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Appendix B: Derivation of resource gradient model of periphyton growth.

We require a simple, general model that captures the essential features of resource-limited growth on a benthic surface. A basic model for periphyton growth is the mass balance model

$$g(R) = P(R) - M(R), \quad (\text{B.1})$$

where $P(R)$ is the rate of biomass gain per unit area ($\mu\text{g cm}^{-2} \text{d}^{-1}$) by photosynthesis and $M(R)$ accounts for losses due to respiration and metabolism ($\mu\text{g cm}^{-2} \text{d}^{-1}$). As the periphyton biofilm develops, cells grow on top of one another so that cells in lower layers become shaded by those above, and the quantity of nutrients diffusing through the biofilm from the stream is depleted by cells in the upper layers. A simple model for $P(R)$ can be derived from the assumption that the photosynthetic rate declines with depth in the periphyton biofilm as a result of these processes, and approximates an extinction curve. Thus,

$$p_z = p_0 e^{-\phi z}, \quad (\text{B.2})$$

where p_z ($\mu\text{g cm}^{-3} \text{d}^{-1}$) is the photosynthetic rate at depth z (cm), p_0 ($\mu\text{g cm}^{-3} \text{d}^{-1}$) is the photosynthetic rate at the surface of the biofilm, and ϕ (cm^{-1}) is a coefficient that determines the rate of decline of photosynthesis with depth in the biofilm. The total photosynthetic rate ($\mu\text{g cm}^{-2} \text{d}^{-1}$) for the full depth of the biofilm is given by integrating over depth, thus

$$\text{total photosynthetic rate} = \int_0^Z p_0 e^{-\phi z} dz = \frac{P_0}{\phi} (1 - e^{-\phi Z}). \quad (\text{B.3})$$

Total depth (Z , cm) is related to biomass per unit area (R , $\mu\text{g cm}^{-2}$) such that $Z = R/q$, where q is biomass per unit volume ($\mu\text{g cm}^{-3}$). We define the new parameters $P_0 \equiv p_0/q$ (d^{-1}) and $\rho \equiv \phi/q$ ($\mu\text{g}^{-1} \text{cm}^2$), which yields:

$$P(R) = \frac{P_0}{\rho} (1 - e^{-\rho R}). \quad (\text{B.4})$$

We assume that losses are a constant function of periphyton density, thus

$$M(R) = mR, \quad (\text{B.5})$$

where m is the rate of biomass loss (d^{-1}). Substituting Eq. B.4 and B5 into Eq. B.1 yields the following model for periphyton growth on a benthic surface:

$$g(R) = \frac{P_0}{\rho} (1 - e^{-\rho R}) - mR. \quad (\text{B.6})$$