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Effects of velocity fluctuations on vertical distributions of phytoplankton

by Greg Holloway¹

ABSTRACT

Effects of vertical velocity oscillations (associated with high frequency internal gravity waves) upon the vertical distribution of horizontally averaged phytoplankton concentration are considered. It is suggested that such effects have been systematically misrepresented in previous modeling efforts. Correction terms are derived both for averaged quasi-Lagrangian (isopycnal) models and for averaged Eulerian models. In quasi-Lagrangian models, an apparent modification to growth rate coefficient is obtained. In Eulerian models, velocity fluctuations are shown to induce a net vertical transport which can be described by a "virtual velocity" and which is seen as a correction to eddy diffusivity parameterizations. Difficulties such as negative or singular diffusivities are circumvented. Convergence of virtual velocity can provide an effective mechanism for formation of a phytoplankton maximum near or below the mean compensation depth. It is hoped that inclusion of effects here derived may extend the realism and utility of averaged plankton models.

1. Motivation

Since the pioneering work of Riley *et al.* (1949), quantitative models for the spatial and temporal evolution of plankton communities have become increasingly complicated. In many cases, models have become increasingly computer intensive. Sources of this complexity arise both in the biology and in the physics. For the most part, these two problem areas have been investigated separately; that is, biological rates and interactions have been studied in circumstances where the physical environment is either uniform or else relatively simple, while physical mixing, stirring and transport in stratified, turbulent flows have been studied for relatively simple substances such as heat or dye. At the level of model synthesis, it is usual to replace the relatively simple dye with biologically active substance. But, had we dealt with biologically active substance all along, might not the character of mixing and transport have appeared differently than in studies based upon simple dyes?

When dealing with complicated interactions in complicated environments, computer simulation has become an increasingly powerful tool, as seen for example in Wroblewski (1977, 1982), Wroblewski and O'Brien (1981) or Woods and Onken

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(1982). Rather than assuming only averaged biology in averaged physical environments, it has become possible, to a limited degree, to follow trajectories of a large number of individual organisms and/or to realize complicated, time-dependent flow fields. However, this approach has definite weaknesses. Even given a dedicated effort employing the most advanced computing technology available, it is unlikely that one could follow a very meagre population in a poorly resolved turbulent flow field.

It seems clear that there will be continuing need for averaged models of plankton distributions, especially as one seeks to explore seasonal cycles or responses to upwelling events or to investigate the dynamics of horizontal inhomogeneities. Then the pressing problem is to find valid representations of the averaged effects of fluctuations in the physical and biological variables.

In this note, we return to the classical type of models for vertical distributions of horizontally averaged plankton concentrations. We will be concerned about the role of fluctuations of vertical velocity, especially velocity associated with high frequency internal gravity waves. Lower frequency waves such as internal tides will not be included based on a rationale that such phenomena can be treated explicitly in computer simulations which resolve diel variation (Kamykowski, 1974, 1976, 1978). See also Joyce and Flierl (1984, in preparation). We will attempt to show that effects of high frequency internal gravity wave fluctuations interacting with growth rate coefficient which varies with depth have been *systematically* misrepresented in previous averaged model calculations. A correction term in the form of a "virtual velocity" will be derived and certain consequences will be considered.

2. Derivation

Let $\phi(z, t)$ be concentration of phytoplankton as function of depth z (directed upward) and time t . In principle, ϕ might be measured as concentration of organic carbon. More convenient measures are chlorophyll concentration or *in vivo* fluorescence although the relations of these measures to organic carbon are widely variable (Cullen, 1982). We may think of $\phi(z, t)$ as an instantaneous profile at time t at a fixed station. In general such a profile will exhibit a great deal of variability on all resolved scales, as seen for example in Figure 1.

Suppose the evolution of ϕ can be written

$$\partial_t \phi + \tilde{w} \partial_z \phi + q = \lambda \phi + \gamma + \partial_z (k \partial_z \phi) + \partial_z (s \phi) \quad (1)$$

where \tilde{w} is the instantaneous (positive upward) vertical fluid velocity, q represents symbolically the effects of horizontal advection, λ is a growth rate coefficient which may be a complicated function of (z, t) γ represents symbolically those biological influences (mainly grazing) which may not be expressed appropriately as λ , k is a small scale diffusivity of biological and/or physical origin, and s is a representative sinking (swimming) speed here expressed so that $s > 0$ is downward sinking. Incompressibility

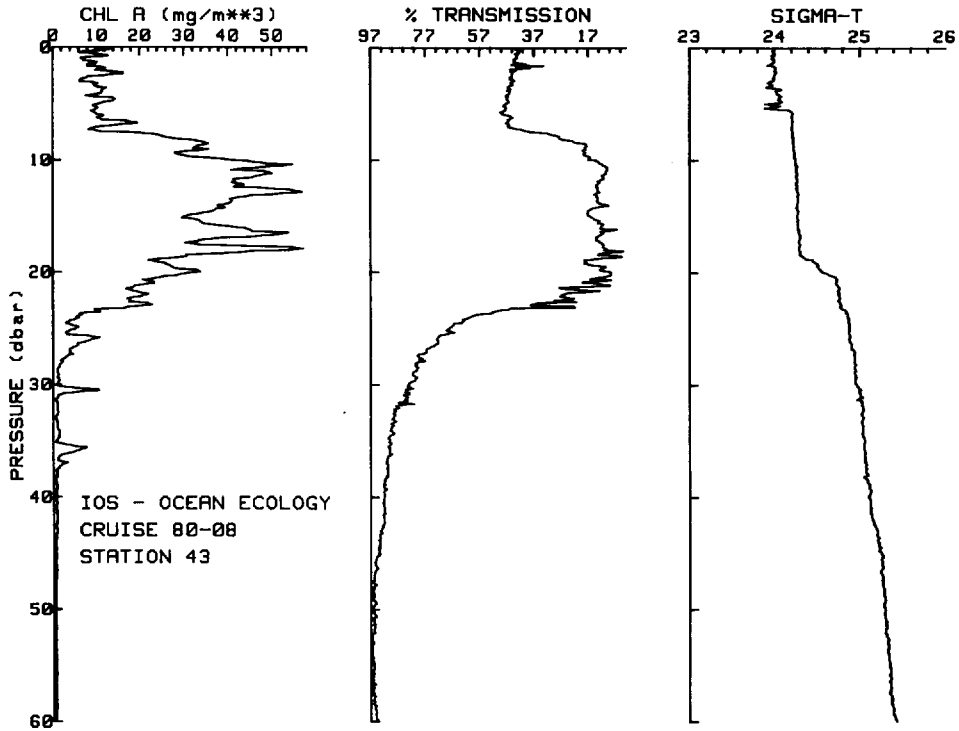


Figure 1. Vertical profiles of chlorophyll *a* (based on fluorescence), transmissivity and potential density are shown for a station over the continental shelf off Vancouver Island, British Columbia during August 1980. Courtesy of Dr. K. L. Denman.

of the fluid motion has been assumed with horizontal divergences cancelling $\partial_z \bar{w}$. Eq. (1) is written in a way that separates physical processes on the left from primarily biological processes on the right.

Now we imagine collecting many such station profiles and forming an ensemble (or horizontal) average denoted by $\langle \rangle$. A usual modeling goal is to obtain an equation for evolution of averaged variable $\Phi = \langle \phi \rangle$ in terms of $\Lambda = \langle \lambda \rangle$, $\Gamma = \langle \gamma \rangle$, $S = \langle s \rangle$ and an effective vertical diffusivity K . The typical form of model equation is

$$\partial_t \Phi - \partial_z (K \partial_z \Phi) = \Lambda \Phi + \Gamma + \partial_z (S \Phi) \quad (2)$$

where advective effects due to \bar{w} and q are "parameterized" by an eddy diffusivity K . K also absorbs any small scale diffusivity k from (1). The term in K has been placed on the left side of (2), reflecting its dominantly physical origin. For assumed horizontal uniformity of mean fields, average vertical velocity $\langle \bar{w} \rangle$ vanishes by incompressibility.

A common criticism is that eddy diffusivity is an *ad hoc* device which is not

fundamentally derived in the theory of fluid dynamics. Nonetheless, eddy diffusivity has enjoyed some success as an engineering approximation. Indeed, if phytoplankton were simply green dye, an eddy diffusivity form might be appropriate. However, the following short calculation shows that, for phototrophic substance in a velocity field which is significantly wavelike, effects arise which cannot be represented appropriately by an eddy diffusivity.

Construct a quasi-Lagrangian coordinate as follows: At any depth z , observe the instantaneous fluid density ρ . Assign an isopycnal deviation $\zeta(z, t)$ as the height of z above that height $z_0(\rho)$ at which one would observe ρ on average; i.e., observe $\langle \rho \rangle$. Assuming that the average density profile is monotonic in z , $\zeta(z, t)$ is a well-defined, single-valued variable. In particular, overturning of instantaneous density does not invalidate the coordinate transformation. Now define a vertical pseudo-velocity

$$w(z, t) = \partial_t \zeta(z, t). \quad (3)$$

In general, the instantaneous velocity \tilde{w} will not equal w . A difference $\tilde{w} - w$ will result from horizontal advection of isopycnal elevations and will contain a "random" component which is assumed to contribute toward a conventional eddy viscosity. Although the pseudo-velocity w is expected to be dominated by internal wavelike dynamics, we have not made a small amplitude assumption, viz. overturning is permitted. A reader should be cautioned that the w here defined is unusual. The essential feature is that w is that part of the vertical velocity field which leads to bounded displacement variance.

We assume that w or ζ fields will be characterized by length and time scales representative of upper ocean internal waves. In the lower euphotic zone, say at depths of 20 to 60 m, typical scales might be

$$\begin{aligned} \langle \zeta^2 \rangle &\approx 10 \text{ m}^2 \\ \langle w^2 \rangle &\approx 10^{-5} \text{ m}^2 \text{ s}^{-2} \\ \text{periods } &10^3 \text{ s} < 2\pi/\omega < 10^4 \text{ s} \\ \text{vertical coherence scale } &l \approx 10 \text{ m} \end{aligned}$$

Note that only periods rather shorter than the internal tide have been retained.

We may observe that, on these internal wave length and time scales, effects of eddy diffusivity K and sinking S may be neglected. Viz., if a conventional value $K \approx 10^{-3} \text{ m}^2 \text{ s}^{-1}$ is assumed, a diffusion time scale $l^2 K^{-1} \approx 10^5 \text{ s}$, while sinking speeds up to 10^{-5} m s^{-1} (i.e., 1 m d^{-1}) are small compared with w . Furthermore, in the quasi-Lagrangian coordinate frame, the grazing community will tend to be carried with the fluid displacement, in addition to some swimming and buoyancy effects, and so the term γ in (1) may be relatively constant. The result is that in the quasi-Lagrangian frame, a dominant source of short term variability in ϕ is due to the variability of λ as experienced following the displacement $\zeta(t)$. To isolate this variability, consider a

simplified model

$$\dot{\phi}(z_0 + \zeta(t)) = \lambda(z_0 + \zeta(t)) \phi(z_0 + \zeta(t)) \quad (4)$$

where $\dot{\phi}$ denotes the advective derivative following w . Next we will take a Taylor expansion of λ in ζ , which is justified for the mean Λ profile whose scale height will tend to be given by the extinction coefficient for optical light, typically $\alpha \approx 0.1 \text{ m}^{-1}$ for a 1% light level at 46 m. Thus $\zeta\alpha \approx .3 < 1$. We have also the opportunity to modify the Taylor expansion in a way that recognizes another aspect of the short term variability: During the internal wavelike oscillation, the nutrient and grazing environment will tend to advect with the phytoplankton profile. Then it is principally the variation of light intensity which affects λ in the quasi-Lagrangian frame. Therefore we take

$$\lambda(z_0 + \zeta) = \Lambda_0 + \Lambda'_0 \zeta + \frac{1}{2} \Lambda''_0 \zeta^2 + O(\alpha \zeta)^3 \quad (5)$$

where

$$\begin{aligned} \Lambda'_0 &= \left(\frac{\partial I}{\partial z} \right)_0 \left(\frac{\partial P}{\partial I} \right)_0 \\ \Lambda''_0 &= \left(\frac{\partial^2 I}{\partial z^2} \right)_0 \left(\frac{\partial P}{\partial I} \right)_0 + \left(\frac{\partial I}{\partial z} \right)_0^2 \left(\frac{\partial^2 P}{\partial I^2} \right)_0 \end{aligned} \quad (6)$$

and all quantities are evaluated at the reference depth z_0 . I is light intensity and $\partial P / \partial I$ is the slope of the photosynthetic-rate-versus-intensity curve (Platt *et al.*, 1977).

It should be remarked that the modified expansion (5), (6) does not take into account self-shading effects (Shigesada and Okubo, 1981). Also, (5), (6) imply that the time constant for changes in P due to changes in I is as short as N^{-1} where $N = \sqrt{-g/\rho_0 \partial \rho_0 / \partial z}$ is the stability frequency. On the other hand, it is assumed that the time constant for photoadaptation, i.e., modification of the P -vs- I curve, is long compared with periods of high frequency waves.

From (4) and (5), following the quasi-Lagrangian displacement,

$$\begin{aligned} \phi(z_0 + \zeta(t)) &= \phi_0 e^{\Lambda_0 t} \exp \int_0^t \left(\Lambda'_0 \zeta + \frac{1}{2} \Lambda''_0 \zeta^2 + \dots \right) d\tau \\ &= \phi_0 e^{\Lambda_0 t} \left(1 + \Lambda'_0 \int_0^t \zeta(\tau) d\tau \right. \\ &\quad \left. + \frac{1}{2} \Lambda''_0 \int_0^t \zeta^2(\tau) d\tau + \dots \right) \end{aligned} \quad (7)$$

where expansion of the exponential has been written out to first order in t . We may conveniently reintroduce effects of omitted terms K , Γ and S by replacing the occurrence of $\phi_0 e^{\Lambda_0 t}$ in (7) by Φ .

Averaging (7) along the quasi-Lagrangian displacement, the term linear in ζ vanishes while the term quadratic in ζ gives an apparent modification of rate

coefficient Λ by an amount

$$\Lambda_L = \frac{1}{2} \Lambda_0'' \langle \zeta^2 \rangle. \quad (8)$$

This effect is easy to explain. There are two terms in (6). If $(\partial^2 I / \partial z^2)(\partial P / \partial I) > 0$, as tends to be the case except at high light levels where photoinhibition $\partial P / \partial I < 0$ can occur, the vertical oscillations cause plankton to visit a more productive environment *on average* than if the plankton remained fixed at a given depth. However, if $\partial^2 P / \partial I^2 < 0$, the vertical oscillations produce oscillations in I resulting *on average* in a lower photosynthetic rate P . Quantitatively, (8) may be rather small compared with Λ_0 . The positive growth enhancement can be estimated as $\frac{1}{2} \alpha^2 \langle \zeta^2 \rangle \approx .05$, or just a few percent of the unmodified growth rate. This will be reduced on account of $\partial^2 P / \partial I^2 < 0$ by an amount dependent upon the shape of the P -vs- I curve. Further discussion on these effects is given by Joyce and Flierl (1984, in preparation).

Although the effect just derived may not appear to be very significant, we will find some further differences arising when we compare the quasi-Lagrangian description with a more common Eulerian description. Consequences will be explored in a following section.

From an Eulerian view, we imagine fastening our attention at a fixed depth z . Large amplitude fluctuations in ϕ will be observed on account of internal wave displacement. However, if we form an average vertical flux $\langle w\phi \rangle$, we'll find that fluctuations in ϕ are nearly in quadrature with fluctuations in w . Indeed, if ϕ were a conservative tracer then fluctuations in ϕ would be nearly in phase with ζ and by (3) we would have $\langle w\phi \rangle = 0$. Here it is important to recall that w is not the instantaneous vertical velocity w . The quasi-random difference $\tilde{w} - w$ is presumed to contribute toward an eddy diffusive-type flux $-K\partial_z\Phi$.

Nonconservation of ϕ alters the flux calculation in a significant way. Whereas a term in (7) linear in ζ vanishes when calculating the Lagrangian growth enhancement Λ_L , the same term linear in ζ dominates a flux, viz

$$\begin{aligned} \langle w\phi \rangle &\approx \Phi \langle \Lambda_0'(\partial_t \zeta) \int_0^t \zeta(\tau) d\tau \rangle \\ &= \Phi(-\Lambda_0' \langle \zeta^2 \rangle) = W_* \Phi \end{aligned} \quad (9)$$

where statistical stationarity of ζ has been used.

We encounter an apparent vertical velocity, or "virtual velocity," given by

$$W_* = - \langle \zeta^2 \rangle \Lambda_0'. \quad (10)$$

The calculation in (9) follows the quasi-Lagrangian displacement ζ . However, the lowest order contribution to the flux is already at order ζ^2 . To this order the quasi-Lagrangian and the Eulerian fluxes agree. Thus W_* and Λ_0' may be evaluated as mean Eulerian properties at any given depth.

The nature of the virtual velocity W_* may seem puzzling. This is not a velocity

associated with any net transport of water. Neither does W_* correspond to any net motion of individual organisms through the water. In particular the process is distinct from sinking. Perhaps the effect can be described as a "pumping" of biomass such that convergence (divergence) of $W_*\Phi$ provides a source (sink) for Φ at any depth. W_* becomes our means of expressing an Eulerian mechanism to support the enhanced quasi-Lagrangian growth Λ_L . The Eulerian balance equation for Φ now reads

$$\partial_t\Phi - \partial_z(K\partial_z\Phi) + \partial_z(W_*\Phi) = \Lambda\Phi + \Gamma + \partial_z(S\Phi). \quad (11)$$

It is interesting to note that it is unclear whether to put W_* on the left or right side of (11) according to our former physical/biological split. W_* arises just through physical-biological interaction. More important is to note the formal similarity between W_* and sinking S . Historically, sinking has been considered to play a role in affecting plankton depth distributions. This is seen both on theoretical grounds, as in Steele and Yentsch (1960), and in numerical modeling efforts, as seen in Jamart *et al.* (1977). Sinking speeds of 1 m/day or more are indicated. Yet, except in cases of larger organisms and more motile flagellates, such assumed sinking speeds seem very large on average (Smayda, 1971, 1974; Happey-Wood, 1976; Burns and Rosa, 1980). For more oligotrophic environments where the bulk of primary productivity may be supported by organisms of typical sizes 1 to 10 μm , average sinking speeds are much smaller, on order of 10^{-2} m/day. On the other hand, W_* can be estimated as

$$\begin{aligned} W_* &\approx -\alpha\Lambda\langle\xi^2\rangle \\ &\approx -(0.1 \text{ m}^{-1})(1 \text{ d}^{-1})(10 \text{ m}^2) \approx -1 \text{ m/day}. \end{aligned} \quad (12)$$

Larger or smaller amplitudes for W_* can easily be obtained. Thus the effect of W_* may readily overwhelm any effect of actual sinking of plankton. Note too that positive or upward W_* seems possible where photoinhibition ($\partial P/\partial I < 0$) occurs.

As a last remark in this section, let us see if the quasi-Lagrangian result (8) can be reconciled with the Eulerian result (10), (11). Even omitting such effects as curvature of P -vs- I or depth dependence of $\langle\xi^2\rangle$, it would appear that

$$-\partial_z W_* \approx \langle\xi^2\rangle \Lambda_0'' \quad (13)$$

or approximately twice Λ_L . This difference actually only reflects a difference between Eulerian and Lagrangian averaging. For a fluid element whose Lagrangian reference level (say, given by the equilibrium depth of the isopycnal) is written z_L , we have seen that the Lagrangian averaged growth rate is

$$\Lambda(z_L) + \frac{1}{2} \langle\xi^2\rangle \Lambda_0''(z_L). \quad (14)$$

At a fixed depth z_E (equal, say, to the same isopycnal equilibrium depth), the Eulerian averaged growth rate may differ from (14) because the depth z_E is visited by fluid elements whose Lagrangian reference level z_L is different from z_E . We ask what is the

value of z_L for any element that is found instantaneously at z_E . It is $z_L = z_E - \zeta(t)$. To obtain the Eulerian averaged growth term, substitute for z_L in (14), Taylor expanding and retaining terms through $O(\zeta^2)$. Expansion of the first term in (14) generates a term identical to the second so that the Eulerian average is

$$\Lambda(z_E) + \langle \zeta^2 \rangle \Lambda''(z_E). \quad (15)$$

Enhancement of the Eulerian apparent growth term is indeed approximately twice the enhancement of the Lagrangian term.

3. Consequences

a. Model results of Wroblewski. For the most part, numerical models for plankton distributions have not explicitly realized a fluctuating velocity field. An exception occurs in the case of Wroblewski (1977) and Wroblewski and O'Brien (1981). Using the flow field from a two-dimensional ($x - z$) numerical circulation model (Thompson, 1974) for coastal upwelling, Wroblewski and O'Brien (1981) integrated a plankton advection model. Explicit sinking was not included in the model. However, due to fluctuations in wind stress the flow field exhibited short period velocity fluctuations which induced plankton concentration fluctuations p' . Denoting the vertical velocity fluctuation by w' , fluxes $w'p'$ were obtained from a model. A systematic pattern emerged showing a downward $w'p'$ flux, counter to the mean gradient $\partial P/\partial z$. Defining conventional eddy diffusivity as

$$K_* = -w'p' / \partial P/\partial z \quad (16)$$

counter gradient fluxes imply "negative diffusivity" as discussed by Wroblewski and O'Brien (1981). Although the computation of Wroblewski and O'Brien (1981) in fact concerns zooplankton, results are much the same as obtained from the phytoplankton model of Wroblewski (1977). Plausibly such close similarity is a consequence of biological dynamics relating zooplankton and phytoplankton populations.

Computations of Wroblewski and O'Brien (1981) are, at once, both enlightening and discouraging. Especially it would be discouraging if realistic plankton simulation required sophisticated, computer-intensive simulation of the detailed space- and time-dependent velocity field. On the other hand, specific inclusion of "negative diffusivity" in an averaged model would cause the model to become strictly ill-conditioned insofar as continuum solutions would become nonunique after arbitrarily short time in the absence of higher derivative terms.

Based upon the derivation in the previous section, we suggest that the fluxes obtained by Wroblewski and O'Brien (1981) would be better modeled by a downward virtual velocity W_* . Essentially, a downward flux of phytoplankton may be driven by the gradient of growth rate coefficient rather than the gradient of phytoplankton

concentration. Removal of the part of the flux describable by W_* will, plausibly, leave a residual flux describable by a more conventional, everywhere positive eddy diffusivity.

b. Formation of deep phytoplankton maxima. Observations by Ryther and Yentsch (1958) as well as numerous subsequent observations (see reviews in Jamart *et al.* (1977), Raymont (1980) or Cullen (1982)) show the common occurrence of chlorophyll or fluorescence maxima near the base of the euphotic zone. Although the relationship of chlorophyll or fluorescence of organic carbon is problematical (Cullen, 1982), the observations are suggestive of deep maxima of phytoplankton concentration. Occurrence of these deep maxima has been an area of long-standing interest among plankton researchers. Explanations often take account of the sinking of cells. Other influences including time-dependence on semi-diurnal to diurnal scales (Kamykowski, 1976, 1978), seasonal dependence (Kiefer and Kremer, 1981), selective grazing (Lorenzen, 1967) or Langmuir circulations (Ledbetter, 1979) may affect plankton distributions. Our interest here focuses on the classical discussion by Steele and Yentsch (1960).

Riley *et al.* (1949) suggested that sinking of phytoplankton might affect the depth of a maximum if the cell sinking rate were a function of depth. Steele and Yentsch (1960) further quantified the argument for such differential sinking, showing that in the absence of differential sinking a steady-state maximum of phytoplankton concentration can only occur above the compensation depth z_c (the depth above which, averaged over the diurnal cycle, photosynthetic production exceeds the sum of respiration plus grazing). See Figure 2. The argument of Steele and Yentsch (1960) is elegant and is given below in slightly more general form. Suppose averaged plankton concentration is governed by

$$\partial_t \Phi - \partial_z(K\partial_z \Phi) = \Lambda \Phi + \Gamma + \partial_z(S\Phi). \quad (17)$$

Here, both Λ and K may vary continuously with depth. The compensation depth z_c is defined by $\Lambda \Phi + \Gamma = 0$. Seeking a steady ($\partial_t \Phi = 0$) maximum ($\partial_z \Phi = 0$, $\partial_{zz}^2 \Phi < 0$), we require

$$\partial_{zz}^2 \Phi = - \frac{\Phi(\Lambda + \partial_z S) + \Gamma}{K} < 0. \quad (18)$$

Below z_c , $\Lambda \Phi + \Gamma < 0$. Therefore (18) can only be satisfied for sufficiently large, positive values of $\partial_z S$. (Note that we assume only that $K > 0$; otherwise K may have any continuous variation in z .) Steele and Yentsch (1960) estimate that observed maxima, at or below z_c , appear to require sinking speeds of 1 to 2 m/day somewhat above z_c decreasing to negligible values below z_c . However, Steele and Yentsch (1960) also suggest that, for temperate latitude, open ocean sites, such large sinking speeds are unlikely.

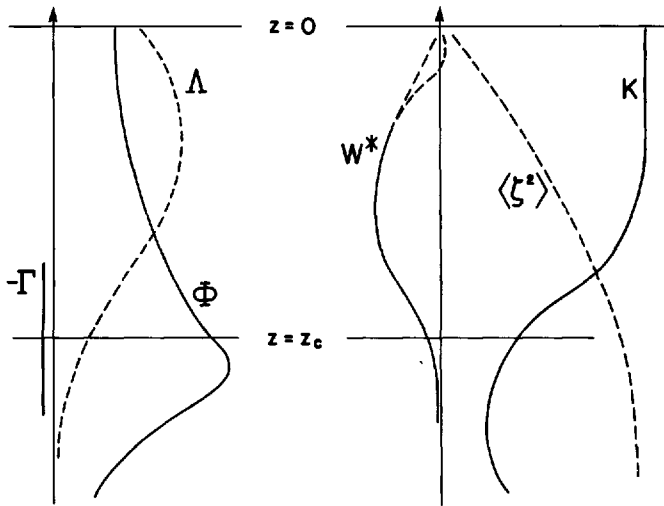


Figure 2. A qualitative sketch suggests possible relationships among mean phytoplankton concentration Φ , growth rate coefficient Λ , net grazing and respiration Γ , eddy diffusivity K , isopycnal displacement variance $\langle \zeta^2 \rangle$, and the derived virtual velocity W_* . This sketch is not claimed to be realistic for any particular location but rather illustrates broadly some of the typical features that may emerge in profiles, averaged over diurnal period. Whereas the depth distribution of grazing pressure is poorly known, a simple constant Γ is shown. Compensation depth z_c is determined by $\Lambda\Phi + \Gamma = 0$. In the upper portion of the euphotic zone, note that $W_* < 0$ although $\partial\Lambda/\partial z < 0$. Such a circumstance may arise on account of nutrient depletion. However, Λ'_0 as defined in (6) is evaluated at fixed nutrient concentration, thereby permitting $\Lambda'_0 > 0$. Very near the free surface, photoinhibition may result in $\Lambda'_0 < 0$, hence $W_* > 0$ according to (10).

Virtual velocity effects may be included in (17), (18) by replacing S by $S - W_*$. As has been noted previously, values of $|W_*|$ may easily be as large as 1 to 2 m/day. The value of $|W_*|$ will decrease with increasing depth over characteristic scales of order $\alpha^{-1} \approx 10$ m.

c. Stability of steady-state distributions. A common theoretical or numerical modeling goal is to obtain steady state solutions to model equations such as (2). Beyond obtaining such solutions, it is important to consider their stability properties. This question has been addressed by Riley (1963) and by Criminale and Winter (1974) and Criminale (1980). For the linear, homogeneous part of (2), a neutrally stable solution (i.e., neither exponentially growing nor collapsing) can only be found for certain choices of the parametric functions $K(z)$, $\Lambda(z)$, $S(z)$, here omitting Γ . The stability studies cited have shown a natural result: increased sinking limits tendencies toward unbounded growth and moves populations toward extinction. For near neutral stability, sinking speeds of order 1 m/day have been indicated. Again we remark that such effects may arise on account of virtual velocities rather than sinking.

4. Discussion

The biology and physics of the upper ocean remain as most complicated problems, far beyond the scope of the present paper. Vigorous research efforts both in the biological and physical domains will certainly lead toward better understanding and, inevitably, more sophisticated modeling efforts. Such modeling efforts are likely to become increasingly computer-intensive. However, it will be prudent at each level of development to employ analysis with a goal of reducing complexity. Toward this end, we have considered the interaction of physics with biology in a relatively simple context. We have tried to show how certain aspects of the fluctuating velocity and plankton concentration fields, namely those aspects related to internal wavelike oscillations, can be given simple representations in terms of both Lagrangian and Eulerian averaged models. Our view is that the simple representations here proposed may be incorporated into models expressing more elaborate biology or physics and resolving, for example, semi-diurnal and longer period variability.

We might remark upon a couple of relatively straightforward extensions of the present calculation. We have considered only a one-dimensional (vertical) model. However if it is possible to define a quasi-Lagrangian vector displacement field $\xi(\mathbf{x}, t)$ where \mathbf{x} is the Eulerian coordinate vector, and if ξ has bounded variances, then a virtual velocity vector \mathbf{U}_* will be given by

$$\mathbf{U}_* = - \langle \xi \xi \rangle \cdot \nabla \Lambda \quad (19)$$

where ∇ is the gradient operator with respect to \mathbf{x} . (19) is the extension of (10). One should note that $\langle \xi \xi \rangle$ is a tensor and so \mathbf{U}_* may not be parallel to $\nabla \Lambda$. In particular, suppose there is some average correlation between vertical and horizontal displacement, i.e., particles tend to move along preferred slantwise paths. Then a vertical gradient in Λ may induce a horizontal component in virtual velocity, for example.

Another point may occur if one wishes to include a balance equation for a nutrient component. Virtual velocities will arise which transport nutrients. For example, if a substance is taken up during photosynthesis, then a virtual velocity will appear with a sense opposite to (10). Such a circumstance has been considered by Kahru (1983) who argues for a net upward flux of phytoplankton concentration resulting from internal wave displacement. Results from the present note appear to be opposite to those of Kahru (1983), and the source of discrepancy is not known.

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