

Adaptive movement of phytoplankton in vertical gradients of light and nutrients

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Phytoplankton

- Microscopic photosynthetic organisms at the base of most aquatic food webs
- Name derived from the Greek word **πλαγκτος**, meaning **wanderer**

Phytoplankton

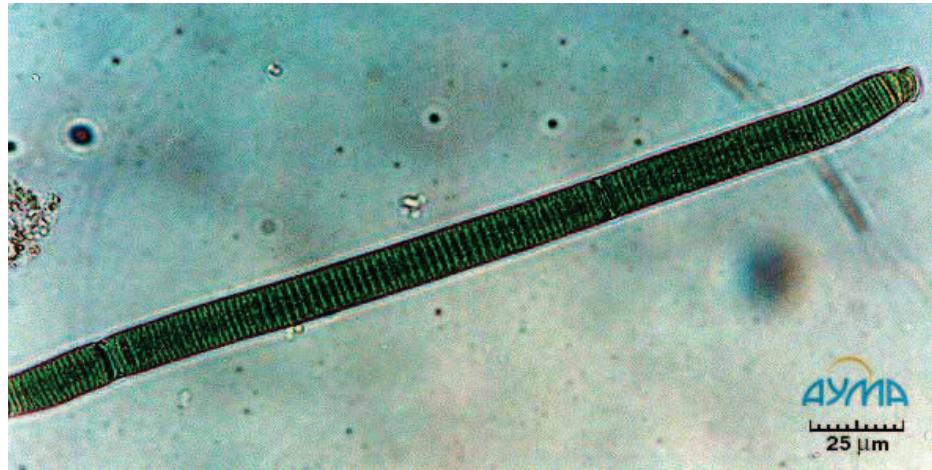
- Microscopic photosynthetic organisms at the base of most aquatic food webs
- Name derived from the Greek word **πλαγκτος**, meaning **wanderer**
- **Not exactly poster children for adaptive movement!**



Cryptophytes



Dinoflagellates



Cyanobacteria

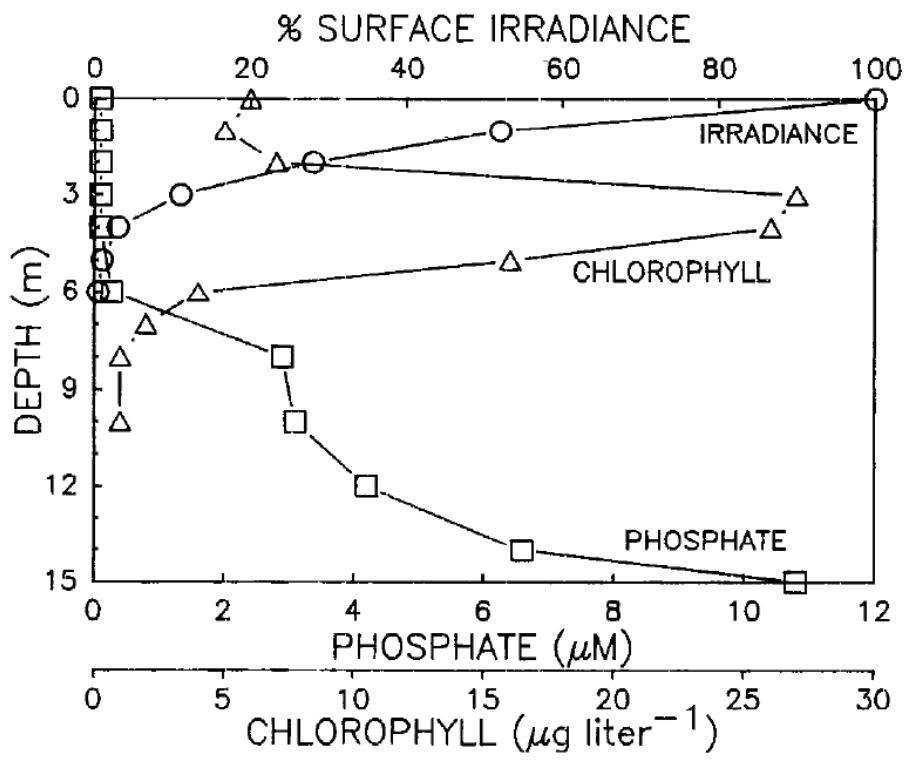


Diatoms

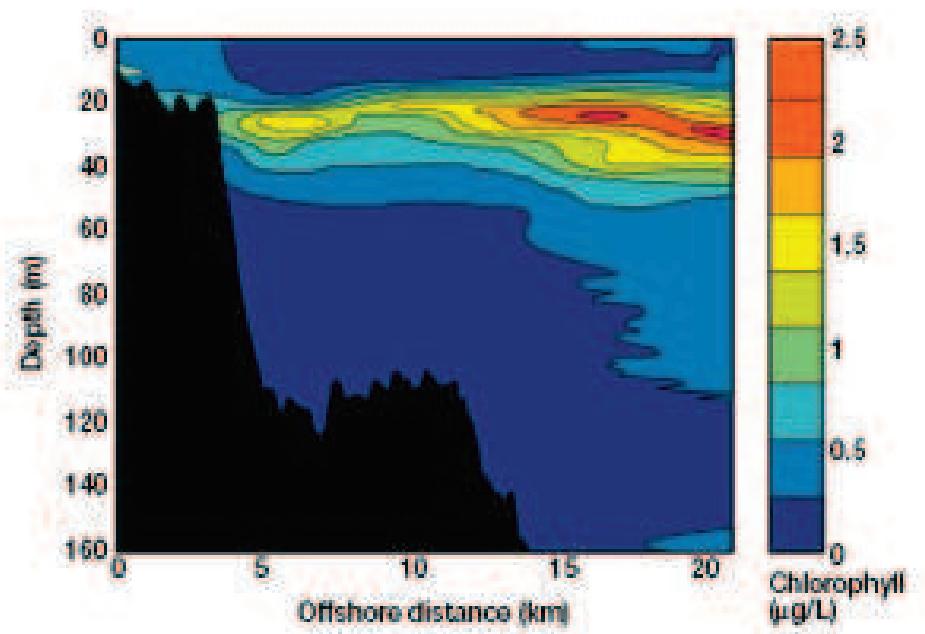
Vertical Distribution of Phytoplankton

- Opposing gradients of 2 essential resources:
 - Light supplied from above
 - Nutrients (N, P, Si) supplied from below
- Many phytoplankton can regulate their depth
- In poorly mixed water columns, these depth-regulating phytoplankton form thin layers

Deep chlorophyll maximum (DCM)



(Konopka 1989)



Surface Scum



Benthic Layer



Questions

- What determines layer type?
- What determines layer location?
- What determines layer thickness?

b – phytoplankton biomass

$$\frac{\partial b}{\partial t} = gb + D \frac{\partial^2 b}{\partial z^2} + \frac{\partial}{\partial z} \left(v \left(\frac{\partial g}{\partial z} \right) b \right)$$

$$= [\text{growth - loss}] + \begin{bmatrix} \text{passive} \\ \text{movement} \end{bmatrix} + \begin{bmatrix} \text{active} \\ \text{movement} \\ = \text{auxanotaxis} \end{bmatrix}$$

$$g = \min(f_R(R), f_I(I)) - m$$
$$\left(D \frac{\partial b}{\partial z} + v \left(\frac{\partial g}{\partial z} \right) b \right) \Big|_{z=0} = 0, \quad \left(D \frac{\partial b}{\partial z} + v \left(\frac{\partial g}{\partial z} \right) b \right) \Big|_{z=z_b} = 0$$

(Klausmeier and Litchman 2001)

R – nutrient


$$\begin{aligned}\frac{\partial R}{\partial t} &= -\frac{b}{Y} \min(f_R(R), f_I(I)) + D \frac{\partial^2 R}{\partial z^2} \\ &= -[\text{uptake}] + [\text{mixing}]\end{aligned}$$

$$\left. \frac{\partial R}{\partial z} \right|_{z=0} = 0, \quad \left. \frac{\partial R}{\partial z} \right|_{z=z_b} = h(R_{\text{in}} - R(z_b))$$

(Klausmeier and Litchman 2001)

I – light

$$I(z) = I_{\text{in}} e^{-\int_0^z (a_{\text{bg}} + ab(Z)) dZ}$$

$$\log I(z) = \log I_{\text{in}} - a_{\text{bg}} z - a \int_0^z b(Z) dZ$$

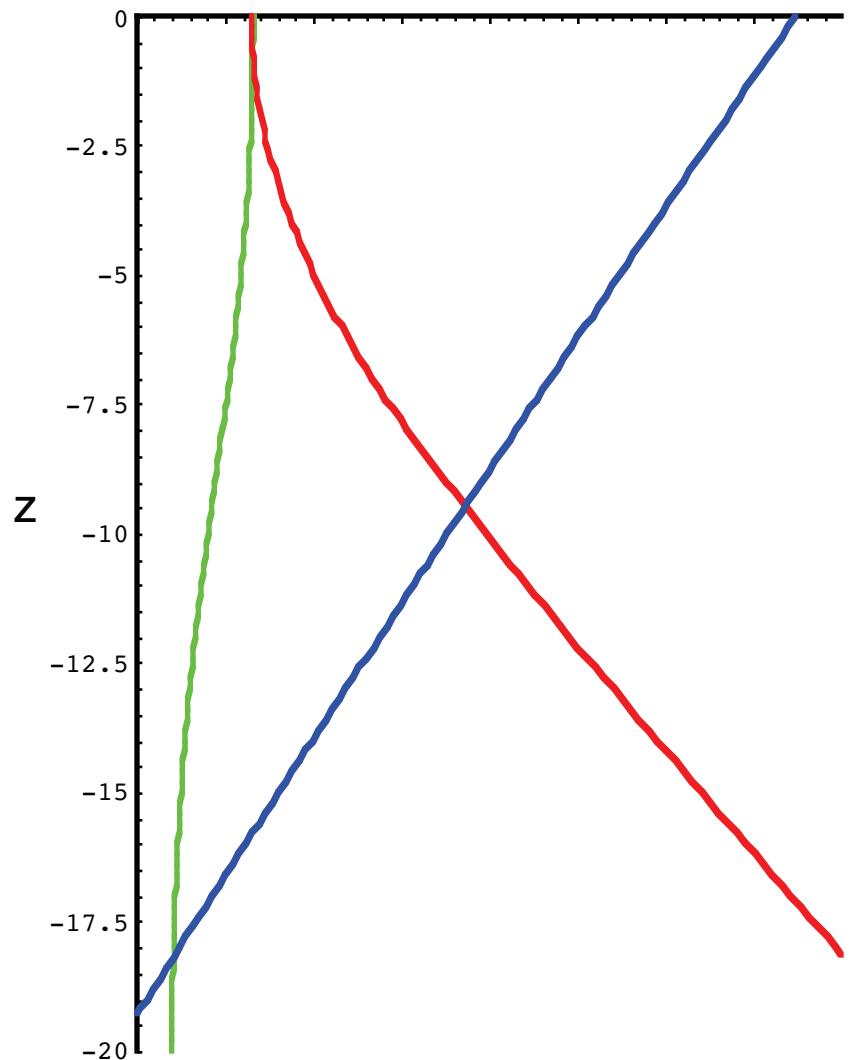
$$= \begin{bmatrix} \text{incoming} \\ \text{light} \end{bmatrix} - \begin{bmatrix} \text{background} \\ \text{attenuation} \end{bmatrix} - \begin{bmatrix} \text{algal} \\ \text{attenuation} \end{bmatrix}$$

(Klausmeier and Litchman 2001)

$v_{max} = 0$



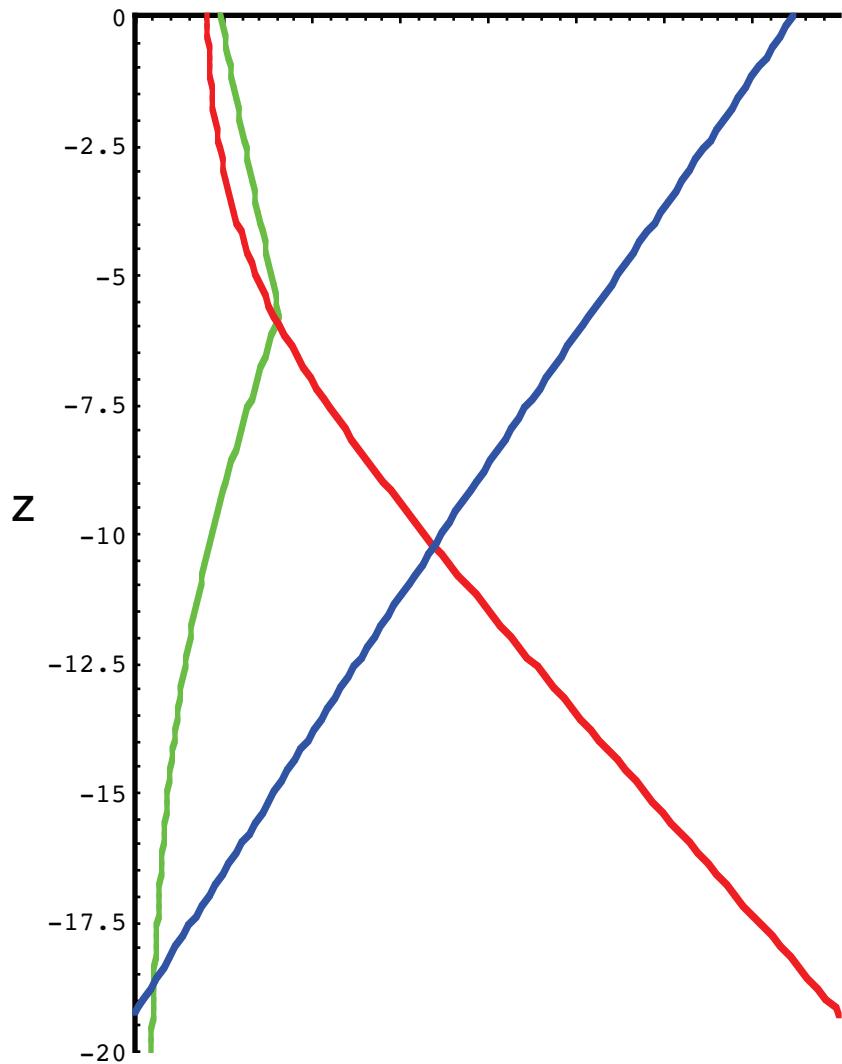
- phytoplankton
- nutrient
- ln light



$$v_{\max} = 1 \text{ m/day}$$



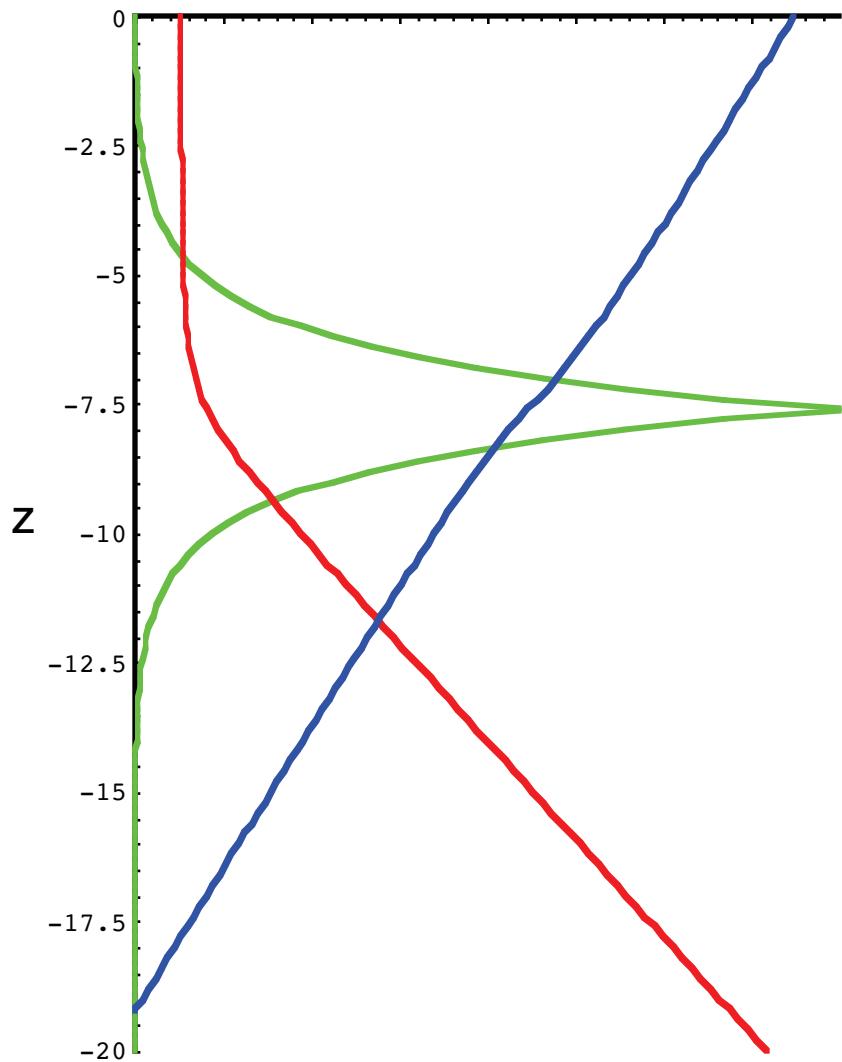
- phytoplankton
- nutrient
- In light



$$v_{\max} = 10 \text{ m/day}$$



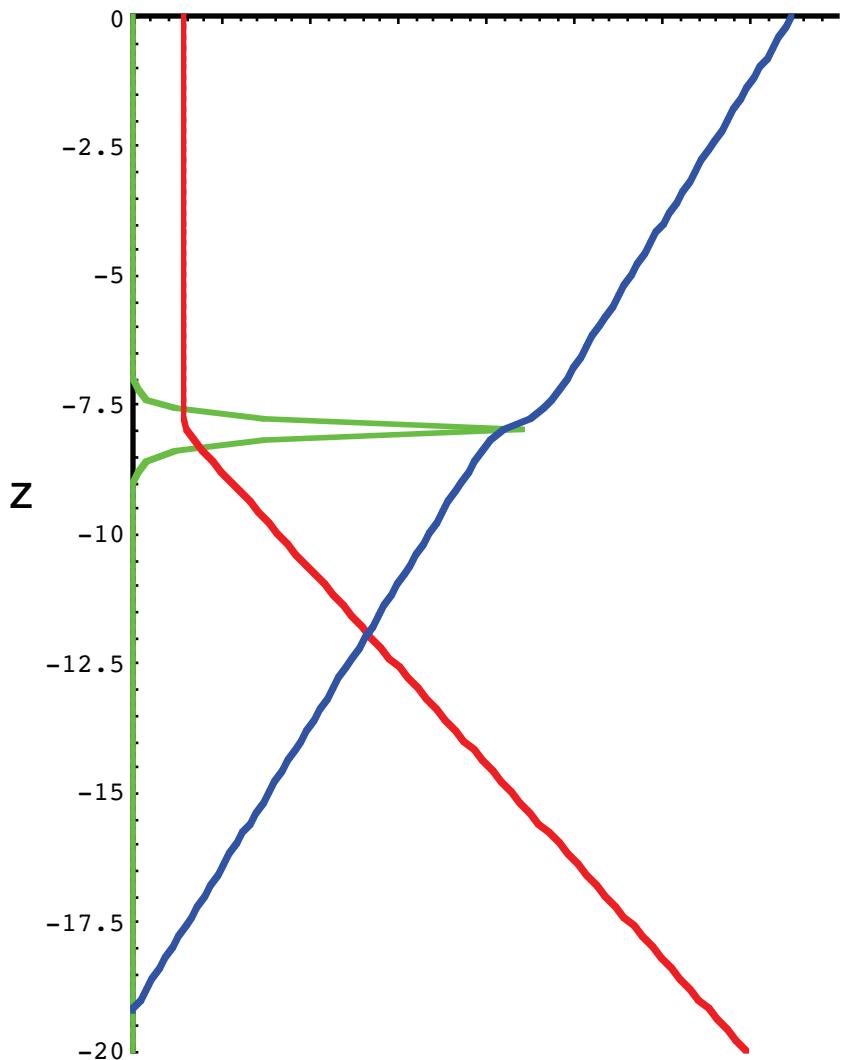
- phytoplankton
- nutrient
- In light



$$v_{\max} = 100 \text{ m/day}$$



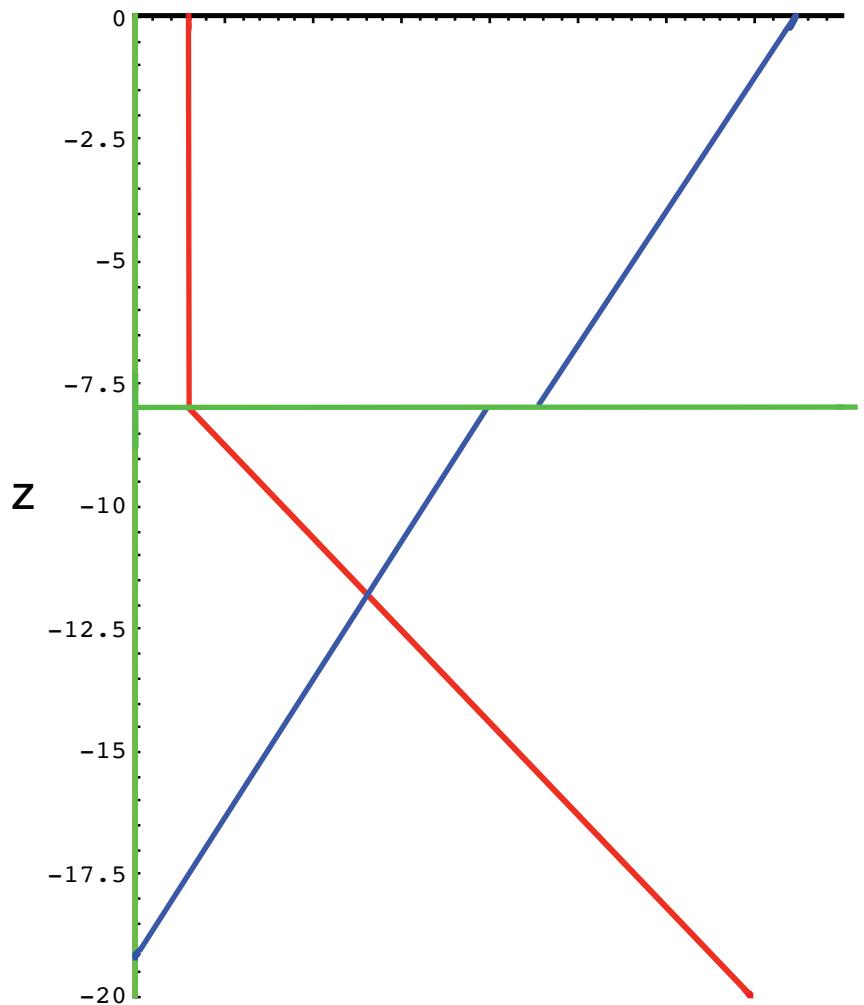
- phytoplankton
- nutrient
- In light



$$v_{\max} = \infty$$



- phytoplankton
- nutrient
- ln light

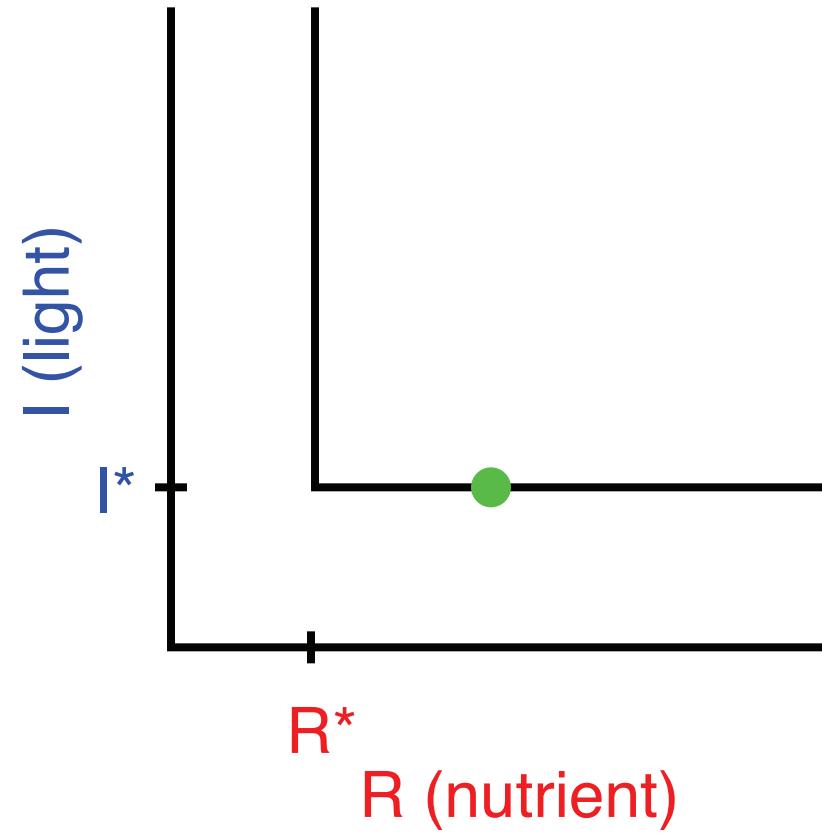
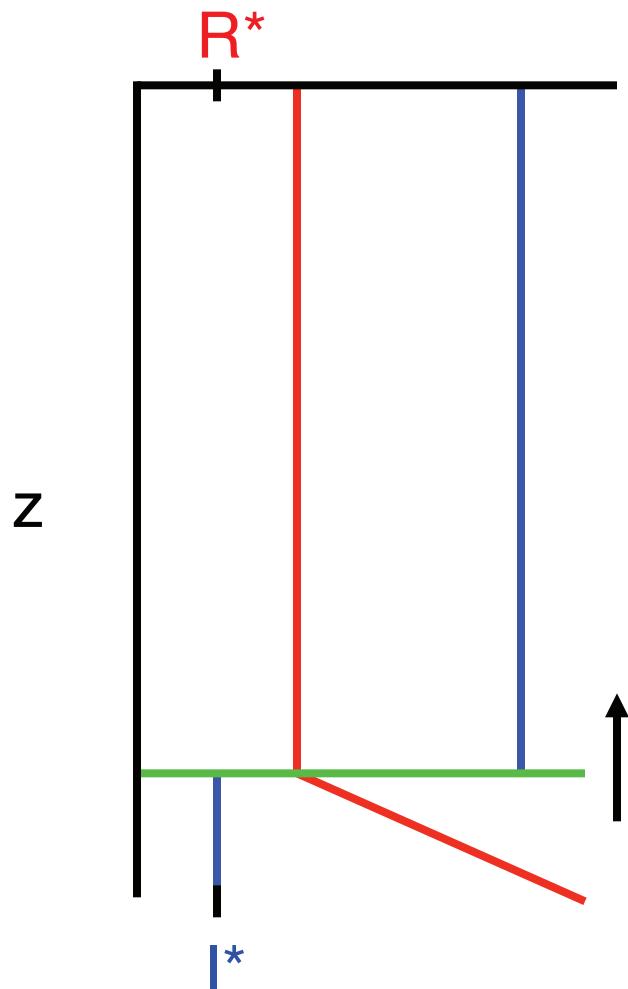


Game Theoretical Approach

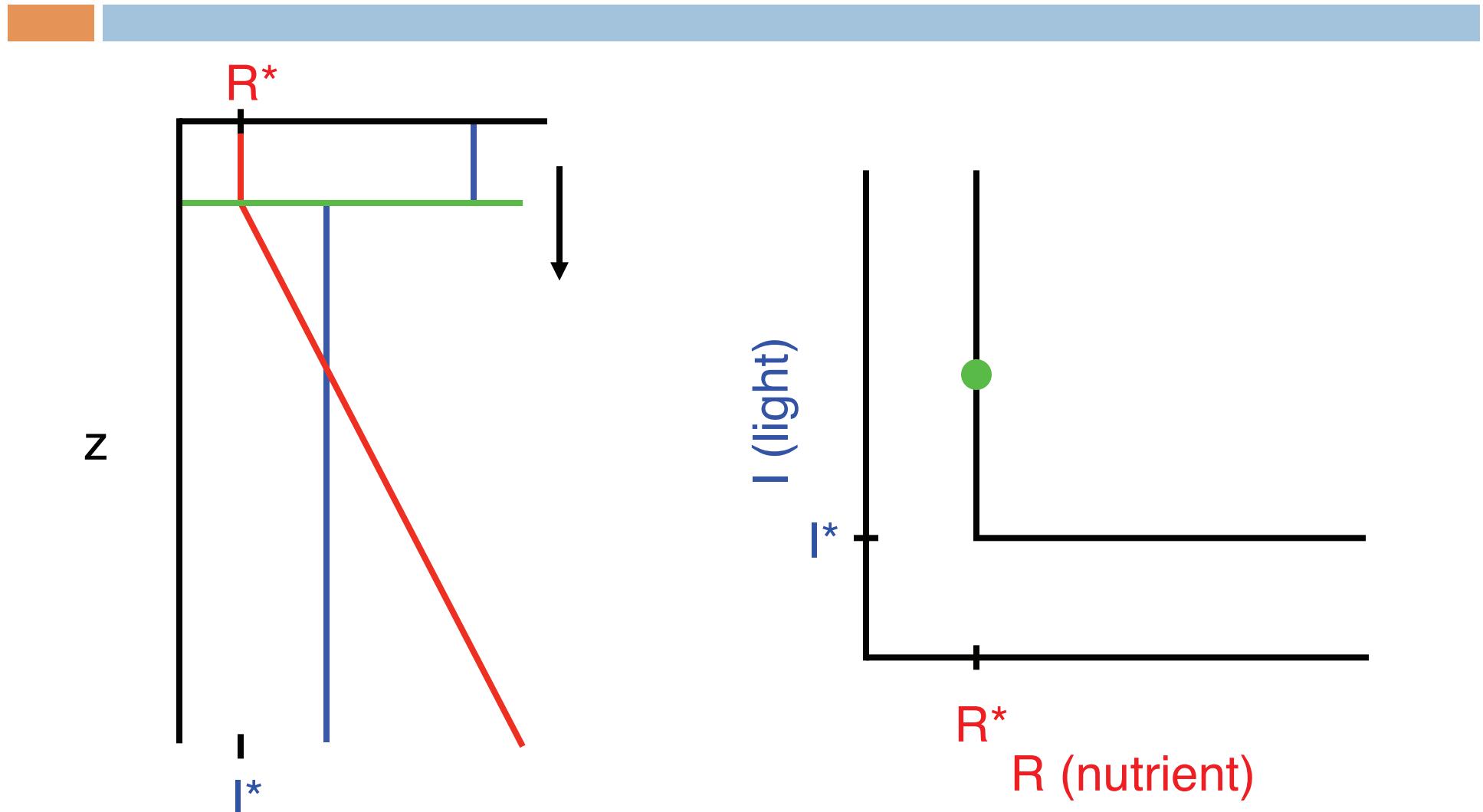
- Assume phytoplankton form thin layer
- Strategy: depth of layer, z_l
- Given layer at z_l , determine equilibrium profile of nutrients and light
- Look for strategy z^* that prevents growth everywhere else (ESS)

(Klausmeier and Litchman 2001)

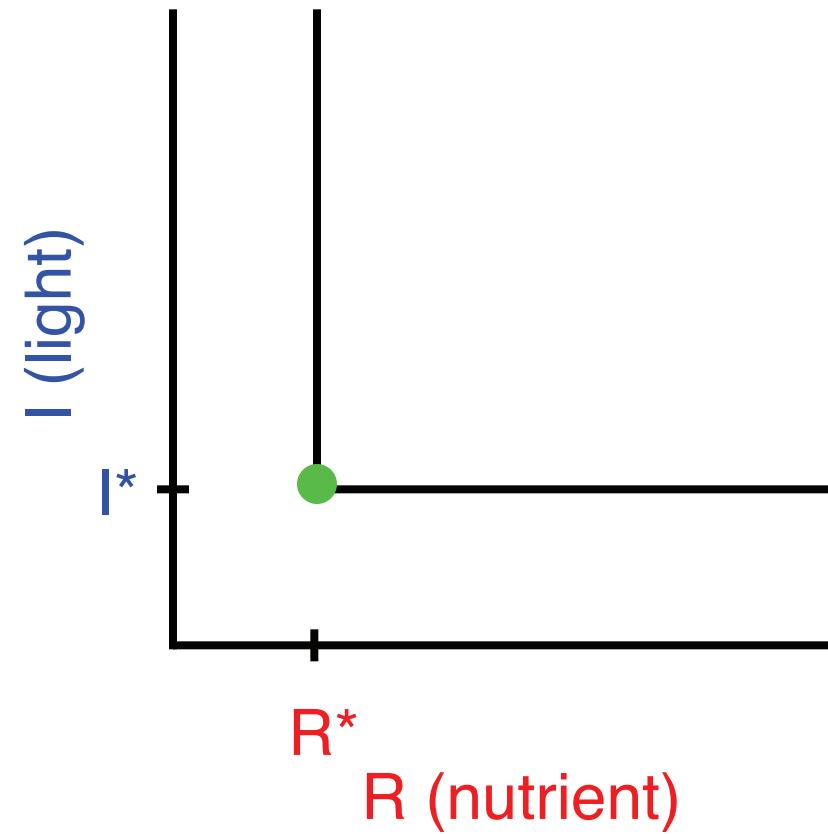
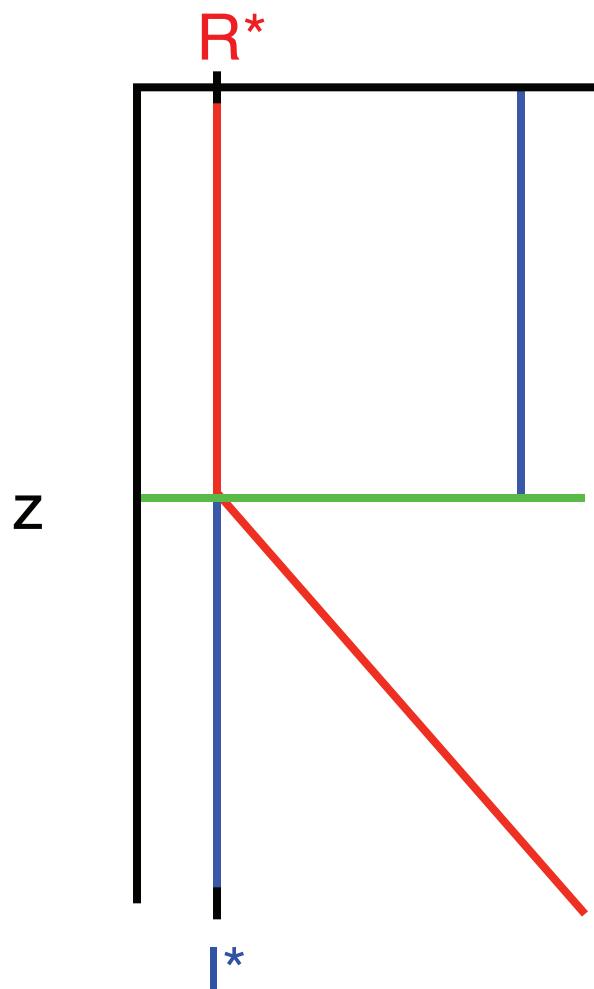
Too Deep – Light-Limited



Too Shallow – Nutrient-Limited



Just Right – Co-Limited



ESS Depth, z^*



$$\frac{\log I_{\text{in}} - \log I^*}{a} - \frac{a_{\text{bg}}}{a} z^* = \frac{YD(R_{\text{in}} - R^*)}{m(1 - \varepsilon)(z_b + 1/h - z^*)}$$

$$\begin{bmatrix} \text{light - limited} \\ \text{biomass} \end{bmatrix} = \begin{bmatrix} \text{nutrient - limited} \\ \text{biomass} \end{bmatrix}$$

Effect of Model Parameters

- Increase light supply / competitive ability

- Increase l_{in}
 - Decrease abg, a
 - Decrease l^*

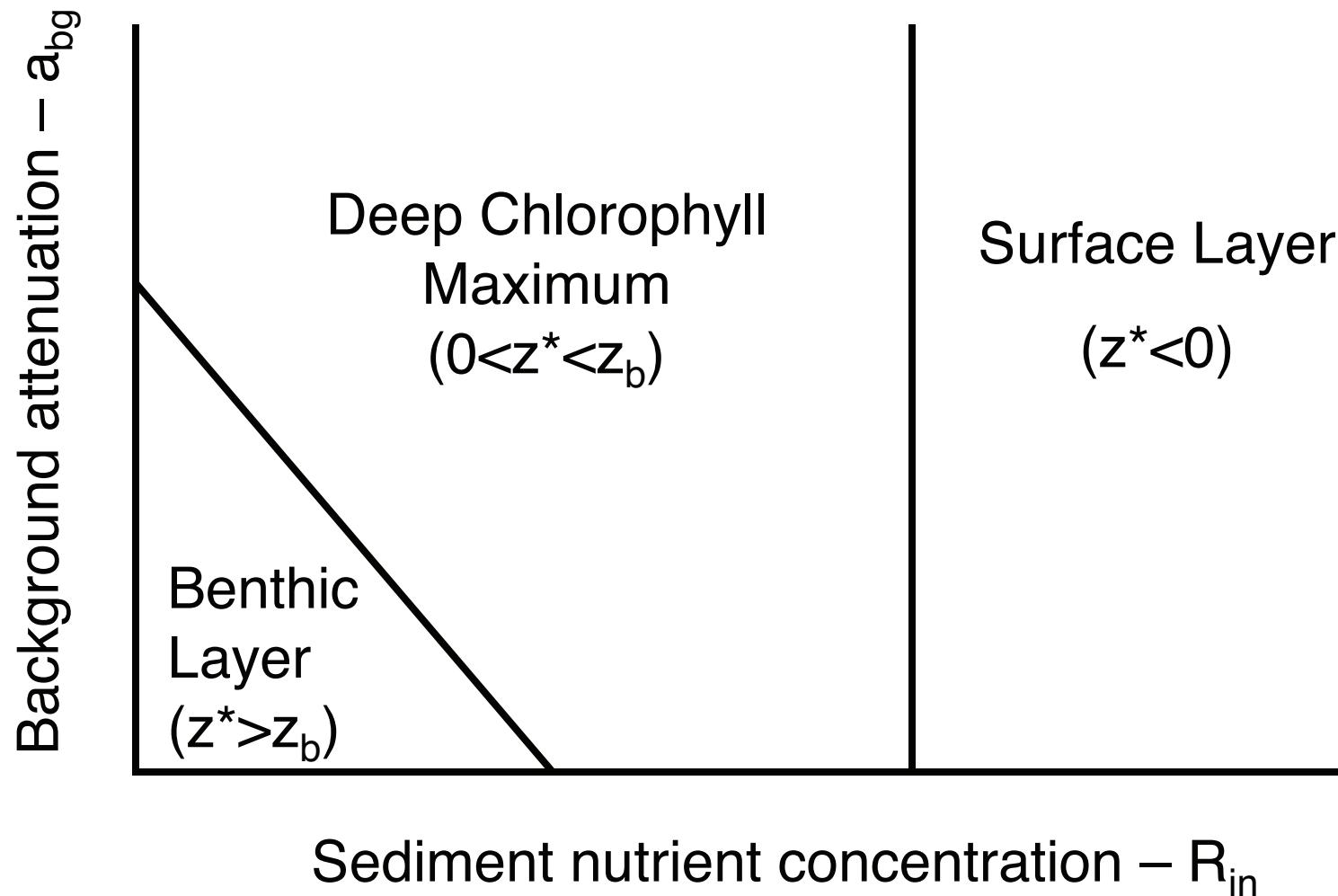
→ Move layer down (increase z^*)

- Increase nutrient supply / competitive ability

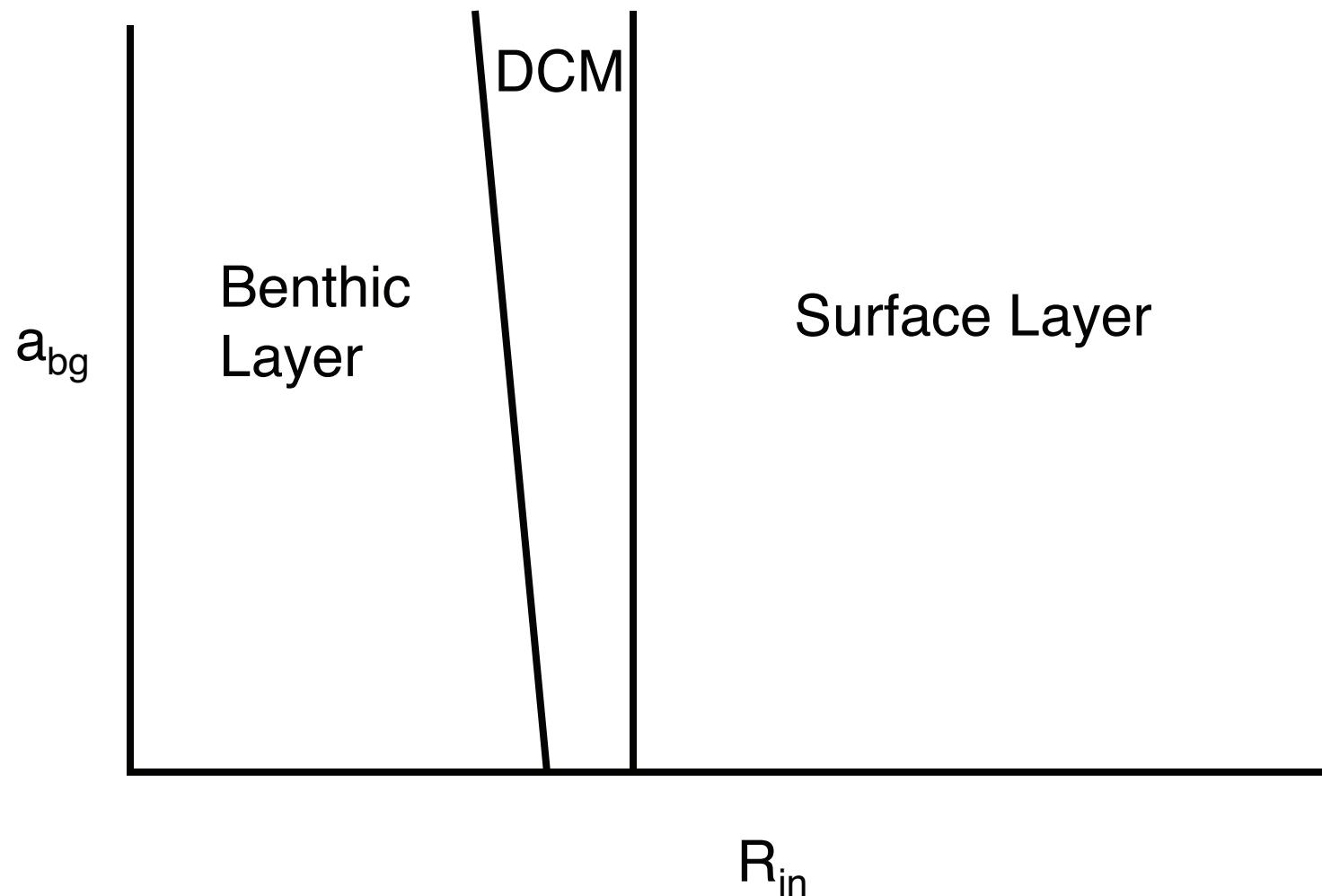
- Increase R_{in}
 - Decrease R^*

→ Move layer up (decrease z^*)

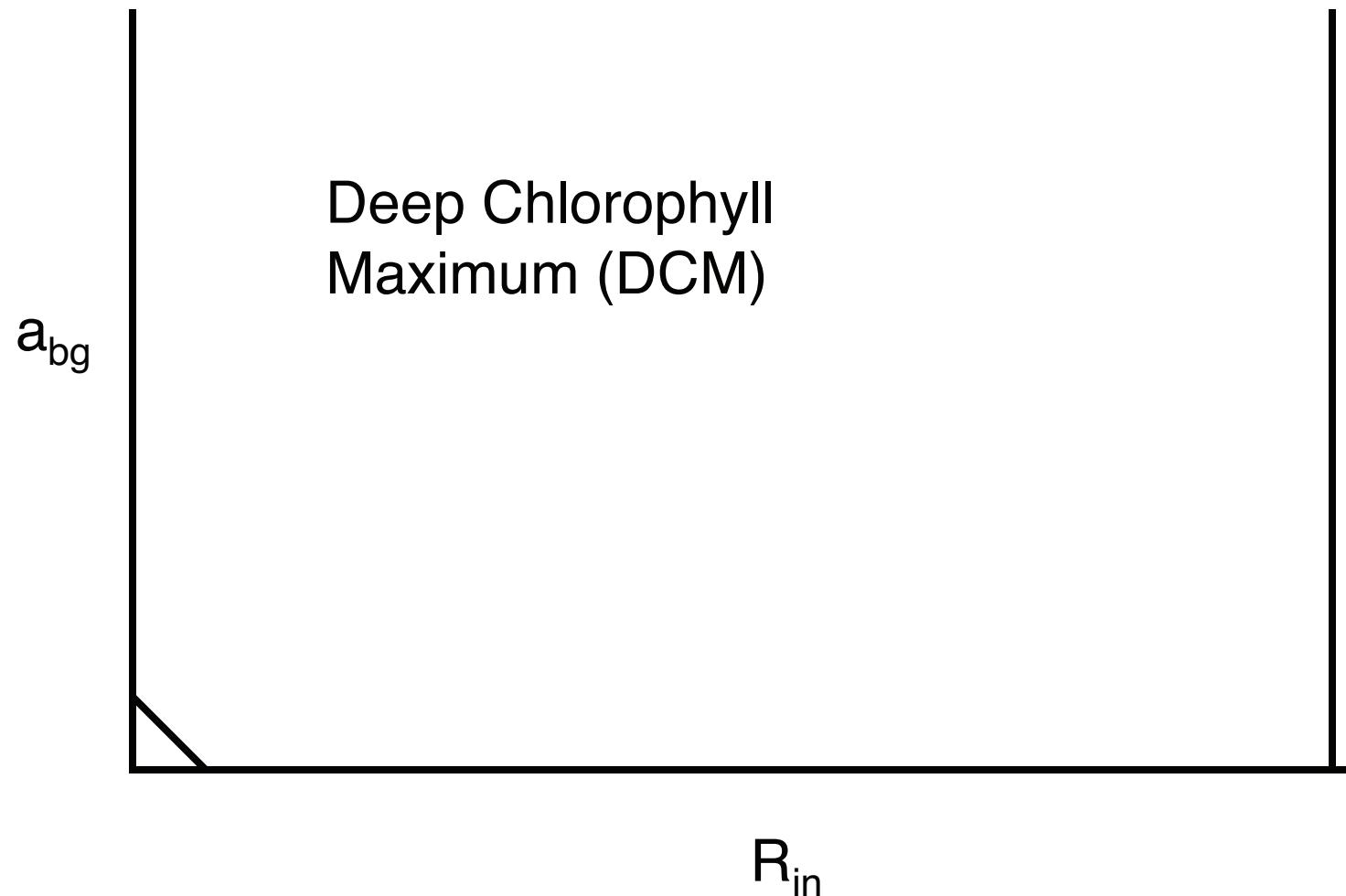
Overview of Outcomes



Shallow Lake (z_b small)



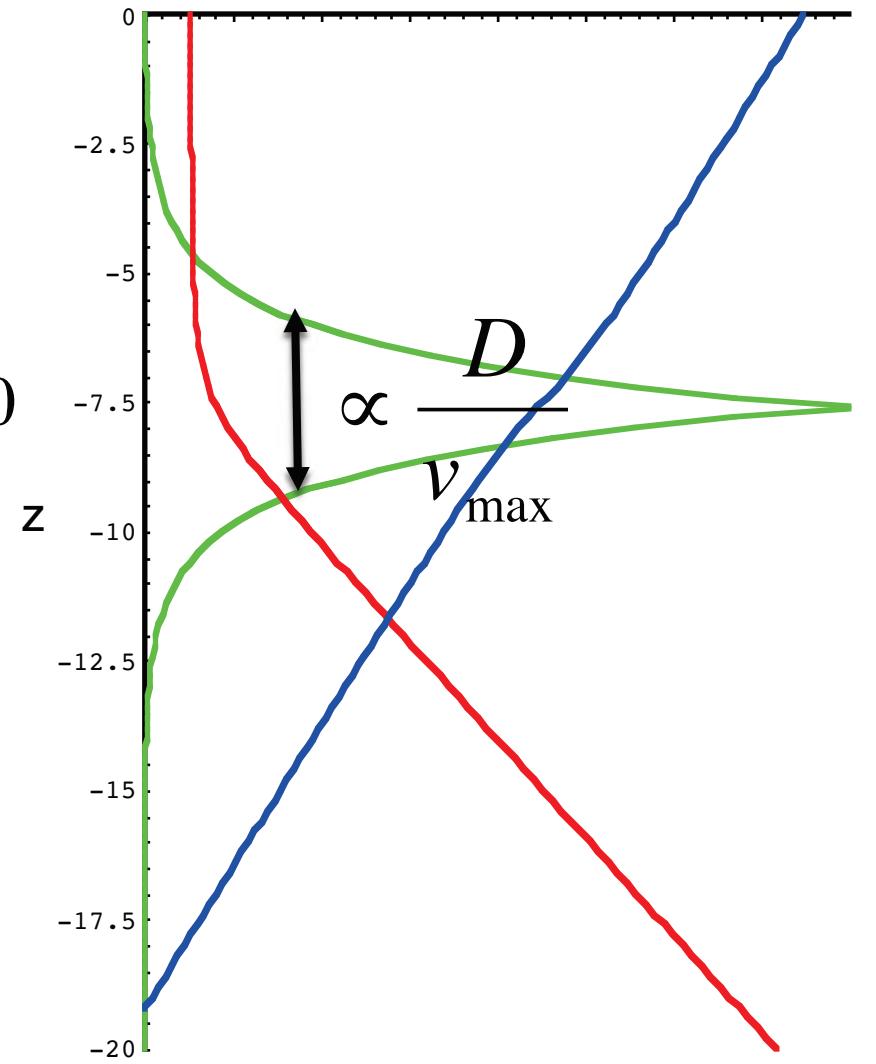
Deep Lake (z_b large)



Width of layer



$$\frac{\partial b}{\partial t} = D \frac{\partial^2 b}{\partial z^2} + \frac{\partial}{\partial z} \begin{cases} -v_{\max} b, & z < z^* \\ v_{\max} b, & z > z^* \end{cases} = 0$$
$$= \begin{bmatrix} \text{passive} \\ \text{movement} \end{bmatrix} + \begin{bmatrix} \text{active} \\ \text{movement} \end{bmatrix}$$



Extending this research...



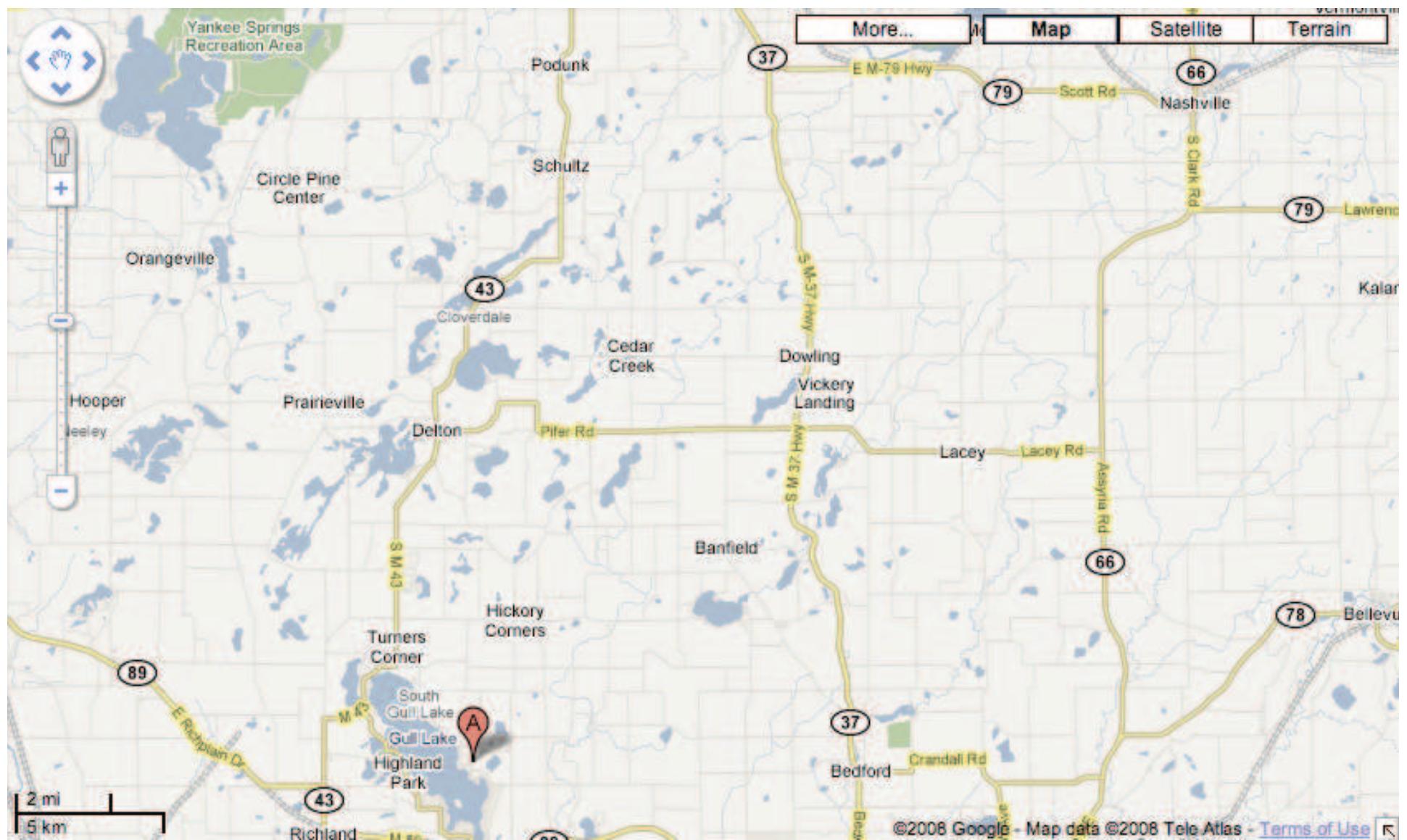
Jarad Mellard [GS]

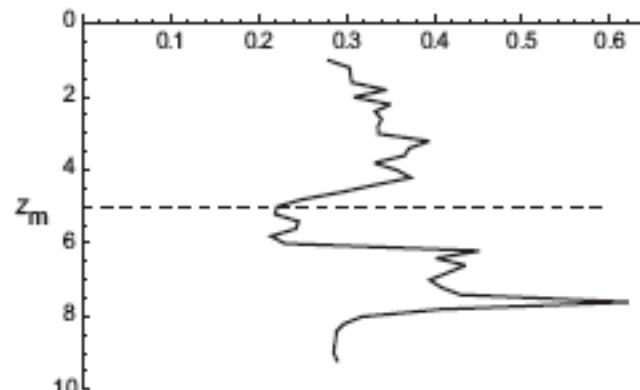
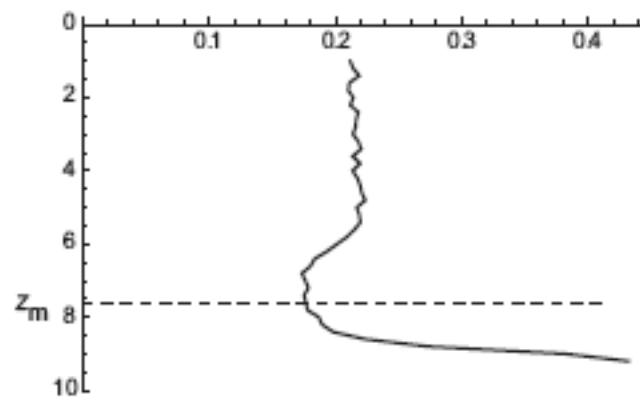
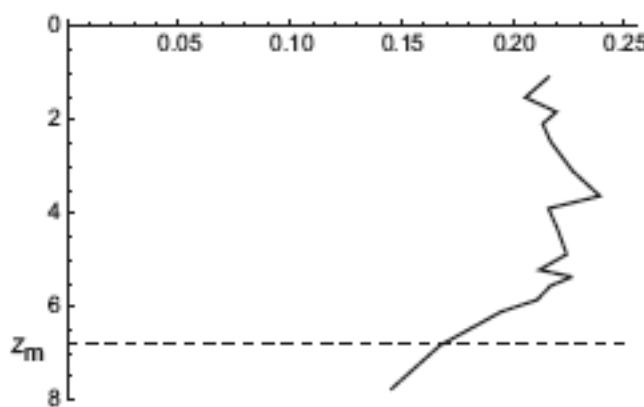
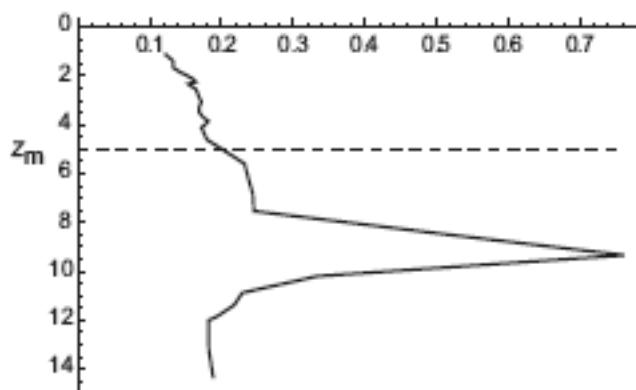
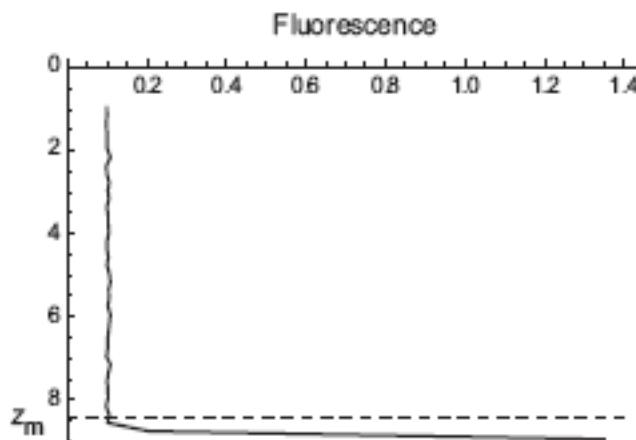
Kohei Yoshiyama [PD]

Laboratory mesocosms

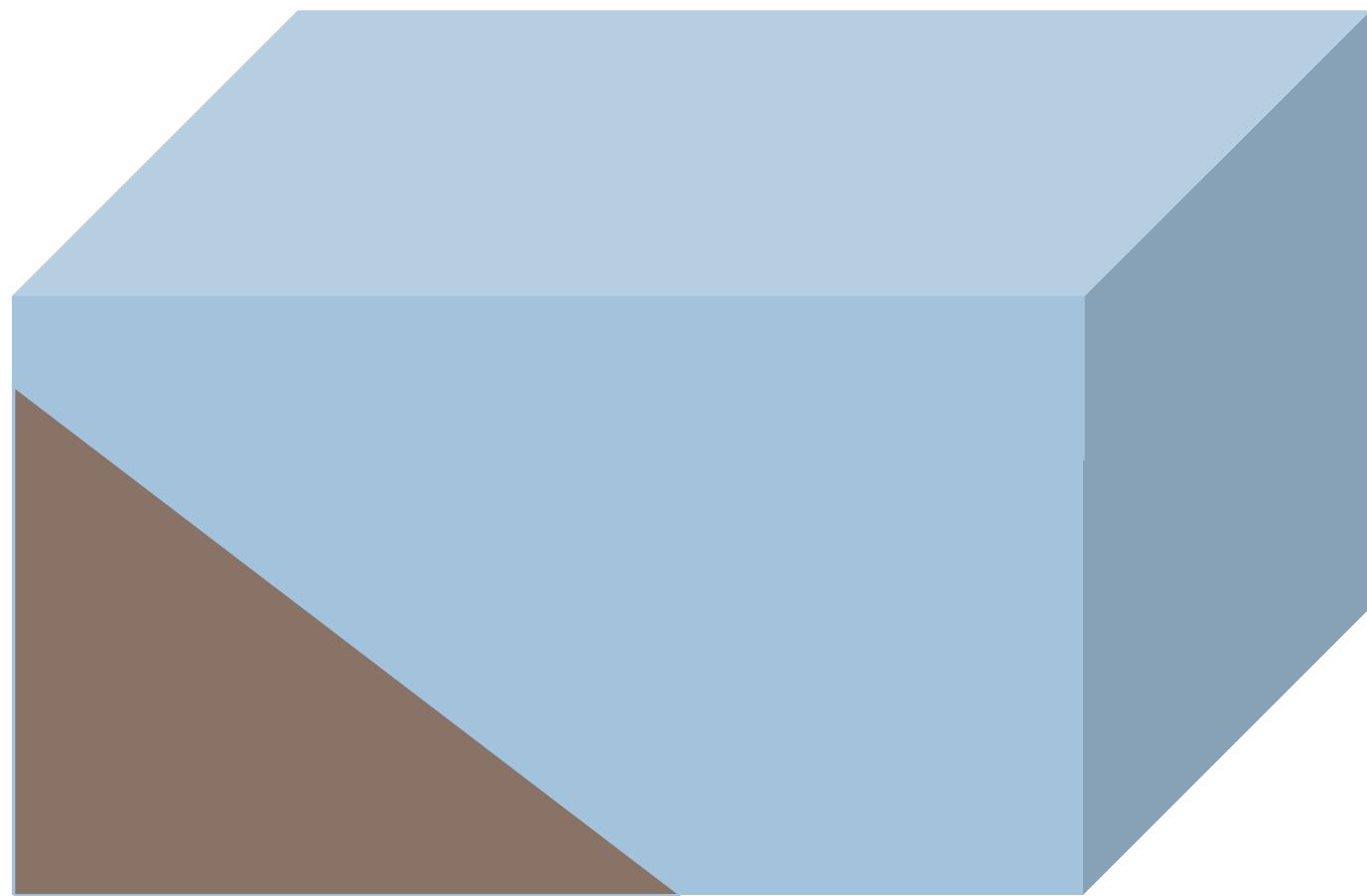


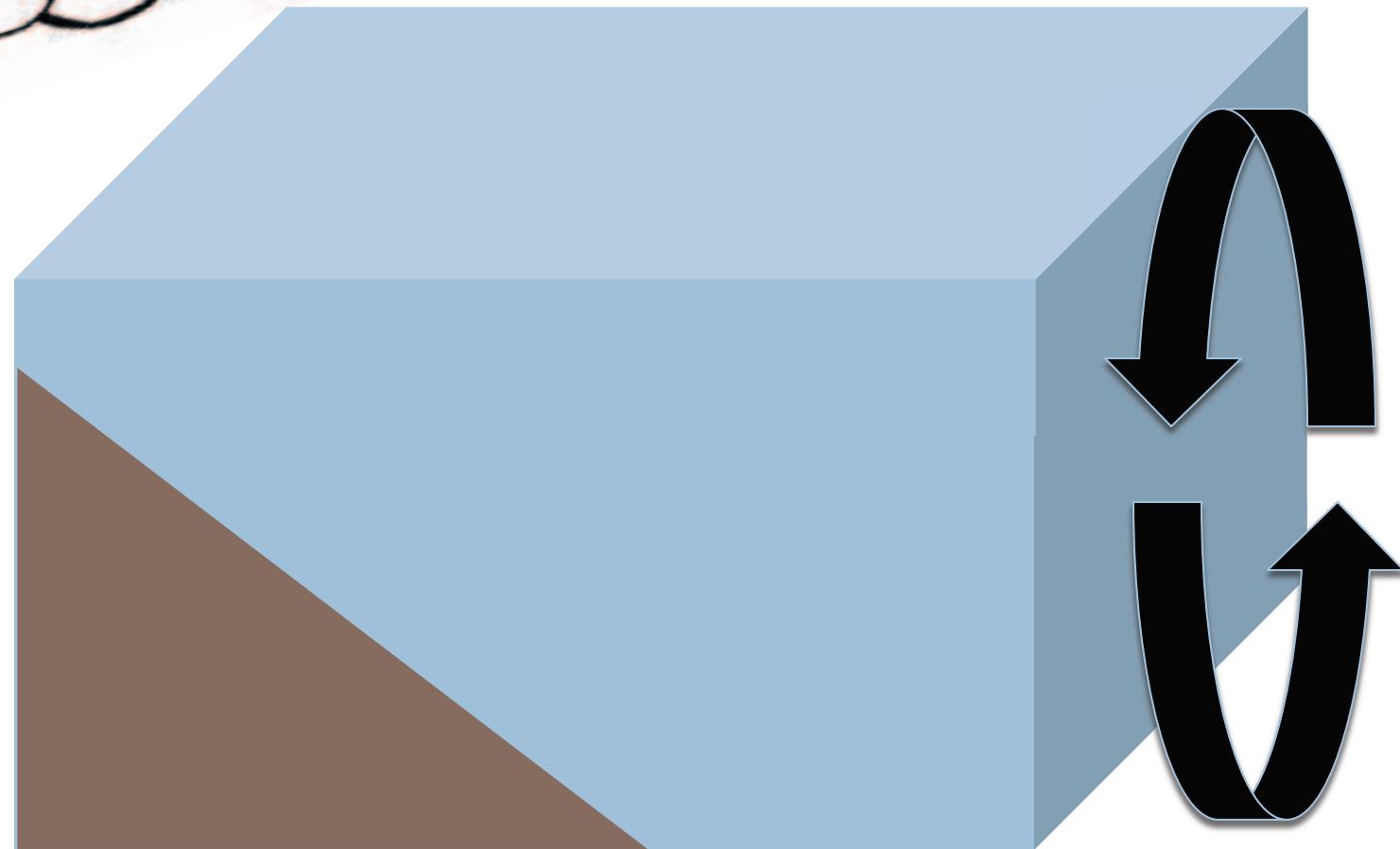
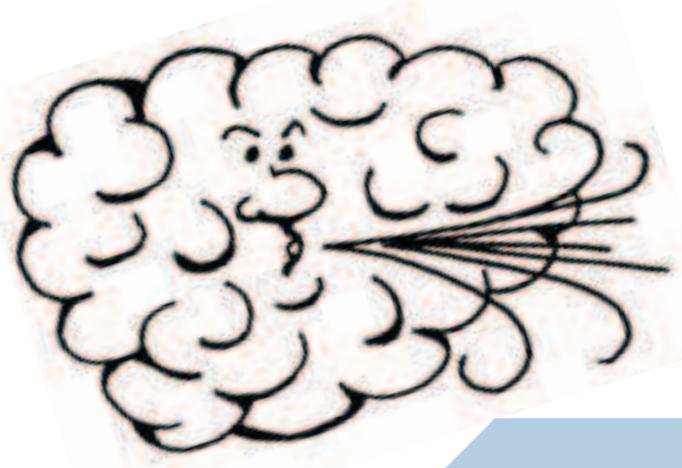
(Mellard et al. *in prep.*)

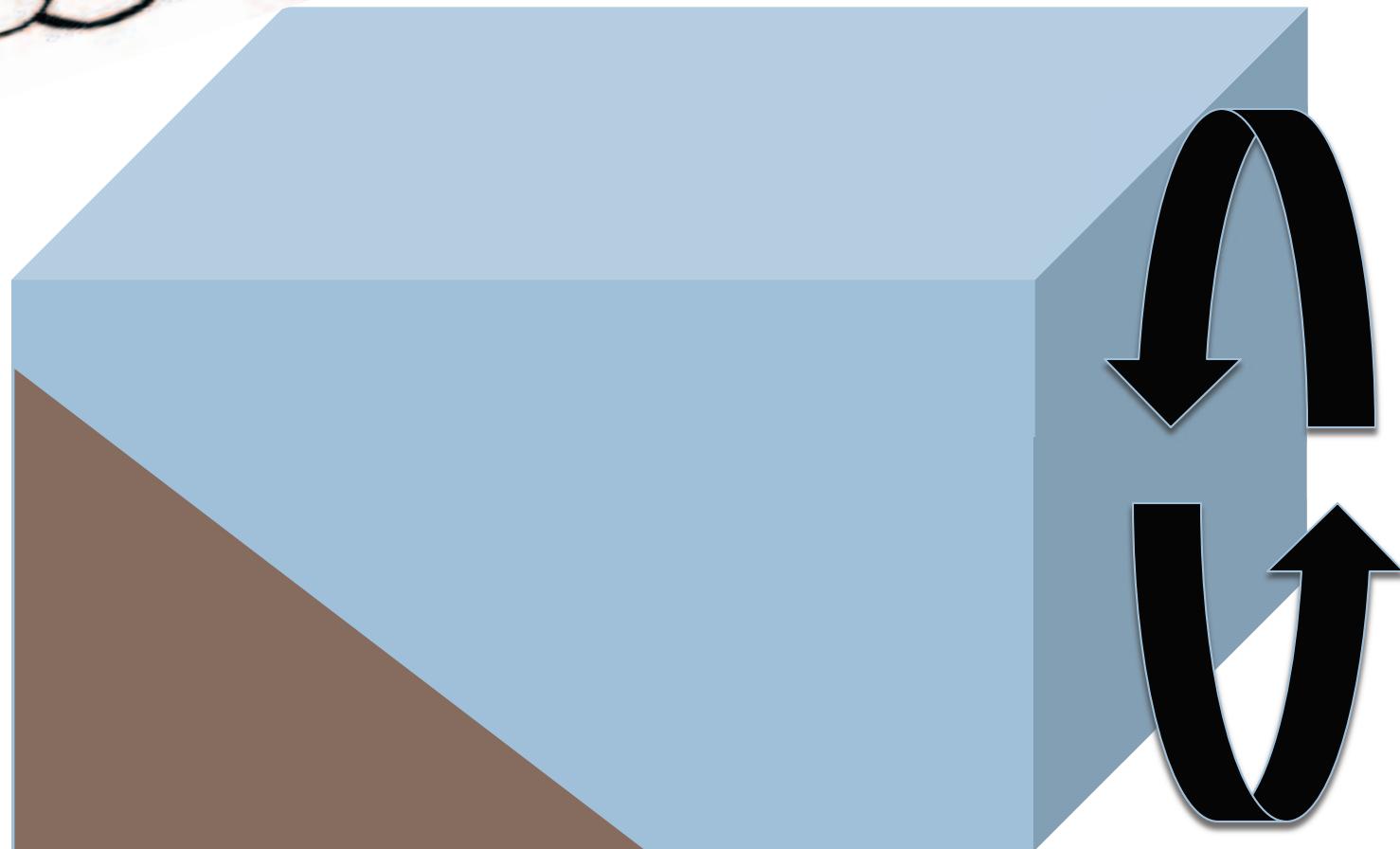
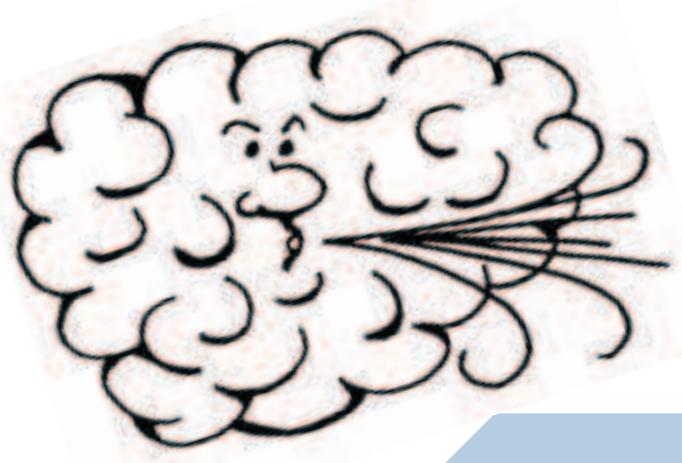


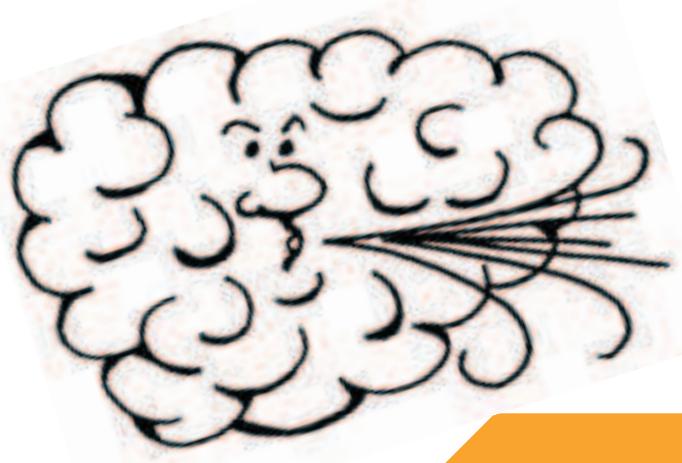


(Mellard et al. *in prep.*)



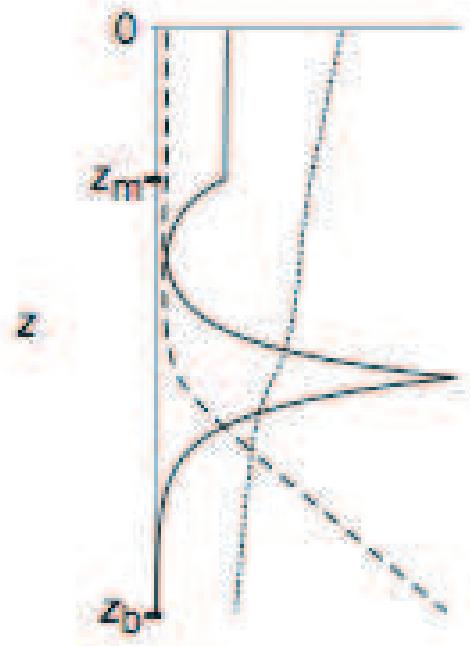






Model Results

A



B



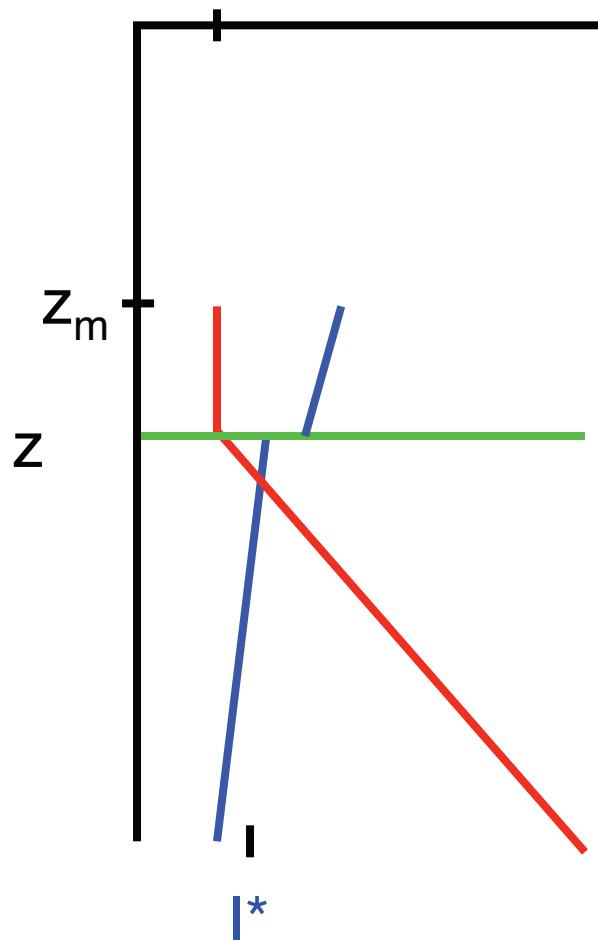
Legend

- biomass (b)
- - - nutrient (R)
- log light ($\log I$)

Figure 2:

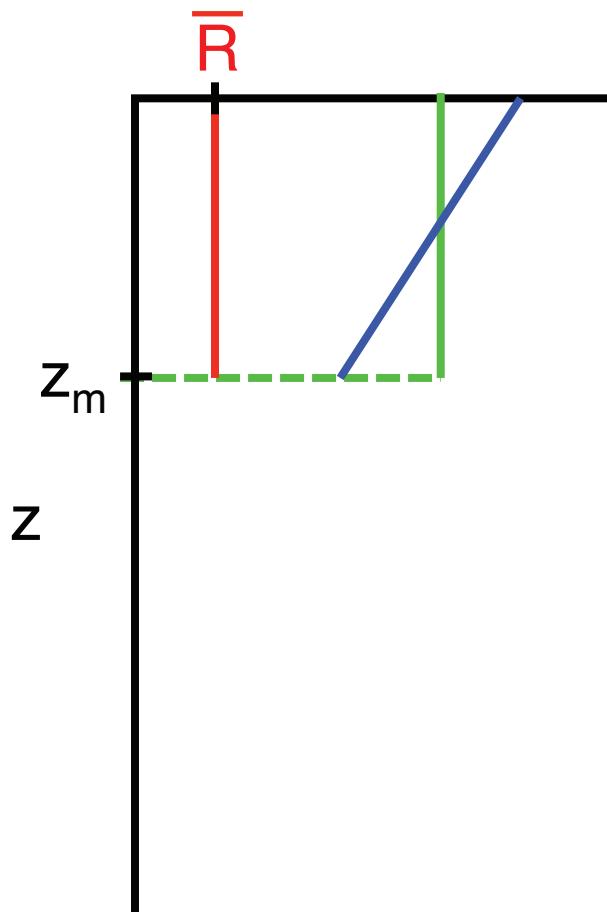
(Mellard et al. *in review*)

Simplified model: deep layer



Klausmeier & Litchman 2001

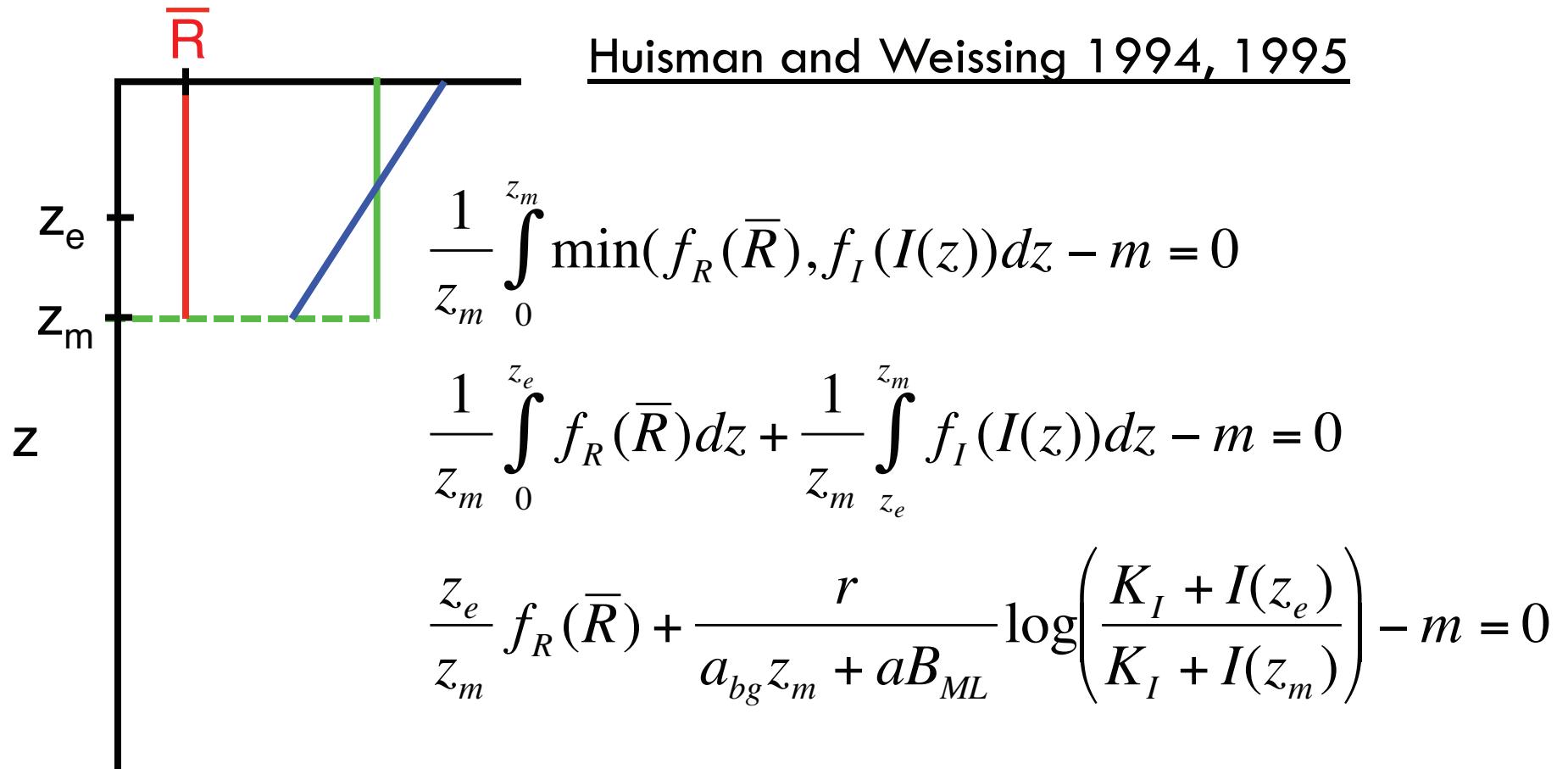
Simplified model: mixed layer



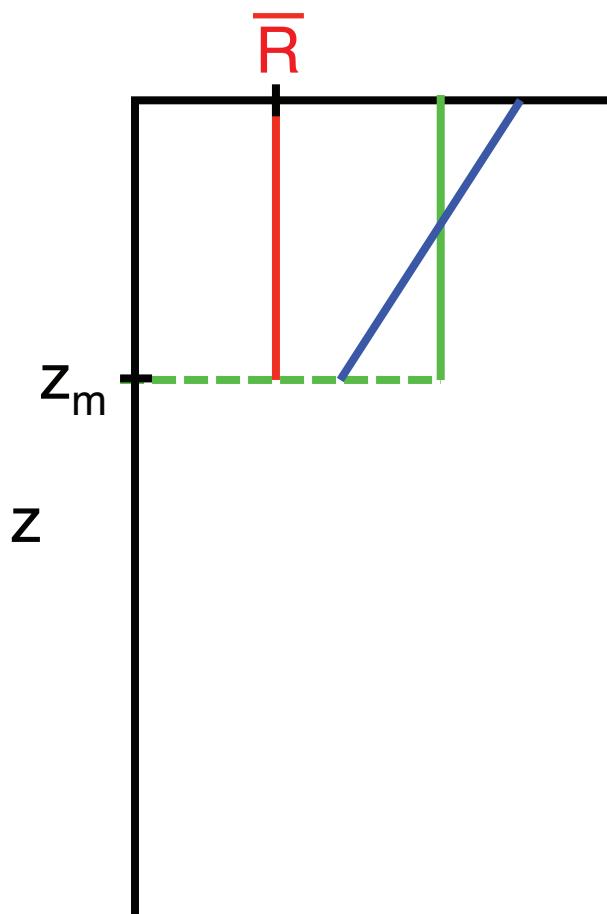
Huisman and Weissing 1994, 1995

$$\int_0^{z_m} \min(f_R(\bar{R}), f_I(I(z))) dz - m = 0$$

Simplified model: mixed layer colimited case



Simplified model: mixed layer light-limited case

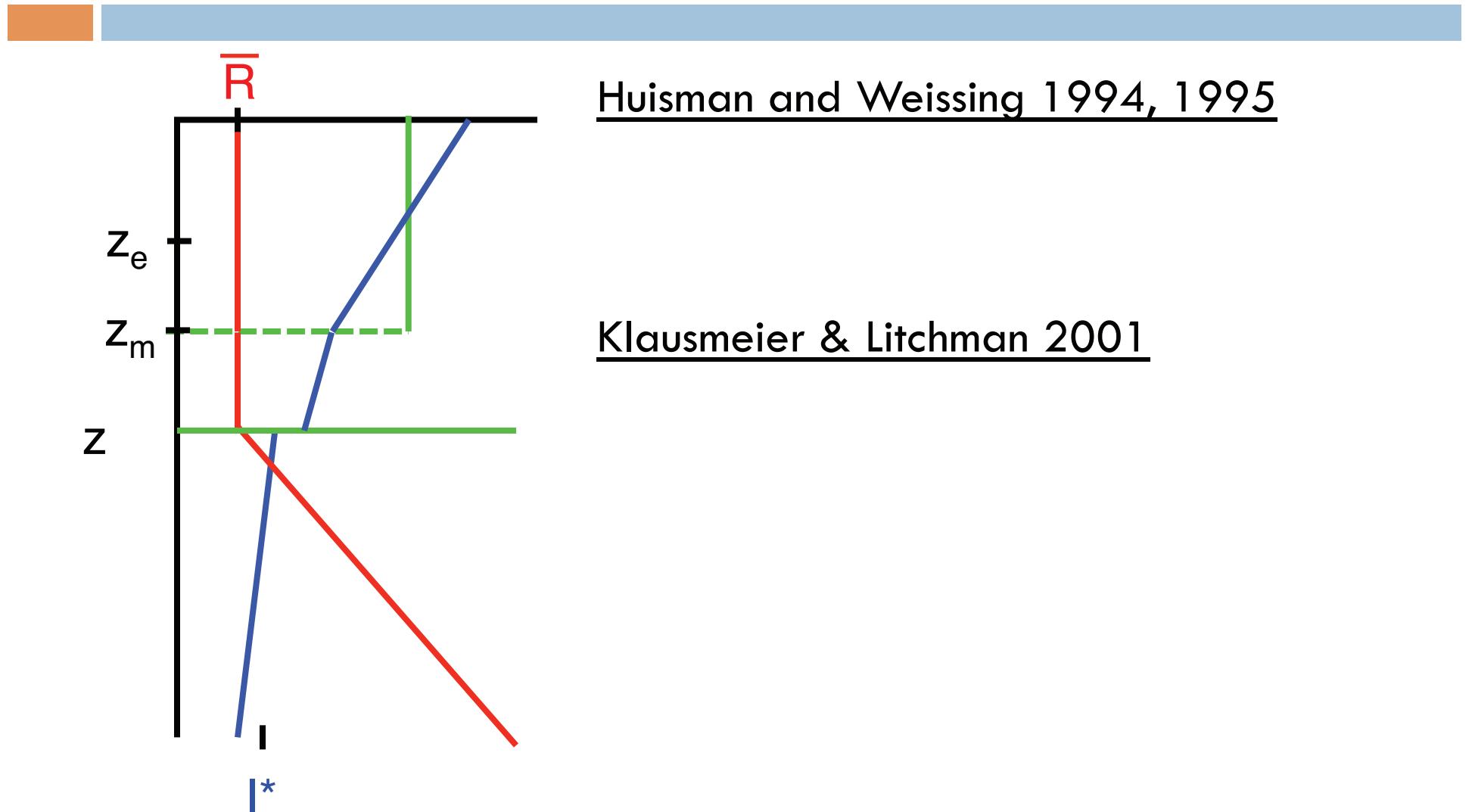


Huisman and Weissing 1994, 1995

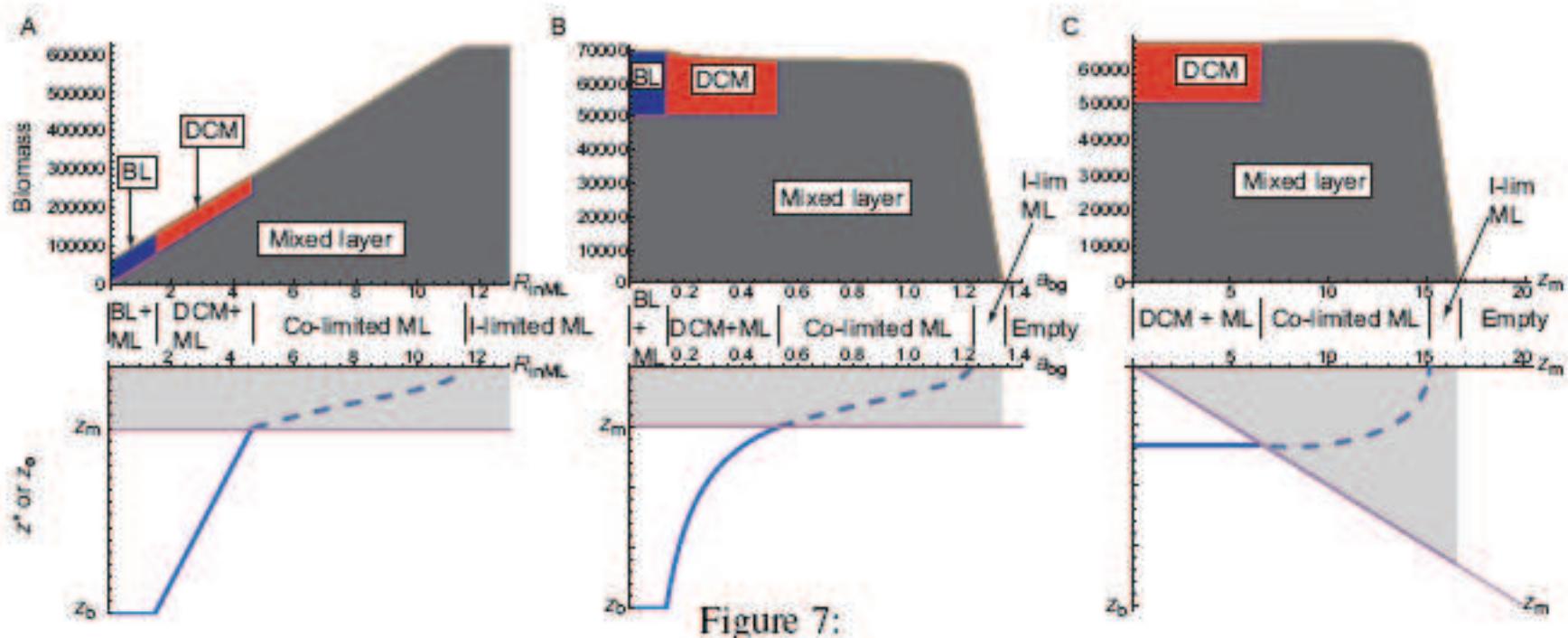
$$\frac{1}{z_m} \int_0^{z_m} \min(f_R(\bar{R}), f_I(I(z))) dz - m = 0$$

$$\frac{r}{a_{bg}z_m + aB_{ML}} \log\left(\frac{K_I + I_{in}}{K_I + I(z_m)}\right) - m = 0$$

Simplified model: stratified

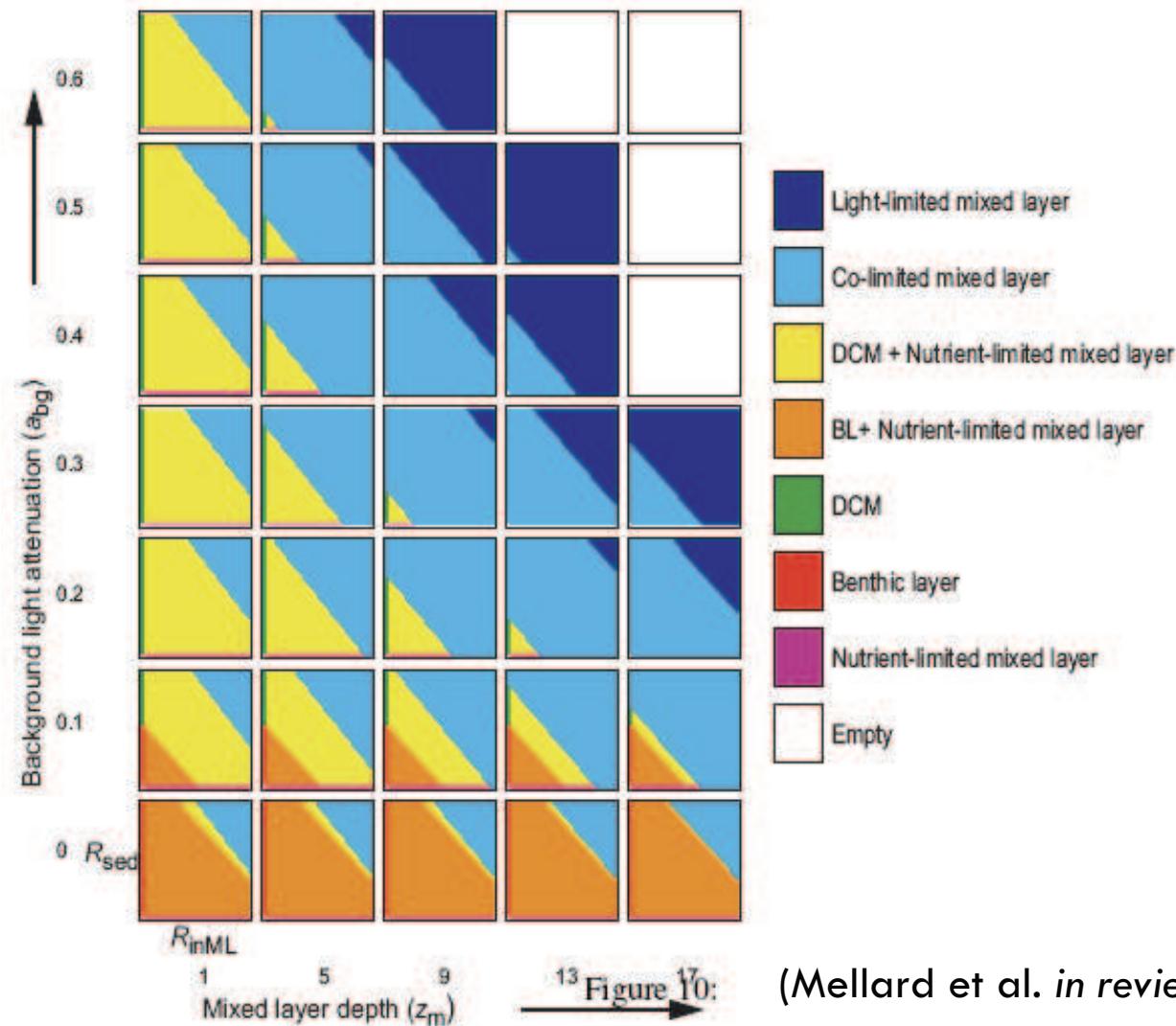


Model Results

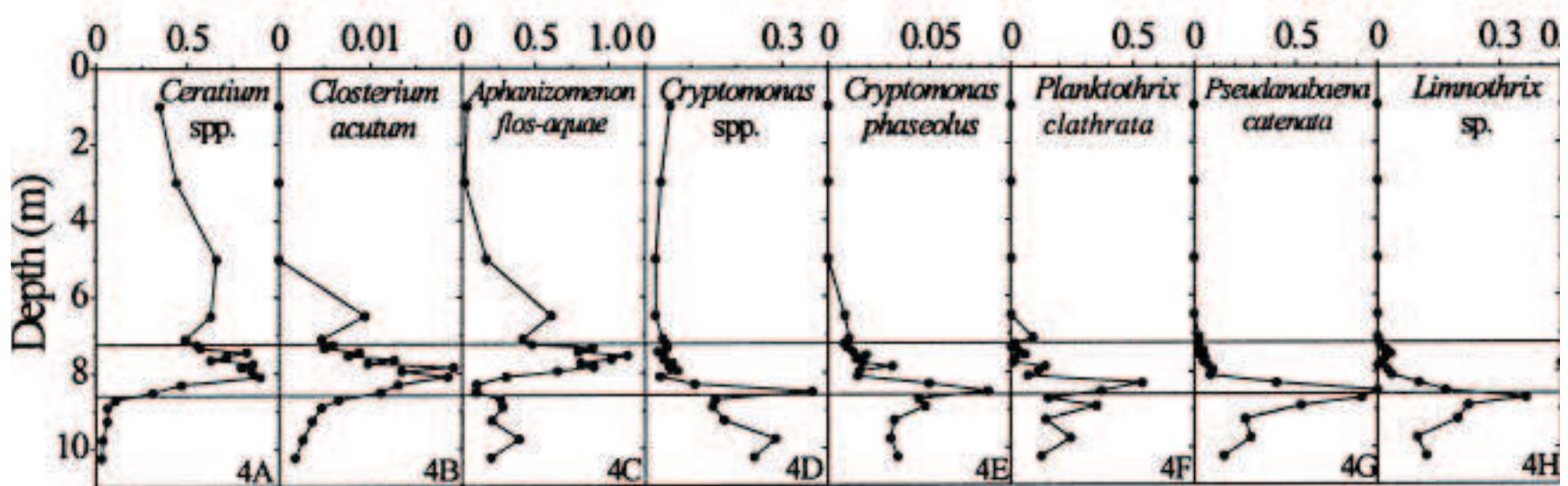


(Mellard et al. *in review*)

Model Results



Multiple competitors



(Gervais et al. 2003)

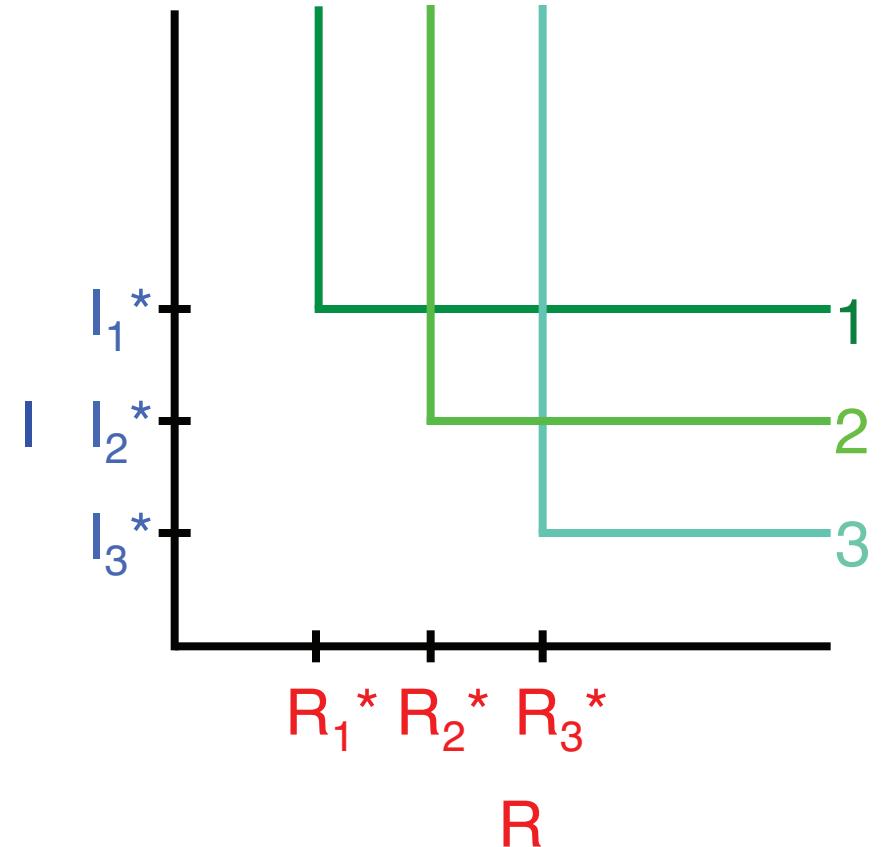
Multiple competitors



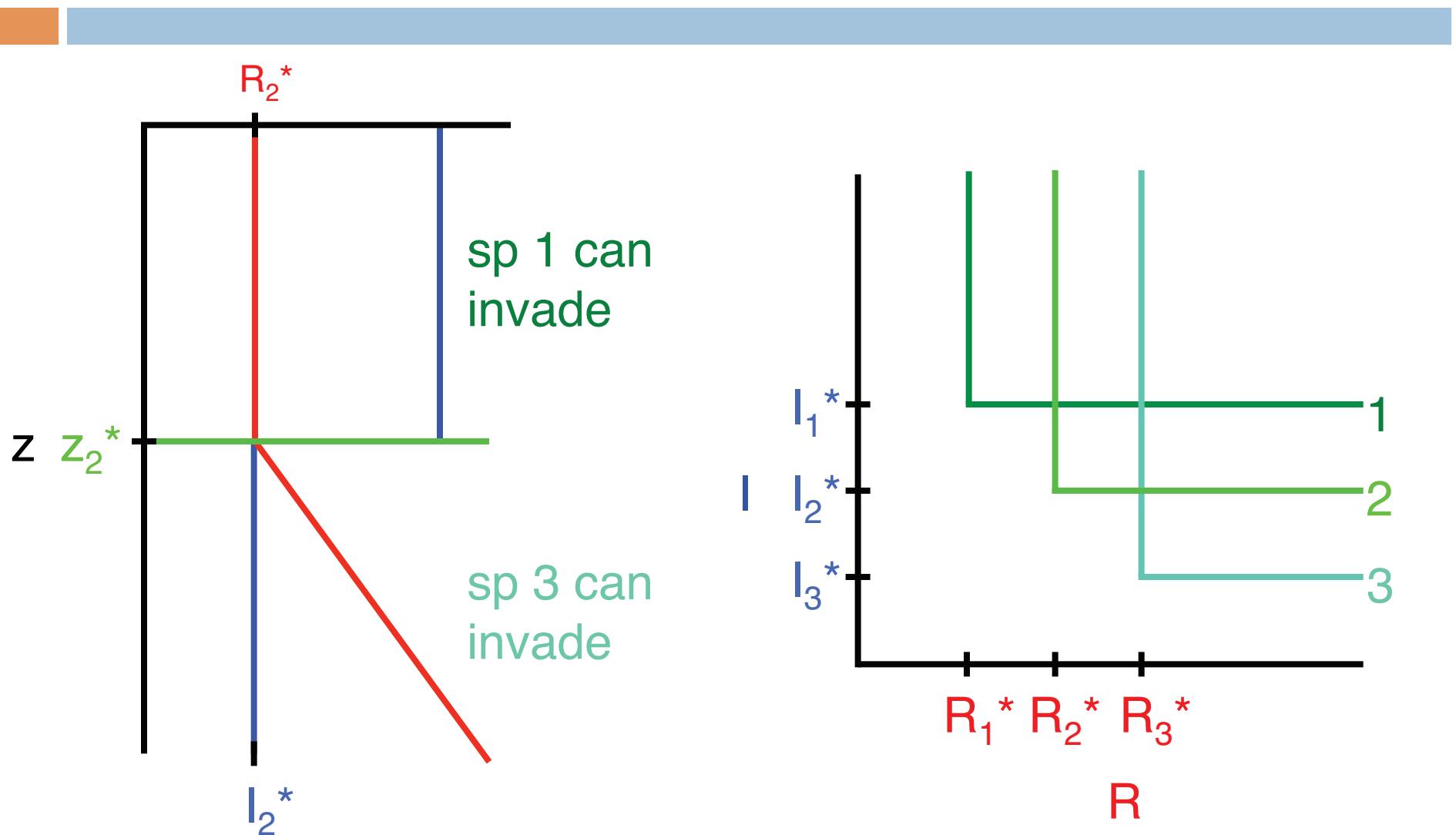
- Q: Can this vertical segregation facilitate species coexistence?

Multiple competitors

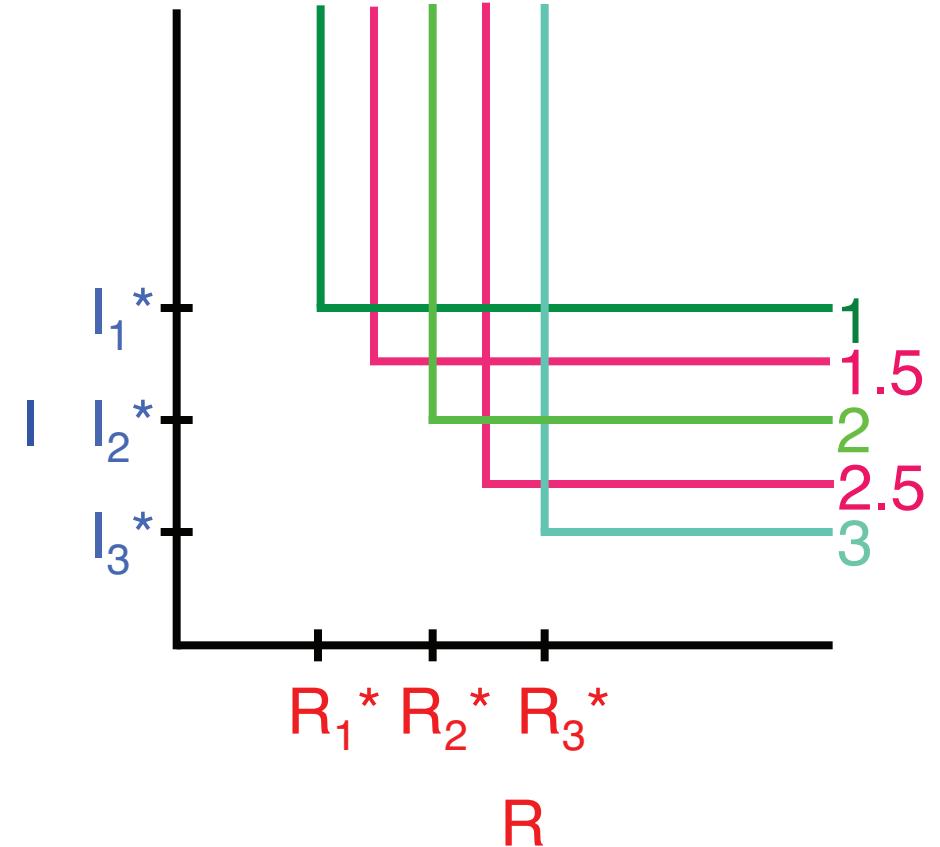
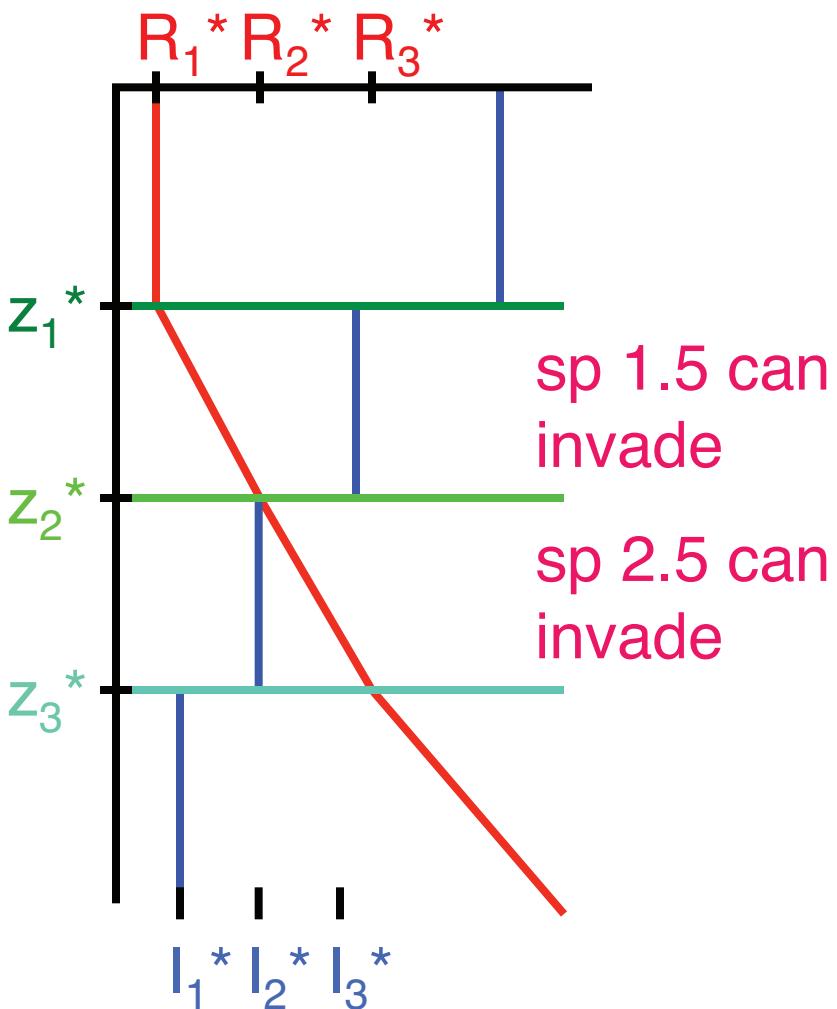
- Trade-off: light vs nutrient competitive ability
- (species 1 is best nutrient competitor, worst light competitor)



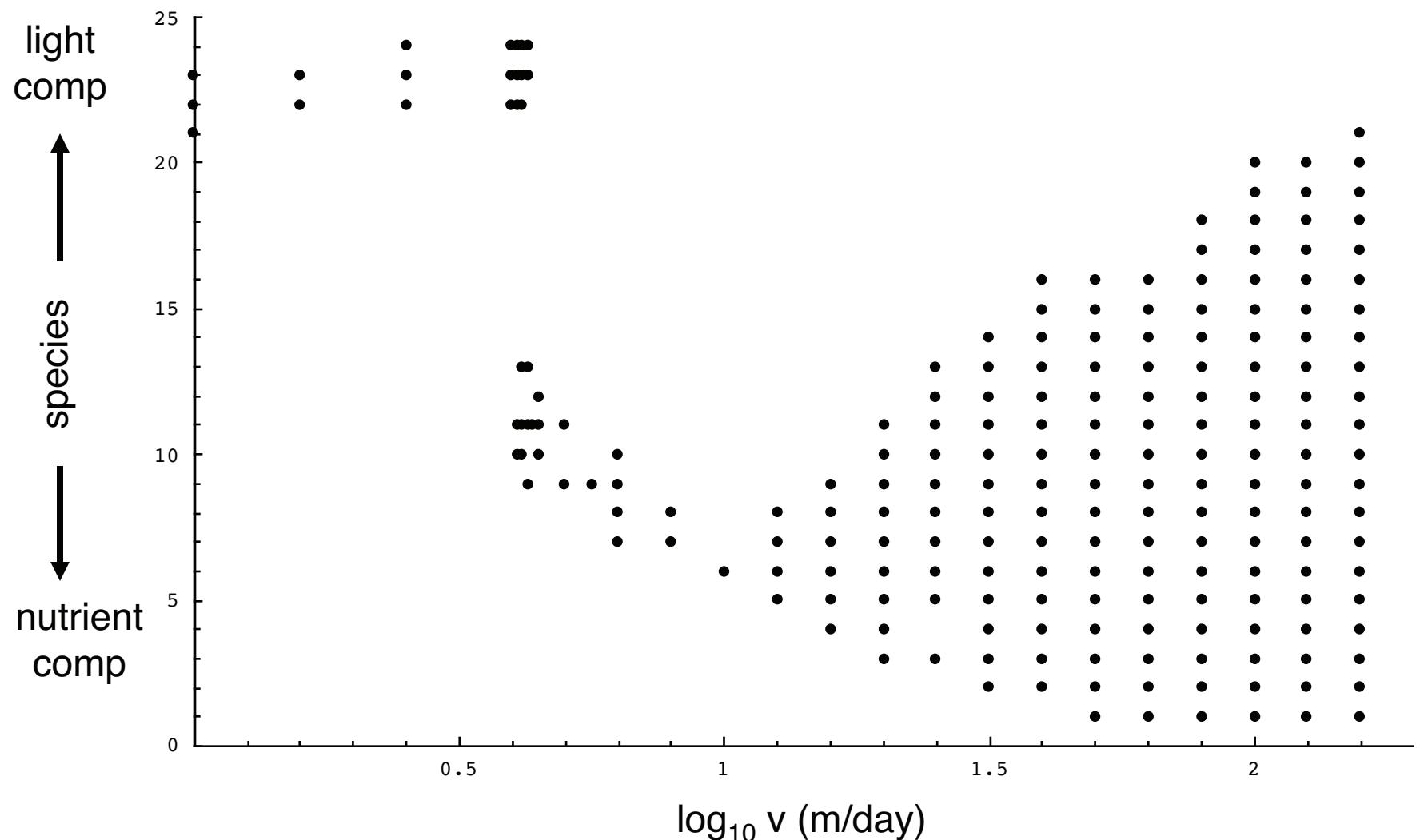
Multiple competitors



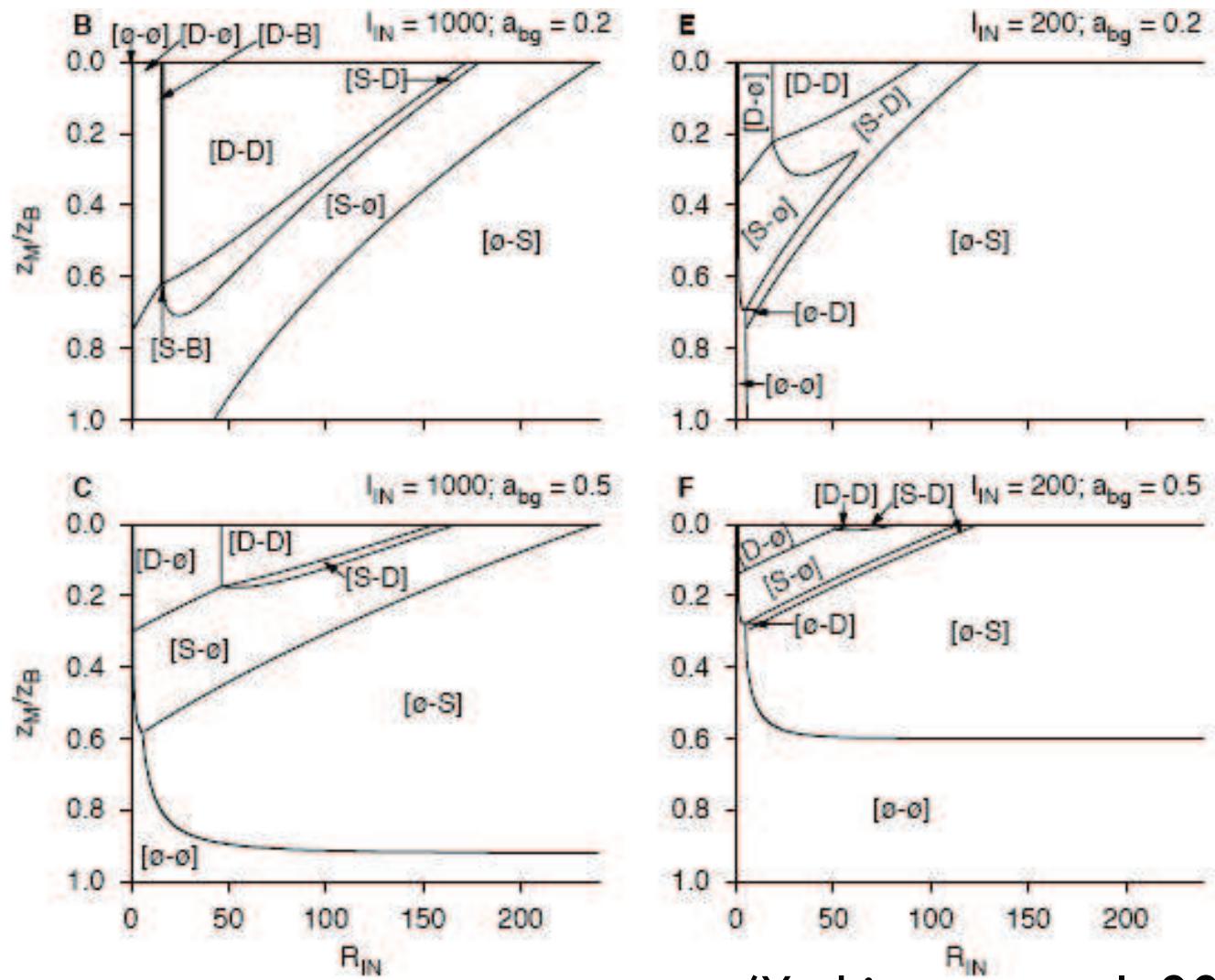
Multiple competitors



Effect of Swimming Ability

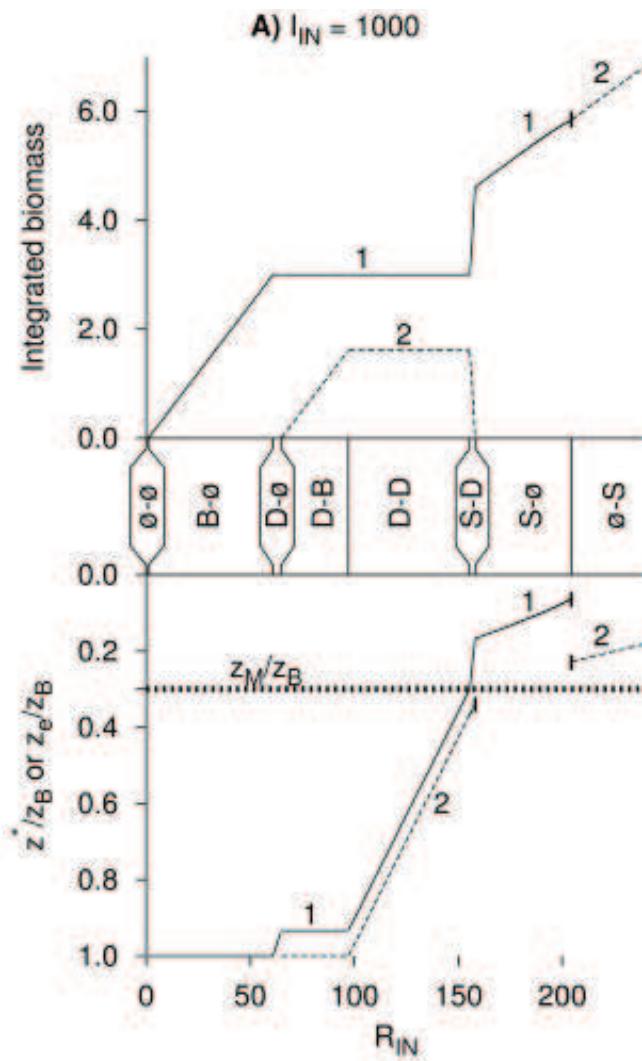


Two competitors, stratified



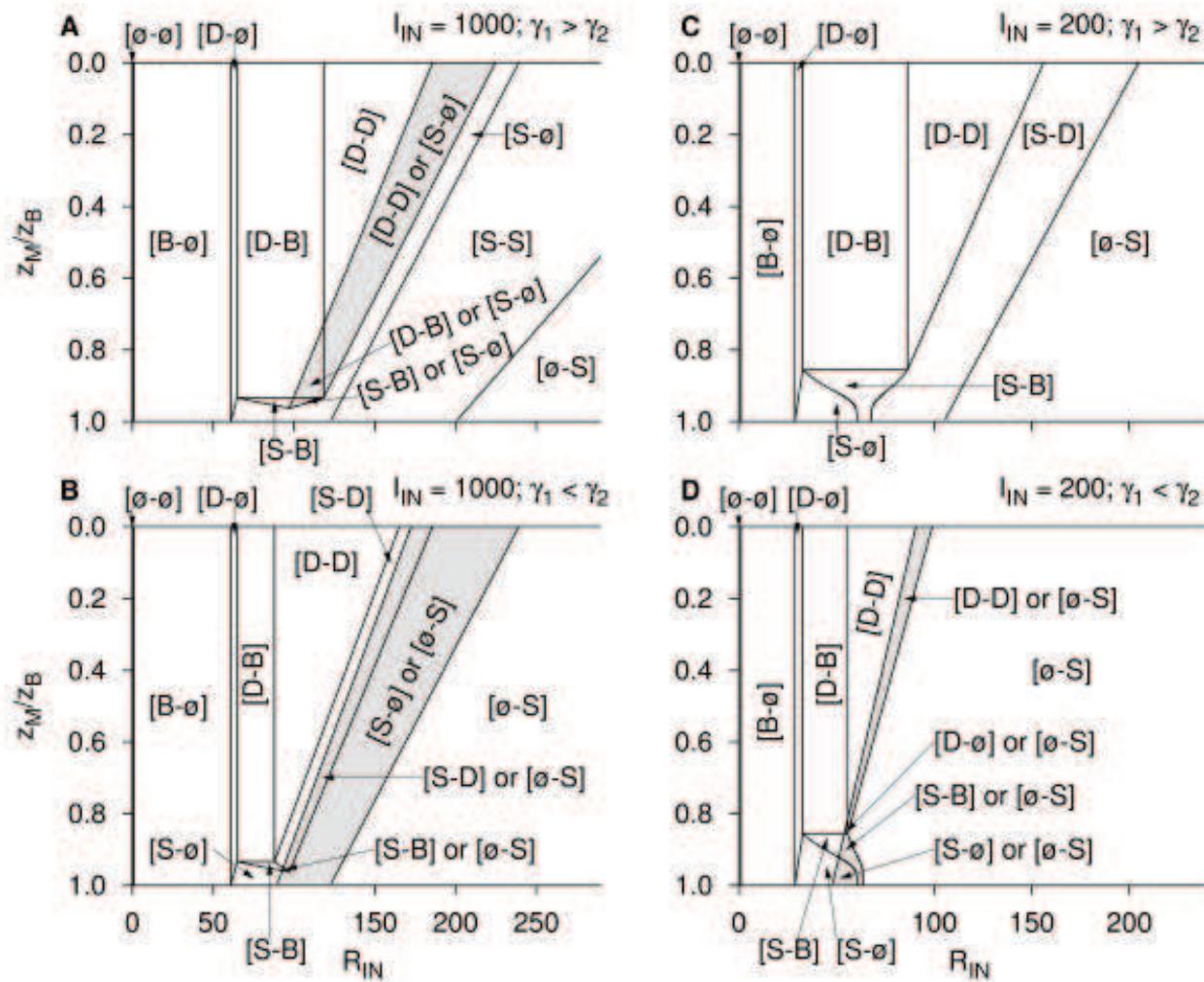
(Yoshiyama et al. 2009 Am Nat)

Two competitors, stratified



(Yoshiyama et al. 2009 Am Nat)

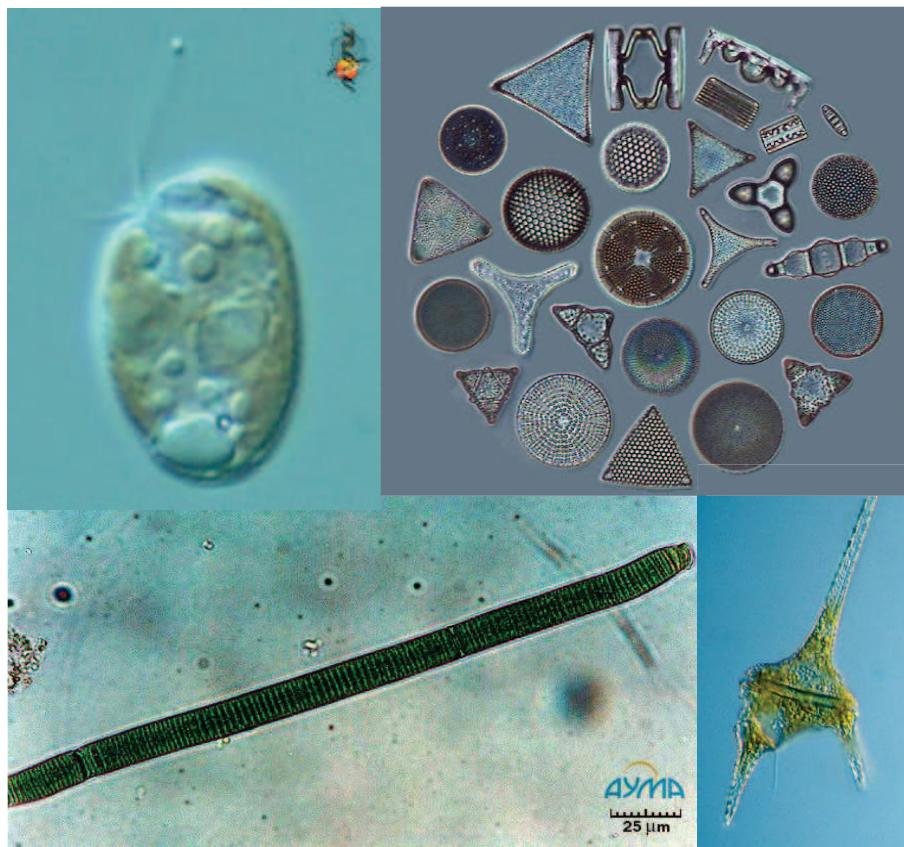
Two competitors, stratified



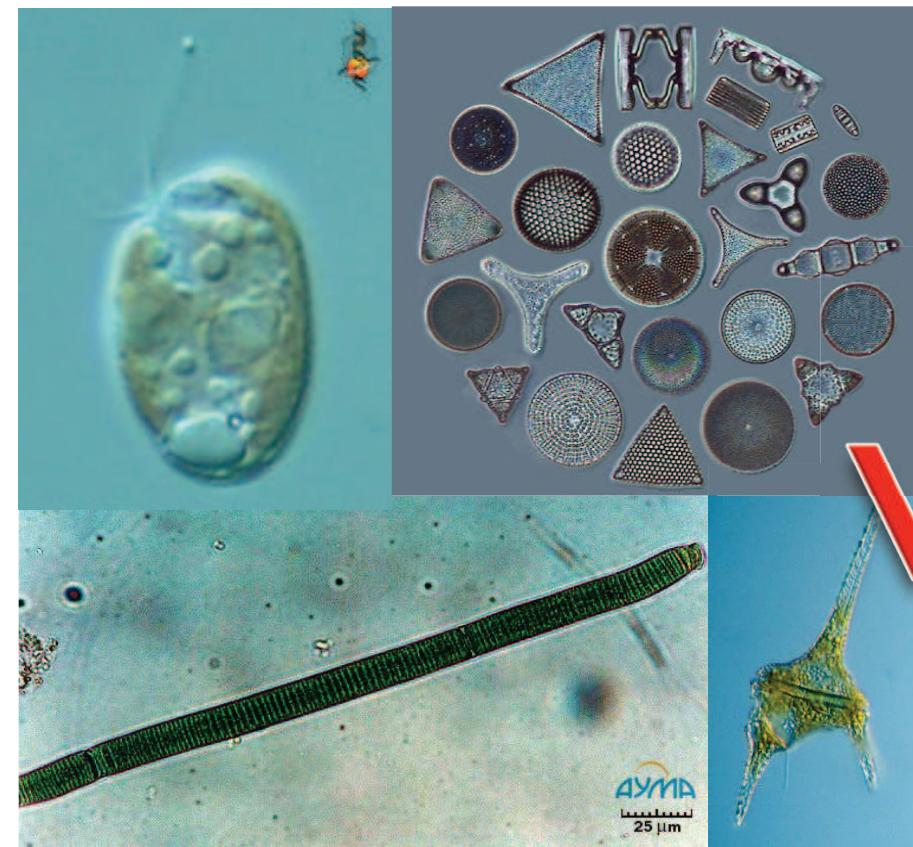
Conclusions: Multiple Competitors



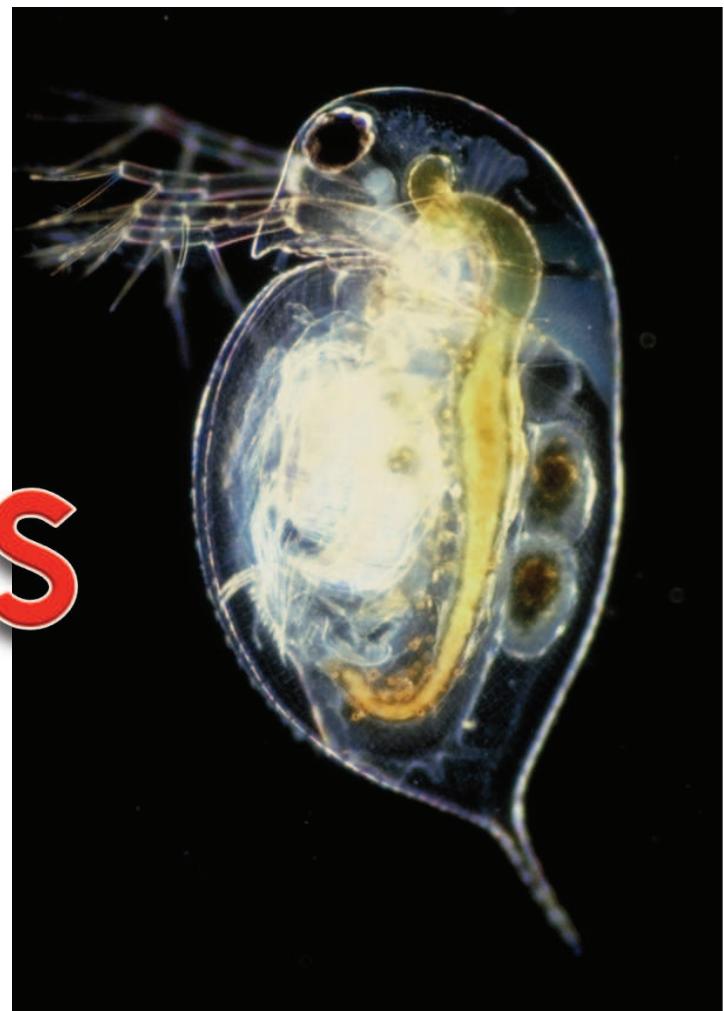
- No limit to diversity if all species stay in water column
- Coexistence due to spatial heterogeneity requires ability to select habitat (or a deep water column?)
- Two distinct, disjunct niches of low-light adapted species in stratified water columns
- Various potential types of founder control in stratified water columns



AYMA
25 μ m



VS





Dennis Ruppe
SUNY Geneseo

b – phytoplankton biomass



$$\frac{\partial b}{\partial t} = gb + D \frac{\partial^2 b}{\partial z^2} + \frac{\partial}{\partial z} \left(v \left(\frac{\partial g}{\partial z} \right) b \right)$$

$$= [\text{growth - loss}] + \begin{bmatrix} \text{passive} \\ \text{movement} \end{bmatrix} + \begin{bmatrix} \text{active} \\ \text{movement} \end{bmatrix}$$

$$g = \min(f_R(R), f_I(I)) - m - f_b(b)Z/b$$

(Ruppe et al. *in prep.*)

Z – zooplankton biomass



$$\frac{\partial Z}{\partial t} = g_Z Z + D \frac{\partial^2 Z}{\partial z^2} + \frac{\partial}{\partial z} \left(v_Z \left(\frac{\partial g_Z}{\partial z} \right) Z \right)$$

$$= [\text{growth} - \text{loss}] + \begin{bmatrix} \text{passive} \\ \text{movement} \end{bmatrix} + \begin{bmatrix} \text{active} \\ \text{movement} \end{bmatrix}$$

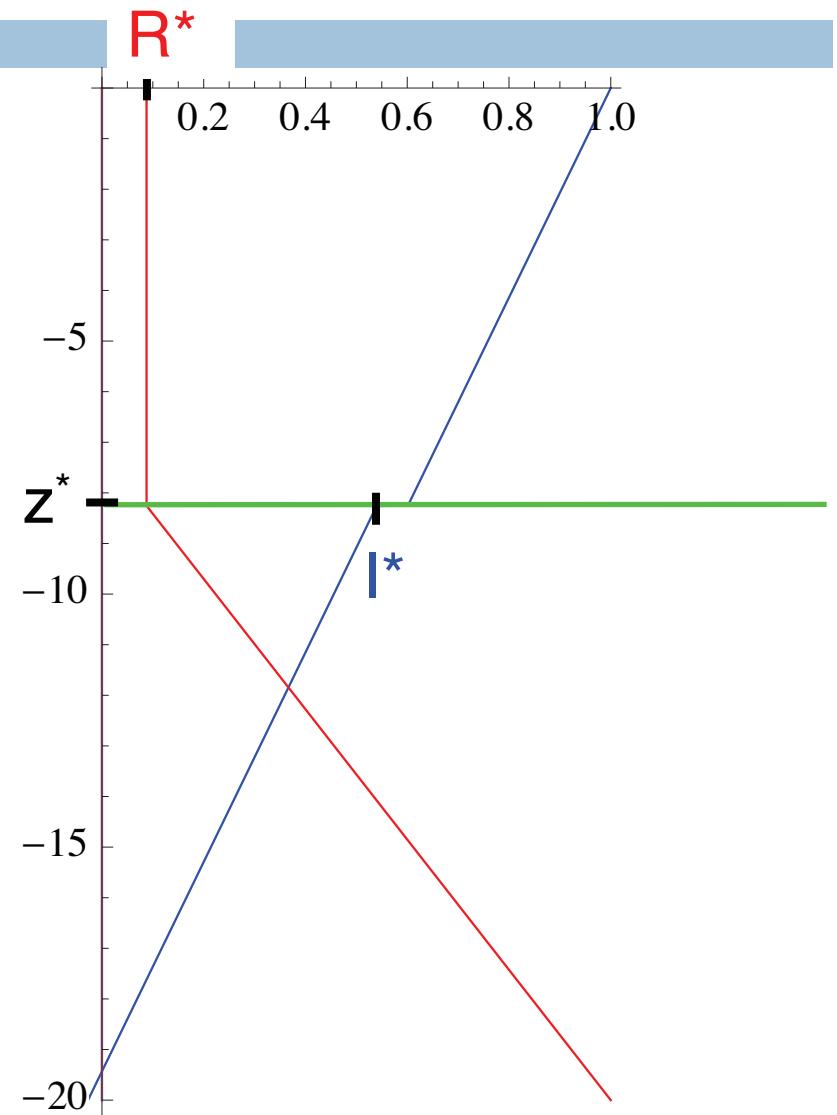
$$g_Z = ef_b(b) - m_Z$$

(Ruppe et al. *in prep.*)

Without zooplankton



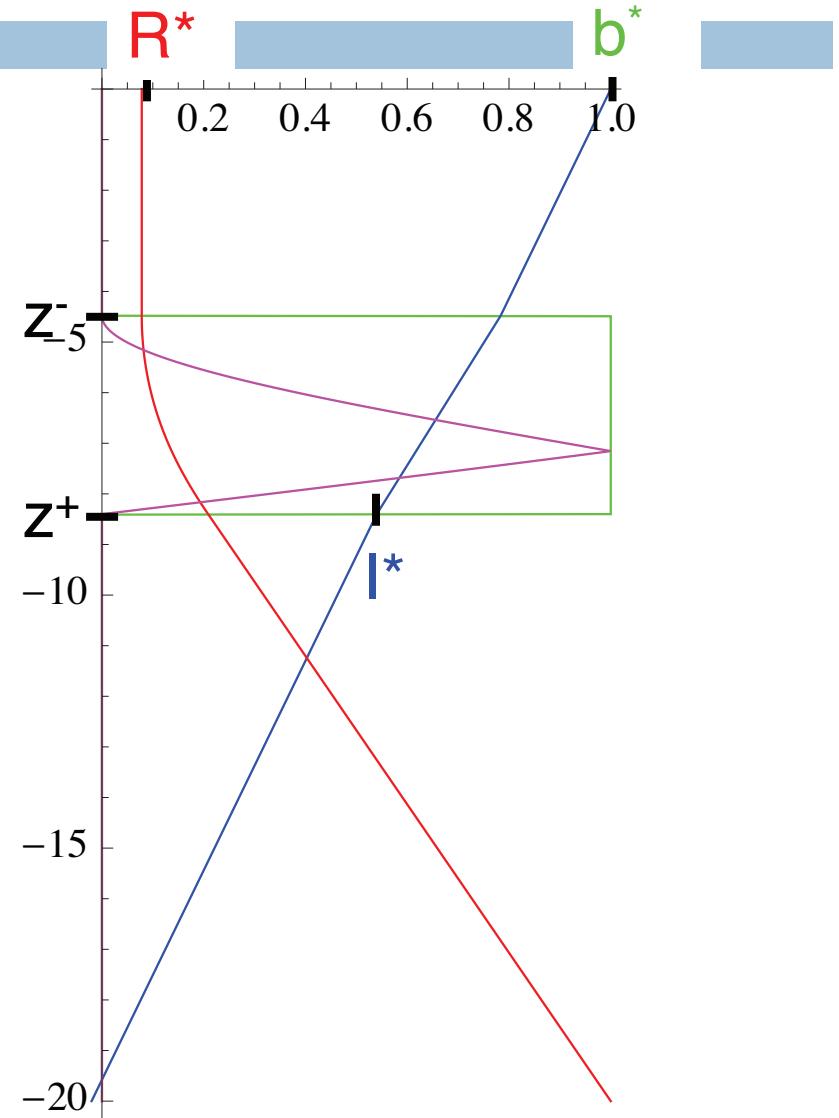
- phytoplankton
- nutrient
- In light



With zooplankton



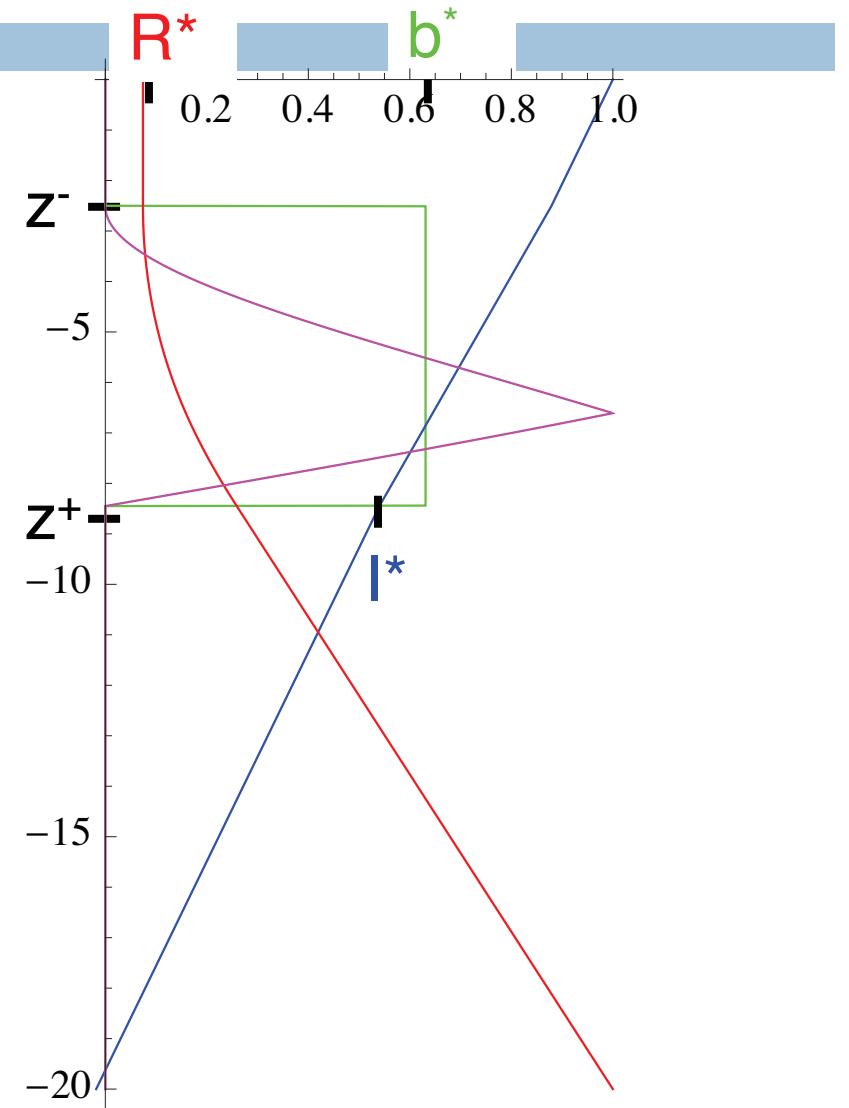
- zooplankton
- phytoplankton
- nutrient
- In light



With zooplankton (more vicious)



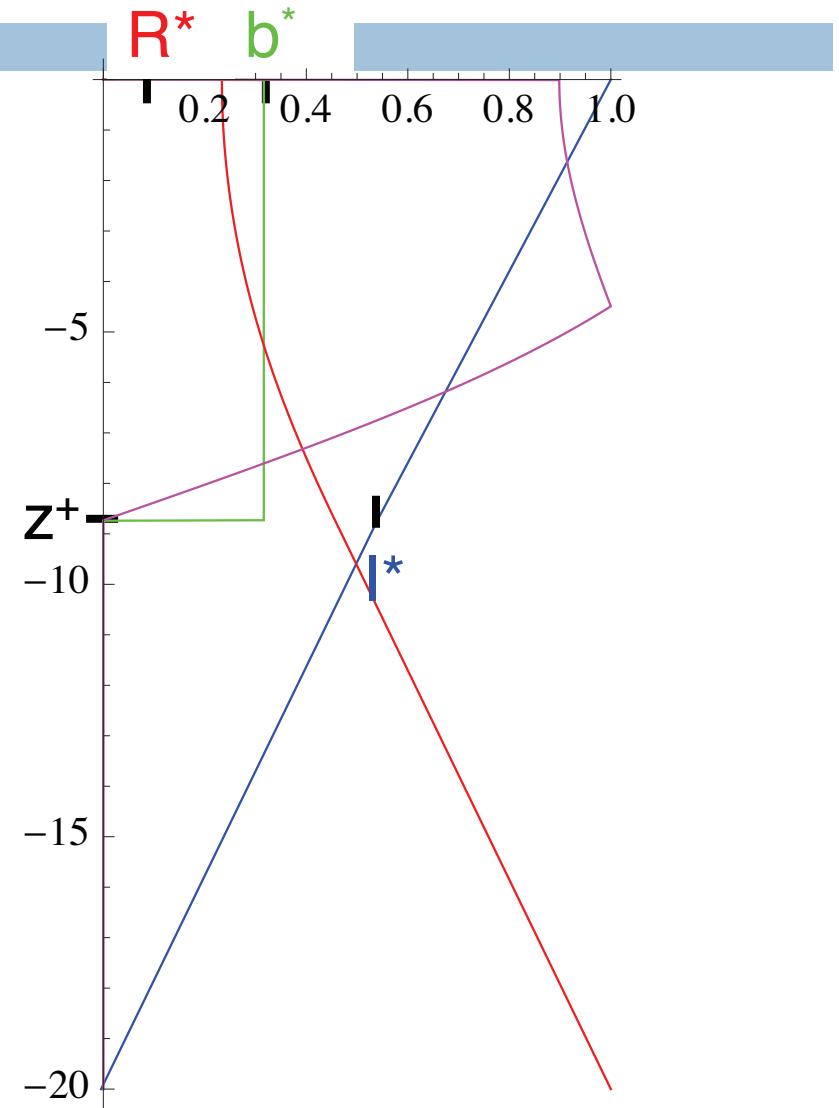
- zooplankton
- phytoplankton
- nutrient
- In light



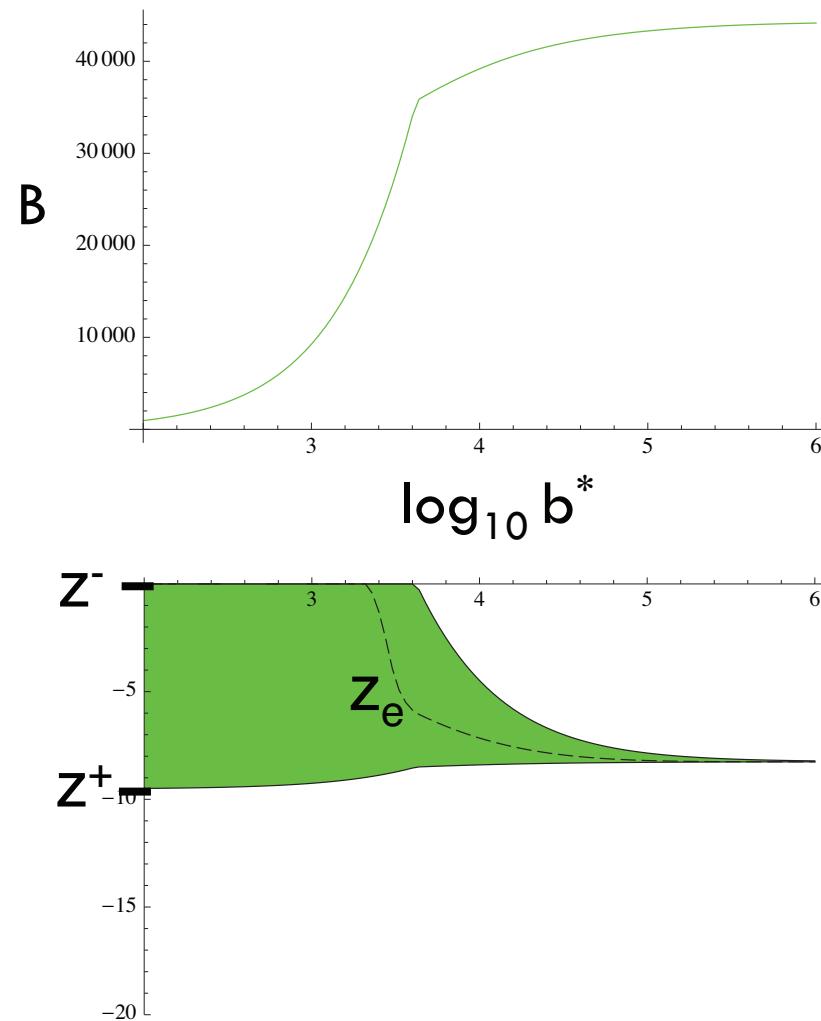
With zooplankton (even more vicious)



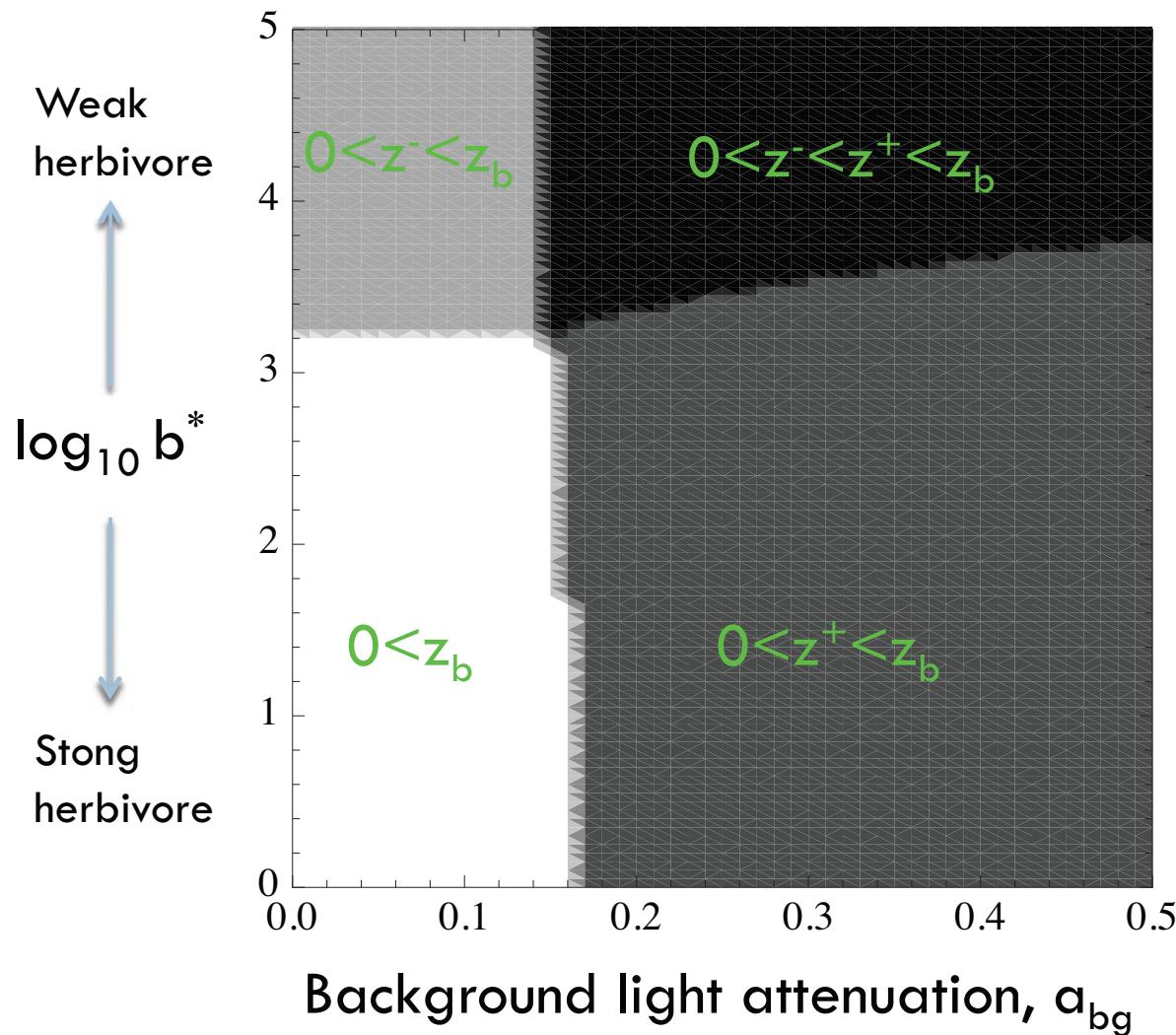
- zooplankton
- phytoplankton
- nutrient
- In light



Along a gradient of herbivore strength



Overview of outcomes



Conclusions: Plant-Herbivore



- Zooplankton grazers lead to thicker phytoplankton layers, with uniform density within
- Increased strength of herbivory has little effect on integrated phytoplankton biomass until layer becomes spatially constrained
- Four qualitative patterns of phytoplankton distribution
- Zooplankton abundance matches phytoplankton growth rate

Future directions

- Rigorous mathematics

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Vol. 40, No. 4, pp. 1439–1460

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CONCENTRATION PHENOMENA IN A NONLOCAL QUASI-LINEAR PROBLEM MODELLING PHYTOPLANKTON I: EXISTENCE*

YIHONG DU[†] AND SZE-BI HSU[‡]

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Vol. 40, No. 4, pp. 1443–1470

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CONCENTRATION PHENOMENA IN A NONLOCAL QUASI-LINEAR PROBLEM MODELLING PHYTOPLANKTON II: LIMITING PROFILE*

YIHONG DU[†] AND SZE-BI HSU[‡]

- Adaptive dynamics on
 - light-nutrient competitive ability
 - swimming speed
- Migration as a strategy

Acknowledgments



- Collaborators

- Kohei Yoshiyama
- Jarad Mellard
- Dennis Ruppe

- Funding sources

- NSF DEB-0610531, DEB-0845825
- James S McDonnell Foundation