Modelling oligotrophic zooplankton production: seasonal oligotrophy off the Azores

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One of the critical issues in large-scale physical/biological coupled models is the survival of zooplankton in a water column circulating an anticyclonic gyre. Survival is most at risk in regions where the phytoplankton food supply is low due to environmental stress by light-limitation (deep mixing in winter) or nutrient limitation (oligotrophy). To investigate this problem we simulated the ecosystem in a 1 m^2 cross-section water column, using the Lagrangian Ensemble method in which plankton are treated as particles following independent trajectories through the changing environment. In this first part of a two-part article we report the results of simulating the ecosystem in a water column located off the Azores, where winter mixing reaches 200 m and there is seasonal, but not permanent oligotrophy. The model features diatoms and herbivorous copepods subject to carnivorous predation, with remineralization of carbon and nitrogen by bacteria attached to detritus and faecal pellets. The copepods become extinct after failing to reproduce in years of low food supply. We show that the risk of extinction can be reduced by allowing cannibalism or by reducing carnivorous predation; we discuss other possibilities: enhancing the food supply by adding new guilds of phytoplankton, and relaxing oligotrophy by allowing other sources of nitrogen injection into the euphotic zone.

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Key words: Azores, copepods, bacteria, cannibalism, model, oligotrophy, phytoplankton, zooplankton.

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Introduction

This article is concerned with zooplankton production during periods of oligotrophy when the food supply is low causing their population to decline (Anderson *et al.*, 1983). It addresses the problem of unrealistic extinction in herbivorous zooplankton which can occur in multi-year simulations of the upper ocean ecosystem (Steele and Henderson, 1993). The primary aim is to understand the environmental causes of seasonal and multi-year decline of herbivore populations in a one-dimensional simulated ecosystem. The secondary aim is to explore how the relationship between population decline and environmental stress is affected by changing the model assumptions. The study is part of a broader investigation into plankton demography. A further article will be submitted to the ICES Journal of Marine Science. In a previous article Woods and Barkmann (1993a) showed how a diatom population responds to deep mixing in winter.

Oligotrophy

The concept of oligotrophy has been recognised in biological oceanography for well over 70 years, the name being imported from limnology (Hutchinson, 1967). It refers to a state in which biological production is low because the concentration of a limiting nutrient, here assumed to be nitrogen, is low. However, the concept remains somewhat hazy, with different authors emphasizing either the lack of nutrient or the lack of primary production, or sometimes the low standing stock of phytoplankton, depending on their measurement technique. The linkage between those three attributes of a water column is not well understood, nor is the quantitative connection between them and the rate of grazing and the concentration of herbivores. To resolve such uncertainty it is necessary to progress from a conceptual model based on the instantaneous state of a water column to one that takes account of its history, describing the processes that brought the water column

to a state of oligotrophy. In the ocean, those processes include circulation around gyres, which may take many years. A theory of oligotrophization in the ocean therefore differs substantially from one for lakes, where it is not necessary to extend the history back beyond one year.

The aim of this introduction is to restate the problem of oligotrophic zooplankton production in a conceptual framework that involves multi-year history. Our hypothesis is that introducing time into the calculation makes it possible to relate the seasonal and regional variations in nutrient concentration and plankton populations to the surface energy fluxes. That is achieved through the following chain: carnivores (predation), herbivores (grazing), phytoplankton (nutrient limited annual new production), nitrogen concentration (entrainment of nitrogen into the mixed layer), winter mixed layer depth (buoyant convection), annual heat budget (surface heat fluxes). To understand what is happening at one location in the ocean it is necessary to ask how those properties and processes have been changing during previous years in a water column that passes through that location after following the gyre circulation. The characteristics of the plankton at that site reflect their response to predictable changes in the physical and chemical environment forced by climatological changes in surface heat fluxes due to a combination of the annual cycle and changing geographical location. Our conceptual model is therefore expressed in terms of a moving water column, and oligotrophic zooplankton growth is simulated by geographically Lagrangian integration of a mathematical model of the ecosystem in such a water column. Before describing the numerical method it will be helpful to elaborate our conceptual model with brief remarks on key elements of the chain linking zooplankton to surface fluxes.

Copepod demography
The multi-year survival of a population of herbivores depends on producing enough young to offset losses due to natural mortality and carnivorous predation. The food supply is crucial: it controls the time taken for copepods to grow to maturity and also the number of eggs produced (Sargent and Henderson, 1986; Sargent and Falk-Petersen, 1988). In those calanoid copepods which produce their young in a batch each year, the population increases sharply during each annual reproduction event and then declines through the rest of the year. The annual production of copepods depends on the concentration of food available for grazing. In the extra-tropical North Atlantic, the spring bloom provides most of the annual food supply. To a first approximation the herbivores graze a constant fraction of the total annual primary production, which is controlled by the annual dose of nitrogen entrained into the euphotic zone (Woods and Barkmann, 1993b).

Environmental stress
Two environmental factors, light and nitrogen, control the rate of primary production and therefore the standing stock of phytoplankton: the food supply for herbivores. Lack of light almost stops primary production in the cooling season when turbulence extends deeper than 50 m even at noon (Woods and Barkmann, 1993a), and the phytoplankton population declines to less than 1% of its annual peak value. Copepods stop feeding and their population declines due to a combination of natural mortality and carnivorous predation. However, the winter loss is made up in the following spring provided the bloom produces enough fodder.

The total annual production of phytoplankton depends on the mass of nitrogen entrained into the euphotic zone each year by deep winter mixing. If the annual maximum depth of the mixed layer stays constant year after year, the annual supply of nitrogen will decline by an amount equal to the particulate flux into the permanent thermocline (Eppley, 1989). The integrated production will be less in each successive bloom, and the herbivore population will decline correspondingly. This decline will be accelerated if the depth of winter mixing becomes less each year due to changes in surface forcing (Woods and Barkmann, 1993b), or when a water column drifts into the oligotrophic zone.

New production
A water column is defined as being oligotrophic whenever the mixed layer concentration of limiting nutrient (assumed here to be nitrogen) has become negligible (Dugdale and Wilkerson, 1992). Using this definition, oligotrophy occurs at mid-latitudes in the North Atlantic ocean after the spring bloom has exhausted the nitrogen stored in the mixed layer during winter. New production each year is defined as the consumption of that initial stock of nitrogen, which may take the form of various chemical species: here we consider nitrate and ammonium. They are injected into the mixed layer each winter when it descends through the nutricline formed during the summer oligotrophic phase the previous year (Wolf and Woods, 1988).

It is important to bear in mind that, when we are considering changes that take several years to complete, it is no longer appropriate to distinguish between new and regenerated production simply by nitrate and ammonium consumption. New production is the consumption of all the nitrogen injected into the euphotic zone by winter convection; regenerated production consumes ammonium injected biologically into the euphotic zone in the same year. This is consistent with the definition of new production by Dugdale and Goering (1967). However, because of the multi-year history involved in our conceptual model, we do not

follow (Eppley, 1989) in equating new production with export of nitrogen through the particulate flux, at least not in the same year.

The key to understanding oligotrophy is to concentrate on new production. Seasonal oligotrophy occurs when the spring bloom consumes all the nitrogen stored in the euphotic zone during the previous winter by deep convection. Permanent oligotrophy occurs in regions where winter convection fails to restock the euphotic zone with nitrogen. The progressive change towards a state of oligotrophy – a process we shall call "oligotrophization" – occurs in a water column when the depth of winter convection decreases in successive years; that occurs when the annual heat budget of the water column is in surplus.

Annual heat budget
If in one year the water column gains less heat from the sun than it loses to the atmosphere, winter convection will drive deeper, and vice versa. (In some regions it is also important to take account of the water balance (Bauer *et al.*, 1991).) Remember that the water column is drifting with the mean flow in the euphotic zone, so the only advective correction needed is for shear and divergence of the geostrophic circulation and for Ekman transport and suction. (Ekman transport occurs in the mixed layer, so the shear in the Ekman current is unimportant for the annual heat budget.) However, surface fluxes normally dominate the heat budget, so it is possible to identify regions where water columns are gaining or losing heat each year by mapping the gyre circulation onto a chart of the net annual heat flux into the ocean (Fig. 1). In principle, that can then be mapped into oligotrophic regimes by considering the trend in mixed layer nitrogen budget of a water column passing through different heating regimes. However, such mapping requires a dynamic model of the ecosystem integrated over several years.

Throughout most of the annual cooling regime, water columns exhibit seasonal oligotrophy. (Only at higher latitudes, in the cyclonic gyre, does winter convection recharge the mixed layer with sufficient nitrate to sustain new production to the end of the summer.) The boundary line between increasing and decreasing oligotrophy is determined by the zero annual heat budget contour. Where annual cooling is weak (less than say 10 W m^{-2}) the annual entrainment of nitrogen from the permanent thermocline may fail to compensate for the loss of nitrogen carried by particles sinking into the permanent thermocline; water columns in that zone show a drift towards permanent oligotrophy (Woods and Barkmann, 1993b). As the water column passes from the annual cooling into the annual heating regime the depth of winter cooling is abruptly reduced (Woods and Barkmann, 1986). In the annual heating regime, winter convection never penetrates the permanent thermocline, so the mixed layer is denied access to its store of nitrogen. Winter convection can still access nitrogen sequestered in the seasonal thermocline during the previous year. But that store is exhausted within a few years, and the water column enters into a state of permanent oligotrophy, which continues until it drifts back into the annual cooling regime, and winter convection once again penetrates the permanent thermocline.

The present investigation

Our investigation has two parts. The first part (reported in this article) explores seasonal oligotrophy and the second (to be reported in a later issue of the journal) explores the transition to permanent oligotrophy.

Here we consider the demographic changes occurring in a water column located off the Azores (41°N 27°W), where the annual net cooling of the water column is less than 10 W m^{-2}, according to Isemer and Hasse (1986). The aim is to show how the populations of phytoplankton and zooplankton change over three years at a site where there is winter stress due to deep mixing, which limits availability of light, and during the summer, after the spring bloom has consumed the annual dose of nitrogen entrained from the thermocline during the previous winter. The emphasis will be on the vertically integrated populations in the water column. It will be shown that although oligotrophy at this site is only a summer phenomenon, the herbivores fail to get enough food to reproduce in the third year and they become extinct. Further numerical experiments show (1) how a modest degree of cannibalism can prevent that happening, and (2) how reducing carnivorous predation further postpones extinction. These results provide the basis for designing the models used in Part 2 of our investigation.

Virtual ecosystems

Virtual ecosystems created by computer simulation have the disadvantage that they can be no more than simplified cartoons of Nature, but they have the advantage that they can be diagnosed in detail. It is possible to learn much more about the virtual ecosystem than one can ever hope to learn about the real world. The answer can be provided to every conceivable question about the evolving environment and the plankton living in and changing it. It is possible to perform numerical experiments to discover how the virtual ecosystem is affected by changes in the model specification. For example, we shall demonstrate the effect of modifying carnivorous predation and introducing cannibalism.

The simulated ecosystems contain many familiar features of the oligotrophic ocean, and reveal aspects that have not previously been clearly diagnosed from

observations. In Part 2 we show how the geographical modulation of the seasonal cycle in mixed layer depth affects the nitrate and ammonium concentrations in a water column drifting around the anti-cyclonic gyre in the North Atlantic ocean. The changes are due, in part, to the direct effect of turbulent mixing, and indirectly to the effect of the changing mixed layer on the plankton ecosystem. It will show how the diel migration of zooplankton brings ammonium into the mixed layer and so sustains growth there after the nitrate has been consumed. The use of the Lagrangian Ensemble method permits detailed demographic diagnosis of the populations of phytoplankton and zooplankton as they decline in the oligotrophic regime.

Those are the strengths of the method. Its weakness is the failure to include some key processes in the model used to create the virtual ecosystems. Given the fact that we are concerned with copepod growth in the oligotrophic ocean when food is in short supply, the most serious shortcomings are concerned with the parameterizations of starvation and the failure to provide the copepods with food other than diatoms. These will be addressed in future models, which will include lipid storage by the copepods as an explicit variable, and picophytoplankton (with negligible sinking speed) and microzooplankton to feed on them and to provide food for the copepods. It will also be necessary to include explicit treatment of copepod growth stages and more realistic parameterization of egg production and spawning mortality.

Another weakness is the adoption of a model containing only one guild of plankton per trophic level: diatoms, copepods, visual carnivorous predators and attached bacteria. Virtual ecosystems based on such a model cannot contain a seasonal succession of species in each trophic level, whereby smaller species with negligible motility dominate primary production and grazing during periods of summer oligotrophy, when nitrogen is in the form of ammonium cycles in the euphotic zone and when there are negligible losses. Neglect of this microbial loop means that the virtual ecosystems described in the two parts of this article do not realistically simulate the observed biology of the oligotrophic ocean. However, they do realistically address the central scientific problem of how a water column becomes oligotrophic and how the relatively large, mobile copepods survive when it does. The microbial loop is a side show for those problems, which depend critically on new production.

Method

Three software tools are needed to address these scientific problems: (1) a mathematical model that treats the relevant processes explicitly, (2) precise demographic analysis of the simulated plankton populations, and (3)

multi-year integrations that simulate the annual cycle, including the oligotrophic regime. In our investigation those requirements were met by using (1) the Lagrangian Ensemble (LE) method (Woods and Barkmann, 1994), in which the biological equations are integrated along the trajectories of individual plankters, and their ensemble development is used to compute biological feedback to the physical and chemical environment, (2) demographic diagnosis of the ensembles of particles simulated by the LE method, and (3) geographically Lagrangian integration of the one-dimensional model around the North Atlantic anticyclonic gyre (Part 2). (Some other models also use Lagrangian integration of the biological equations, but only the LE method simulates biological feedback to the environment with sufficient realism for this study.)

The simulation model

The investigation used the LE'93 model described by Woods and Barkmann (1993a, b, 1994). The model explicitly represents ensembles of several thousand particles each carrying a changing load of identical plankters, either phytoplankton (with functions like diatoms) or herbivorous zooplankton (with functions like calanoid copepods). Phytoplankton detritus and faecal pellets are also tracked explicitly as particles. The functions of bacteria (extraction of dissolved inorganic nitrogen and carbon from detritus and faecal pellets) and of carnivorous zooplankton (visual predation on herbivores) are treated parametrically. The physical environment is controlled by fluxes through the sea surface by means of a mixed layer model (Woods and Barkmann, 1986a) designed accurately to simulate the response of turbocline depth to changes in surface heat flux as well as the less important changes due to turbulent entrainment due to varying windstress. The limiting nutrient is nitrogen, which occurs as nitrate (injected initially) and ammonium (generated by bacteria and by herbivore excretion).

The behaviour of the plankton is as follows. The diatoms sink steadily through the water at 1 m d^{-1}. The herbivores exhibit diel migration controlled by solar irradiance, depending on their recent feeding success; their maximum swimming speed depends on body weight. Dead diatoms (detritus) and faecal pellets also sink steadily through the ocean at 1 m d^{-1} as bacteria extract their carbon and nitrogen. (The LE'93 model does not take account of aggregation of dead organic matter, and consequent changes in its fall speed.)

Integration

The model is integrated in half-hour steps, during which the physical and chemical environmental variables are updated, taking account of the divergence of vertical fluxes and interaction with the plankton. (For example,
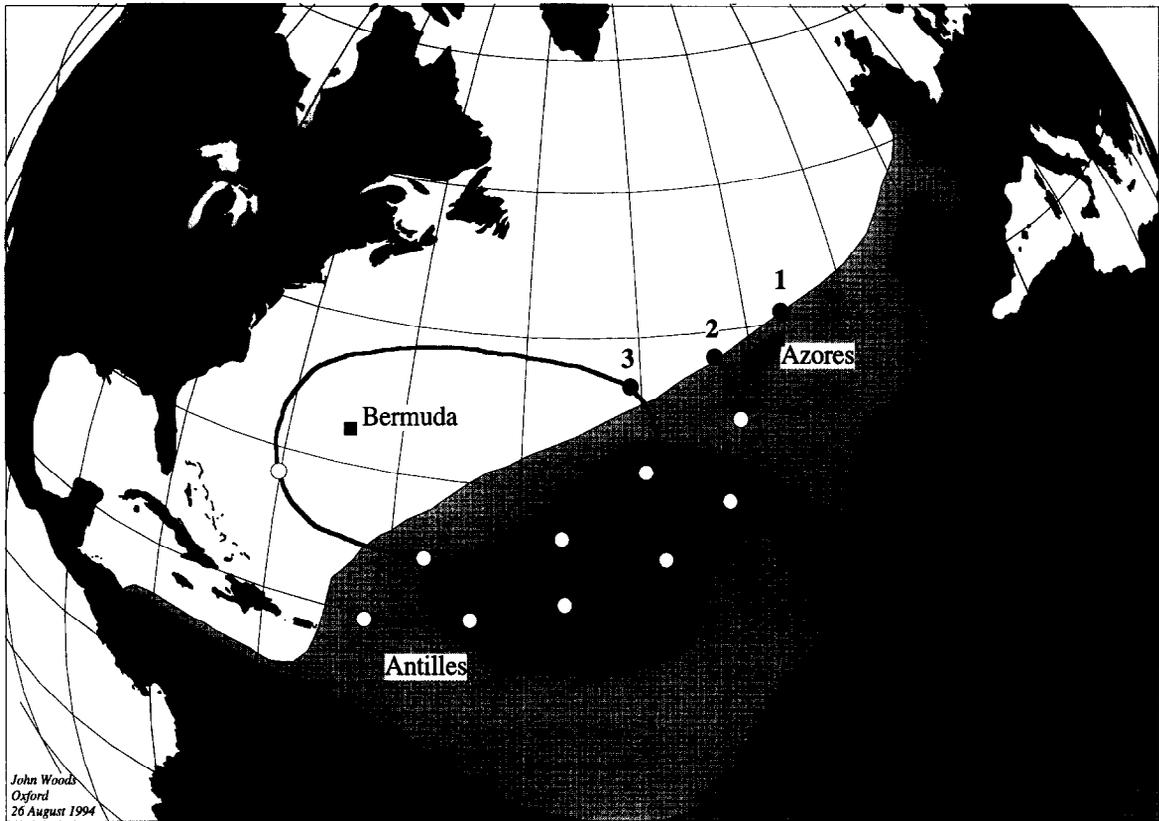
Figure 1. The location of the numerical simulation off the Azores (1). The shading indicates the annual net heat balance of the ocean according to Isemer and Hasse (1986) used in the integrations. In the unshaded region the annual ocean heat loss exceeds 10 W m^{-2}, and in the darker region the ocean gains heat each year. [The other two locations (2) and (3) refer to Part 2 of this article.]

the solar irradiance profile in each waveband is influenced by the plankton-controlled turbidity and in turn it controls the solar heating profile, and therefore the depth of the mixed layer. Self-shading severely limits the depth of phytoplankton production in the spring (Woods and Barkmann, 1993).) During each time step the model computes the change in depth of every plankton particle as it responds independently to a combination of the ambient motion of the seawater (turbulence and upwelling) and the plankter's own behaviour. (The ambient environment $_iE^*(t)$ is defined as the value that a changing environmental field $E(x, y, z, t)$ has at the location $[x, y, z]_i$ of a particular plankter i at time t.) Finally, the change in physiological state of the plankters in each particle is computed as their ambient environment changes during its half-hour trajectory from initial to final depth.

The model is integrated for several years, during which interval the simulated ecosystem changes in response to two factors: (1) the environmental response to the surface fluxes of energy, water, and gases, and (2) the internal physical – chemical – biological dynamics of the ecosystem. The former is determined by the

boundary conditions, which change at each time step in response to geographical location, solar elevation (computed astronomically), and atmospheric conditions interpolated between monthly mean values in the Bunker climatology of Isemer and Hasse (1986, 1987). The boundary conditions at each time step were selected by the geographically Eulerian procedure, in which the location is fixed. This is justified by the relatively small annual displacement of the water column in this weak return flow region of the gyre. A water column starting at 41°N,27°W and drifting with the mean flow experiences a very small change in annual heat budget over the next three years (Fig. 1). The surface climate stays almost stationary despite the advection of the water column, so it is not necessary to adopt the geographically Lagrangian method used for the faster moving water columns to be reported in Part 2 of our investigation.

Results

We now report the results of a numerical experiment designed to simulate the ecosystem in a water column in the North Atlantic anticyclonic gyre (Fig. 1). The first
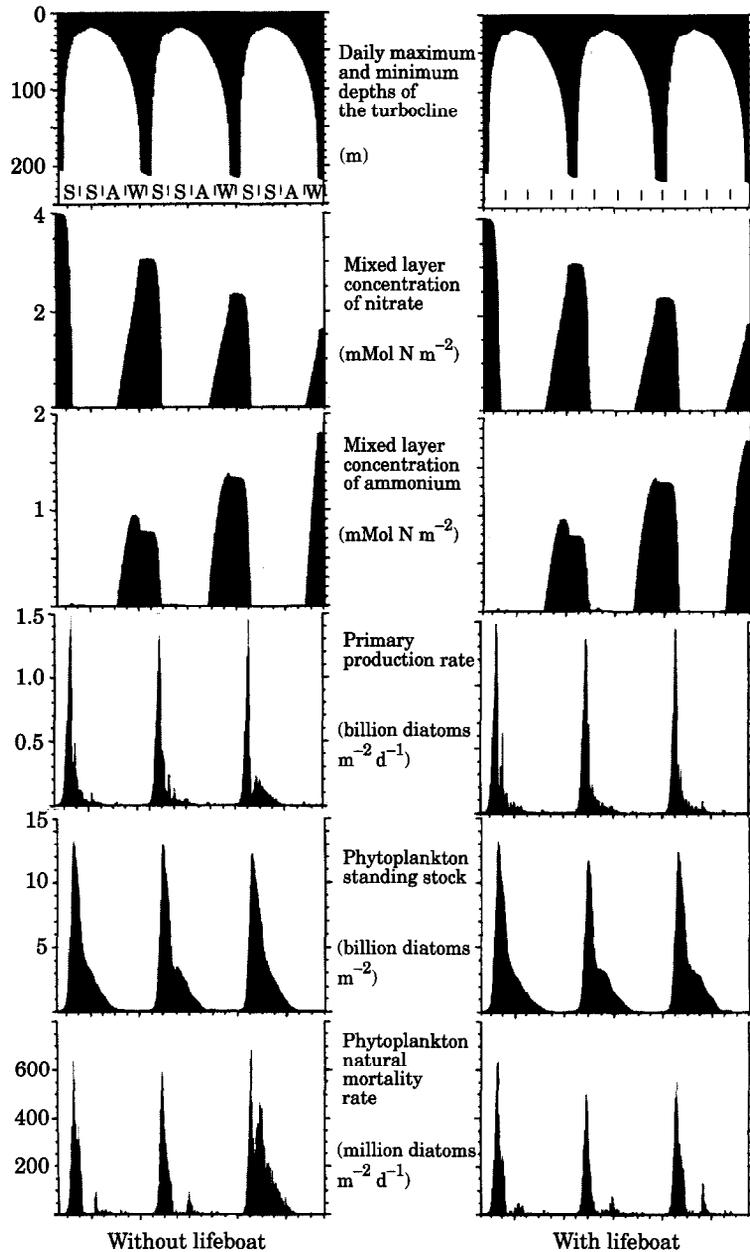
Figure 2. Plankton demography at a fixed location off the Azores with and without the lifeboat routine.

experiment simulates changes occurring off the Azores over three years. The results will be presented as a set of time series of the vertically integrated properties of the simulated ecosystem (Fig. 2). The experiment was then repeated for a simulation in which cannibalism was permitted (Fig. 2, right). Finally, we show what happens to the diatom and copepod populations when the carnivorous predation is eliminated (Fig. 3).

The water column was held at a fixed location (41°N, 27°W) near the Azores, at a site where it loses heat at a modest annual rate of < 10 W m^{-2}. (The experimental uncertainty in heat flux maps exceeds ± 10 W m^{-2}.) We have already reported many aspects of the ecosystem simulated at this site by the same LE'93 model (Woods and Barkmann, 1993a, b, 1994). Here we concentrate on the annual cycles of demographic variables, including time series of daily birth-rate, death-rate (by natural mortality and by predation), life expectancy and biomass; these are presented in Figure 2, together with supporting information about the mixed layer environment. The principal features are now summarized.
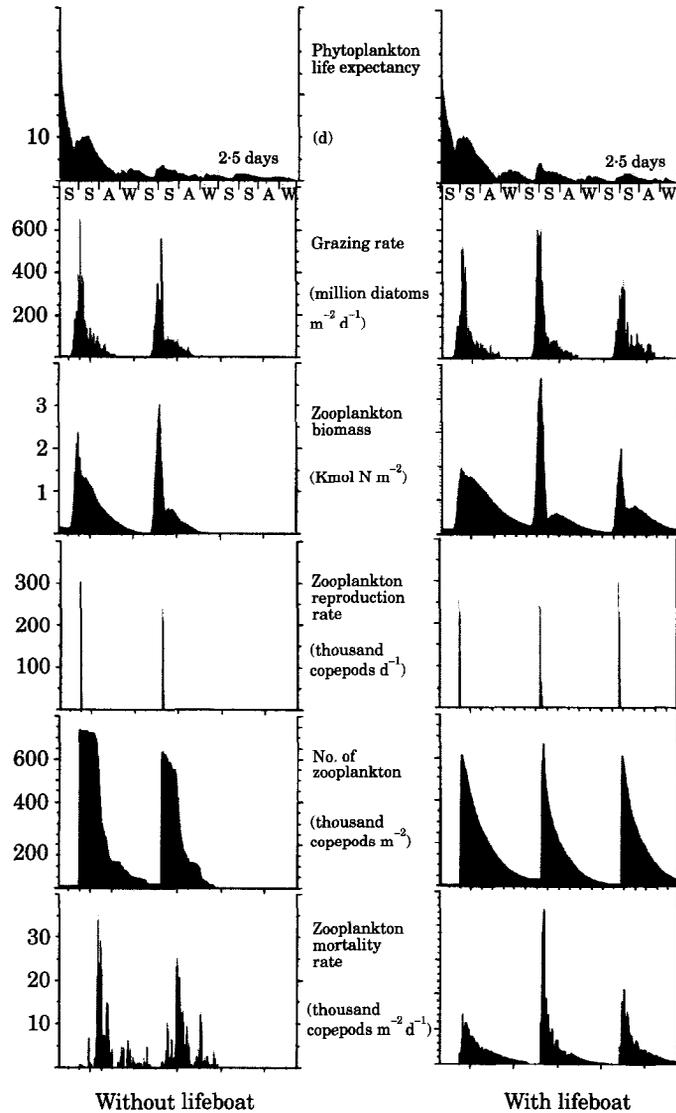
Figure 2. (cont.)

Turbulence

The integration starts just before the Vernal Equinox, a week before the mixed layer depth attains its annual maximum of 205 m. This defines the vertical extent of the seasonal boundary layer and the upper limit of the permanent thermocline at this location. This is much deeper than the Ekman depth, so buoyant convection rather than windstress is the principal factor determining the annual maximum depth of the mixed layer. The net annual cooling of 250 MJ m^{-2} drives winter convection to deepen the seasonal boundary layer by nearly 5 m each year. Each winter, turbulence in the mixed layer homogenizes the vertical distribution of particles and dissolved chemicals between the surface and the annual maximum depth of the mixed layer. That sets the initial conditions for the following growing season; in particular

it determines the initial concentrations of nitrate and ammonium in the euphotic zone. This annual dose of nutrients comes mainly from the seasonal thermocline, but (as we have just seen) there is also a contribution from the top 5 m of the permanent thermocline.

Once the daily heat budget becomes positive (on 1 April at this site according to the Isemer–Hasse climatology) nocturnal convection weakens and the mixed layer depth decreases sharply. During the spring bloom, which follows the shoaling of the mixed layer, its depth is modulated by ±3 m due to daily variation in the turbidity of the water. Convection is quenched by solar heating, causing diurnal variation in the depth of the turbocline marking the base of the surface mixing layer, starting at the Winter Solstice. As we have noted previously (Woods and Barkmann, 1993a), the growing
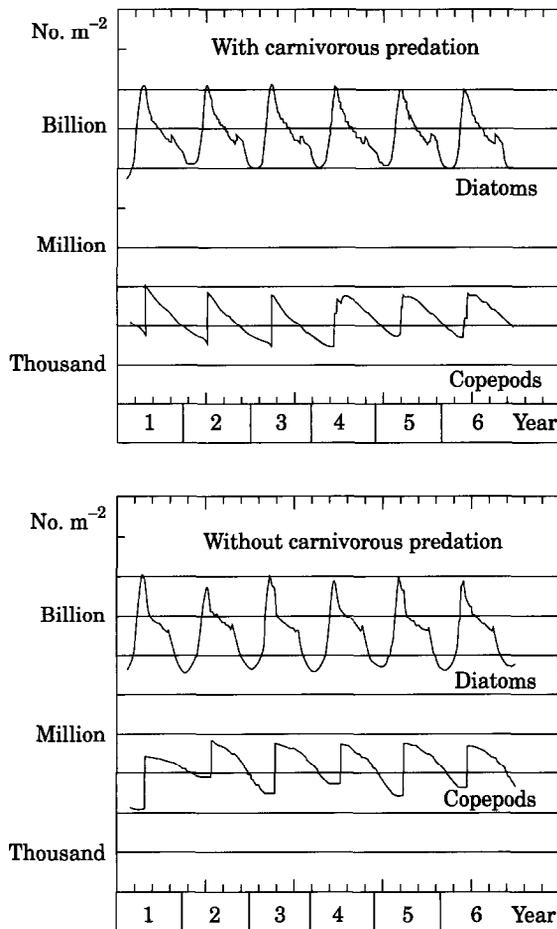
Figure 3. The influence of carnivorous predation on the numbers of diatoms and copepods in a water column off the Azores: (a) with predation, (b) without predation.

season begins a month later, when the noon depth of the turbocline becomes shallower than 50 m, despite the fact that the mixed layer is still deepening.

Phytoplankton

Although growth starts in mid-winter the phytoplankton population is then so low that it takes three months for the bloom to reach its peak of some 13 billion diatoms m^{-2}, following a peak production rate of 1.5 billion diatoms d^{-1}. In years 1 and 2 natural mortality and grazing each run at about half the production rate. In year 3 there is no grazing, so all the diatoms die naturally. It is interesting to note that this has little effect on their life expectancy: energy exhaustion or grazing provides an equally speedy death for these diatoms, largely because of their high sinking rate (1 m d^{-1}). (Each phytoplankter has an energy pool which fills and empties in response to energy gain by photosynthesis and loss due to respiration. Natural mortality is due to energy exhaustion, when the pool is empty.)

Nutrients

The integration started with an initial nitrate concentration of 4 mM N m^{-2} and zero ammonium. The phytoplankton completed their consumption of that initial dose early in May of year 1; thereafter the mixed layer concentration remained negligible until late November, when the deepening mixed layer reached the nutricline and began to re-entrain nitrate. The mixed layer concentration then rises until the start of the next growing season. In subsequent years the annual maximum concentration of nitrate in the mixed layer declines by nearly 1 mM N m^{-2} per year, but this decline is largely offset by the rise in annual maximum concentration of ammonium, entrained from the thermocline, where it had been injected by microbial action on dead diatoms and faecal pellets. The timing of the decline in ammonium owing to consumption during the spring bloom matches that in nitrate. (The model does not discriminate between uptake of nitrate or ammonium by the diatoms.) However, there is evidence of low concentrations of ammonium during the summer, the result of a lag between zooplankton excretion and consumption by phytoplankton.

Seasonal oligotrophy, defined as the period during which the nitrogen in the mixed layer comes only from biogenic sources that are both local and recent, extends from early May until late November. We note that the phytoplankton biomass remains significant for much of this time, and primary production continues fitfully throughout the period of seasonal oligotrophy, nourished by ammonium from zooplankton swimming up at night in search of food and, when successful, excreting in the mixed layer.

Zooplankton

In year 1, zooplankton ingest 200 million diatoms d^{-1} during the last week of spring and grazing peaks at 650 million d^{-1} at the Summer Solstice when the phytoplankton biomass has already declined to half its peak value. Thereafter it declines fitfully to a minimum of under 1 million d^{-1} just before the Winter Solstice. The zooplankton population peaks at 750 000 copepods m^{-2} immediately after the reproduction event, one week before the Summer Solstice, and thereafter declines to a minimum of 30 000 m^{-2} immediately before the reproduction event in year 2, which occurs on the Solstice, one week later than in year 1. The annual minimum population was twice the number at the start of the integration, but the total biomass was much less. This explains the delay in reproduction in year 2: the individual copepods were less mature at mid-summer, and needed an extra week of grazing before they reached the prescribed body weight for egg production to start. Spring feeding to put on body weight comes at the cost of egg production. The delay proved costly in terms of the number of eggs produced:

the peak population was 100 000 fewer than in year 1. The subsequent decline of the population in year 2 was faster than in year 1 and by mid-winter the population was extinguished by a combination of natural mortality and carnivorous predation. No zooplankton remained to graze on the phytoplankton in year 3.

Discussion and supplementary experiments

The most remarkable feature of this experiment was the extinction of the zooplankton before the spring bloom in year 3. This poses a technical problem for modellers seeking to simulate the upper ocean ecosystem. It is an artifact of the model which is deficient in many ways, not least the limitation of only one plankton guild per trophic level. The model must be elaborated to eliminate this problem. By trying different solutions we might learn something useful about the working of the upper ocean ecosystem. We shall now consider a number of physical and biological possibilities and report the results of numerical experiments on two of them.

Physics

Starvation leading to extinction of the copepods may represent a realistic simulation of what happens to the average water column in the oligotrophic sector of the gyre. It may be that, in Nature, copepod survival is due to exceptional environmental conditions providing abundant food in a few more fortunate water columns, which then seed their neighbours by lateral mixing. The mechanism of such local "hotspots" has been discussed by Woods (1988), Strass (1992), Strass *et al.* (1992); this solution will not be pursued here. In Part 2 we shall show that copepod extinction may be avoided in gyre trajectories that pass only briefly through the heating regime: perhaps water columns drifting along such trajectories seed those that have spent longer in the heating regime.

Biology

However, it may be more realistic to expect every water column circulating around the gyre to avoid copepod extinction on its own without help from neighbours with more favourable physical environment. To some extent, survival of a viable population depends on the area of the water column; premature extinction might occur merely because the numbers are too small. However, that is avoided in our numerical experiments by adopting a 1 m² cross-section, which allows us to simulate copepod population densities as low as 1 m⁻³ without extinction due to numerical causes.

Increasing the food supply

The biological solution to preventing extinction is to provide an alternative food supply. In the LE'93 model there are only four possible food sources: diatoms (living and dead), and copepods (or their eggs). In the Azores experiment, grazing exclusively on living diatoms is insufficient to prevent extinction in the second winter. Permitting grazing on dead diatoms (detritus) can at best double the food supply and prevents extinction so long as the annual supply of nitrogen remains high, as it does in this geographically Eulerian integration. The increase in food supply depends on the fraction of annual new production escaping as detritus to the deep ocean. That in turn depends on the fall speed of the detritus, which is not realistically parametrized in the LE'93 model.

The alternative to eating detritus is for the copepods to eat each other, or their eggs, in years when some are produced. There are no eggs to eat in the third year when the adult copepods are approaching death, so the only possibility is cannibalism. We now present the results of a repeat of the Azores experiment with cannibalism introduced into the model by means of what we call the lifeboat routine.

Permitting cannibalism

The LE'93 model has an explicit routine for increasing the natural mortality rate of herbivores during periods of famine, defined as time steps in which the ingestion of carbon from phytoplankton by a particle is less than the collective respiration of the zooplankters contained in it. When ingestion exceeds respiration, all the zooplankters in a particle put on weight (or, if they are mature, produce more eggs). But when respiration exceeds ingestion the plankters do not lose weight; they lose biomass by natural mortality, each survivor maintaining constant body weight. This parametrization is called the lifeboat routine, after the ancient practice of survivors eating the cabin boy when all face starvation.

Introducing cannibalism by the lifeboat routine has a large effect on the population dynamics of the upper ocean ecosystem. Without it (left-hand column of Fig. 2), the whole population succumbs in periods of famine: but with it the number of zooplankton declines gracefully, postponing extinction until the food supply comes available the next spring. The right-hand column of Figure 2 shows the demography of phytoplankton and zooplankton populations simulated with the lifeboat routine. Natural mortality continues to be an erratic process, but the decline in the number of copepods becomes monotonic.

The success of cannibalism contains two messages: the first technical, the second ecological. The technical message concerns the packaging of the zooplankton population in hundeds of particles, each like a spaceship with its own trajectory through the changing

environment which creates a unique life history for all the identical copepods on board. Without the lifeboat routine, all the passengers starve together and eventually die. With it, the excess respiration loss of the whole community on board is attributed to a few, which die immediately, so that the others can retain body weight. Weight loss is traded for a few deaths at each time step. The net effect on the total community is dramatic: the population declines at a much slower rate, because those that survive are in good condition to reproduce when the next spring bloom comes and feeding recommences.

This result is, of course, an artifact of the computer code in the LE method, but helps clarify the key problem to be solved if the copepod population is to survive: its members must keep up body weight so that, when abundant grazing resumes in the next spring, ingestion will not be wasted on rebuilding body weight but can be devoted to maximizing the number of eggs. The lifeboat routine has a major impact on population dynamics in our simulations because the LE method incorporates the process of growth and egg production explicitly at the level of individual zooplankters. Expressed in terms of population management, the lifeboat routine ensures the survival of the population by maintaining a sufficient breeding stock; it does that by culling when food is short.

How does Nature address this problem? In the short term, the solution must be to increase ingestion, even at the expense of increasing visibility to predators, or taking other categories of food, not necessarily through cannibalism. If that does not work, if starvation continues, the copepod can reduce respiration by abandoning the energy-consuming search for food: it can hibernate. To explore these possibilities takes us beyond the scope of the present article. However, we can indicate the way ahead on the basis of the results reported above. Priority will be given to modifying the model to allow the copepods new sources of food, which means adding new guilds.

Adding new guilds

Our modelling philosophy is to add new plankton guilds only when it is necessary to prevent some unrealistic behaviour in the simulated ecosystem, and to define new guilds in terms of functions that will most economically solve the problem. In that spirit of "designer ecology" we identify two possible solutions to the problem of providing more food for the copepods. One is to introduce a guild of phytoplankton that has negligible sinking speed and therefore avoids the fate of diatoms that die from energy exhaustion soon after they sink out of the mixed layer. Such picoplankton will be nourished by ammonium injected into the mixed layer by the migrating zooplankton. We would also have to introduce micro-zooplankton which graze efficiently on the tiny phytoplankton and, in turn, provide food for the copepods (Burkill et al., 1993). The problem with this solution is that it makes copepod survival dependent on the phytoplankton that are growing at a rate determined by the supply of ammonia, which comes from copepod excretion. This is only a fraction of the nitrogen consumed by the copepods, so while picoplankton may postpone copepod extinction it cannot prevent it. For survival during long periods of oligotrophy, the zooplankton need a source of new production which draws on the nitrate in the thermocline.

This might be achieved by adding a guild of phytoplankton designed to exploit nitrate at the deep chlorophyll maximum. They will need to swim alternately up to avoid self-shading and down below nutricline to take up nitrate. They may functionally resemble dinoflagellates. Survival based on new production at the nutricline would be consistent with the observed deepening of the deep chlorophyll maximum during summer oligotrophy (Strass and Woods, 1991). The results of numerical experiments with simulated ecosystems incorporating dinoflagellates will be reported elsewhere.

Carnivorous predation

The alternative to increasing the food supply is to reduce losses to predation. Steele and Henderson (1992) and Steele (1995) have shown that simulated plankton populations are sensitive to the high trophic level closure assumption in models. They argue that problems arise when the loss rate to implicit carnivores is assumed to be proportional to the prey concentration and recommend quadratic variation. In our model, carnivorous predation is assumed to be visual. (The LE'93 model does not take account of loss to predators which hunt acoustically or by drift-netting, and the corresponding avoidance procedures, but these may be added in future versions.) The probability that a herbivore is eaten by carnivores in a given time step depends on its visibility, which is controlled by its cross-section area (mass to the 2/3 power) and by the ambient irradiance mapped onto the spectrum of the predator's visual pigments. The copepod's strategy for minimizing loss to visual predators is its diel migration, whereby it seeks to avoid being seen by following a dim isolume as it descends through the water column each day after sunrise. The choice of isolume depends on recent feeding success. The functional relationship between choice of isolume and recent feeding success, measured by the copepod's satiation index, was determined by Burkert (1980) using a method equivalent to that described by Fiksen and Giske (1995). Choosing a brighter isolume increases feeding success at a higher risk of death by predation; and vice versa. The former is favoured by small copepods, the latter by adults.

This parametrization favours survival of large herbivores which use their superior swimming speed to descend into low illumination water, and young herbivores which are too small to be seen even in surface waters, where they pass the daylight hours because they cannot yet swim fast enough to descend into deep water. The herbivores with the highest risk of being eaten are the hungry ones that linger near the surface in search of sparse food during the summer. Their control routine for diel migration is to vary the target isolume with satiation, i.e. with how well they have been feeding during the previous couple of days. So oligotrophy not only reduces the chance of herbivores growing, but increases the chance of their being seen and eaten by carnivores. In contrast, during the spring bloom self-shading greatly reduces the depth of the diurnal migration of isolumes, so zooplankton do not have to swim down so far to reduce their visibility; their respiration cost due to swimming is reduced and their daily feeding time is extended.

We have investigated the impact of predation on the populations of phytoplankton and zooplankton during two six-year integrations of the water column off the Azores, with cannibalism by the lifeboat routine to prevent extinction (Fig. 2, right). In the first integration, incorporating the standard carnivorous predation of LE'93, the diatom population per square metre varies seasonally between a maximum of around 10 billion in the spring bloom, to a minimum of about 100 000 000 in January; while the copepod population per square metre varies seasonally between a maximum of nearly 100 000, just after reproduction during the spring bloom, to a minimum of a few tens of thousands. Starting in year 4, the seasonal decline in copepod population is postponed for a couple of months, and the minimum in years 5 and 6 is much less than in the first four years. We conclude that the model is stable for multi-year integrations, but that there are significant trends and inter-annual variation in the seasonal variation of copepod population.

In the second integration (lower panel of Fig. 3) the model was modified to eliminate carnivorous predation. In general, this led to a rise of an order of magnitude in the copepod population, with the annual maximum approaching $1\,000\,000$ m^{-2} and the minimum averaging 30 000. However, eliminating predation led to much greater inter-annual variability, caused by substantial differences in reproduction success in successive years. The diatom population showed an annual maximum slightly lower than with predation, but with enhanced inter-annual variation. However, eliminating predation led to reduced autumn bloom and consequently a much lower annual minimum diatom population. This numerical experiment appears to support the trophic cascade hypothesis of Verity (in press).

Conclusion

We have introduced a conceptual model for oligotrophy in which the state of the ocean depends on its history in previous years. The idea is that the process of oligotrophization occurs in a water column that accumulates heat progressively over a number of years. The mechanism will be examined in Part 2 of this article. In Part 1 we have provided a reference simulation for a water column that does not gain heat each year. Exploiting the power of the Lagrangian Ensemble method we have examined the demographic changes that occur in the water column over a period of three years during which the climate was held constant (i.e. the annual cycle of solar and atmospheric forcing was the same each year). Surprisingly, despite a vigorous spring bloom each year, the herbivore population is not robust. The copepods get barely enough food to reproduce, and in the second year they fail to do so, and the population dies out in the third. That catastrophe can be prevented by permitting a modest level of cannibalism, using the "lifeboat routine". Eliminating carnivorous predation increases the copepod population by an order of magnitude, at the expense of enhanced inter-annual variability. The microbial loop cannot prevent extinction. The survival of copepods in a water column depends on there being a sufficient supply of new primary production each year.

Acknowledgements

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