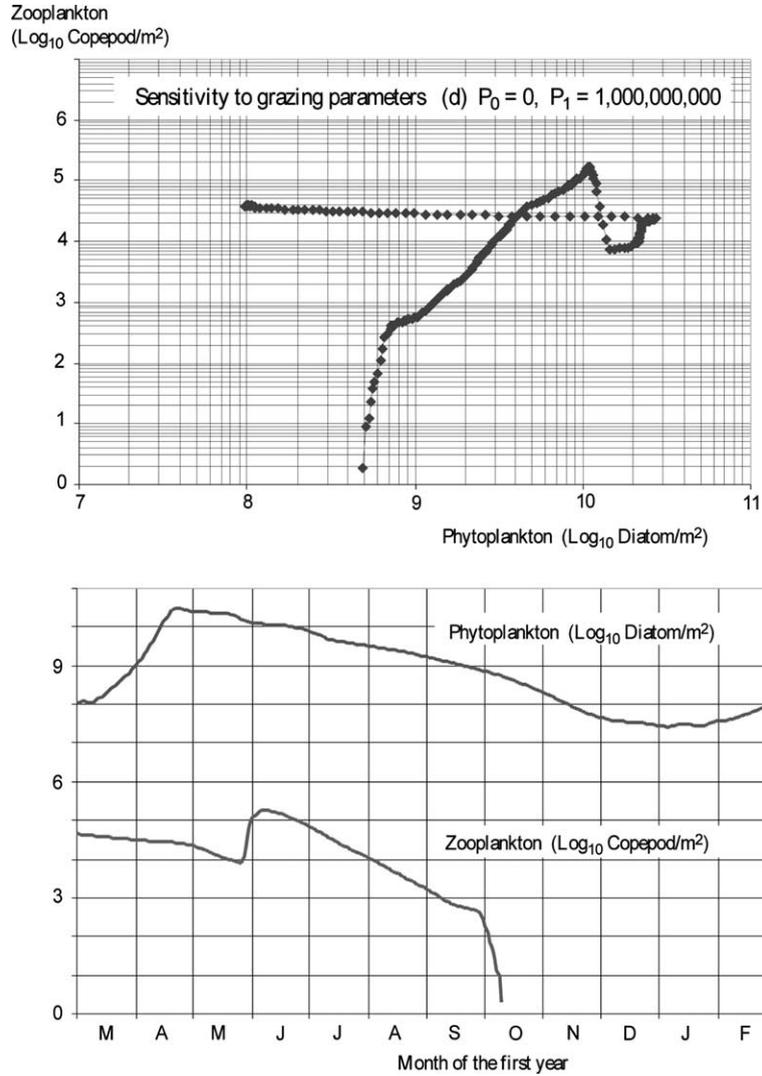


Fig. 14. The Azores VE with parameter set (d), for which the zooplankton become extinct in the first year after a feeble reproduction: (upper panel) the Poincaré map $[P(d, y = 1):Z(d, y = 1)]$; (lower panel) time series of $P(d)$ and $Z(d)$ during the first year.

required to start making eggs ($W_m = 100 \mu\text{g}$), the birth weight ($W_b = 0.2 \mu\text{g}$), and the grazing efficiency (p_0, p_1):

$$N_i = (W_i + G_i - R_i - W_m)/W_b.$$

Copepods that over-winter with a high body weight $W_i(0)$ produce the most offspring; because they graze more effectively than those with lower weight, and reach maturity (W_i) earlier, when the food supply is less depleted. Under default conditions, there is enough food for even those copepods with the lowest weight to reproduce. All the copepods produce fewer offspring when p_1 is higher. When $p_1 > 10^8$ the smallest copepods fail to reach maturity before the food concentration becomes too low for ingestion. They are then exposed to 12 months of losses to predators and cannibalism before food becomes available in the next year's

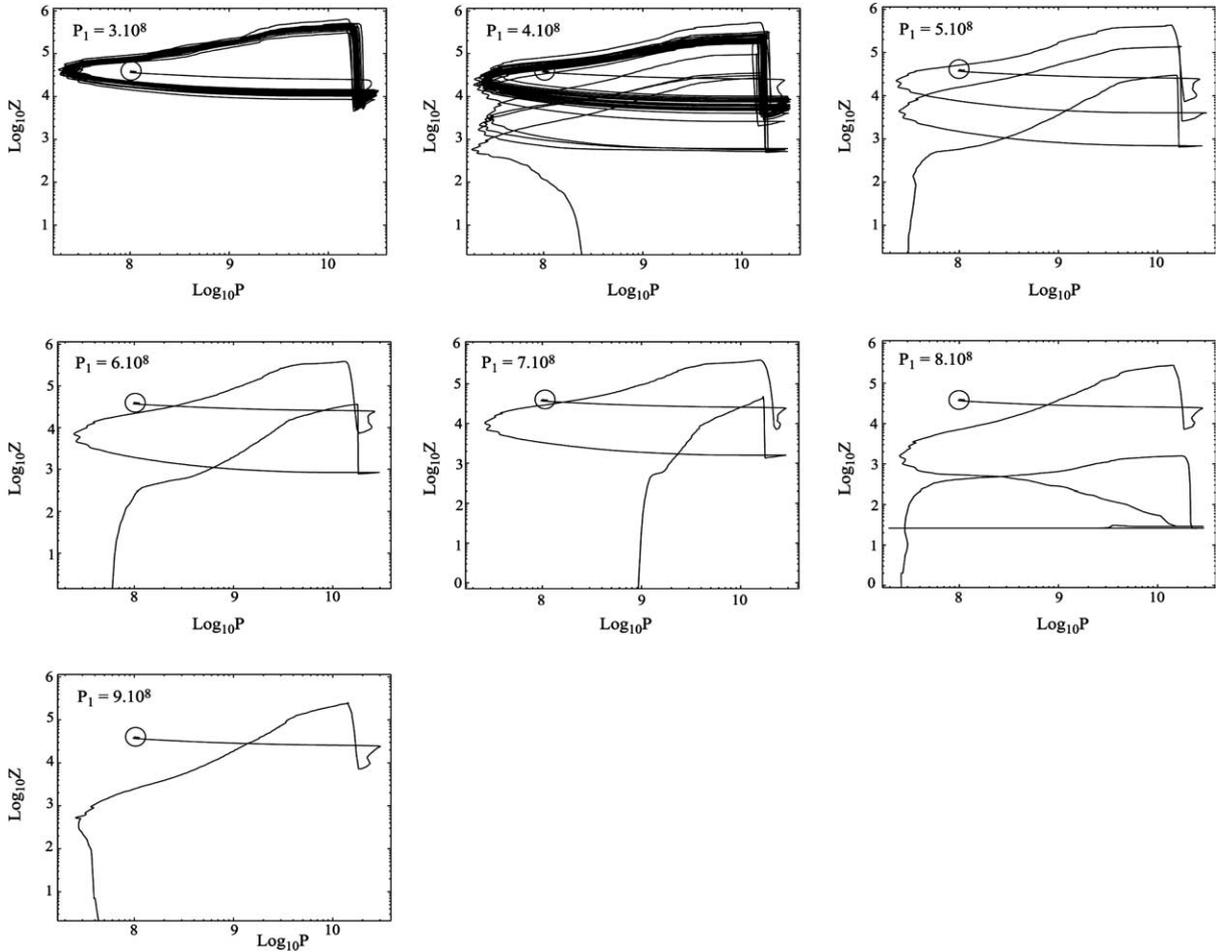


Fig. 15. Transition to extinction as p_1 increases from 10^8 to 10^9 .

spring bloom. The incidence of copepods skipping reproduction in a year increases with p_1 . The combination of fewer offspring and missed years, causes secondary production to decline, until it does not balance the annual losses to predators and starvation. The copepod population is then on a downward spiral to extinction. Fig. 16 shows how the time to extinction gets progressively shorter as p_1 increases. It occurs in the first year when $p_1 = 9 \times 10^8$ and earlier in the first year when $p_1 = 10^9$ (Fig. 14).

The progressive decline in secondary production as p_1 rises is not smooth: it involves fluctuations (Fig. 15). But examination of audit trails shows that those fluctuations are the rational response of changes in the date of reproduction, number of offspring, their growth rate and the incidence of missed years. The transition to copepod extinction occurs without chaotic instability. The attractor adjusts gracefully to the new regime of an ecosystem without zooplankton.

In the years after the copepod population becomes extinct, the phytoplankton experience only one cause of death, energy starvation. All diatoms end up as detritus, and the biological pump increases, transporting more particulate nitrogen down into the permanent thermocline. The ecosystem runs down faster because there are no longer any copepods to keep nitrogen in the euphotic zone, by fertilising summer regrowth (see Woods, 2005).

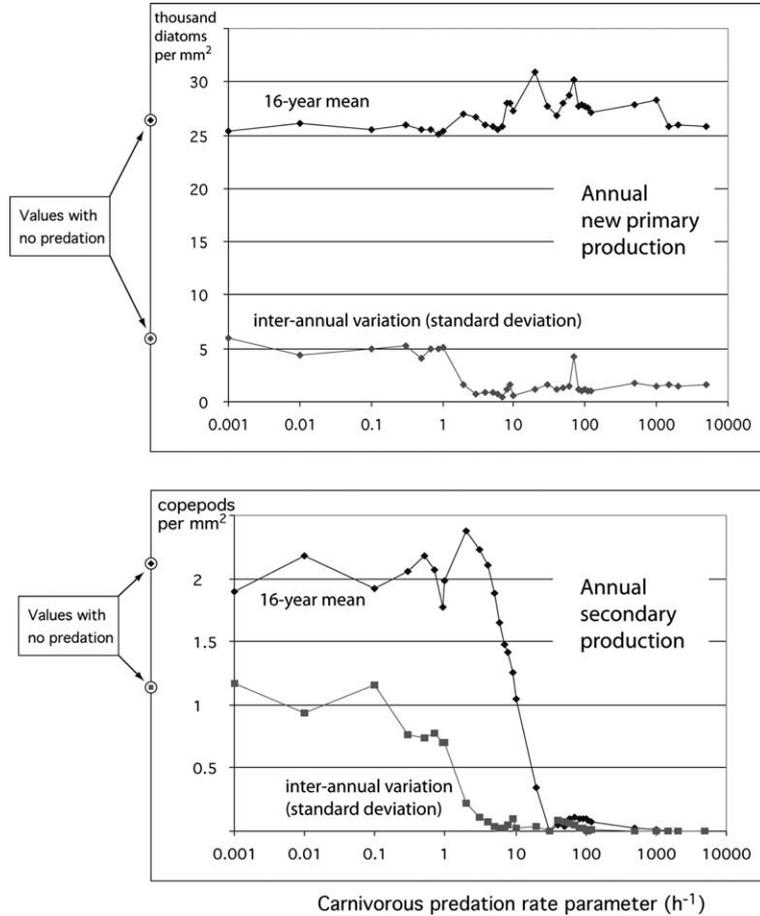


Fig. 16. The sensitivity to carnivorous predation parameter. (Upper panel) Annual new primary production, estimated from $P_{\max} - P_{\min}$: (a) 16-year mean value and (b) inter-annual variation (standard deviation). (Lower panel) Annual secondary production estimated from $Z_{\max} - Z_{\min}$: (a) 16-year mean value and (b) inter-annual variation (standard deviation).

4.3. Predation by carnivores on copepods

In NPZD models, carnivory is not effected by an explicit population of carnivorous zooplankton feeding on the herbivorous zooplankton (copepods). It is treated by a closure term in the equation for zooplankton growth. Most Field models use the quadratic closure of [Steele & Henderson \(1995\)](#). [Caswell & Neubert \(1998\)](#) showed that this Z^2 non-linearity can cause instability. In our WB model the closure term applies to individual zooplankton sub-populations. It is based on the visibility of the copepods in the sub-population, V_i , defined as the product of the ambient irradiance and the plankter cross-section area. This is linear so it is not a source of instability. There is no predation at night; and it is reduced by diel migration during the day.

[Woods & Barkmann \(1995\)](#) investigated an unbalanced Azores VE with no carnivorous predation; copepod mortality is then due solely to cannibalism, which is also described by a linear equation. We repeated that test in a 36-year simulation of the balanced Azores VE. Eliminating carnivorous predation does not affect stability: the attractor adjusts to the new regime ([Fig. 16](#)). It reduces P_{\min} by 30% and P_{\max} by a few percent, Z_{\min} and Z_{\max} both increase by an order of magnitude. Cannibalism is negligible when

phytoplankton are abundant; it does not occur during the spring bloom as the copepods fatten to maturity and produce eggs. More copepods survive to reproduce; so secondary production rises by a factor of 10, even though primary production is little affected by turning off carnivorous predation.

Fig. 16 shows multi-year mean primary and secondary productions (and associated inter-annual variances) in a set of 36-year simulations of the Azores VE covering 28 different values of the carnivorous predation parameter ranging from zero to 10,000. The default value in the WB model is 10. Annual primary production ($P_{\max} - P_{\min}$) changes by only a few percent, which reflects the fact that new production is controlled by the nitrogen supply. Note, however, that the inter-annual variance remains low for all predation rates.

Annual secondary production ($Z_{\max} - Z_{\min}$) is steady when the predation parameter is less than 1. But when the parameter exceeds 2, production declines sharply to become negligible when the parameter exceeds 30. A detailed investigation of the changes occurring when the predation rate is high will be published elsewhere. In brief, rising predation losses change the balance between number of copepods surviving to breed and the number of offspring the survivors produce each year. At very high predation rates the zooplankton population becomes extinct during the 36-year period of the simulation. The attractor adjusts gracefully to the new regime with no copepods.

4.4. Sensitivity to seawater temperature

The respiration of an individual plankter varies with temperature. We have investigated the sensitivity of plankton populations to seawater temperature on 1st March $T(60)$. At the Azores site $T(60) = 14.5\text{ }^{\circ}\text{C}$. The sensitivity study extended over the range (10.5–25.5 $^{\circ}\text{C}$) encountered in the NOAA climatology along the line of annual heat balance ($B = 0$). The study was based on a set of 16, 36-year, simulations of the WB model for the Azores scenario, apart from the mixed layer temperature.

All 16 VEs had stable attractors, with modest inter-annual variation (Fig. 17). As the temperature deviated from that at the Azores, biofeedback produced a small drift in the ambient nitrogen content of the euphotic zone, measured by $N(60)$. That led to corresponding drifts in the plankton populations, but the

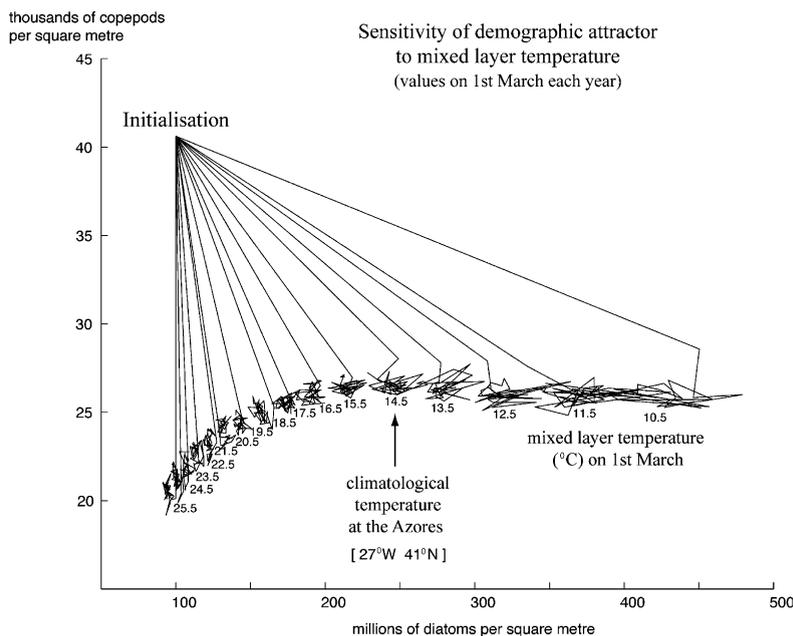


Fig. 17. The sensitivity of the demographic attractor for 1st March to mixed layer temperature.

Table 2
Response of attractor to change in mixed layer temperature

	Emergent property	% change per Kelvin degree
$P(60)$	Phytoplankton population on 1st March	6
$Z(60)$	Zooplankton population on 1st March	2
P_{\max}	Primary production (new)	1 ^a
Z_{\max}	Secondary production	1.3 ^a

^a Rises for temperatures lower than the Azores.

change over 35 years was in each case less than the demographic noise. At all temperatures the annual maximum depth of the mixed layer was stationary (168.5 m) with inter-annual variation of 0.5 m. After correcting for nitrogen drift, the demographic sensitivities to seawater temperature are given in Table 2.

The demographic response to change in temperature is an emergent property which depends on a number of competing processes. The direct processes are (1) reduced phytoplankton reproduction when respiration is higher, and (2) enhanced grazing efficiency when food supply is reduced. The indirect processes involve biofeedback to the chemical environment: the change in grazing modifies the source of dissolved inorganic nitrogen through excretion from the zooplankton and microbial action on faecal pellets and dead plankton. Although the balance between these processes changes with $T(60)$ the ecosystem remains stable over the range of temperature encountered from Scotland to Florida.

4.5. Sensitivity to temperature response parameter

The temperature sensitivity arises from the temperature parameter T_r in the plankton respiration equation. The WB default value is 10 °C. The question is whether this is the optimal parameter value for the ambient climate of the Azores. Fig. 18 shows how the annual primary and secondary productions in the Azores VE vary with T_r . We conclude that the VE is stable for all values of T_r in the range 10–25 °C. The diatoms with $T_r = 10$ °C are best fitted to the ambient climate at the Azores. They have the lowest demographic noise. Varieties with less-optimal T_r survive there in the absence of competition, but would suffer competitive exclusion if living with diatoms that are better fitted to the ambient climate at the Azores (Al-Batran et al., 1998).

4.6. Sensitivity to the limiting nutrient (nitrogen)

We have demonstrated that the Azores VE is stable when $N_0 = 5.4$ mmol N/m³. That is the value from the NOAA climatology (Levitus, 1998). Due to lack of data in February and March, it must be treated as a best estimate, but it is uncertain to a factor of 2. We investigated the sensitivity of the Azores VE to N_0 over the greater range, $0 < N_0 < 30$ mmol N/m³. Each 36-year simulation used the standard Azores scenario, apart from the value of N_0 . The results are summarised in Fig. 19, which shows a Poincaré map for the annual primary and secondary productions for 13 values of N_0 . In each case the VE adjusts to a stable attractor within three years.

The 13 attractors fall into three regimes, in which N_0 is (1) close to the climatological value, (2) much less, and (3) much more. Primary production increases monotonically through the range $0.4 < N_0 < 30$ mmol N/m³, but secondary production is markedly different in the three regimes. We shall now discuss each regime.

4.6.1. Variation around the NOAA value

The annual mean demographic attractors are stable for Azores VEs initialised with values of $N_0(60)$ in the range 2.4–9.4 mmol N/m³. The demographic noise is smallest in this regime. As the resource level

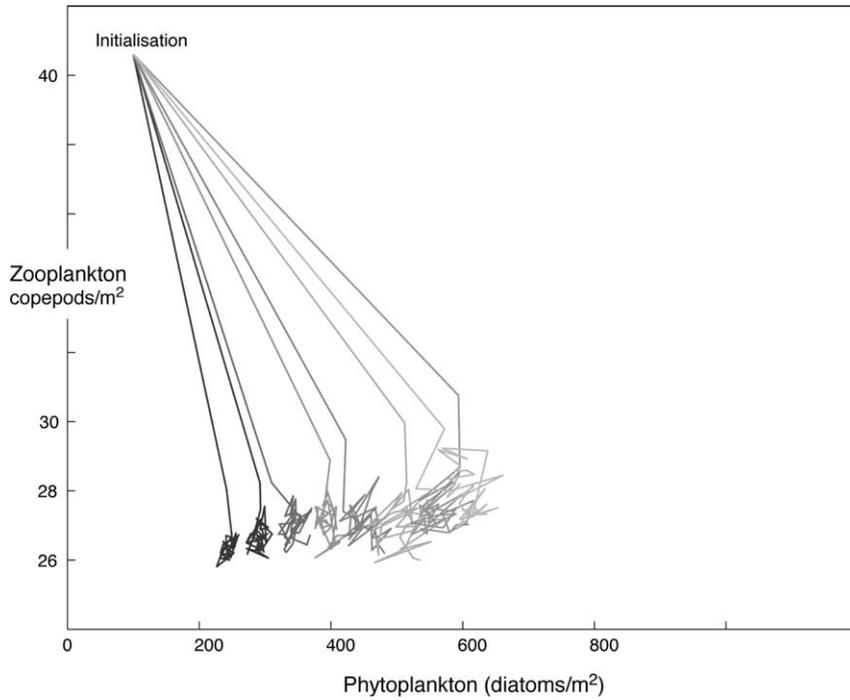


Fig. 18. The sensitivity of the annual demographic attractor for 1st March to the temperature parameter in the phytoplankton respiration equation. 36-year time series of Azores VEs with different temperature parameter in the diatom respiration equation.

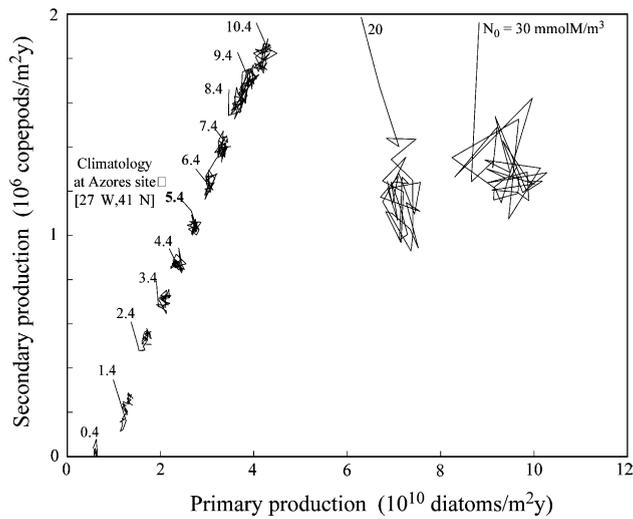


Fig. 19. Poincaré map of the time series of annual primary and secondary production for VPEs at the Azores site (27°W, 41°N) initialised with different values of N_0 the concentration of dissolved nitrogen in the mixed layer on the 1st March.

declines below 2.4 mmol N/m^3 , the attractor for phytoplankton P_A continues to fall linearly, but Z_A declines faster. This emergent property of the ecosystem is caused by the non-linear grazing efficiency curve (Fig. 12). The winter populations P_{\min} and Z_{\min} do not change significantly with N_0 .

4.6.2. Decline to copepod extinction at low nutrient concentration

In VEs with $N_0 < 2.4 \text{ mmol N/m}^3$ the annual mean phytoplankton population is so low that copepod grazing efficiency decreases significantly. Secondary production becomes too low to cover annual losses to carnivorous predation and cannibalism (which extends over a longer period of each year, as the growing season shrinks). When $N_0 < 0.4 \text{ mmol N/m}^3$, the zooplankton population survives for only 13 years (Fig. 20). The decline to extinction is accompanied by enhanced inter-annual variation, with a two-years limit cycle. Every other year, poor secondary reproduction reduces grazing allowing the phytoplankton to rise. Next year, that enhanced food supply allows better zooplankton reproduction followed by over-grazing of the under-nourished diatoms. For a dozen years, this resource-starved VE is poised on the edge of extinction. In the years when it is low, secondary production barely covers losses to predation and cannibalism, so the population is vulnerable to small fluctuations. Eventually, demographic noise superimposed on the limit cycle tips it over the edge. In this instance that happens in the 13th year; but the time to extinction has a broad spread in an ensemble of VEs differing only in the seed value of the random number generator.

Fig. 20 reveals enhanced inter-annual variation superimposed on the limit cycle during the decline to extinction. This is due to inter-annual variation in the over-wintering weight of lineages containing zooplankton so weak that they cannot reproduce every year. The threshold weight for this to occur fluctuates with the demographic noise. The amplitude increases at low resource levels; a consequence of enhanced intra-population variability. It is not a symptom of chaotic instability. That is confirmed by the rapid adjustment to the attractor from an initially unbalanced condition.

4.6.3. Reduced secondary production at very high nutrient concentration

Finally we consider how the VE responds to very high resource levels. At $N_0 = 10.4 \text{ mmol N/m}^3$ the annual production attractor lies close to the linear trend established at lower N_0 . When $N_0 > 10.4$ the VE passes into a new regime, defined by continued rise in $\mathbf{P}(y)$ with N_0 , but a sharp decline in $\mathbf{Z}(y)$; there is increased inter-annual variation of both $\mathbf{P}(y)$ and $\mathbf{Z}(y)$. As N_0 increases from 20 to 30 mmol N/m^3 , the secondary production recovers a little (from 1.1 to 1.3 million copepods/ m^2), but the rise in primary production is less than between 10 and 20 mmol N/m^3 . Inter-annual variation continues to rise.

What makes this new regime so different? The answer is that high N_0 nourishes such a rich food supply for the zooplankton that some of the lineages produce twice in the same year. In principle, double reproduction can occur in two ways: by adults producing two broods a few weeks apart (siblings), or by their offspring reproducing in the year they were hatched (grand-children). The first possibility is forbidden in the WB model because the prescribed time for death by senility equals the gestation time, preventing copepods from reproducing more than once. The second possibility is that their offspring put on weight fast enough to reproduce before the food runs out. Such double events are clearly seen in Fig. 18. Copepodites hatching earliest have the best chance of reproducing in the same year; they are the offspring of adults that had the highest ranking body weight during the previous winter (Fig. 8). Marshall & Orr (1955) report double reproduction in *Calanus finmarchicus* under similar conditions.

4.6.4. Stability regimes

One of the hallmarks of chaos is the progression from stability to oscillation to erratic fluctuations in different regions of model parameter space and in different ranges of exogenous properties, such as ambient climate. PFOR reported such regimes in their Field simulations of the plankton ecosystem. But that is not the cause of the regime shift in Fig. 19 when the $N > 10 \text{ mmol N/m}^3$. Even when $N = 20$ and 30 mmol N/m^3 the multi-year mean remains independent of initial conditions. The increased inter-annual variance is due to intra-population variation in reproduction.

We can divide the plankton lineages into two classes. The first reproduces once per year. All the copepods are in this class at the Azores. The second class occasionally produce two generations in the same year.

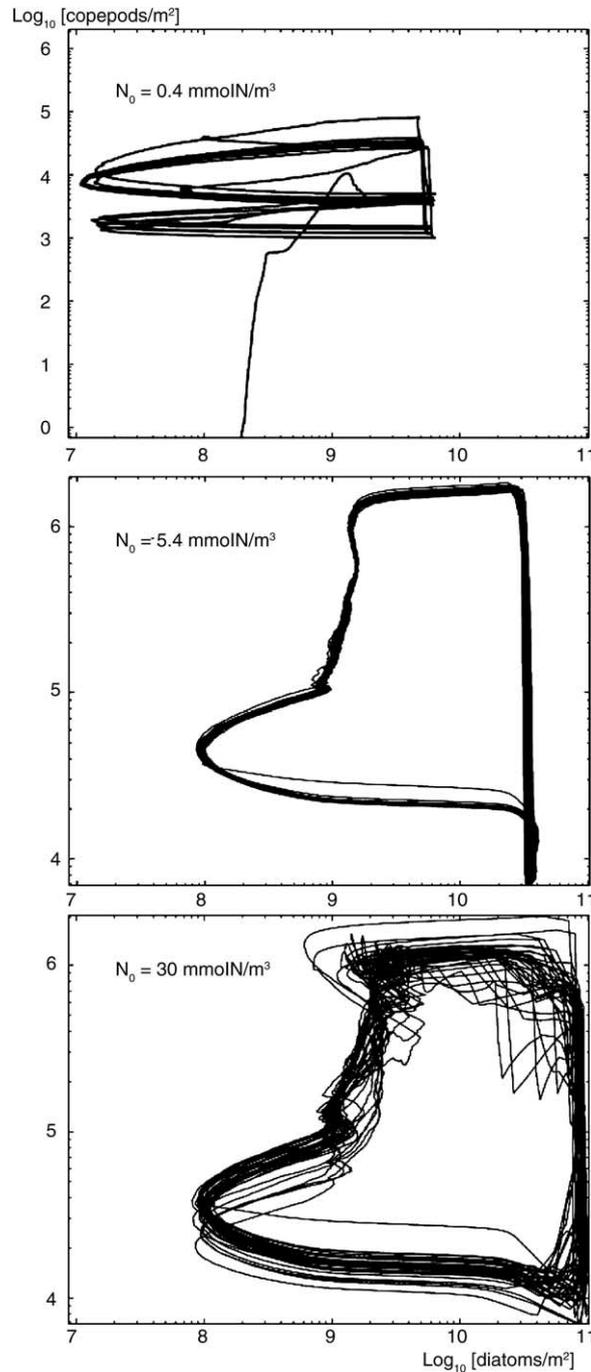


Fig. 20. The annual demographic attractor for three values of N_0 the dissolved nitrogen concentration in the mixed layer on 1st March: $N_0 = 0.4 \text{ mmol N}/\text{m}^3$, showing copepod extinction in the 13th year; $N_0 = 5.4 \text{ mmol N}/\text{m}^3$, the climatological value at the Azores site [41°N, 27°W]; $N_0 = 30 \text{ mmol N}/\text{m}^3$, showing the new regime in which some copepod lineages occasionally produce two generations in the same year.

They start the growing season in that year with the highest ranked body weight and reproduce early, so that their daughters grow rapidly to reach maturity and reproduce before the food is exhausted by the copepods in the other lineages. Mothers and daughter die, leaving the granddaughters to survive the coming winter. They hatched just before the food ran out so they do not put on much weight before the end of the growing season. That means they start the next growing season with a low body weight, and are unlikely to reproduce once in that year. However, they put on sufficient weight to highly ranked at the start of the following year. Thus the copepods in the second class reproduce intermittently, with granddaughters in one year followed by no offspring in the next, then back to granddaughters. On average the secondary production in this second class of lineages is lower than the first class. The tortoises win the race against the hares. The separation into the two classes increases the inter-annual variability. Increasing N_0 by 50% (from 20 to 30 mmol N/m³) produces less than 20% increase in secondary production, reflecting the near balance between gain and loss in the two classes of lineage. The change also affects the changed efficiency of grazing on the phytoplankton and therefore the mean primary production ($P_{\max} - P_{\min}$). To conclude, the enhanced inter-annual variability is a rational response of the zooplankton to a high resource regime: it is not an example of chaos.

5. Influence of ocean circulation

The numerical experiments reported above neglected advection. They simulated the ecosystem in a virtual mesocosm moored off the Azores (position 1 in Fig. 1). The contribution of advection to the annual heat budget of the mesocosm is zero at that site; the surface fluxes are in balance (solar heating equals cooling to the atmosphere). The influence of baroclinic advection was assumed to be zero, too. In other words the horizontal flux divergences of the other ecosystem properties (heat, nutrients, plankton, etc.) were all assumed to zero in every layer in the virtual mesocosm. The error arising from that assumption is quite small for the gyre circulation and scalar fields at the Azores, which lies in the weakly flowing re-circulation regime. The error in primary production arising from neglecting mesoscale advection has been estimated to be around 10% (Martin, Richards, & Fasham, 2001).

5.1. Research strategy

The boundary conditions at the sea surface are defined by fluxes. They were computed from Bunker's climatology, which describes a stationary annual cycle at each geographical location with a resolution of one month and one degree of latitude and longitude. The Azores VE was driven by the annual cycle at the location where the mesocosm was moored [27°W, 41°N]. Now we consider the stability in the mesocosm if it were allowed to drift with the ocean circulation, while remaining upright. We assume that it moves with the mean flow in the top 100 m of the ocean; we call this barotropic drift. As in the previous experiments, we shall ignore the flux divergences at every level due to the baroclinic component of the flow. As the mesocosm drifts around the ocean it samples the climate at each location along its track. So the ambient surface fluxes will not follow a stationary annual cycle. The VE in the drifting mesocosm will not therefore be able to adjust to an attractor of the kind we computed when the mesocosm was moored.

Nevertheless, if the ecosystem were intrinsically stable it would adjust to a different kind of attractor, one that is prescribed by the upstream history of surface fluxes, which is determined by the mesocosm's track. We call this a Geographically-Lagrangian (GL) attractor. (The attractor in the moored mesocosm will be called a geographically-eulerian attractor.) Our hypothesis was that this GL attractor would be independent of initial conditions, provided the integration was started far enough upstream for the legacy of initialisation errors to have decayed to less than the noise in the VE. If that were true, then the virtual

ecosystem in the drifting mesocosm would be stable and predictable. That would be a useful first step towards showing that ocean circulation does not make the plankton ecosystem become unstable.

5.2. Two numerical experiments

We performed two numerical experiments with drifting mesocosms. The tracks are shown in Fig. 1. They were derived from a velocity field obtained from an ocean circulation model (New et al., 1995). The first experiment (Track 2) was designed to show how the virtual ecosystem changes as it drifts into the tropics, passing from the regime of seasonal oligotrophy (like that experienced off the Azores) to the regime of permanent oligotrophy. The second experiment (Track 3) was designed to test our hypothesis that the legacy of the initialisation errors would decay, leaving a stable GL attractor.

5.2.1. Track 2 – Transition to extinction

Fig. 21 shows the demographic changes occurring in the mesocosm as it drifts from the Azores to the Antilles. As the water column enters the heating zone, the mixed layer shoals. The annual maximum depth of the mixed layer becomes less each year. The lower portion of the seasonal thermocline is subducted into the permanent thermocline each spring. The dissolved and particulate nitrogen in the subducted water is exiled from the euphotic zone, reducing new production next year. The decline in annual primary production puts a stress on the zooplankton. Secondary production declines in the first four years. There is no reproduction in the fifth year. The zooplankton decline towards extinction. The final decline is slow because daily carnivorous predation has fallen to less than 1 copepod/m². That is because the diatoms have sunk in the permanent thermocline where the copepods forage, without migrating up into the mixed layer where they can be seen and eaten.

5.2.2. Track 3 – Recovery from tropical stress

Fig. 22 shows the changes occurring in the water column as it makes 13 five-year laps of the closed circuit around Bermuda (track 3 in Fig. 1). The surface heat budget around the circuit is close to zero; a small correction (4 W/m²) was introduced to close the budget. This ensures that the scenario follows a stationary five-year cycle.

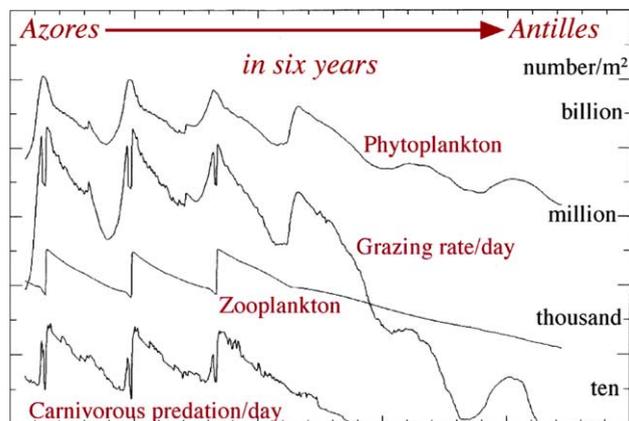


Fig. 21. The transition to copepod extinction in a virtual mesocosm drifting from the Azores to the Antilles (from location 2 in Fig. 1).

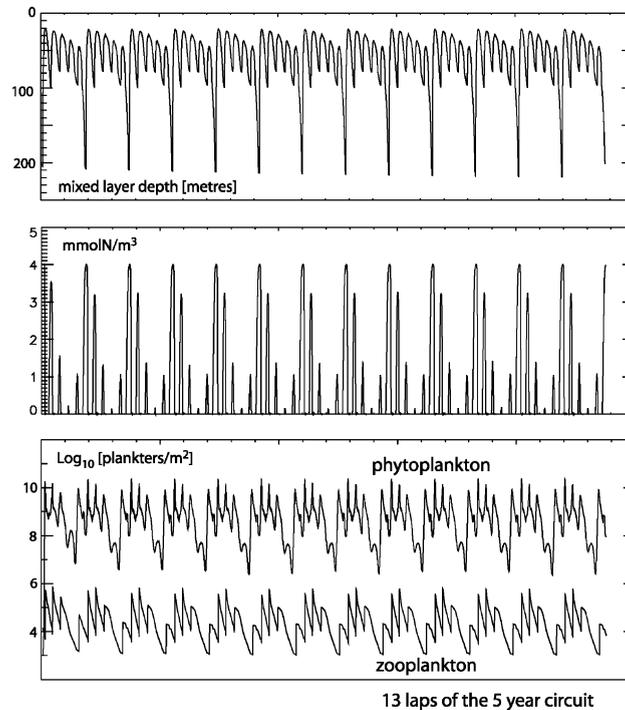


Fig. 22. Plankton demographic history in a water column circulating 13 times around the 5-year circuit in the Sargasso Sea (track 3 in Fig. 1). Time series of 65 years with stationary climate. (a) Depth of the mixed layer, (b) mixed layer nitrogen concentration, (c) phytoplankton and zooplankton biomass.

The result is that the ecosystem also follows a stationary five-year cycle, after an initial period of 15 years (three laps of the circuit) during which initialisation errors decay. The VE in the drifting mesocosm then settles to a stable GL attractor. The mesocosm passes through a geographical location on the track once every five years. It does so on precisely the same day of the year. The emergent properties of the VE have the same values every time the mesocosm passes through that location.

The VE experiences great changes around the track, but they are reversible. The mixed layer is shallow in the tropics, the phytoplankton population declines to such a low level that the zooplankton fail to reproduce. They are on the way to extinction as in the previous experiment. However, before they become extinct the mesocosm drifts back into the cooling zone where the mixed layer deepens entraining nutrients from the permanent thermocline; the phytoplankton population grows again in a spring bloom and the zooplankton reproduce. Despite resource stress in the tropics, the phytoplankton and zooplankton populations recover fully.

5.2.3. Comment

The behaviour reported here, in which the plankton ecosystem recovers quickly from a period of climate stress, is reminiscent of results reported by Taylor et al. (2002), who found similar adjustment within a few years to changes in the North Atlantic climate. They concentrated on the multi-year correlation of observed copepod populations with the latitude of the Gulf Stream. A time series of this correlation from 1966–1998 is characterised by periods of around five years in which the correlation is very high separated by transitions lasting from one to three years. A similar pattern was found in a one-dimensional simulation derived from

integrating ERSEM (Baretta, Ebanhoh, & Ruardij, 1997) under boundary conditions from the time series of weather recorded at Dublin. The sharp transitions between periods of stable correlation are consistent with our results in which the ecosystem takes one to three years to adjust to the attractor after a step change in ambient climate. However, there has been no systematic investigation of the multi-year stability of ERSEM (Dr. Icarus Allen, personal communication).

6. Predictability

6.1. The plankton multiplier

The stability found in our virtual ecosystems offers useful predictability for problems involving changes over many years. We illustrate this by simulating the response of the VE to a progressive rise in the atmospheric concentration of carbon dioxide (ApCO_2) during the next 50 years, following the IPCC “Business-as usual” scenario (Houghton et al., 2001). The greenhouse effect changes the infrared radiation at the sea surface by about 5 W/m^2 as the atmospheric carbon dioxide concentration doubles over those 50 years. Woods & Barkmann (1995) showed that a VE forced by twice present ApCO_2 had significantly reduced H_{max} , which caused corresponding reductions in N_{max} , primary and secondary production. Those differences from present climate led to reduced carbon dioxide uptake, which represented positive feedback in the greenhouse effect; a phenomenon named the “Plankton multiplier”.

That investigation compared two VEs each in equilibrium with steady ApCO_2 . Simulating the progressive change in the VE over 50 years as ApCO_2 rises provides a more challenging test of predictability. The numerical experiment was based on 13 laps of the closed five-year circuit in the Sargasso Sea (track 3 in Fig. 1). During the first three laps (15 years) the ApCO_2 was held constant at the present value. That allowed the VE to adjust to the GL attractor. For the next ten laps (50 years) ApCO_2 was increased progressively following the IPCC business-as-usual scenario, so that it had doubled at the end of the simulation.

The resulting changes in the VE are shown in Fig. 23. As expected from the earlier study, there is a progressive decrease in H_{max} , N_{max} , P_{max} , and Z_{max} , and in the sequestration of carbon in the permanent thermocline carried by sinking detritus (dead plankton and faecal pellets). As we have seen before, the grazing efficiency [$Z(y)/P(y)$] rose as $P(y)$ declined. So a smaller fraction of the phytoplankton died by starvation and sank into the deep ocean. This positive feedback in the biological pump is an emergent property; it accelerated the decline in oceanic uptake of atmospheric carbon dioxide. Over 50 years the sequestration of carbon by the biological pump was reduced by 15%. The demographic noise in the VE, and hence the inter-annual variability, is low enough to track the subtle changes in grazing as the ambient climate changes due to pollution with greenhouse gases. The same skill will be achieved in predicting the impact on the VE of two other processes, stratospheric dust from volcanoes (Genin et al., 1995), and the Milankovich ice age cycle (Berger et al., 1984), both of which change the radiation at the sea surface by a few W/m^2 . Such subtle radiative forcing represents a stringent test of the predictability of the VE. The results augur well for useful predictability in practical problems where the forcing is less subtle.

7. Discussion

We now address the question: Why are some simulations of the plankton ecosystem stable and others not? We start from the fact that our virtual ecosystems are globally stable. That has been established by the numerical experiments reported in this paper. The challenge is to explain what is different in other simulations that exhibit instability. We limit the discussion to one-dimensional modelling.

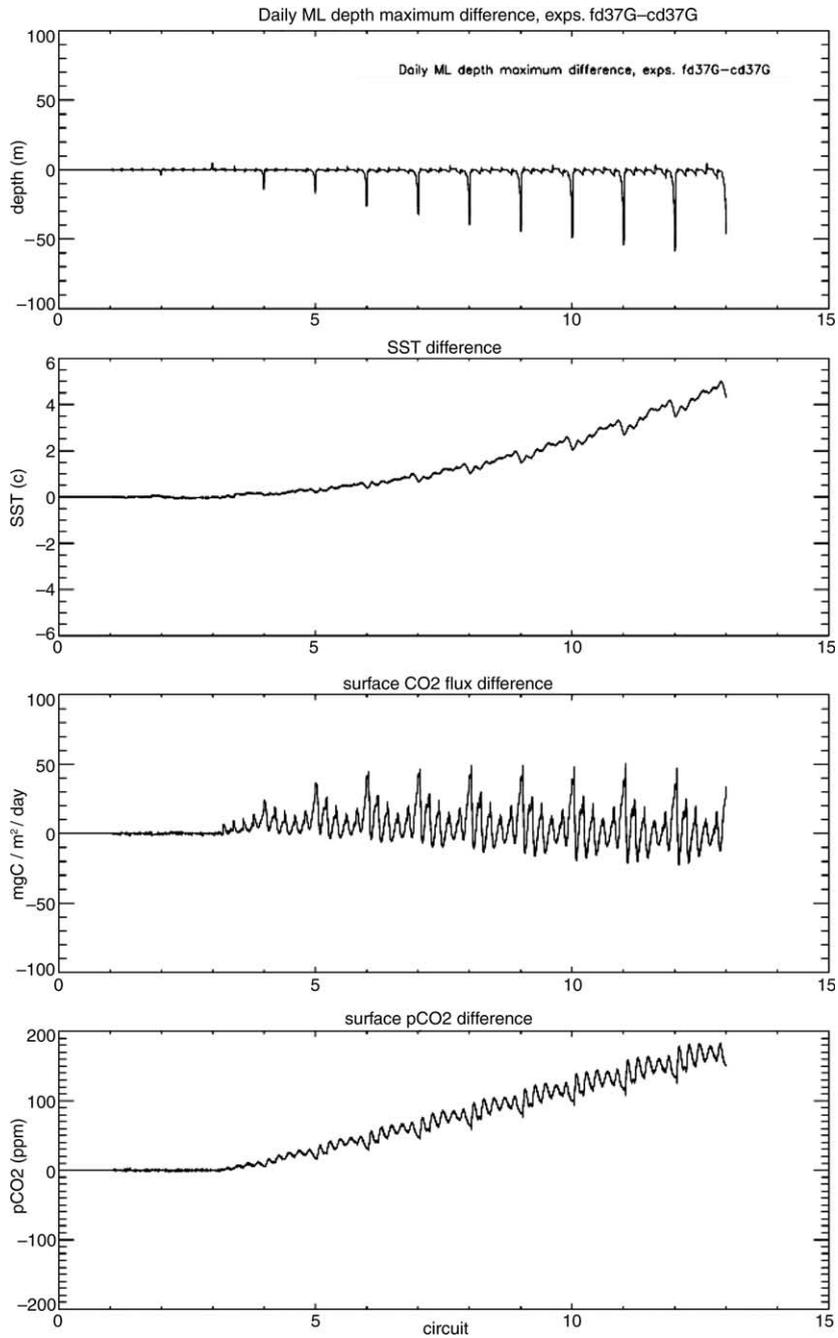


Fig. 23. Changes in the Sargasso Sea VE due to rising atmospheric carbon dioxide over 50 years according to the IPCC Business-as-usual scenario. The figure shows the difference between two VEs in water columns drifting for 13 laps of the Sargasso Sea circuit (track 3 in Fig. 2). The surface physical climate follows the same stationary annual cycle at each geographical location in both VEs. The atmospheric partial pressure of carbon dioxide was constant in the first (reference) VE. In the second VE it was held constant for the first three laps (15 years) then allowed to rise according to the IPCC Business-as-usual scenario. The four panels show the differences for the IPCC and reference VEs: (1) mixed layer depth, (2) sea surface temperature, (3) carbon dioxide flux, (4) sea surface OpCO_2 .

7.1. *The attractor*

We focus on the attractor, which is the epitome of stability. Virtual ecosystems are free to adjust to an attractor, which has properties determined by the specification of (1) the model and (2) the scenario for exogenous conditions. The attractor is independent of the initial conditions. It exhibits a low level of demographic noise due to ecological processes, not chaotic instability. The attractor changes with the model parameters, and with the limiting resource available to the plankton. When the parameter values and/or resource level are inadequate to sustain all the species in the initial conditions, the unsustainable species become extinct, and the attractor adjusts gracefully to one with the remaining species. At high resource levels the attractor adjusts to a new regime in which the zooplankton produce more than one generation per year. That transition is gradual: as the resource level rises, an increasing fraction of the zooplankton lineages produce two generations per year.

Ocean circulation affects the form of the attractor. For heuristic reasons, we started our investigation with a simplified scenario in which there was no circulation. To make that work we chose a location (off the Azores) where the surface annual heat flux is in balance, so advection makes no contribution. This produces a Geographically-Eulerian Attractor (GEA) characterised by an adjustment time of less than three years. The legacy of any initialisation error decays to below the demographic noise in that adjustment time.

The next set of numerical experiments investigated the influence of ocean circulation simulating the virtual ecosystem in a mesocosm that took five years to drift barotropically around a closed circuit in the Sargasso Sea passing deep into the permanently oligotrophic and eutrophic regimes. This produced a Geographically-Lagrangian Attractor (GLA) with a five-year periodicity. The adjustment time was 15 years. The legacy of any initialisation error decayed to below the demographic noise in three laps of the circuit. The nature of the two classes of attractor is rather different. The GEA is in local balance with the stationary annual cycle of surface fluxes. The GLA is in balance with the stationary five-year cycle. But it is not in local balance with the stationary annual cycle of surface fluxes. The GLA attractor is in a perpetual state of lagged response to the history of upstream forcing. But that lagged response is an attractor. The virtual ecosystem has the same state each time it passes through the same geographical location. The demographic noise is small and attributable to ecosystem processes. These two numerical experiments were designed to establish the stability of a virtual ecosystem, whether it is stationary or drifting with the ocean circulation. The experiments used stationary cycles of forcing to prove the point. We have since confirmed the result for tracks across the ocean, which do not have stationary periodic forcing.

7.2. *The adjustment process*

The attractor describes the state of all the emergent properties of a virtual ecosystem when it is in balance with the upstream history of external forcing. The virtual ecosystem takes a few years to adjust to the attractor after being initialised with an assumed state that is not on the attractor for that time and place. There is a similar period of adjustment when the virtual ecosystem experiences an internal regime shift; for example, when one of its species becomes extinct. Regardless of the cause, adjustment is effected by a variety of ecological feedbacks. These include the predator–prey feedback familiar from simple Lotke–Volterra models. Also bio-optical feedback, which affects primary production (“self-shading”), secondary production (“darkness at noon”), and the depth and temperature of the mixed layer. Another familiar ecological phenomena is the trophic cascade, by which the attractor adjusts to changes in top predators. Any artificial constraint on these processes may impede the virtual ecosystem from adjusting freely to the attractor. In that case the virtual ecosystem might not adjust to the attractor: it might oscillate, or fluctuate chaotically. It might adjust to a strange attractor that involves substantial inter-annual variation. That would limit predictability.

7.3. Constraints on adjustment

We now consider what might constrain the free adjustment of the virtual ecosystem to the attractor. There are two broad issues. The first is the metamodel; the second is the specification of a particular simulation. The specification comprises the model and scenario. The model includes the equations and parameter values. The scenario describes exogenous conditions, including solar elevation and atmospheric conditions, the ocean circulation and the resources (nutrients). If the system is free to adjust it will respond to change by shifting smoothly to a new attractor. If that adjustment is prevented by some aspect of the metamodel or the specification, the simulation will respond by vacillating between two attractors, or by entering into a strange attractor. Classical stability analysis maps the values of model parameters or resource levels lying on the boundaries between those three regimes defined by a stable attractor, vacillating or strange attractor. Our investigation shows that the first regime extends over all values of model parameters and resource levels expected in the ocean. We follow ecological practice in saying that our virtual ecosystems are therefore “globally stable”.

7.4. Metamodel

All simulations are based on a metamodel, which constrains the specification of the model and scenario. The investigations of plankton ecosystem stability reported in the scientific literature are based on many different metamodels. Some of them introduce constraints on the feedback processes needed for free adjustment to an attractor.

7.4.1. Lagrangian Ensemble metamodel

The virtual ecosystems described in this paper are all based on the Lagrangian Ensemble (LE) metamodel. It uses agent-based computing. The agents are used to describe the plankton. Each agent describes the trajectory of a single plankter, taking account of its motion with the water (advection by currents and random displacement by turbulence), plus its motion relative to the water (by sinking or swimming). At each location along this trajectory the agent experiences an ambient environment, which comprises the values of all the environmental fields interpolated to that location and time. These fields include the concentrations of every species, including both predators and prey. The change in biological state of the plankton associated with a particular agent is computed using biological rules, which depend on its current state and ambient environment. This permits the use of phenotypic equations. Each agent follows a unique trajectory. The differences are caused by turbulence in the mixed layer. They lead the plankton associated with each agent to develop and behave individually. So intra-population variation is a free emergent property of the simulation. The demographic properties of each population are expressed as fields. They are computed by summing over all the agents in each layer of the mesh used to define the fields. Predation rules use the field of prey concentration. Bio-optical feedback is computed from the field equations for phytoplankton. Bio-chemical feedback is computed from the actions of every agent in each layer.

7.4.2. Field metamodel

Most models designed to simulate the plankton ecosystem are based on the Field Metamodel (FM), which treats plankton as though the biomass of each species were a continuum with its biological state varying in space and time. Models created under this metamodel have differential equations that describe the rate at which the biomass of one species changes at each location in a fixed mesh. The population-based equations describe biological processes that are described phenotypically in individual-based models: photosynthesis, predation, etc. They also describe the feedback processes that are so important for the adjustment of the simulated ecosystem to an attractor. However, it is difficult to represent plankton behaviour in FM, whether it is foraging or diel migration.

To what extent does FM constrain adjustment of the ecosystem, so that it may not reach the attractor? It clearly has fewer degrees of freedom than the LE metamodel. Both use field descriptions of each plankton population. They are emergent properties of the LE metamodel, but explicit state variables of FM models. As the result, FM biofeedback is immediate and local, whereas LE biofeedback is dispersed through many thousands of agents following different trajectories. FM lacks the intra-population variability, which disperses biofeedback in space and time to create a more fluid adjustment to change. That is especially important under conditions that require a phase shift in attractor, whether due to extinction or more than one generation per year. The constraint imposed by not permitting intra-population variability is a prime suspect in the chaos at high resource levels reported by PFOR. It leads to a strange attractor, where LE produces a smooth transition between stable attractors.

7.4.3. *Box metamodel*

The simplest metamodel, adopted widely by theoretical population ecologists, does not describe the spatial distribution of each plankton population, but the changes occurring in each of a set of boxes. They might be defined as, for example, the mixed layer, the seasonal thermocline and the permanent thermocline. The depths of the boundaries between these three boxes may be fixed or exhibit annual variation prescribed in the scenario. This was the metamodel adopted by PFOR for their investigation of stability. The boundaries specified in box models should be variables of the ecosystem. They should be free to change as part of the process of adjustment to the attractor. Fixing how they change in the scenario is a constraint that will impede that adjustment. The ecosystem may respond by vacillating or becoming chaotic. It is therefore not surprising that most examples of instability in plankton ecosystem modelling are based on the box metamodel.

7.5. *The specification*

Having chosen the metamodel, the investigator must now specify the model and the scenario. The model includes the physics (including air–sea interaction, optics and turbulence), the chemistry (including carbon, nutrients and pigments) and the biology (the plankton community and biofeedback). It comprises the equations and parameter values needed to describe those processes at the level permitted by the metamodel. The specification includes all the exogenous phenomena which, by definition, are unaffected by feedback from the ecosystem. An essential feature of the specification is that phenomena must not be allocated to the scenario when they should be part of the model, or vice versa. We have already encountered an example, namely the allocation of the annual cycle of the mixed layer to the scenario rather than to the model.

7.5.1. *The model*

The model defines the scope of the ecosystem. It determines how fine-grained is the resolution of the physics, chemistry and biology. For example, the radiation equations in the WB model describe the absorption of solar radiation by the plankton in 25 wavebands, but it does not describe the way plankton scatter light. The chemical equations are limited to nitrogen and carbon, both in solution and in the plankton, with accurate budgeting of the changing balance between those components. It computes the flux of carbon dioxide through the sea surface, but not that of nitrogen. The biological state variables are limited to a simple community of plankton comprising explicit populations of diatoms, copepods and their corpses and faecal pellets, plus implicit populations of attached bacteria which remineralised carbon and nitrogen in the detritus. Trophic closure was effected by an implicit population of carnivorous zooplankton which eat copepods at a rate determined by their visibility.

The WB model can be described as an NPZD model designed for the LE metamodel. The scientific literature contains many examples of similar models designed for the Field or Box metamodels. PFOR is an

example. To the extent that the biological functions are equivalent the model does not introduce any obvious constraint preventing free adjustment to the attractor. We have dealt separately with the constraints arising from the choice of metamodel.

However, there is one significant difference between the biological functions used in the WB model and most of the others. That is in the formulation of the trophic closure. The use of a visibility closure in WB allows free adjustment. Woods & Barkmann (1993) showed that changing the closure parameter merely led to a different stable attractor. However, that is not the case with the commonly used quadratic closure (Steele & Henderson, 1995), which is known to constrain the ecosystem so severely that it causes transition to a strange attractor.

7.5.2. *The scenario*

The scenario defines the initial and boundary conditions used to integrate the model.

7.5.3. *Initial conditions*

If the ecosystem is globally stable, the only properties that must be specified in the initial conditions are those that define the resource level in the ecosystem. In our numerical experiments, the resource was nitrogen, for which the only source was the initial profile of nitrate concentration in the water column. (Our WB model contained no microbial process for fixing nitrogen from the atmosphere.) All other ecosystem variables in the initial conditions were eventually adjusted to values on the attractor.

7.5.4. *Ocean circulation*

A four-dimensional velocity field is derived from an ocean circulation model. This is used to compute the track along which the mesocosm will drift. The changing geographical location determines the history of surface fluxes.

7.5.5. *Boundary conditions*

The simulation is driven by surface fluxes. The flux of solar radiation is computed from an astronomical formula for solar elevation and a meteorological formula for the reduction due to clouds. The cloud cover is specified in the scenario. All the other surface fluxes can be computed using bulk aerodynamic formulae which depend on the difference between the atmospheric and oceanic values of a variable such as the partial pressure of carbon dioxide. The former is specified in the scenario, the latter is an emergent property of the virtual ecosystem. That is how the WB model computes the flux of carbon dioxide through the sea surface. It is a free variable of the ecosystem and therefore offers no constraint on adjustment to the attractor. The same cannot be said for surface fluxes of sensible, latent and radiative heat. These, too, should be free variables responding to the emergent mixed-layer temperature and the prescribed atmospheric surface temperature. In fact, we prescribed the surface heat fluxes in the scenario, using the ERA40 data. That was a mistake. It introduced a constraint that prolonged the initial adjustment by several years (see Fig. 2). It did not provoke instability, but the lesson is that one must be careful not to transfer to the scenario properties that should be in the model.

8. Conclusion

We have shown that Virtual Ecosystems based on Lagrangian Ensemble integration of the WB individual-based model are globally stable. When forced by a stationary cycle of surface fluxes all the emergent properties follow stable stationary annual cycles. The VE has a little inter-annual variability in environmental and demographic variables due to turbulence, which randomly displaces plankton in the surface mixing layer, causing intra-population variability. The VE deviates slightly from ergodicity because of inheritance

through zooplankton lineages. It has a stable attractor, which is insensitive to initial conditions. The legacy of initialisation error decays within three years. The attractor varies with parameter values. At extreme parameter values, the zooplankton population becomes extinct. The attractor adjusts gracefully, without chaotic instability.

The VE remains stable over a wide range of resource level, with primary and secondary production varying linearly with resource (nitrogen) over a wide range. When the nitrogen content is very low the copepod population becomes extinct after a few years, and the attractor adjusts to a new regime for the truncated community. When the resource level rises the attractor enters a new regime, in which some of the zooplankton lineages occasionally produce two generations in one year. In this regime secondary production rises with the VE nitrogen content as an increasing fraction of the zooplankton lineages produce two generations per year. The attractor remains insensitive to initial conditions in this new regime.

A virtual ecosystem in a mesocosm drifting with the ocean circulation is also stable. This was demonstrated by geographically-lagrangian integration along a closed track that circumnavigated Bermuda in five years. The surface heat budget was in balance over those five years, but the track passed deep into the oligotrophic and eutrophic zones. The attractor for such a moving virtual ecosystem is called a geographically-lagrangian attractor. The VE is in a state of continuous adjustment to different upstream forcing. So it is not in local balance with the annual cycle at any location along the track, because it is in a perpetual state of lagged response to the history of upstream forcing. But it passed through each location in the same state on successive laps, with only a small inter-lap variability caused by turbulence in the ecosystem.

The drifting mesocosm experiences changing ambient climate. That modulates the annual maximum depth of the mixed layer depth, and therefore the available nitrogen load. The plankton populations respond to this changing resource level. The nutrient level is so low in the tropics that the zooplankton cannot reproduce there. However, they recover when the water column drifts back into the cooling zone with its deeper mixed layer and increased available nutrient content. The legacy of initialisation error is lost in three laps of the closed circuit.

We explain the global stability of our virtual ecosystems in terms of biofeedback processes that effect rapid adjustment to the attractor. Any impediment to those processes can prevent free adjustment, and lead to vacillation between two attractors, or transition to a strange attractor. We consider three factors that are important for free adjustment to a stable attractor. The first is the choice of metamodel. We have shown that the lagrangian ensemble metamodel leads to global stability. Instability reported by other authors using the alternative Field and Box metamodels is attributed to the constraints they impose on the free adjustment to an attractor. The second factor is the specification for the simulation. This has two parts: the model and the scenario. The latter contains the exogenous conditions. Using the scenario to fix key ecosystem variables can constrain adjustment to a stable attractor. So too can some specifications of model equations, for example the trophic closure.

The stability of a virtual ecosystem on a geographically-lagrangian attractor offers the prospect of useful prediction of ecosystem response to climate change. This was demonstrated by computing the response of the drifting virtual ecosystem to IPCC “Business as usual” conditions.

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References

- Al-Batran, S., Field, A. J., Wiley, R. L., & Woods, J. D. (1998). Parallel simulation of plankton ecology. In *Proceedings of the IASTED international conference modelling & simulation*. Philadelphia: IASTED.
- Allen, J. T., Smeed, D. A., Nurser, A. J. G., Zhang, J. W., & Rixen, M. (2001). Diagnosis of vertical velocities with the QG omega equation: An examination of the errors due to sampling strategy. *Deep-Sea Research*, 48(2), 315–346.
- Ascioti, F. A., Beltrami, E., Carroll, T. O., & Wirick, C. (1993). Is there chaos in plankton dynamics? *Journal of Plankton Research*, 15, 603–617.
- Baretta, J. W., Ebanhoh, W., & Ruurdij, P. (1997). The European Regional Seas Ecosystem Model (ERSEM) II. *Journal of Sea Research*, 38(3/4), 229–483.
- Berger, A., & Imbrie, J., et al. (Eds.). (1984). *Milankovich and climate*. Dordrecht: Reidel.
- Berryman, A. A., & Millstein, J. A. (1989). Are ecological systems chaotic – And if not, why not? *Trends in Evolutionary Ecology*, 4(1), 26–28.
- Casti, J. (1997). *Would be worlds: How simulation is changing the frontiers of science*. New York: John Wiley.
- Caswell, H., & Neubert, M. G. (1998). Chaos and closure terms in plankton food chain models. *Journal of Plankton Research*, 20, 1837–1845.
- Cushing, D. (1995). *Population production and regulation in the sea: A fisheries perspective*. Cambridge: Cambridge University Press, 354 pp.
- Cushing, J. M., Costantino, R. F., Dennis, B., Desharnais, R. A., & Henson, S. M. (2003). *Chaos in ecology – Experimental non-linear dynamics*. Amsterdam: Academic Press, 225 pp.
- Edwards, A. M., & Brindley, J. (1996). Oscillatory behaviour in a 3-component plankton population mode. *Dynamics and Stability of Systems*, 11, 349–372.
- Edwards, A. M., & Brindley, J. (1999). Zooplankton mortality and the dynamical behaviour of plankton population models. *Bulletin of Mathematical Biology*, 61, 303–341.
- Evans, G. T., & Fasham, M. J. R. (Eds.). (1993). *Towards a model of biogeochemical processes. NATO ASI series*. Berlin: Springer Verlag.
- Fasham, M. J. R., Sarmiento, J. L., Slater, R. D., Ducklow, H. W., & Williams, R. (1993). Ecosystem behaviour at Bermuda station “S” and ocean weather station “India”: A general circulation model and observational analysis. *Global Biogeochemical Cycles*, 7(2), 379–415.
- Fu, L. L. (2001). Ocean circulation and variability from Satellite Altimetry. In G. Siedler, J. Church, & J. Gould (Eds.), *Ocean circulation and climate* (pp. 141–172). London: Academic Press.
- Garnier, E., Barnier, B., Siefridt, L., & Beranger, K. (2000). Investigating the 15 years air–sea flux climatology from the ECMWF reanalysis project as a surface boundary condition for ocean models. *International Journal of Climatology*, 20(14), 1653–1673.
- Genin, A., Lazar, B., et al. (1995). Vertical mixing and coral death in the Red Sea following the eruption of Mount Pinatubo. *Nature*, 377, 507–514.
- Glendinning, P. (1994). *Stability, instability and chaos: An introduction to the theory of nonlinear differential equations*. Cambridge: Cambridge University Press, 388 pp.
- Godfray, H. C. J., & Blythe, S. P. (1990). Complex dynamics in multi-species communities. *Philosophical Transactions of the Royal Society of London B*, 330, 221–233.
- Houghton, J. T. et al. (Eds.). (2001). *Climate change 2001: The scientific basis*. Cambridge: Cambridge University Press.
- Isemer, H. J., & Hasse, L. (1987). *The Bunker Climate Atlas of the North Atlantic Ocean*. Berlin: Springer Verlag.
- Johnson, S. (2001). *Emergence*. London: Allen Lane, 288 pp.
- Kot, M. (2001). *Elements of mathematical ecology*. Cambridge: Cambridge University Press, 453 pp.
- Lack, D. L. (1954). *The natural regulation of animal numbers*. Oxford University Press.
- Large, W. G., & Nurser, A. J. G. (2001). Ocean surface water mass transformation. In G. Siedler, J. Church, & J. Gould (Eds.), *Ocean circulation and climate* (pp. 317–336). London: Academic Press, and Plates 5.1.9 & 5.1.11.
- Levitus, S. (1998). *World Ocean Atlas 1998*. NOAA, Washington, DC: Government Printing Office.
- Liu, C.-C., & Woods, J. D. (2004a). Prediction of ocean colour: Monte Carlo simulation applied to a virtual ecosystem based on the Lagrangian Ensemble method. *International Journal of Remote Sensing*, 25, 921–936.
- Liu, C.-C., & Woods, J. D. (2004b). Deriving four parameters from patchy observations of ocean color for testing a plankton ecosystem model. *Deep-Sea Research*.
- Lomnicki, A. (1988). *Population ecology of individuals*. Princeton, NJ: Princeton University Press.
- Lomnicki, A. (1999). Individual-based models and the individual-based approach to population ecology. *Ecological Modelling*, 115(2–3), 191–198.
- Longhurst, A. (1998). *Ecological geography of the sea*. London: Academic Press.
- McGillicuddy, D. J., & Robinson, A. R. (1997). Eddy-induced nutrient supply and new production in the Sargasso Sea. *Deep-Sea Research*, 44(8), 1427–1450.

- McGlade, J. (1999). *Advanced ecological theory*. Oxford: Blackwell, 353 pp.
- Marshall, S. M., & Orr, A. P. (1955). *The biology of a marine copepod*. Edinburgh: Oliver & Boyd, 188pp.
- Martin, A. P., Richards, K. J., & Fasham, M. J. R. (2001). Phytoplankton production and community structure in an unstable frontal region. *Journal of Marine Systems*, 28, 65–89.
- May, R. (1976). Simple mathematical models with very complicated dynamics. *Nature*, 261, 459–467.
- May, R. M. (1973). *Stability and complexity in model ecosystems*. Princeton, NJ: Princeton University Press, 265pp.
- Michaels, A. F., & Knap, A. W. (1996). Overview of the U.S. JGOFS Bermuda Atlantic Time-Series Study and the Hydrostation S program. *Deep-Sea Research Part II*, 43, 157–198.
- Mueller, L. D., & Joshi, A. (2000). *Stability in model populations*. Princeton, NJ: Princeton University Press, 319 pp.
- New, A. L., Bleck, R., et al. (1995). An isopycnic model study of the North Atlantic. Part 1: Model experiment. *Journal of Physical Oceanography*, 25, 2667–2699.
- Popova, E. E., Fasham, M. J. R., Osipov, A. V., & Ryabchenko, V. A. (1997). Chaotic behaviour of an ocean ecosystem model under seasonal external forcing. *Journal of Plankton Research*, 19(10), 1495–1515.
- Rhines, P. (1979). Geostrophic turbulence. *Annual Reviews of Fluid Mechanics*, 11, 401–441.
- Scheffer, M. (1991). Should we expect strange attractors behind plankton dynamics and, if so, should we bother? *Journal of Plankton Research*, 13, 1291–1305.
- Siegel, D. A., Karl, D. M., & Michaels, A. F. (2001). HOT and BATS: Interpretations of open ocean biogeochemical processes. *Deep-Sea Research Part II*, 1400–2140.
- Steele, J. H., & Henderson, E. W. (1995). Predation control of zooplankton demography. *ICES Journal of Marine Science*, 52, 565–573.
- Sugihara, G., Grenfell, B., & May, R. (1990). Distinguishing error from chaos in ecological time series. *Philosophical Transactions of the Royal Society of London B*, 330, 235–251.
- Sverdrup, H. (1953). On conditions for the vernal blooming of phytoplankton. *Journal of the International Council for Exploration of the Sea*, 18, 287–295.
- Taylor, A. H., Allen, J. I., & Clark, P. A. (2002). Extraction of a weak climatic signal by an ecosystem. *Nature*, 416, 629–632.
- Totterdel, I. J. (1993). An annotated bibliography of marine biological models. In G. T. Evans & M. J. R. Fasham (Eds.), *Towards a model of biogeochemical processes* (pp. 317–339). Berlin: Springer Verlag.
- Traub, J. F., & Werschulz, A. G. (1998). *Complexity and information*. Cambridge: Cambridge University Press, 139 pp.
- Truscott, J. E., & Brindley, J. (1994). Equilibria, stability and excitability in a general class of plankton population models. *Philosophical Transactions of the Royal Society of London A*, 347, 703–718.
- Wijffels, S. E. (2001). Ocean transport of fresh water. In G. Siedler, J. Church, & J. Gould (Eds.), *Ocean circulation and climate* (pp. 475–488). London: Academic Press.
- Woods, J. D. (1988). Mesoscale upwelling and primary production. In B. J. Rothschild (Ed.), *Towards a theory of biological–physical interactions in the world ocean* (pp. 7–38). Dordrecht: Kluwer.
- Woods, J. D. (2001). Laminar flow in the Ocean Ekman Layer. In R. Pearce (Ed.), *Meteorology at the millennium* (pp. 204–216). London: Academic Press.
- Woods, J. D. (2002). Primitive equation modeling of plankton ecosystems. In N. Pinardi & J. D. Woods (Eds.), *Ocean modeling: Conceptual basis and applications*. Berlin: Springer Verlag, 472 pp.
- Woods, J., & Barkmann, W. (1994). Simulating plankton ecosystems by the Lagrangian Ensemble method. *Philosophical Transactions of the Royal Society of London B*, 343, 27–31.
- Woods, J. D., & Barkmann, W. (1995). Modelling oligotrophic zooplankton production: Seasonal oligotrophy off the Azores. *ICES Journal of Marine Science*, 52, 723–734.
- Woods, J. D., & Barkmann, W. (1993). Diatom demography in winter. *Fisheries Oceanography*, 2, 202–222.
- Woods, J. D. (2005). The Lagrangian Ensemble metamodel for simulating plankton ecosystems. *Progress in Oceanography*, in press. doi:10.1016/j.pocean.2005.04.003.