

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

## Appendix A: Uniqueness and local stability of the interior equilibrium of the closed system model.

For a given incident light intensity, background turbidity, and mixing depth, light availability depends only on total algal biomass. The integral in Eqs. 1a and 1c can therefore be written as  $P(R, W)$ , where  $P$  is total algal production summed over the mixed layer. Substitution of  $P(R, W)$  into Eqs. 1a and 1c and multiplication of Eq. 1a with  $z$  yields

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

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

$$\frac{dR}{dt} = \frac{r}{z} R_s - \frac{c}{z} P(R, W) \quad (\text{A.3})$$

where  $l(v, z) = l_{bg} + v/z$  (Eq. 1a). Eq. A.2 can be eliminated from the dynamical system described by Eqs. A.1-A.3 because of the mass balance constraint specified by Eq. 1d. Eq. A.3 takes then on the form

$$\frac{dR}{dt} = r \left( R_{tot} - \frac{c}{z} W - R \right) - \frac{c}{z} P(R, W) \quad (\text{A.4})$$

Some properties of the dynamical system specified by Eqs. A.1 and A.4 can be derived graphically, if the shape of the isoclines  $dW/dt = 0$  and  $dR/dt = 0$  in the  $W$ - $R$ -phase plane is known. The slopes of these isoclines can be derived after setting Eqs. A.1 and A.4 to zero and subsequently differentiating Eq. A.1 with respect to  $R$  and Eq. A.4 with respect to  $W$ . This yields

$$\frac{dW}{dR} = \frac{\frac{\partial P}{\partial R}}{l(v, z) - \frac{\partial P}{\partial W}} \quad (\text{A.5})$$

$$\frac{dR}{dW} = - \frac{r + \frac{\partial P}{\partial W}}{\frac{zr}{c} + \frac{\partial P}{\partial R}} \quad (\text{A.6})$$

Huisman and Weissing (1995) have shown that  $\partial P / \partial R > 0$  and that  $\partial P / \partial W = p(I_{out}, R) > 0$ . Because of the unidirectional nature of the light gradient, algal production decreases with depth within the mixed layer. In contrast, because of homogeneous mixing, losses occur uniformly over the entire mixed layer. Thus, algal biomass can only be at steady state, if production exceeds losses at the top of the mixed layer and if losses exceed production at the bottom of the mixed layer, i.e., if  $p(I_{out}, R) < l(v, z)$  at  $dW/dt = 0$  (Huisman and Weissing 1995). Given these inequalities, the slope of the biomass isocline in the  $W$ - $R$  plane is positive and the slope of the nutrient isocline is negative. Furthermore, algae require a minimal nutrient concentration,  $R_c$ , to invade an empty system. The biomass isocline intersects the nutrient axis at this threshold, which is given by the nutrient level at which algal production exactly balances losses, i.e.,

$$\frac{1}{z} \int_0^z p\left(I_{in} e^{-K_{bg}s}, R_c\right) ds = l(v, z) \quad (\text{A.7})$$

Finally, the nutrient isocline intersects the nutrient axis at  $R = R_{tot}$ . Thus, if  $R_{tot} < R_c$ , the isoclines do not intersect and the system has only one equilibrium state at which  $R = R_{tot}$  and  $W = 0$ . Whenever  $R_{tot} > R_c$ , the isoclines do intersect and the system has an interior equilibrium with  $W^*$  and  $R^*$  both positive. Because of the opposite signs of the slopes of the isoclines, there is only one interior equilibrium. This interior equilibrium is locally stable (see below). The boundary equilibrium  $R = R_{tot}$  and  $W = 0$  is unstable, if  $R_{tot} > R_c$ . Because  $R_s^* = cIW^*/r$  (Eq. 1b),  $R_s^* > 0$  for  $R_{tot} > R_c$  and  $R_s = 0$  for  $R_{tot} < R_c$ .

The stability of the interior equilibrium is derived from the Jacobian matrix of the system described by Eqs. A.1 and A.4. The elements of the Jacobian matrix are given by

$$\begin{aligned} A_{11} &= \left. \frac{\partial(dW/dt)}{\partial W} \right|^* = \frac{\partial P}{\partial W} - l(v, z) < 0 \\ A_{12} &= \left. \frac{\partial(dW/dt)}{\partial R} \right|^* = \frac{\partial P}{\partial R} > 0 \\ A_{21} &= \left. \frac{\partial(dR/dt)}{\partial W} \right|^* = -\frac{cr}{z} - \frac{c}{z} \frac{\partial P}{\partial W} < 0 \\ A_{22} &= \left. \frac{\partial(dR/dt)}{\partial R} \right|^* = -r - \frac{c}{z} \frac{\partial P}{\partial R} < 0 \end{aligned}$$

where the asterisk indicates that the matrix is evaluated at equilibrium. According to the Routh-Hurwitz criteria, local stability requires that  $A_{11} + A_{22} < 0$  and  $A_{11}A_{22} - A_{12}A_{21} > 0$  (e.g., Gurney and Nisbet 1998). Both conditions are fulfilled. Therefore, if an interior equilibrium exists, it is also locally stable.

Because, in an infinitely shallow mixed layer, specific algal production is bounded by  $p(I_{in}, R_{tot})$ , whereas algal loss rate,  $l(v, z)$  approaches infinity, existence of the interior equilibrium requires a minimal mixing depth to be exceeded. This depth is given by the depth  $z_c$  at which algal production exactly balances losses, i.e.,

$$\frac{1}{z_c} \int_0^{z_c} p\left(I_{in} e^{-K_{bg}s}, R\right) ds = l(v, z_c). \quad (\text{A.8})$$