On Advection in Phytoplankton Models†

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Scale analysis is used to deduce a new non-dimensional number, \( S = \frac{C}{[(A H)^{1/2} V_m]} \) which defines the importance of advection of phytoplankton by organized fluid motion in spatial models of marine food chains. When \( S \gg 1 \), advection greatly affects biological productivity; when \( S \ll 1 \), advection may be neglected. When \( S \) is order one, advection and biological productivity play competing roles in determining the spatial configuration of the plankton biomass.

1. Introduction

The marine ecologist interested in modelling the lower trophic levels in an aquatic environment must consider the effect of the water movement on the concentrations of the biological and chemical components of his models. Most biological oceanographers intuitively understand the role of organized water circulation and disorganized water motion (turbulence) in determining the spatial structure of phytoplankton and zooplankton distributions. There is a tendency for modern marine food chain models to include advection (by organized motion) and diffusion (by disorganized motion) in spatial models (Walsh & Dugdale, 1971). In this note we would like to explore the question: when does advection need to be included in a marine food chain model? We will demonstrate that it is instructive to non-dimensionalize the dynamic equations of a phytoplankton model to glean an answer to this question.

A non-dimensional ratio, \( S \), is derived which categorizes the importance of advection in a food chain model. When \( S \gg 1 \), advection is the foremost factor in plankton dynamics; when \( S \ll 1 \), advection is unimportant to the plankton dynamics. When \( S \) is of the order unity, advection plays a strong competing role with the other environmental conditions determining the spatial distribution of the plankton.

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2. Dynamic Equations for Plankton Models

Let us consider a marine environment with a biological component, \( P \). The symbol \( P \) represents the concentration of the component \( P \) at an arbitrary point in the fluid. For convenience we can assume \( P \) is the phytoplankton biomass concentration. It is convenient to assume that there exists a maximum specific growth rate, \( \nu_m(\text{sec}^{-1}) \) of \( P \). This characterizes the fundamental specific uptake of nutrients by the phytoplankton (Dugdale, 1967). We may assume quite generally that the dynamics \( P(x, y, z, t) \) is governed by

\[
\frac{\partial P}{\partial t} + u \frac{\partial P}{\partial x} + v \frac{\partial P}{\partial y} + w \frac{\partial P}{\partial z} = \frac{\partial}{\partial x} \left( \nu H \frac{\partial P}{\partial x} \right) + \frac{\partial}{\partial y} \left( \nu H \frac{\partial P}{\partial y} \right) + \frac{\partial}{\partial z} \left( \nu v \frac{\partial P}{\partial z} \right) + V_m R_P - Q_P + F. \tag{1}
\]

The independent variables are \( x, y, z, t \) where we choose by convention that \( x, y \) are the horizontal coordinates and \( z \) is the vertical coordinate. The specific orientation of the axes is not essential. The velocity components, \( u, v, w \), are the \( x \)-directed, \( y \)-directed and \( z \)-directed components respectively of the organized motion. The four terms on the left-hand side represent collectively the change of \( P \) following a water parcel moving with the fluid. The first term is the local change and the other terms are the advective changes.

The first three terms on the right-hand side are the turbulent dispersion terms where \( \nu_H \) and \( \nu_v \) are the horizontal and vertical eddy diffusivities, respectively. We have assumed that the eddy diffusivity is isotropic in the horizontal but not in the vertical, i.e., \( \nu_H \neq \nu_v \). Terms involving molecular diffusion have not and should not be considered. Implicit in equation (1) is the understanding that a finite difference type solution will be sought for any particular model. The model equations have been Reynolds’ averaged and turbulent fluxes of \( P \) have been approximated by a Fickian diffusion law (Hess, 1959; Fofonoff, 1962). These diffusion terms represent the collective diffusion of \( P \) by all scales of motion not represented by the grid size used in the model. This includes, besides chaotic motion, motion whose time and space scales are smaller than can be resolved by the computational model.

The term, \( V_m R_P \), represents the principal growth term for the phytoplankton; \( V_m \) is the maximum specific uptake rate (sec\(^{-1}\)); \( R \) is a non-dimensional function which includes the details of the uptake formulation. In general, \( R \) is a function of many variables (which vary from model to model) such as nutrient concentration, light availability, chelating inhibition etc.

The term, \( Q_P \), represents collectively the biological processes which diminish the phytoplankton stock such as predation by higher trophic levels, excretion, mortality etc. The term \( F \) represents any losses or additions to the system which are biological in nature but not dependent on the concentration, \( P \).
Equation (1) is quite general and includes any biological, chemical, or physical oceanographic process which might be included in a marine food chain model.

The water motion, u, v, w, may be a function of x, y, z, t. In a particular model it may be specified or, in itself, calculated from the dynamic equations of motion. For the purpose of this note and without loss of generality we shall assume that γ-directed variations of all variables may be neglected. In addition, we expect the water to be non-divergent, i.e.

\[
\frac{\partial u}{\partial x} + \frac{\partial w}{\partial z} = 0. \tag{2}
\]

This is an excellent assumption for almost all aquatic ecosystems. Since detailed knowledge of the sub-grid scale motions will not be available, it is customary to assume that the best estimates of \(v_H\) and \(v_v\) are positive constants. It is doubtful that a more sophisticated relationship can be formulated at this time. This is not the situation for the fluid eddy diffusivities for momentum \(A_H\), \(A_v\), e.g., see O'Brien (1970).

Equation (1) reduces to

\[
\frac{\partial P}{\partial t} + u \frac{\partial P}{\partial x} + w \frac{\partial P}{\partial z} = v_H \frac{\partial^2 P}{\partial x^2} + v_v \frac{\partial^2 P}{\partial z^2} + V_m RP - QP + F. \tag{3}
\]

3. Non-Dimensionalization

The principal technique used to deduce the relative importance of advection and diffusion in a spatial trophic level model is non-dimensionalization and scale analysis. Since we are often concerned in an aquatic ecosystem model with the rate of primary production, we select \(V_m^{-1}\) as the appropriate parameter for scaling time, \(t\), in equation (3). Let \(C\) be a typical value of the organized horizontal flow; \(W\) is a typical value of the vertical velocity; \(L\) and \(H\) are horizontal and vertical length scales which have to be determined. Let \(P\) be the average or a typical value of \(P\).

The scaling equations are

\[
P = PP^*,
V_m t = t^*,
u = Cu^*,
w = Ww^*,
x = Lx^*,
z = Hz^*,
F = V_m PF^*,
Q = V_m Q^*. \tag{4}
\]
Equations (4) are used to non-dimensionalize equation (3). If we adopt the common practice of dropping asterisks immediately, equation (3) becomes

$$\frac{\partial P}{\partial t} + S \left[ \frac{\partial P}{\partial x} + w \frac{\partial P}{\partial z} \right] = E_H \frac{\partial^2 P}{\partial x^2} + E_v \frac{\partial^2 P}{\partial z^2} + R_P - Q_P + F$$  \hspace{1cm} (5)

where $S, E_H$ and $E_v$ are defined

$$S \equiv C/LV_m,$$  \hspace{1cm} (6)

$$E_H \equiv \nu_H/L^2 V_m,$$  \hspace{1cm} (7)

$$E_v \equiv \nu_v/H^2 V_m.$$  \hspace{1cm} (8)

The scaled non-dimensional form of equation (2) implies

$$W = CH/L.$$  \hspace{1cm} (9)

This relationship has been used in equation (5). It is important to realize that all quantities in equation (5) are non-dimensional. We also insist that $P, u, w$ and all derivatives of $P$ have been scaled such that these quantities are of the order unity. Thus the non-dimensional numbers, $S, E_H, E_v$, measure the relative importance of advection by organized motion and diffusion by disorganized motion.

If $S$ is of order unity, then advection is as important as biological and chemical processes in determining the temporal variations of $P$. If $S \ll 1$, advection may be neglected. If $S \gg 1$, advection is extremely important. In this case equation (5) is not valid since the advection term is larger than every other term and the model must be redefined.

How can $S$ vary? It increases directly with the characteristic water speed, $C$. It varies inversely with $V_m$. When the maximum specific uptake rate is high, the biological reproduction rate is large and the importance of advection is diminished. We have yet to specify a physical meaning of the horizontal length, $L$.

The length scales may not be related to the biological dynamics in any way. It is meaningless to relate $L$ to grid size or the size of the ocean under consideration. However, it is natural for our present discussion to relate $L$ to the turbulent part of the flow. Let us define

$$L = (A_H \tau)^{1/2},$$  \hspace{1cm} (10)

where $\tau$ is interpreted as a time scale associated with the eddies in the disorganized motion which contain the most kinetic energy; $\tau$ may be called the eddy turnover time. $S, E_H, E_v$ become

$$S = C/V_m(A_H \tau)^{1/2},$$  \hspace{1cm} (11)

$$E_H = \frac{\nu_H}{A_H} 1/V_m \tau,$$  \hspace{1cm} (12)

$$E_v = \frac{\nu_v}{A_v} \left( \frac{L}{H} \right)^2 (1/V_m \tau).$$  \hspace{1cm} (13)
We have related the non-dimensional ratio, $S$, to the advection speed, the maximum uptake rate of nutrients and the turbulent part of the flow field. Where the flow is geostrophic the choice for the time scale is $\tau = f^{-1}$, $f$ being the Coriolis parameter.

It is constructive to consider some real oceanographic situations where the \textit{a priori} importance of advection in a spatial marine food chain model is uncertain. For the Sargassa Sea, we may obtain from the literature the parameter values: $C = 1 \text{ cm sec}^{-1}$, $A_u = 5 \times 10^7 \text{ cm}^2 \text{ sec}^{-1}$, $f = 7.3 \times 10^{-5} \text{ sec}^{-1}$, and $V_m = 2.8 \times 10^{-5} \text{ sec}^{-1}$ (Munk & Carrier, 1950; Thomas & Dodson, 1968). The resulting value of $S$ is $4 \times 10^{-2}$, indicating horizontal advection may be neglected when modelling the phytoplankton.

In a rapidly moving system advection must be important. For the Gulf Stream, with a value of $C$ equal to 100 cm sec$^{-1}$ and $f = 10^{-4} \text{ sec}^{-1}$, $S$ increases to 5. Thus the horizontal advection is a dominant factor. For the Peru upwelling region, we estimate that $C = 20 \text{ cm sec}^{-1}$, $A_u = 10^8 \text{ cm}^2 \text{ sec}^{-1}$, $|f| = 3 \times 10^{-5} \text{ sec}^{-1}$, and $V_m = 1.4 \times 10^{-5} \text{ sec}^{-1}$ (Beers, Stevenson, Eppley & Brooks, 1971), thus $S = 1.0$. Here advection and biological productivity play competing roles in determining the spatial configuration of the phytoplankton biomass.

It is our thesis that $S$ is a measure of the importance of advection in determining the spatial structure of plankton distributions in marine food chain models.

4. Conclusion

We have used scale analysis to deduce a new non-dimensional number, $S$, whose magnitude indicates the importance of including advection in a marine ecosystem model. We are presently utilizing this technique in a lower trophic level model of the West Florida continental shelf. Here the flow is geostrophic, thus

$$\tau = f^{-1}$$

where $f$ is the Coriolis parameter.

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