

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

Appendix E: Effects of nutrient enrichment 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. The equilibrium equations can thus be written as

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

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

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

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

$$\frac{dW^*}{dR_{tot}} = \frac{\frac{\partial P}{\partial R} \frac{dR^*}{dR_{tot}}}{l(v, z) - \frac{\partial P}{\partial W}} \quad (\text{E.4})$$

$$\frac{dR_s^*}{dR_{tot}} = \frac{cl(v, z)}{r} \frac{dW^*}{dR_{tot}} \quad (\text{E.5})$$

$$1 = \frac{c}{z} \frac{dW^*}{dR_{tot}} + \frac{1}{z} \frac{dR_s^*}{dR_{tot}} + \frac{dR^*}{dR_{tot}}. \quad (\text{E.6})$$

Substitution of Eqs. E.4 and E.5 into Eq. E.6 yields

$$\frac{dR^*}{dR_{tot}} = \frac{1}{\frac{c}{z} \frac{\partial P / \partial R}{[l(v, z) - \partial P / \partial W] \left(1 + \frac{l(v, z)}{r}\right)} + 1}. \quad (\text{E.7})$$

Huisman and Weissing (1995) have shown that $\partial P / \partial R > 0$ and that, at equilibrium, $l(z) - \partial P / \partial W > 0$. Thus the denominator of Eq. E.7 is positive and $dR^* / dR_{tot} > 0$.

Substitution of Eq. E.7 into Eq. E.4 and of Eq. E.4 into Eq. E.5 reveals that also $dW^* / dR_{tot} > 0$ and $dR_s^* / dR_{tot} > 0$. Finally, substitution of $\omega^* z = W^*$ into Eq. E.4 reveals that $d\omega^* / dR_{tot} > 0$. In other words, at an interior equilibrium (i.e., $W^* > 0$),

nutrient availability and algal biomass concentration as well as the standing stocks of algal biomass and of sedimented nutrients are all positively related to enrichment with nutrients.

The concentration of total nutrients in the mixed layer, R_m , is defined as the sum of the concentrations of free nutrients, R , and nutrients stored in biomass. Implicit differentiation with respect to R_{tot} yields

$$\frac{dR_m^*}{dR_{tot}} = \frac{dR^*}{dR_{tot}} + c \frac{d\omega^*}{dR_{tot}}. \quad (E.8)$$

This expression is positive. In other words, at an interior equilibrium, the concentration of total nutrients in the mixed layer is positively related to enrichment with nutrients.

Finally, inspection of Eq. 4 reveals that $dI_{out}^*/dR_{tot} < 0$, because $d\omega^*/dR_{tot} > 0$. Hence, at an internal equilibrium, I_{out}^* is negatively related to enrichment with nutrients.