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Vertical Mixing and its Effects on Phytoplankton Growth in a Turbid Estuary[1]

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Using a hydrodynamical model, in conjunction with current meter observations, vertical eddy diffusivities, and associated vertical mixing time-scales are estimated for the Bristol Channel, U.K. In this shallow region, the mixing time-scale appears to be more useful than the commonly employed stratification parameter in assessing the potential for thermal stratification of the water column.

Chlorophyll *a* concentrations in the Bristol Channel are observed to be vertically well-mixed throughout the year. This is shown to be a consequence of the short vertical mixing time-scales in comparison with phytoplankton generation times. These time-scales are of particular importance to phytoplankton in the region because the mixed depth is much greater than the depth of the euphotic zone. Photoinhibition is unlikely to occur in the rapidly mixing water column because phytoplankton cells experience high light conditions for only very short periods. In addition, the rapid mixing does not appear to allow time for photosynthetic adaptation of the phytoplankton population of the Bristol Channel.

Key words: Bristol channel, phytoplankton growth, vertical mixing, vertical eddy viscosity

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A l'aide d'un modèle hydrodynamique, concurremment avec des observations au courantomètre, nous estimons les propriétés diffusibles des tourbillons verticaux et les périodes de mélange verticaux qui lui sont associées dans le chenal de Bristol (R.-U.). Dans cette région peu profonde, l'échelle temporelle de mélange semble plus utile que le paramètre de stratification communément utilisé pour évaluer le potentiel de stratification thermale de la colonne d'eau.

On constate que les concentrations de chlorophylle *a* dans le chenal de Bristol sont verticalement bien mélangées tout au long de l'année. Nous démontrons que ceci est la conséquence de courtes périodes de mélange vertical, comparativement aux temps de génération du phytoplancton. Ces périodes de mélange sont particulièrement importantes pour le phytoplancton de la région, car la zone mélangée se trouve à une profondeur beaucoup plus grande que la zone euphotique. Il est peu probable qu'il y ait photoinhibition dans la colonne d'eau se mélangeant rapidement, car les cellules phytoplanctoniques rencontrent des conditions de forte intensité lumineuse pendant de courtes périodes seulement. En outre, le mélange rapide ne semble pas donner à la population phytoplanctonique du chenal de Bristol suffisamment de temps pour une adaptation photosynthétique.

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PHYTOPLANKTON respond to variations in light intensity on two different time-scales. A variation in light intensity produces rapid change in the rate of photosynthesis (i.e., a photochemical time-scale); longer term changes in light intensity may induce a physiological response in the algal cell as it accommodates to the new light conditions (a biochemical and physiological time-scale). There have been many studies of the physiological changes induced by varying solar illumination, but it is only recently that the effect of vertical movement within the water column has been investigated (Marra 1978, 1980a). Vertical movement may result in changes in light available to a phytoplankton cell as great as, or greater than, those caused by variation in cloud cover or seasonal and daily irradiance curves. It is particularly important to discount whether the time-scale of vertical mixing is sufficiently long for phytoplankton cells to become biochemically and physiologically adapted to this varying light regime.

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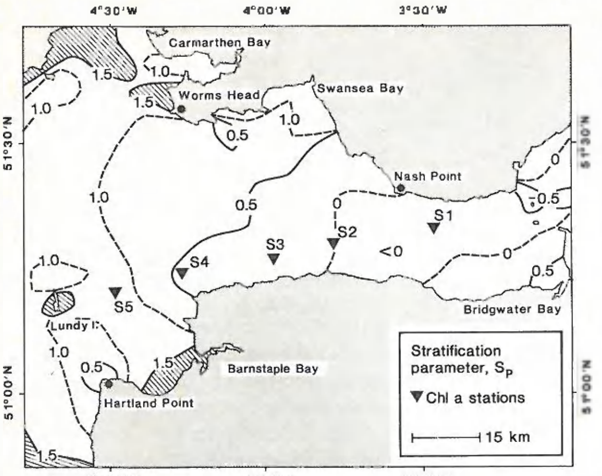

FIG. 1. Stratification parameter, S_p. Areas with $S_p > 1.5$ are hatched. Vertical profiles of chlorophyll *a* were observed at stations S1 to S5 during April 1976.

Recent work suggests that physiological changes which allow cells to adapt to new light regimes may occur over relatively short periods. Marra (1980b), working with a diatom in continuous culture, found a physiological adaptation to reduced irradiance within 10 h. Prezelin and Matlick (1980) found full photosynthetic adaptation within 12 h of a shift from high to low light and a very rapid change, within 3 h, of a chlorophyll *a*–pigment complex. Physiological changes occurring within such short time-scales would be very important processes for inclusion in models of primary production, and at least as important as the effect of diel variations in irradiance. However, there have been few studies of the importance of vertical mixing to phytoplankton, because of the absence of physical models which can be used to set time-scales to the mixing process.

The purpose of this paper is to determine vertical eddy diffusivities and associated time-scales of vertical mixing for the Bristol Channel, which is a large, turbid estuary in the southwest of the U.K. Vertical mixing in this estuary is very relevant to the phytoplankton because the substantial turbidity of the water results in a euphotic zone which is often much shallower than the mixed layer; in the turbid regions of the estuary, phytoplankton are severely light-limited and vertical mixing results in transport from surface light into darkness. Water samples taken from the turbid regions of the Bristol Channel show significant photosynthesis when incubated under simulated in situ conditions, that is under conditions equivalent to a static depth within the water column (Joint and Pomroy 1981). However, as discussed by Joint and Pomroy (1981), the significance of such static light regime incubations is dependent on the time-scale of vertical mixing.

Vertical mixing and stabilization of water on the continental shelf determine the availability of light and nutrients required for phytoplankton growth. A convenient measure of the relative degree of vertical mixing where tidally induced turbulence dominates is given by the Simpson–Hunter stratification parameter, S_p (Simpson and Hunter 1974):

$$S_p = \log_{10}[\rho h/\epsilon], \qquad \text{(c.g.s. units)}$$

where ϵ is the tidally averaged rate at which energy is dissipated by seabed friction, ρ is the density of seawater, and h is the depth of water. S_p has been derived for the case of M_2 tidal flows in the Bristol Channel using a hydrodynamical model (Uncles 1981), and is contoured in Fig. 1. During summer months, the boundary between vertically well-mixed and thermally stratified shelf water is given by $S_p = 1.5$. Regions having $S_p > 1.5$, and which should, therefore, be subject to seasonal stratification, are hatched in Fig. 1. The stratified region in the southwest corner of Fig. 1 extends across the Celtic Sea, and has also been identified in previous theoretical and experimental studies (Fearnhead 1975; Simpson 1976; Pingree 1978). Other regions where $S_p > 1.5$, in Fig. 1, lie in bays and off Lundy Island; however, these areas do not exhibit stratification. This is possibly because of horizontal tidal advection effects, or wind–wave mixing. An alternative explanation is that, despite large values of S_p, the vertical mixing time-scales in these regions are too short to allow stratification to occur. This possibility is examined later. Elsewhere in the Bristol Channel the stratification parameter shows that the water column does not stratify due to summer heating, and that vertical mixing becomes intense as S_p decreases rapidly progressing into the Severn Estuary.

Methods

Vertical mixing depends on the vertical eddy diffusivity, K_z. In the well-mixed water of the Bristol Channel, K_z can be estimated from the vertical eddy viscosity, N_z. Values of N_z are deduced from current meter data obtained at the stations shown in Fig. 2, and are parameterized in terms of local water depth and depth-averaged currents. A numerical model of the depth-averaged M_2 (principal lunar semidiurnal) tide is then used to draw contours of the depth-averaged and tidal cycle-averaged vertical eddy viscosity and vertical mixing time-scale in the Bristol Channel and Severn Estuary (west and east of Nash Point, respectively, in Fig. 2). The numerical model has been verified for the M_2 tide by comparing computed and observed water elevations and currents (Uncles 1981). Data for the elevations were taken from tide-gauge stations shown in Fig. 2.

Vertical Chlorophyll *a* Distributions

Chlorophyll *a* was routinely measured on 64 cruises, covering the Bristol Channel and western Severn Estuary, at all seasons between 1972 and 1980, and was always homogeneously distributed with depth. Vertical profiles of chlorophyll *a* sampled during April 1976 at stations S1 to S5 (see Fig. 1) are shown in Fig. 3A; overall, there were no systematic variations with depth, and the distributions may be considered essentially vertically homogeneous. Simulated in situ, depth-integrated primary production varied from 0.20 mg C fixed$\cdot$m$^{-2}\cdot$h^{-1} at S1, to 15 mg C$\cdot$m$^{-2}\cdot$h^{-1} at S5. Secchi disc depths, D, for these profiles are also shown in Fig. 3A; D decreased from 6 m at station S5 in the western Bristol Channel (see Fig. 1) to less than 1 m at station S1 in the Severn Estuary, in response to the much higher turbidity of

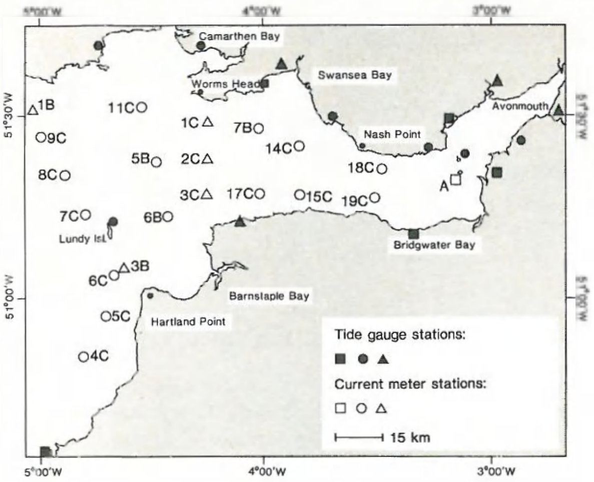

FIG. 2. Locations of tide-gauge stations (■, ●, ▲), and current meter stations (□, ○, △). (■, ●, ▲) denote observations over 15 d, 1 mo, and 1 yr, respectively. (○, △) denote stations at which two or three recording current meters were deployed on a mooring for a few tidal cycles and 1 mo, respectively. A direct reading current meter was used for current profiling over three tidal cycles at station A (□).

the Severn. D is generally a very small fraction of the depth, h. We define a scale depth:

$$h_D = h/D,$$

and a scaled "critical depth":

$$h_{CD} = h_C/D,$$

where h_C is the maximum value of h for which the depth-averaged light intensity is sufficiently high to initiate rapid growth for a homogeneous distribution of phytoplankton. Both h_D and h_{CD} are easily related to the incident light intensity, I_O, and the depth-averaged intensity over the water column, $\bar{I}$. The light intensity at any depth is:

$$I = I_O \exp - (1 - \eta)\kappa h,$$

where η is non-dimensional depth, with $\eta = 0$ at the bed and $\eta = 1$ at the surface, and κ is extinction coefficient, which is related to Secchi disc depth by (Sinclair et al. 1981):

$$\kappa = 1.44/D.$$

The depth-averaged light intensity is:

$$\bar{I} = I_O[1 - \exp(-\kappa h)]/\kappa h \simeq I_O/\kappa h,$$

using $\kappa h \simeq 1.44h/D \gg 1$.

It follows that:

$$h_D = h/D = 0.69 I_O/\bar{I}.$$

In a well-mixed water column, rapid production occurs when a critical, depth-averaged light intensity is exceeded, $\bar{I}_C$ (Sinclair et al. 1981):

$$\bar{I} > \bar{I}_C \simeq 19\ W\ m^{-2}$$

so that:

$$h_{CD} = h_C/D = 0.69 I_O/\bar{I}_C \simeq 3.6 \times 10^{-2} I_O,$$

where I_O has units $W\ m^{-2}$. For a stratified water column, the depth, h, must be taken as the thickness of the surface mixed layer.

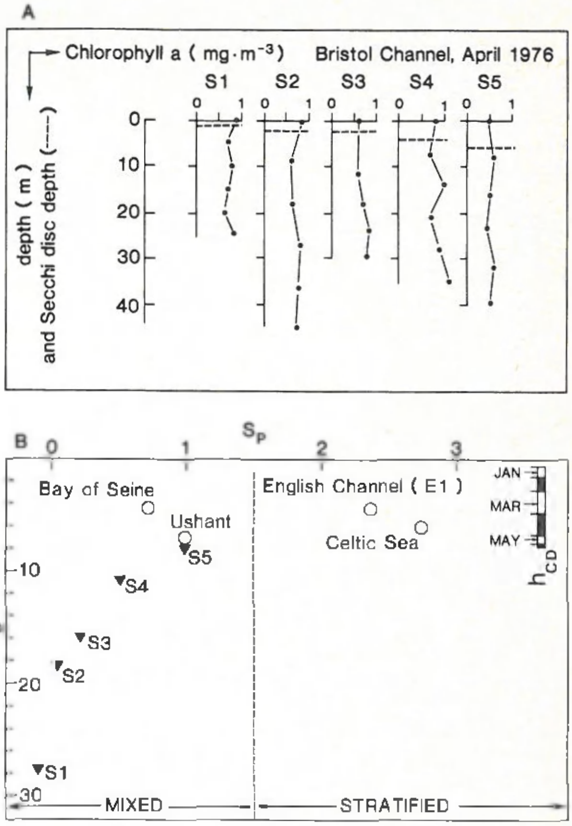

FIG. 3. Vertical profiles of chlorophyll a and the physical conditions governing phytoplankton growth: A, Profiles at stations S1 to S5; B, Stratification parameter, S_p, against scaled depth, h_D, for S1 to S5 and other coastal and shelf stations. Also shown is the scaled critical depth, h_{CD}.

Pingree (1978) has shown that the scaled depth and the stratification parameter provide a useful physical framework for a study of processes governing phytoplankton growth. Accordingly, h_D and S_p were plotted in Fig. 3B for stations S1 to S5 and for four stations in the English Channel and Celtic Sea (taken from Pingree 1978, and also applicable to M_2 tides). The diagram divides into either a mixed or seasonally stratified regime according to whether S_p is less than or greater than 1.5. Scaled critical depths (h_{CD}), typical for the area, are shown as approximate values for the months January to mid-June in Fig. 3B.

Stations S1 to S5 form a progression in Fig. 3B: station S5 occupies a position which is comparable to other thermally, vertically mixed ($S_p < 1.5$) coastal stations, although its scaled depth h_D, is slightly greater. Because the scaled depth of station S5 exceeded the scaled critical depth for April ($h_D > h_{CD}$ during April, see Fig. 3B), it follows that phytoplankton were light limited during this period of observations. Moreover, at station S5 h_D marginally exceeded h_{CD} even for mid-June, so that light limitation appears to occur throughout the year; however, the degree of light limitation is reduced during summer because Secchi disc depth at S5 increases to about 10 m (Joint and Pomroy 1981), hence decreasing h_D.

Progressing into the channel from station S5 to S1, Fig. 3B shows that the physical conditions governing phytoplankton growth within the Bristol Channel and Severn Estuary are very different from those generally applicable to coastal and shelf waters, being characterized by intense vertical mixing ($S_p \ll 1.5$) and severe light-limitation ($h_D \gg h_{CD}$). These conditions also seem atypical when compared with other estuaries: Sinclair et al. (1981), in a review of phytoplankton growth cycles in a large number of estuaries, show that h_D is typically less than about five. Nevertheless, the large values of h_D do not preclude primary production. Significant standing stocks of phytoplankton exist throughout the region (Joint and Pomroy 1981; Radford 1981), although the annual production decreases rapidly progressing up-channel — from about 150 to less than 5 g $C \cdot m^{-2} \cdot yr^{-1}$.

Despite the fact that photosynthesis in the eastern Bristol Channel and Severn Estuary can occur only in a thin surface layer ($h_D \gg 1$), vertical mixing is, nevertheless, sufficient to maintain vertical homogeneity of the phytoplankton population (see Fig. 3A). To understand why this is the case, it is necessary to estimate time-scales for vertical mixing (rather than merely compute the thermal stratification parameter) and compare these with cell division times. The following sections are concerned with the derivation of vertical eddy diffusivities arising from tidal currents, and with the estimation of associated mixing time-scales.

Eddy Viscosity

A brief review of available formulations for the vertical eddy viscosity, N_z, is given in Bowden and Hamilton (1975). For vertically mixed conditions the eddy diffusivity, K_z, applicable to tidal flows, can be equated to N_z.

For steady, homogeneous, unidirectional flow in a wide channel of depth h, Rossby and Montgomery (1935) proposed an eddy viscosity of the form:

$$(1) \qquad N_z = k_O h u_* \eta (1 - \eta),$$

where k_O is Von Karman's constant (0.41), u_* is friction velocity, h is depth, and η is again the nondimensional depth ($\eta = 0$ at the bed and $\eta = 1$ at the surface); in the absence of surface stress this leads to a logarithmic velocity profile throughout the column. N_z is a quadratic function of depth, with a maximum value, $(N_z)_{max} = k_O u_* h/4$, at mid-depth ($\eta = \frac{1}{2}$), and minimum values, $(N_z)_{min} = 0$, at surface and bed; the depth-mean value is $\bar{N}_z = k_O u_* h/6$. Friction velocity is commonly related to depth-mean velocity, $\bar{u}$, for such flows; the seabed stress in the 'x' direction is:

$$(2) \qquad \tau = \rho u_*^{\,2} = \rho k \bar{u}^2 = -\rho h g \frac{\partial \zeta}{\partial x},$$

which defines u_* and k. The stress at the bed is balanced by the surface slope forcing, where g is the acceleration due to gravity, and $\partial\zeta/\partial x$ is the slope of the sea surface. Taking $k = 2.5 \times 10^{-3}$ (Proudman 1953), then:

$$(3) \qquad (N_z)_{max} = 5.1 \times 10^{-3} h\bar{u}, \qquad (N_z)_{min} = 0 \text{ and } \bar{N}_z = 3.4 \times 10^{-3} h\bar{u}.$$

McGregor (1972) considered a rather more general logarithmic profile of velocity, in which the current vanishes at the bed, and where the slope of the profile vanishes at the surface in absence of surface stress. In this case the maximum value of N_z again occurs at mid-depth, and the small (but nonzero) minimum values occur at surface and bed.

For tidal flows the definition of N_z is uncertain because of the importance of accelerations in the momentum balance. However, near times of maximum flood or ebb streams in homogeneous water there are indications that a logarithmic, or similar power-law profile is applicable. From a considerable number of observations of tidal streams near their maximum flood and ebb, Van Veen (1938) concluded that:

$$(4) \qquad u = \beta \eta^{\delta}$$

where δ varies somewhat according to location, but typically has the value $\delta = 1/5.2$. The eddy viscosity is:

$$(5) \qquad N_z = \{\eta^{1-\delta}(1 - \eta)/\delta(1 + \delta)\} \cdot k h \bar{u},$$

which reaches a maximum near mid-depth (at $\eta = 0.45$ for $\delta = 1/5.2$) and a minimum at surface and bed:

$$(6) \qquad (N_z)_{max} = 3.1 \times 10^{-3} h\bar{u}, \qquad (N_z)_{min} = 0 \text{ and } \bar{N}_z = 2.1 \times 10^{-3} h\bar{u},$$

using $k = 2.5 \times 10^{-3}$ and $\delta = 1/5.2$.

Dyer (1970), observing current profiles near a dune field, found that up-stream of the dunes the profiles were logarithmic throughout the column, whereas some distance from the field the profiles followed a power law, with $\delta = 1/5$ at high flow rates. Bowden (1967) used observations of tidal currents in homogeneous water to show that the maximum value of N_z occurred near mid-depth during peak streams, and had the value:

$$(7) \qquad (N_z)_{max} = 2.5 \times 10^{-3} h\bar{u}.$$

From equations (3), (6), (7), and other investigations, the agreement between coefficients of $(N_z)_{max}/h\bar{u}$ is within a factor of two. Current meter data from the vertically homogeneous Bristol Channel are subsequently used to improve knowledge of this coefficient for the region.

N_z from Bristol Channel Data

If the depth-averaged momentum balance for semidiurnal tides is considered, with the 'x' axis pointing in the direction of the maximum depth-averaged semidiurnal tidal current, $\bar{u}_m$, then at maximum flood (see equation (2)):

$$g\frac{\partial\zeta}{\partial x} = -\frac{k\bar{u}_m^{\,2}}{h}$$

in which the mean depth, h, is used because maximum streams occur near midwater in an estuary, and where advection, horizontal viscosity, and density gradients are ignored because of their insignificance to the semidiurnal tide.

If the momentum balance is considered now at any nondimensional depth, η, in the column, and if a new 'x' axis is defined to be in the direction of the local maximum current, u_m, then at maximum streaming:

$$g\frac{\partial\zeta}{\partial x} = \frac{1}{h^2}\frac{\partial}{\partial\eta}\left(N_z\frac{\partial u_m}{\partial\eta}\right).$$

Therefore, the equations reduce to those for steady, unidirectional flow provided the orientations of the semidiurnal tidal currents and their phases do not vary appreciably down the column. For most stations in Fig. 2 the differences in current orientation and phase through the column are less than 4°; at the western, seaward end of the Bristol Channel, however (stations 6C, 7C, 8C, and 9C), the differences can be in the range 10°–20°. Nevertheless, there is reasonable indication from those stations where three or more observations were made (see Fig. 4), that a logarithmic profile is applicable near times of maximum streaming, although such data can be made to fit a power law of Van Veen form, equation (4), equally well. For the remaining stations in Fig. 2 only two observations were made down the column, so that these fit exactly any two-parameter representation of the profile.

If the data are fitted to equation (4), with an eddy viscosity of the form of equation (5), then the results are (using 95% confidence intervals):

$$\delta = 1/(5.2 \pm 0.3)$$

in agreement with Van Veen's (1938) data. The maximum value of N_z occurs at $\eta = 0.45 \pm 0.03$, which with $k = 2.5 \times 10^{-3}$ gives:

$$(8) \quad (N_z)_{\max} = (3.3 \pm 0.5) \times 10^{-3} h\bar{u}_m,\ (N_z)_{\min} = 0,$$

$$\text{and} \quad \bar{N}_z = (2.3 \pm 0.3) \times 10^{-3} h\bar{u}_m.$$

This result is not significantly different from either equation (6), or from results obtained by fitting a logarithmic profile of McGregor's (1972) form to the data. Therefore, at maximum tidal streams, the vertical mixing deduced from data fitted to logarithmic or power law profiles in the Bristol Channel is essentially the same as that predicted from data presented by Van Veen (1938) for the Straits of Dover, and for areas in the neighborhood of the Dutch coast.

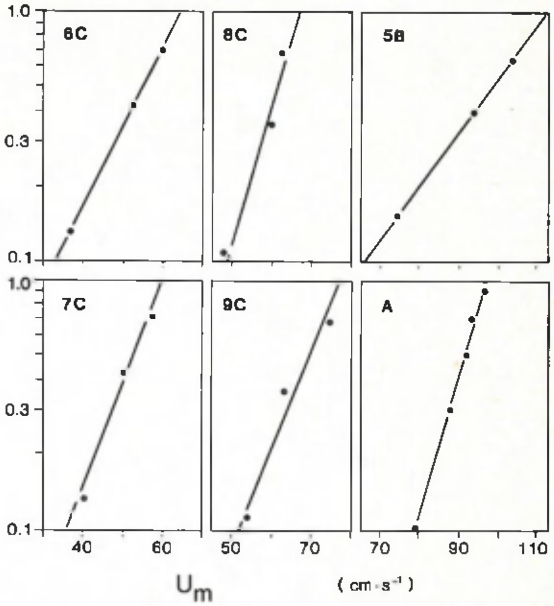

FIG. 4. Maximum semidiurnal tidal currents, u_m, against nondimensional depth. See Fig. 2 for station positions.

Tidal Averages and Vertical Mixing

Equation (8) for N_z applies during maximum streams, and is based on the assumption that a power law profile is applicable throughout the column. During other times in the tidal cycle, N_z may have a very different profile shape from that predicted by equation (5), and will also probably have smaller values at lower current speeds. Therefore, in estimating an effective N_z over a tidal cycle with the limited data available, it seems reasonable to ignore vertical variations in N_z and consider an instantaneous depth mean value of the form (see equation (8)):

$$\bar{N}_z = 2.3 \times 10^{-3} h|\bar{u}| = 2.3 \times 10^{-3} h\bar{u}_m|\sin\omega t|,$$

where ω is the semidiurnal tidal angular frequency, and where tidal currents are taken to be rectilinear for this region (Uncles 1981). The average value over a tidal cycle is:

$$(9) \quad \langle\bar{N}_z\rangle = 1.5 \times 10^{-3} h\bar{u}_m,$$

which is contoured in Fig. 5A for the case of M_2 tidal streams. Values range from 100 cm$^2 \cdot$s^{-1} in the shallow bays where currents are low, to 700 cm$^2 \cdot$s^{-1} in the region of intense tidal streaming and moderately deep water near Nash Point.

A time-scale for vertical mixing can now be derived from equation (9) by assuming that "Reynolds analogy" holds in the vertically homogeneous water of the Bristol Channel, so that the vertical eddy diffusivity, K_z, equals N_z. Ignoring vertical variations in K_z, then a typical time-scale for complete mixing of a passive tracer released from mid-depth is (Fischer et al. 1979):

$$T = 0.1h^2/\langle\bar{K}_z\rangle.$$

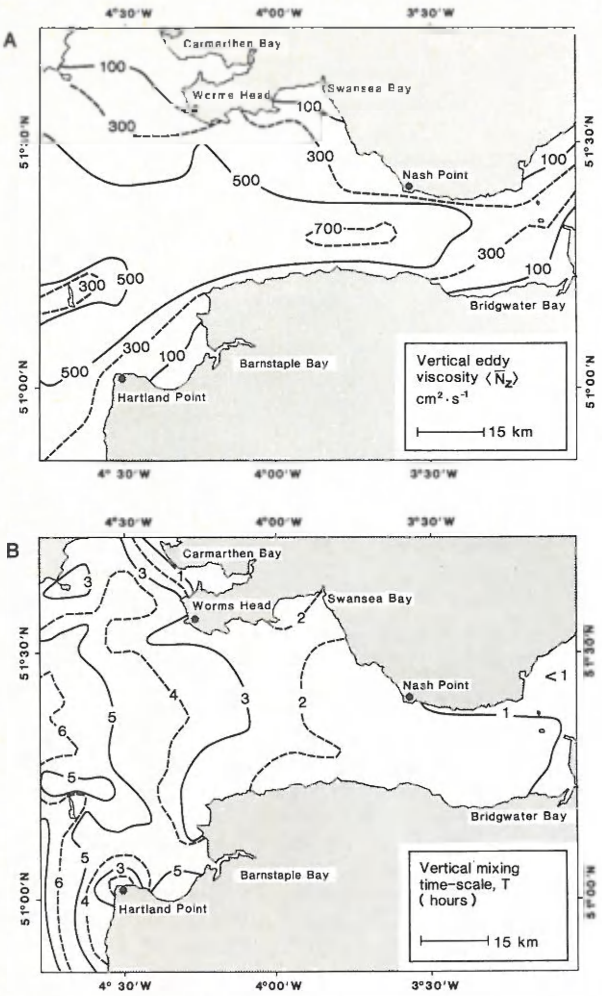

FIG. 5. Vertical eddy viscosity and vertical mixing times: A, $\bar{N}_z$ (cm^2·s^{-1}); B, Time-scale, T(hours).

However, because phytoplankton photosynthesis occurs in a thin layer near the surface (see Fig. 3A), it is more appropriate to investigate the time-scale for complete mixing of a passive tracer released at the surface, which is:

$$(10) \quad T = 0.4h^2/\langle\bar{K}_z\rangle = 2.7 \times 10^2 h/\bar{u}_m,$$

using equation (9). This time-scale is contoured in Fig. 5B. In the Severn Estuary the mixing time is between 1 and 2 h. Progressing down-channel, T increases, exceeding 7 h in the southwest of the region where seasonal stratification can occur. This time-scale is an effective value over a tidal cycle; naturally, at peak currents the mixing will be faster than depicted in Fig. 5B, and near slack water it will be slower (see later).

Discussion

During maximum tidal streams, the vertical eddy viscosity deduced from current meter data in the Bristol Channel and Severn Estuary has a similar form, and magnitude, to that observed for other shallow, well-mixed coastal regions. The associated time-scales for vertical mixing in the Channel, T (equation (10) and Fig. 5B), can be compared with the stratification parameter, S_p, in Fig. 1. The Celtic Sea front, a segment of which is shown in the southwest corner of Fig. 1, occurs at $T \sim 8$ h. Plotting T for the whole of the northwest European shelf (using modeled currents and depth data supplied by R. D. Pingree, personal communication) shows that the observed seasonal frontal regions on the shelf occur for mixing time-scales between 8 to 12 h. No attempt has been made to define a "critical" T at which fronts develop. On this basis, one would expect the short mixing time-scales in Carmarthen Bay and Barnstaple Bay (less than about 5 h, see Fig. 5B) to result in vertically homogeneous conditions, as was observed. S_p (Fig. 1) indicates that stratification can occur in these bays, which suggests that, in shallow water at least, the mixing time-scale may be a more useful indicator of stratification than S_p.

This paper has shown the physical reason for the observed homogeneous distribution of phytoplankton within the water column of the Bristol Channel. Even at the seaward end of the Channel, where the euphotic zone may be 15 m deep or more, tidally induced mixing has a time-scale of the order of 5 h; this is significantly less than the generation time of phytoplankton. We have no measurements of carbon : chlorophyll *a* ratios for Bristol Channel phytoplankton that would allow us to calculate precise cell division times. Nevertheless, a reasonable value to assume for the carbon : chlorophyll *a* ratio is 25. Dividing the depth-integrated chlorophyll *a* concentrations at stations S1 and S5 by the respective rates of primary production, gives doubling times of the order of 70 d at the turbid station, S1, and one day at S5. A cell division time of 1 d is comparable with that found from a number of other investigations, and is supported by work with cultures of phytoplankton (Brand and Guillard 1981). Therefore, even at station S5, generation times are much longer than the vertical mixing time-scales in the Bristol Channel, and there is no possibility of a chlorophyll maximum developing at any depth in the water column.

Consideration should also be given to whether sinking of phytoplankton cells can affect the vertical distribution in this estuary. Bienfang (1981) observed sinking rates for natural populations of temperate phytoplankton in a CEPEX bag; these were in the range 0.32–1.69 m·d^{-1}, and the mean sinking rate, w, was 0.64 m·d^{-1} (7×10^{-4} cm·s^{-1}). Walsby and Reynolds (1980) have briefly reviewed a number of models which take into account the effects of sinking in the presence of vertical mixing. If growth and decay are ignored, and if the phytoplankton concentration, P, is in a steady-state, then a balance exists between sinking and mixing in the form (Walsby and Reynolds 1980, p. 400):

$$\langle\bar{K}_z\rangle \frac{\partial^2 P}{\partial \eta^2} + hw \frac{\partial P}{\partial \eta} = 0,$$

which has the solution:

$$P = P_O \exp\left(-hw\eta/\langle\bar{K}_z\rangle\right),$$

where P_O is the concentration at the bed ($\eta = 0$). The relative surface ($\eta = 1$) to bed difference in concentration is thus:

$$\delta P/P_O = -1 + \exp(-hw/\langle\bar{K}_z\rangle) \simeq -0.4\%$$

using $w = 7 \times 10^{-4}\ \mathrm{cm \cdot s^{-1}}$, $h = 30m$, and $\langle\bar{K}_z\rangle = 500\ \mathrm{cm^2 \cdot s^{-1}}$ as typical values for the region (see Fig. 5A). The effects of sinking are thus negligible in the presence of this intense vertical mixing.

It is of interest to enquire how phytoplankton achieve net production in the severely light-limited conditions that exist in the turbid region of the Bristol Channel. Joint and Pomroy (1981) estimated the yearly averaged primary production in this region to be only 6.8 g $\mathrm{C \cdot m^{-2} \cdot yr^{-1}}$. The observed low production at station S1, coupled with the estimated doubling time of about 70 d, implies that only marginally more energy is assimilated by the phytoplankton than is needed to meet the maintenance energy requirement. Moreover, this long doubling time means that advection and dispersion by currents effectively determines phytoplankton concentrations in this region. In deriving estimates of primary production, Joint and Pomroy (1981) assumed that the depth-integrated production for a well-mixed water column was equivalent to the integration of a number of static-depth incubations. Support for this assumption comes from Platt and Gallegos (1980) and Gallegos and Platt (1982), who attempted to simulate the effect of vertical motion on photosynthesis using a conceptual model and an analogue incubation technique. They concluded that vertical mixing has very little quantitative effect on primary production in the column. However, they were considering the Canadian Arctic, where the surface mixed layer is shallower than the euphotic zone. The opposite situation applies in the Bristol Channel, and further work is required to study the effect of vertical mixing (with time-scales determined in this paper) on estimates of depth-averaged primary production in a turbid water column.

Such rapid mixing times have obvious implications for phytoplankton physiology. With time-scales of 5 h or less, physiological changes of the type described by Marra (1980b), and Prezelin and Matlick (1980), are unlikely to occur in the Bristol Channel. Photoinhibition is also unlikely to occur in a well-mixed water column, because of the short time that phytoplankton cells are in high light levels. Marra (1978) found an enhancement of integral photosynthesis in incubations when bottles were moved vertically when compared with bottles incubated at fixed depths; part, but not all, of this enhancement was assumed to be due to the absence of photoinhibition in the vertically cycled bottles. Generally, Joint and Pomroy (1981) could not detect photoinhibition in surface incubations of less than 2 h, although photoinhibition sometimes occurred within this time-scale on summer days with very high irradiance. Therefore, for a well-mixed water column, simple models of primary production may be appropriate; models of the type recently derived to describe both the linear and the photoinhibited part of the photosynthesis irradiance curve (Platt et al. 1980) may be unnecessarily complex.

In the Bristol Channel, vertical mixing brings phytoplankton cells from darkness into high irradiance in a random way, and processes other than photosynthesis may be important for the survival of phytoplankton. If a cell is only briefly exposed to light once an hour, as may occur in the most turbid regions of the Channel, respiratory losses from the cells become important. Intuitively, one would expect a phytoplankton cell that is exposed to light for only a few minutes each hour to have difficulty in surviving, yet the population seems viable — water samples taken from the turbid estuary and incubated at constant light show substantial rates of carbon fixation (Joint and Pomroy 1981). We have no information on whether phytoplankton from this region are physiologically adapted to long periods in the dark by alteration of respiration rate, but clearly maintenance requirements of the cells are met by brief exposure to light; the population remains viable and able to exploit longer exposure to light.

Individual cells may experience longer periods of illumination if they are in the euphotic zone at slack tide, when vertical mixing is negligible; however, they will be quickly mixed within the water column as the tide turns and currents increase in speed. The population as a whole cannot benefit from the longer periods of illumination at the surface because the rest of the population will spend longer in darkness at times of low mixing. In general, vertical mixing is more rapid than that shown in Fig. 5B (time-scale less than T) for 60% of the time. Mixing time-scales are less than $2T$ for 80% of the time, and less than $3T$ for 90% of the time. On hot, windless days at slack water, it is possible that stabilizing temperature gradients might form just beneath the surface, but these would escape detection on the scale of our observations. In any event, such gradients would have a small effect on the water column as a whole; and would rapidly decrease with increasing current speed.

Finally, there appears to be no photosynthetic adaptation of the phytoplankton population of the Bristol Channel. Demers and Legendre (1982) suggest that increased vertical mixing in an estuarine water column results in a lower assimilation number ($P'_{\max}$). Nevertheless, $P'_{\max}$ values determined in the turbid region of the Bristol Channel, with mixing times of 1 h or less, are not significantly different from those in regions with euphotic depths in excess of 10 m, and with mixing times longer than 5 h (I. R. Joint unpublished data). However, the degree of vertical mixing occurring in the Bristol Channel is greater than that studied by Demers and Legendre (1982), and differences in physiological adaptation may only be obvious in regions with a wider range of vertical mixing than is found in the Bristol Channel. Such regions would include partially mixed estuaries in which vertical stratification (and thus the stability of the water column) depends strongly on freshwater inputs, as well as tidal currents (Bowden 1967).

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