

Sebastian Diehl. 2002. Phytoplankton, light, and nutrients in a gradient of mixing depths: theory. *Ecology* 83:386-398.

Appendix C: Effects of algal sinking velocity on equilibrium conditions in the closed system model with mixing depth-dependent algal loss rate.

For a given incident light intensity, background turbidity, and mixing depth, light availability depends only on algal biomass and algal losses (l) depend on sinking velocity. The equilibrium equations can thus be written as

$$\frac{dW}{dt} = P(R^*, W^*) - l(v, z)W^* = 0 \quad (C.1)$$

$$\frac{dR_s}{dt} = cl(v, z)W^* - rR_s^* = 0 \quad (C.2)$$

$$zR_{tot} = cW^* + R_s^* + zR^* \quad (C.3)$$

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

$$\frac{dW^*}{dv} = \frac{1}{b} \left(\frac{\partial P}{\partial R} \frac{dR^*}{dv} - \frac{\partial}{\partial v} W^* \right) \quad (C.4)$$

$$\frac{dR_s^*}{dv} = \frac{cl(v, z)}{r} \frac{dW^*}{dv} + \frac{c}{r} W^* \frac{\partial}{\partial v} \quad (C.5)$$

$$0 = c \frac{dW^*}{dv} + \frac{dR_s^*}{dv} + z \frac{dR^*}{dv} \quad (C.6)$$

with $b = l(v, z) - \partial P / \partial W$. Substitution of Eqs. C.4 and C.5 into Eq. C.6 yields

$$\frac{dR^*}{dv} = \frac{\frac{cW^*}{rb} \frac{\partial}{\partial v} \left(r + \frac{\partial P}{\partial W} \right)}{z + \frac{c}{b} \frac{\partial P}{\partial R} \left(1 + \frac{l(v, z)}{r} \right)}. \quad (C.7)$$

Algal loss rate increases with sinking velocity, i.e., $\partial l / \partial v > 0$. Huisman and Weissing (1995) have shown that $\partial P / \partial W > 0$ and $\partial P / \partial R > 0$ and that, at equilibrium, $b = l(v, z) - \partial P / \partial W > 0$. Thus, all terms in Eq. C.7 are positive and $dR^* / dv > 0$. In other words, nutrient availability at an interior equilibrium (i.e., $W^* > 0$) is positively related to algal sinking velocity.

Substitution of Eqs. C.7 and C.5 into Eq. C.6 and rearrangement yields

$$\frac{dW^*}{dv} = \frac{-\frac{cW^*}{r} \frac{\partial l}{\partial v} - z \frac{dR^*}{dv}}{c \left(1 + \frac{l(v,z)}{r} \right)} \quad (C.8)$$

which is negative. Substitution of $\omega^* z = W^*$ into Eq. C.8 reveals that also $d\omega^*/dv < 0$. In other words, at an interior equilibrium, algal biomass concentration and the standing stock of algal biomass are both negatively related to algal sinking velocity.

The effect of algal sinking velocity on the standing stock of sedimented algae is derived as follows. The second term in Eq. C.5 is positive, whereas the first term is negative (as revealed by substitution of Eq. C.8 into Eq. C.5). Thus, the sign of dR_s^*/dv is indeterminate. The effect of algal sinking velocity on the concentration of total nutrients in the mixed layer, R_m^* , is also indeterminate, because

$$dR_m^*/dv = d\omega^*/dv + dR^*/dv.$$

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

$$\frac{dI_{out}^*}{dv} = I_{out}^* \left(-k \frac{dW^*}{dv} \right). \quad (C.9)$$

This expression is positive. Hence, at an interior equilibrium, I_{out}^* is positively related to algal sinking velocity.