

Coupling plankton population models to hydrodynamical studies

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Abstract

The population dynamics of plankton are strongly affected by the hydrophysical conditions in which they reside. In this article I discuss in general terms the motivation behind and a common method for coupling plankton population models to numerical studies of the flow and transport in environmental fluid bodies. I then give an example of such an ecological study in Lake Baikal, Siberia.

Introduction

The steady increase in the power of computers has made a range of fluid problems amenable to the techniques of Computational Fluid Dynamics (CFD). A particular advance is the ability to model environmental flows (such as those in rivers, lakes and oceans) with a grid resolution which permits the study of relatively small-scale phenomena. This enables the modeller to examine the importance of flows to localised populations of plankton, microscopic organisms which exist virtually everywhere in natural fluid bodies.

Phytoplankton are the tiny plants which grow in the surface layers of a water body, and are visible as a green sludge in over-nutriented garden ponds. They require sunlight and nutrients to grow, and are the primary producer of energy in an aquatic ecosystem. Zooplankton are microscopic animals which feed on the phytoplankton and each other. Both classifications are extremely general in that they represent organisms of many different species and classes, ranging over scales from unicellular to the barely-visible.

The modern practice of coupling plankton population models to CFD in two or three dimensions has precipitated a significant advance in our understanding of the interaction between the physics and ecology of natural water bodies and is extremely useful in addressing a range of practical problems. Determining maximum release concentrations of nutrient-rich effluent (such as sewage sludge or fertiliser runoff from fields) can help to avoid provoking massive plankton blooms, which have been responsible for upsetting the balance of aquatic ecosystems by releasing toxins or consuming large portions of the available oxygen as they decompose [1]. Alternatively, predicting blooms in the ocean may one day enable fishermen and ecologists to surmise the likely location of fish and other organisms higher up in the food chain [2]. In other situations the modelled plankton distributions can be used to infer details of flow regimes, as in the case of assimilation of remotely-sensed ocean colour data into physical ocean models [3]. Oceanic plankton play a vital role in the cycle of various important elements, such as Carbon, and should therefore be resolved in long-term coupled models of the Earth's climate [4].

Plankton models in one (vertical) dimension have been in development for decades and have addressed a wide range of scientific questions [5]. The inclusion of one or two horizontal

dimensions allows us to take these well-understood parameterisations of biological processes and extend them to the study of new phenomena, such as horizontal currents, eddying, and turbulence.

N-P-Z modelling

A class of multidimensional models in common usage are the so-called *N-P-Z* models, which have a three-component ecosystem featuring state variables for a universal limiting nutrient (*N*), phytoplankton (*P*), who utilise this nutrient, and a herbivorous zooplankton (*Z*) who feed on the phytoplankton. Although defining single compartments for phytoplankton and zooplankton, with accompanying averaged values for growth, mortality, etc., is an extremely rough approximation, such models can still be of great use in answering well-defined ecological questions [6]. All three components are expressed in units of chemical concentration (e.g. mg-at Nitrogen l^{-1} , where 1 g-at = 1 atomic mass unit = mass of 1 Hydrogen atom) and are evaluated at each cell of the computational grid used to discretise the governing differential equations. In the very simplest *N-P-Z* models the nutrient is supplied by a mortality rate of both plankton species and this is sufficient to close the system of equations.

The three components are each governed by a scalar transport equation of the model in question, such as the two-dimensional advection-diffusion equation for an incompressible fluid:

$$\frac{\partial C}{\partial t} + u \frac{\partial C}{\partial x} + w \frac{\partial C}{\partial z} = \frac{\partial}{\partial x} \left(K_h \frac{\partial C}{\partial x} \right) + \frac{\partial}{\partial z} \left(K_v \frac{\partial C}{\partial z} \right) + S_C \quad (1)$$

where $C = N, P, Z$ is the component of interest, K_h and K_v are horizontal and vertical eddy diffusivities (representing turbulent mixing on a scale finer than that of the grid), t is time and u, w are velocities in the x, z plane. S_C represents a series of source terms which account for the interactions between plankton components.

The model used as an example here [7] consists of the following source terms:

$$S_P = PV_m \left(\frac{N}{N + k_s} \right) e^{-\eta d} - m_P P - IZ \quad (2)$$

$$S_Z = (1 - \gamma)IZ - m_Z Z \quad (3)$$

$$S_N = -PV_m \left(\frac{N}{N + k_s} \right) e^{-\eta d} + m_P P + m_Z Z + \gamma IZ \quad (4)$$

where d represents depth and descriptions of the various model parameters and their units are given in table 1. A schematic diagram of the model described by (2) - (5) is shown in figure 1. The zooplankton grazing rate I is given by

$$I = R_m \Lambda P (1 - e^{-\Lambda P}) \quad (5)$$

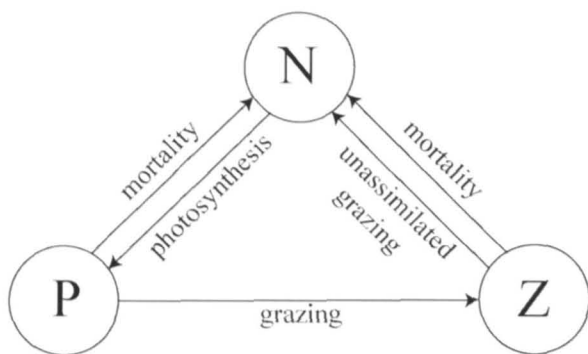


Figure 1 Schematic diagram of the transfer mechanisms in the *N-P-Z* plankton population model adopted as an example in this study

and is a food-acclimatised formulation, which means that it has no asymptotic value for increasing phytoplankton concentrations because the zooplankton adapt their feeding rate to the food abundance.

Table 1 Parameters in the *N-P-Z* model.

Parameter	Description	Value
V_m	Maximum phytoplankton growth rate	2 day^{-1}
k_s	Nutrient uptake half-saturation constant	$0.2 \text{ mg-at N l}^{-1}$
η	Light extinction coefficient	0.1 m^{-1}
R_m	Maximum ingestion rate of zooplankton	0.5 day^{-1}
Λ	Ivlev constant	$0.5 \text{ mg-at N l}^{-1}$
m_p	Phytoplankton mortality rate	0.1 day^{-1}
m_z	Zooplankton mortality rate	0.2 day^{-1}
γ	Unassimilated fraction of zooplankton grazing	0.3

It can be seen that phytoplankton photosynthesis (the first term on the right-hand side of equation (2)) responds to two limiting factors in this formulation: nutrient shortage and lack of light. Growth follows an exponential decrease with depth due to the attenuation of available light while the Michaelis-Menten ratio (first used in the description of enzyme catalysis) describes the effect of nutrient supply and limitation. The exact response of this formulation to variation in N and d is shown in figure 2, for the fixed value $P = 1$.

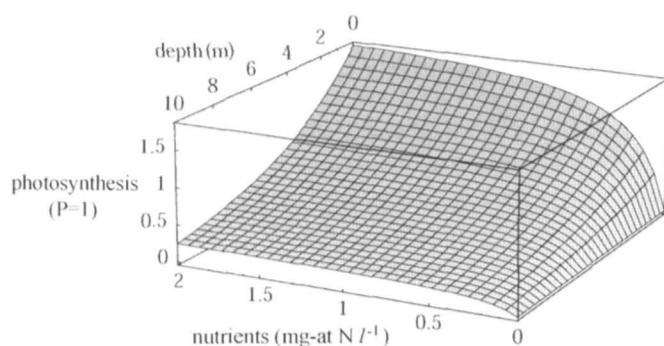


Figure 2 The response of the photosynthesis formulation to variation in light and available nutrients.

Example Application - the thermal bar in Lake Baikal

The model described above has been successfully used to investigate the localised plankton bloom which accompanies the Spring thermal bar in Lake Baikal, Siberia [7]. The thermal bar is a downwelling plume of dense water which forms when the shallows of a lake warm or cool through 4°C , the temperature of maximum density for fresh water. Water on each side of the plume is either warmer or cooler than 4°C and is therefore lighter and does not sink, resulting in a localised plume at which the horizontal surface flows converge. The thermal bar moves toward the open lake as the surface heat flux continues, and figure 3 shows a snapshot of a simulated travelling thermal bar after 20 days of warming [7]. The physics and ecology of this phenomenon are the subject of a recent review by the author [8].

The Spring thermal bar of Lake Baikal is known to have an important interaction with its plankton populations [9], with various species reacting differently to the flow patterns generated. The growth of all diatoms, to varying degrees, is found to be promoted inshore of and at the position of the thermal bar.

The ecological model is coupled to a hydrodynamical formulation which has successfully predicted the transient thermal structure and position of the Spring thermal bar [7]. This allows the plankton blooms at the position of the thermal bar to be qualitatively predicted in the presence of accurate flow and density conditions. It can be seen that population growth is strongly promoted just inshore of the moving thermal bar (figure 3), which agrees with observations taken in Lake Baikal [9].

This result is of great value because a study of the various terms in the ecosystem model can subsequently reveal a lot of useful information about plankton behaviour within this bloom. For example the rate of photosynthesis in the bloom is found to be fairly constant throughout the simulation, revealing that the limitation of growth due to depletion of nutrients is balanced by a continual influx of photosynthesising phytoplankton carried by the converging surface flows [7]. Examining the variables quantifying photosynthesis in equation (2), P , N and d , it is clear that the bloom occurs at the position where the surface flows converge because the effects of nutrient limitation there (low N) are countered by an influx of phytoplankton (high P) and abundant light (low d). In the original paper [7] this argument is supported by a

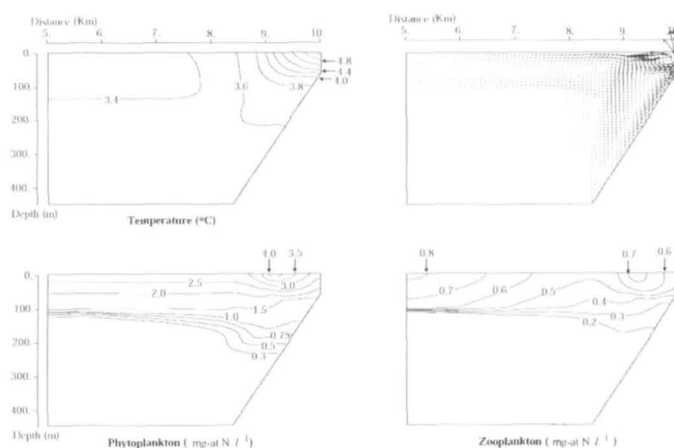


Figure 3 Results from the example simulation [7]: velocity vectors and contours of temperature, phytoplankton and zooplankton after 20 days of simulation.

detailed analysis of each biological interaction term, which is omitted here in the interest of brevity.

The study also finds that the plankton model is fundamentally dependant upon the vertical diffusion term in the plankton transport equation (1), and in particular upon the value of K_v which quantifies the amount of vertical turbulent mixing. When applied to large bodies of water, K_v is usually modelled by a simple function of the vertical density structure of the fluid, as buoyancy effects may help to generate or suppress turbulence. The study shows that plankton growth near the surface is strongly responsive to the value of K_v , as blooms can be trapped near the surface for small K_v or diffused away from the growth region rapidly when K_v is large. In this way the plankton responds to the lake's density structure, which is predicted by the two-dimensional flows of the model.

Discussion

In this article I have attempted to give a flavour of the coupled physical-ecological modelling which is now possible using computational techniques, and I have given a brief example of such an application which has been performed on an ordinary desktop computer.

It should be noted that the formulation I have used as an example here is at the simpler end of the spectrum of plankton models. It is possible to adopt models with many more state variables, representing different species of plankton and nutrient types and additionally modelling such factors as Oxygen concentrations, the benthic (bottom-dwelling) communities, and even the effects of higher organisms such as fish. However, extending models in this way can be problematic due to uncertainty in the mathematical representations of ecological processes and the increasing number of poorly-known parameters which arise from such increased complexity. The model used as an example here is merely the first step in a series of attempts to capture mathematically the interaction between the physics and ecology of the thermal bar circulation [10].

The most important consideration is to find accurate results which are of relevance to the real world, regardless of the complexity of the model used to obtain them. With a host of parameters to be set in each ecosystem model, increasing rapidly with every new sophistication, it is the lack of in-situ hydrobiological

data required to validate these parameters, rather than computing power, which now limits the numerical modelling of plankton ecology. □

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