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Appendix B: Effects of mixing depth on equilibrium conditions in the closed system model with constant algal loss rate.

For a given incident light intensity and background turbidity, light availability depends on mixing depth and total algal biomass. The equilibrium equations for the case of a constant algal loss rate $l = l_{bg}$ (Eq. 1a) can thus be written as

$$\frac{dW}{dt} = P(R^*, W^*, z) - lW^* = 0 \qquad \text{(B.1)}$$

$$\frac{dR_s}{dt} = clW^* - rR_s^* = 0 \qquad \text{(B.2)}$$

$$zR_{tot} = cW^* + R_s^* + zR^* \qquad \text{(B.3)}$$

where $P(R, W, z)$ is total algal production in the mixed layer and corresponds to the integral in Eq. 1a. Implicit differentiation of Eqs. B.1-B.3 with respect to z yields

$$\frac{\partial P}{\partial R}\frac{dR^*}{dz} + \frac{\partial P}{\partial W}\frac{dW^*}{dz} + \frac{\partial P}{\partial z} - l\frac{dW^*}{dz} = 0 \qquad \text{(B.4)}$$

$$cl\frac{dW^*}{dz} - r\frac{dR_s^*}{dz} = 0 \qquad \text{(B.5)}$$

$$R_{tot} = c\frac{dW^*}{dz} + \frac{dR_s^*}{dz} + R^* + z\frac{dR^*}{dz} \qquad \text{(B.6)}$$

Eqs. B.4 and B.5 can be solved for dW^*/dz and dR_s^*/dz, respectively, and the results substituted into Eq. B.6, which yields

$$\frac{dR^*}{dz} = \frac{R_{tot} - R^* - \frac{a}{b}\frac{\partial P}{\partial z}}{z + \frac{a}{b}\frac{\partial P}{\partial R}} \qquad \text{(B.7)}$$

with $a = c + cl/r$ and $b = l - \partial P/\partial W$. The sign of Eq. B.7 is derived as follows. Huisman and Weissing (1995) have shown that $\partial P/\partial R > 0$ and that, at equilibrium, $b > 0$ (see also Appendix A). Furthermore, $\partial P/\partial z < 0$, because, at constant W and R, an increase in mixing depth means that more light is being absorbed by background turbidity and is thus not available for algal growth. Finally, z and a are positive constants and $R_{tot} - R^* > 0$ if $W^*>0$. Thus the numerator and the denominator of Eq. B.7 are both positive and

$dR^*/dz > 0$. In other words, nutrient availability at an interior equilibrium (i.e., $W^*>0$) is positively related to mixing depth.

Because $W = \omega z$, Eq. B.3 can be solved for the equilibrium concentration of algal biomass

$$\omega^* = \frac{1}{c}\left(R_{tot} - \frac{R_s^*}{z} - R^*\right) \tag{B.8}$$

Substitution of $R_s^* = clW^*/r$ (Eq. B.2) and of $W^* = \omega^* z$ and subsequent implicit differentiation with respect to z yields

$$\frac{d\omega^*}{dz} = -\frac{1}{a}\frac{dR^*}{dz} \tag{B.9}$$

As just shown, $dR^*/dz > 0$ and, consequently, $d\omega^*/dz < 0$. In other words, algal biomass concentration at an interior equilibrium is negatively related to mixing depth.

The concentration of total nutrients in the mixed layer, R_m, can be calculated from Eq. B.3 as

$$R_m^* = c\omega^* + R^* = R_{tot} - \frac{1}{z}R_s^* \tag{B.10}$$

Substitution of $R_s^* = clz\omega^*/r$ into Eq. B.10 and subsequent implicit differentiation with respect to z yields

$$\frac{dR_m^*}{dz} = -\frac{cl}{r}\frac{d\omega^*}{dz} \tag{B.11}$$

As just shown, $d\omega^*/dz < 0$. Hence, $dR_m^*/dz > 0$. In other words, at an interior equilibrium, the concentration of total nutrients in the mixed layer is positively related to mixing depth.

Rearrangement of Eq. B.4 yields

$$\frac{dW^*}{dz} = \frac{1}{b}\left(\frac{\partial P}{\partial R}\frac{dR^*}{dz} + \frac{\partial P}{\partial z}\right). \tag{B.12}$$

The first term in parantheses is positive and the second term is negative, i.e., the sign of dW^*/dz is indeterminate. How does the sign of dW^*/dz change along a gradient of mixing depths? In the limit of $z \to 0$, Eq. B.12 reduces to

$$\frac{dW^*}{dz} = \frac{1}{a}\left(R_{tot} - R^*\right)$$

which is positive if $W^*>0$. In the limit of $z \to \infty$, Eq. B.12 reduces to

$$\frac{dW^*}{dz} = \frac{1}{l}\left[\frac{\partial P}{\partial R}\frac{(R_{tot} - R^*)}{\infty} + \frac{a}{l}\frac{\partial P}{\partial z}\right]$$

When z approaches infinity, $\partial P/\partial R$, $(R_{tot} - R^*)$, and $\partial P/\partial z$ all approach zero. The first term in square brackets, however, approaches zero more quickly than the second term. The sign of dW^*/dz thus depends on the sign of $\partial P/\partial z$ which is negative. Along a gradient of mixing depths, the standing stock of algal biomass per area therefore first increases but eventually decreases and has a maximum at an intermediate mixing depth. In simulation runs, I have always found a unimodal pattern (e.g., Fig. 1a).

The mixing depth z' at which the maximum of W^* occurs is found through substitution of Eq. B.7 into Eq. B.12, setting Eq. B.12 to zero, and solving for z:

$$z' = \left(R^* - R_{tot}\right)\frac{\partial P/\partial R}{\partial P/\partial z} \tag{B.13}$$

Both factors are negative and, consequently, z' is always positive. Implicit differentiation of Eq. B.13 with respect to K_{bg} yields

$$\frac{dz'}{dK_{bg}} = \frac{dR^*}{dK_{bg}}\frac{\partial P/\partial R}{\partial P/\partial z} + \left(R^* - R_{tot}\right)\frac{d\left(\dfrac{\partial P/\partial R}{\partial P/\partial z}\right)}{dK_{bg}}. \tag{B.14}$$

It can be shown that $dR^*/dK_{bg} > 0$ (see Appendix C). Furthermore,

$$\frac{d\left(\dfrac{\partial P/\partial R}{\partial P/\partial z}\right)}{dK_{bg}} = \frac{\dfrac{d(\partial P/\partial R)}{dK_{bg}}\dfrac{\partial P}{\partial z} - \dfrac{d(\partial P/\partial z)}{dK_{bg}}\dfrac{\partial P}{\partial R}}{(\partial P/\partial z)^2}.$$

An increase in background turbidity means that less light is available for algal growth. Consequently, an increase in background turbidity diminishes the positive effect of nutrients, and enhances the negative effect of mixing depth, on algal production. The two derivatives with respect to K_{bg} on the right hand are thus both negative and the entire expression is positive. Hence, $dz'/dK_{bg} < 0$, i.e., the mixing depth at which the maximum of algal biomass per area occurs is a decreasing function of background turbidity.

Because $R_s^* = clW^*/r$ (Eq. B.2), the effects of mixing depth on R_s^* are qualitatively similar to the effects of mixing depth on W^*. Thus, the standing stock of nutrients lost through algal sedimentation first increases and eventually decreases with mixing depth and has a maximum at an intermediate mixing depth. The mixing depth at which this maximum occurs is a decreasing function of background turbidity.

Finally, implicit differentiation of Lambert-Beer's law with respect to z yields

$$\frac{dI_{out}*}{dz} = I_{out}*\left(-K_{bg} - k\frac{dW*}{dz}\right). \qquad \text{(B.15)}$$

This expression is clearly negative over ranges of z for which $dW*/dz \geq 0$. A little logic reveals that Eq. B.15 must be negative also over ranges of z for which $dW*/dz < 0$. We already know that $dR*/dz > 0$. Thus, with an increase in mixing depth, algal production becomes less limited by nutrients. A decrease in total standing stock of algae with increasing mixing depth (i.e., $dW*/dz < 0$) is therefore only possible, if algal production becomes increasingly limited by light (i.e., if $dI_{out}*/dz < 0$). Hence, at steady state, $I_{out}*$ is negatively related to mixing depth over the entire range of z.