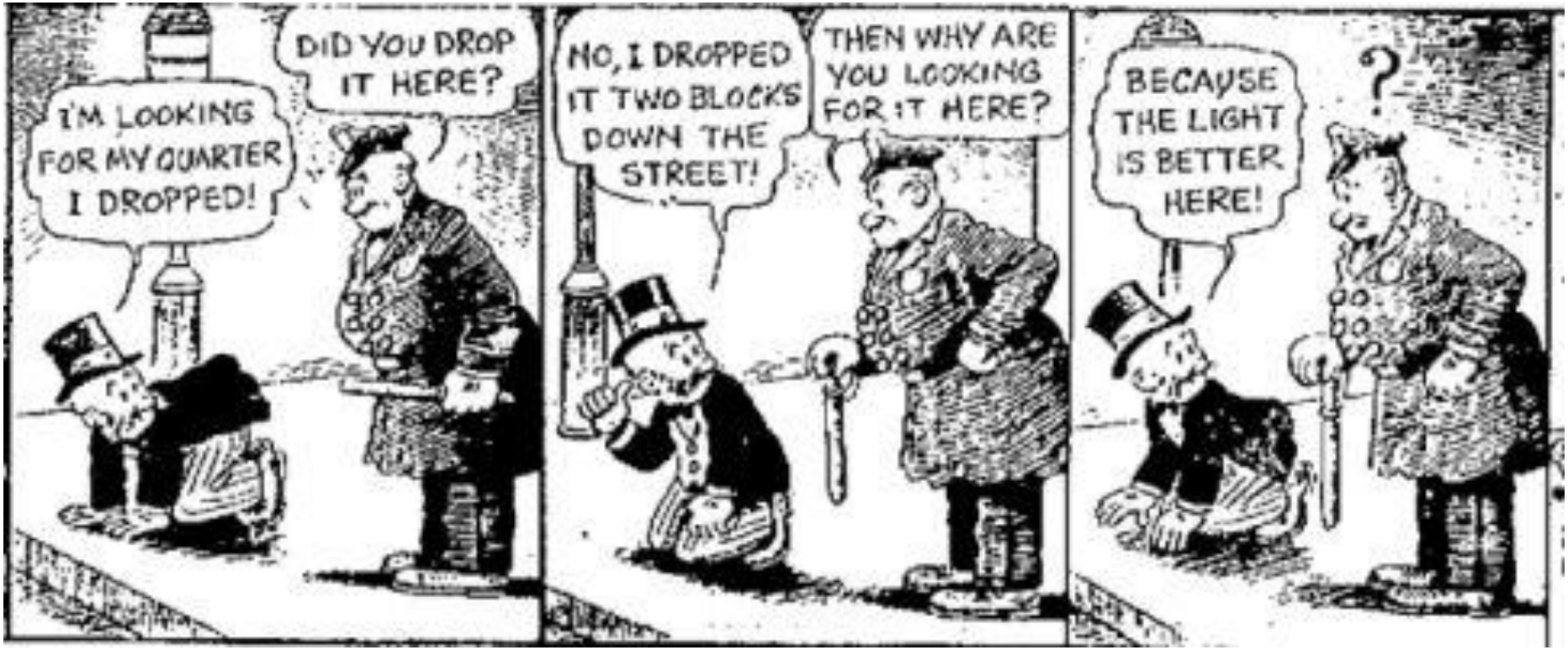
Ecological and physical processes underlying *some* phytoplankton blooms

Emmanuel Boss (in close collaboration with M. Behrenfeld)



Today I will:

1. Introduce a simple 1&0-D framework to describe upper-ocean phytoplankton dynamics.

2. Show that autonomous observations of a spring bloom in the NA are not consistent with stratification being necessary to initiate the bloom.

3. Speculate about other processes needed to explain the observations.

4. Discuss the notion of quasi-steady-state dynamics and their implications for constraining rate processes.

Denoting by *p* the phytoplankton concentration in the upper ocean's mixed layer [e.g. mg Chl m^{-3}]:

$$\frac{\partial p}{\partial t} + w_s \frac{\partial p}{\partial z} = \mu p + \frac{\partial}{\partial z}\left(k \frac{\partial p}{\partial z}\right) - loss$$

We will concentrate on the fall-winter-spring transition,
Hence we will assume:

a. The mixed-layer is a mixing layer: except for light all other parameters are constant in the mixed layer. $\tau_{mixing} << \tau_{ecology}$
b. When deepening, ML entrain water with no phytoplankton (concentration per m^2 is conserved).
c. When shallowing, ML concentration per m^3 is conserved.

Denoting by P as the integrated phytoplankton concentration in the upper ocean's mixed layer [e.g. mg Chl m^{-2}]:

$$\frac{dP}{dt} = P\bar{m} - \frac{mP + w_+P + w_sP}{H_{ML}} - Loss$$

Sverdrup's simplification:

$$\frac{dP}{dt} = P\left(\bar{m} - loss\right)$$

For phytoplankton in the ML to accumulate: $\bar{m} > loss$

On Conditions for the Vernal Blooming of Phytoplankton.

By

H. U. Sverdrup,
Norsk Polarinstitutt, Oslo.

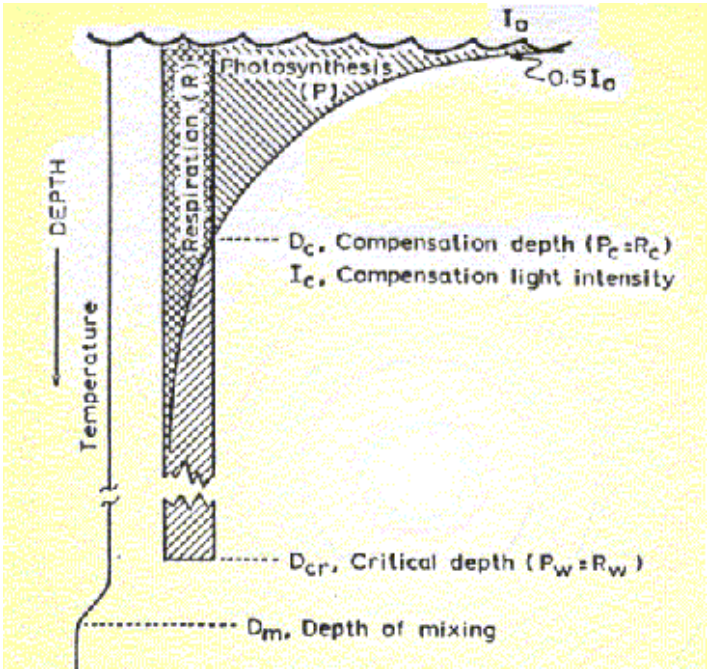
Sverdrup, H. U. 1953. *J. Cons. Perm. Int. Explor. Mer*. **18:** 287-295.

$$\frac{\partial P}{\partial t} = \left(a\bar{I} - loss\right)P, \qquad a, loss - const.$$

'Blooming': $\partial P/\partial t > 0$.

In the oceans: $I(z) = I_0 e^{-kz}$

When phytoplankton are mixed too deep they cannot bloom.



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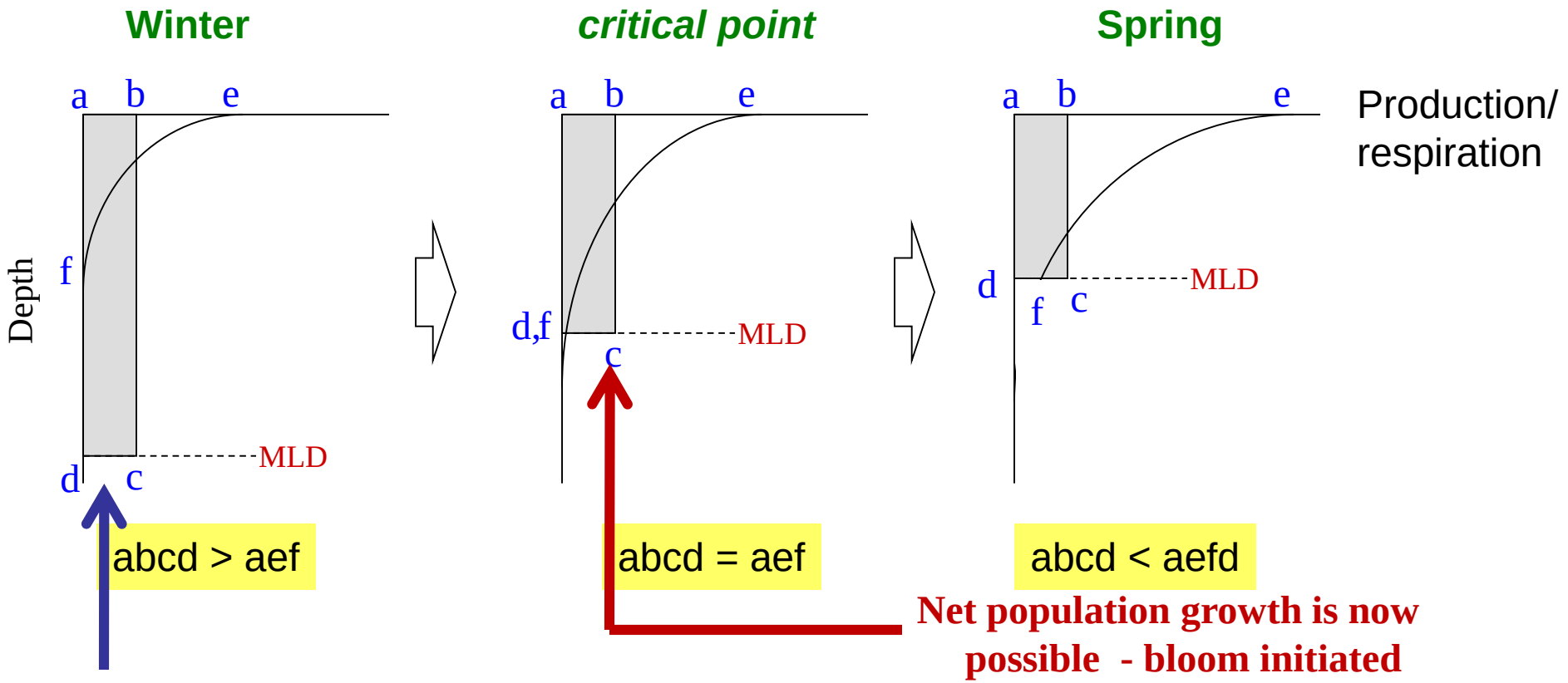
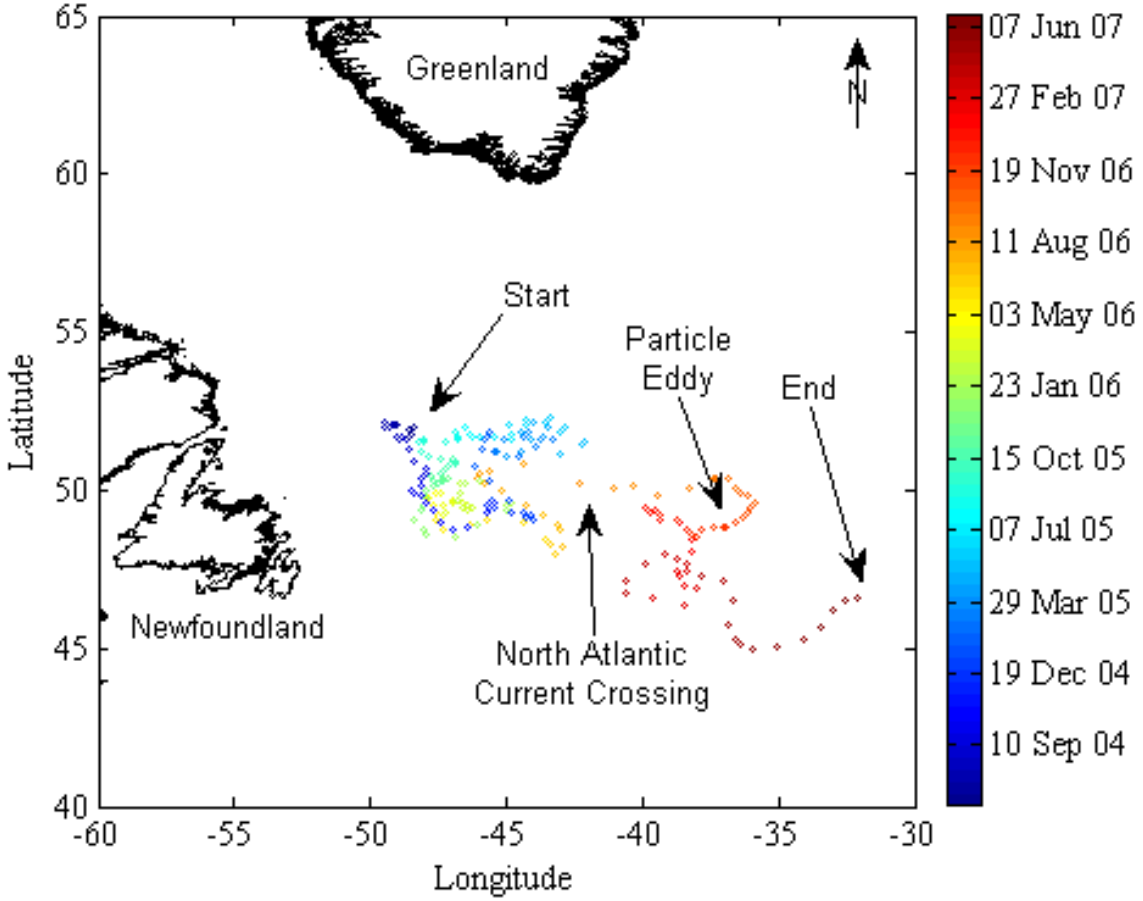
•The Critical Depth Hypothesis attempts to explain what *initiates* a vernal (spring) bloom (not what controls its magnitude or duration).



In-situ observations of phytoplankton bloom



- Coverage under clouds
- Vertically resolved Chlorophyll and Phytoplankton Carbon (b_{bp})
- Accounting for entrainment & detrainment
- 3 indices of MLD
- Advection issues

Boss et al., 2008

Introduction to optical properties (demo)

1. Absorption

2. Scattering (+backscattering)

3. Fluorescence

Functions of concentration, wavelengths, size, shape, composition (physiology) & packaging.

Direct and inverse approaches in optics:

e.g. Given particles → scattering coef.

'well' posed

Scattering coef. → [particles]

'ill' posed

Bohren and Huffman, 1987

If so complicated, why should we use it?

If so complicated, why should we use it?

Answer: given the large dynamic range of concentrations of biogeochemical material (in time and space) relatively large uncertainties (e.g. +/- 50%) can be tolerated (but watch out for biases).

List of optical proxies:

Temperature –NIR radiance.

Nitrate, Sulphides – UV absorption.

DOM, Hydrocarbons – fluorescence (UV-ex, VIS-em), absorption.

PM, POC, C_{phyto} – attenuation, scattering, ocean color.

Phytoplankton pigments – fluorescence, absorption, ocean color.

Particulate size distribution – spectrum of attenuation and scattering, near forward scattering, ocean color.

Particulate composition (index of refraction) – back-scattering to scattering ratio, degree of polarization.

Accumulation begins before stratification at time when light conditions are deteriorating (MLD deepens faster then days are getting longer).

Note the role of entrainment in reducing the upper ocean's concentration per m^3 while it starts increasing per m^2.

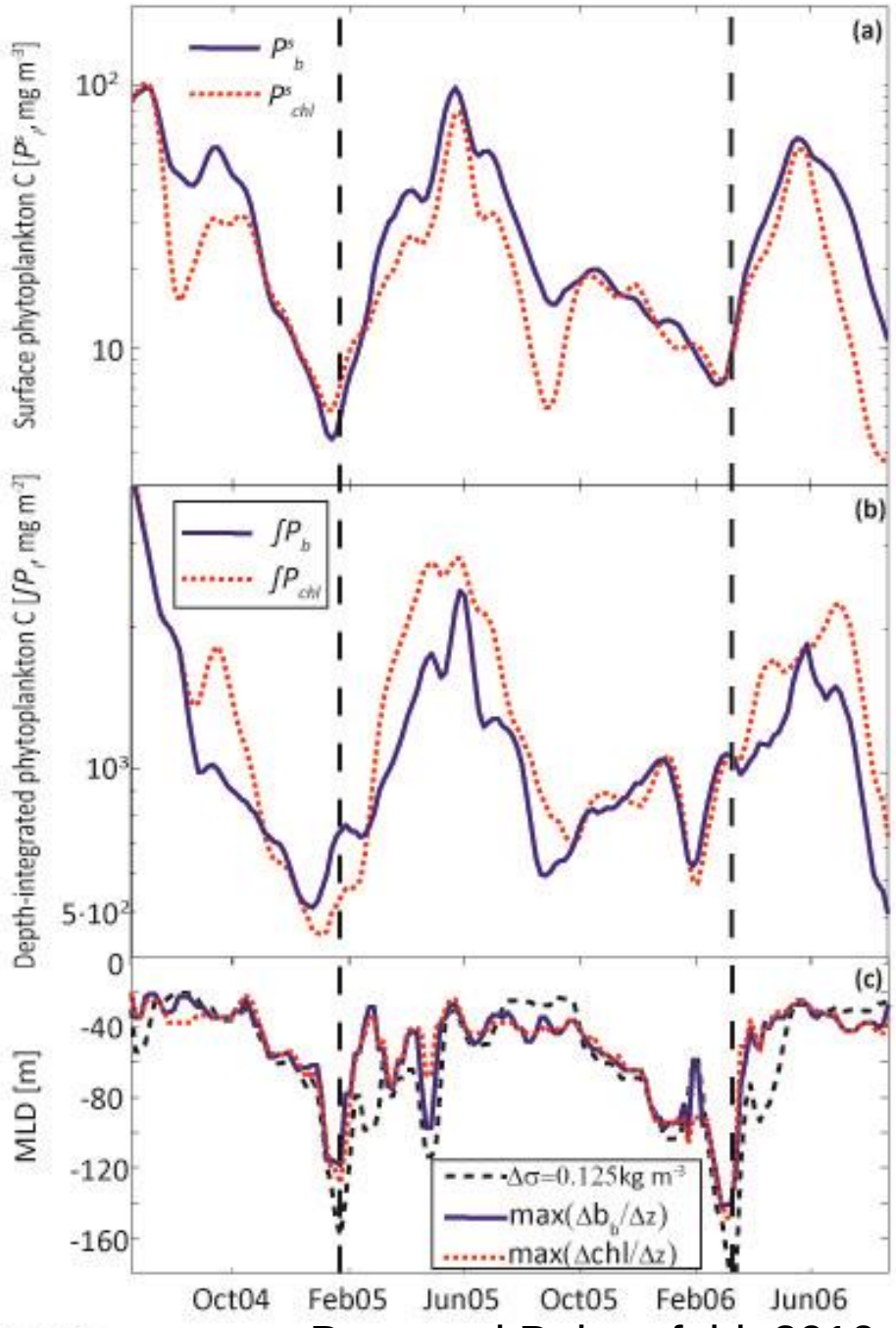


Figure 2.

Boss and Behrenfeld, 2010

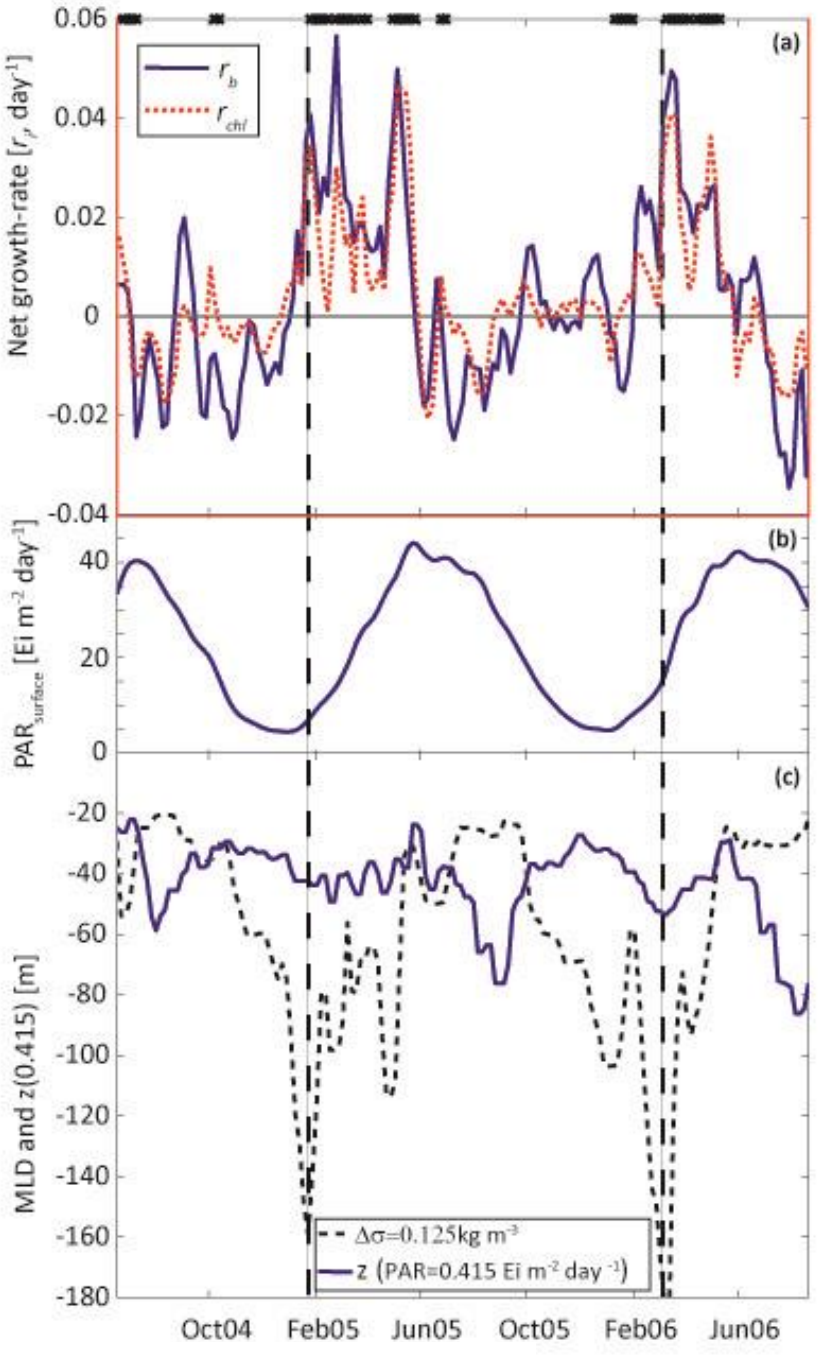
Two annual cycles:

Net growth is positive even when mixing is deepest and light is least.

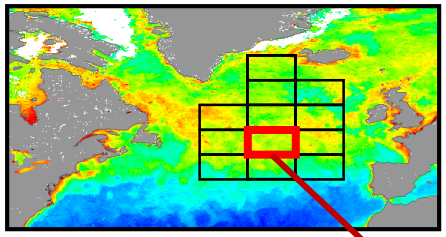
$$r \equiv \frac{d \ln P}{dt}$$

Computed from depth-integrated biomass down to max(MLD, z_{eu}), except when MLD shallows but is deeper than z_{eu}.

r=0.02 → doubling every two weeks.

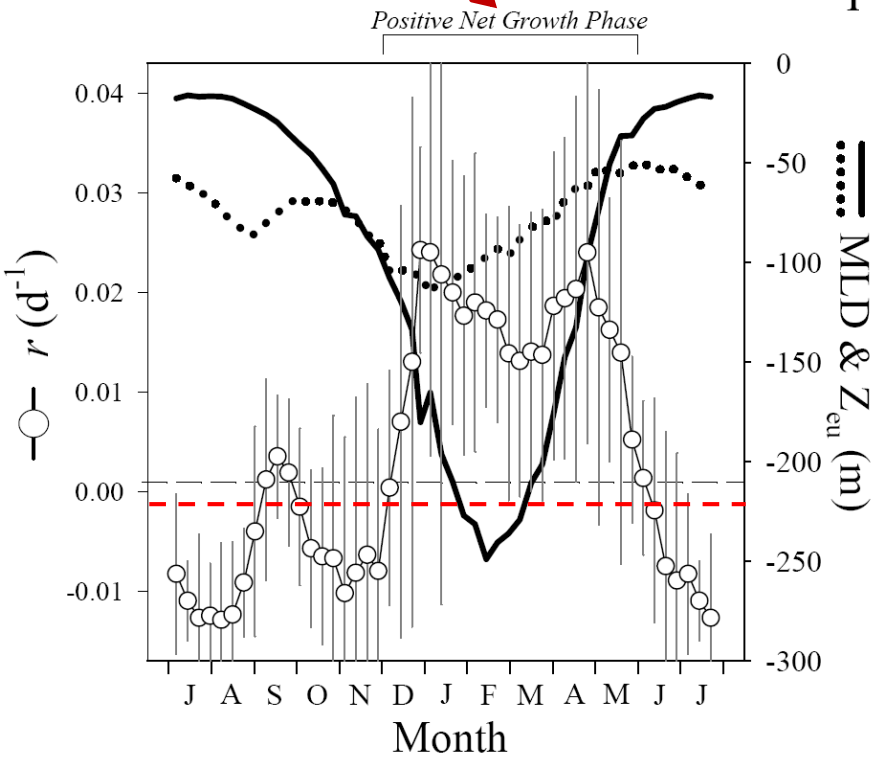


Boss & Behrenfeld, 2010



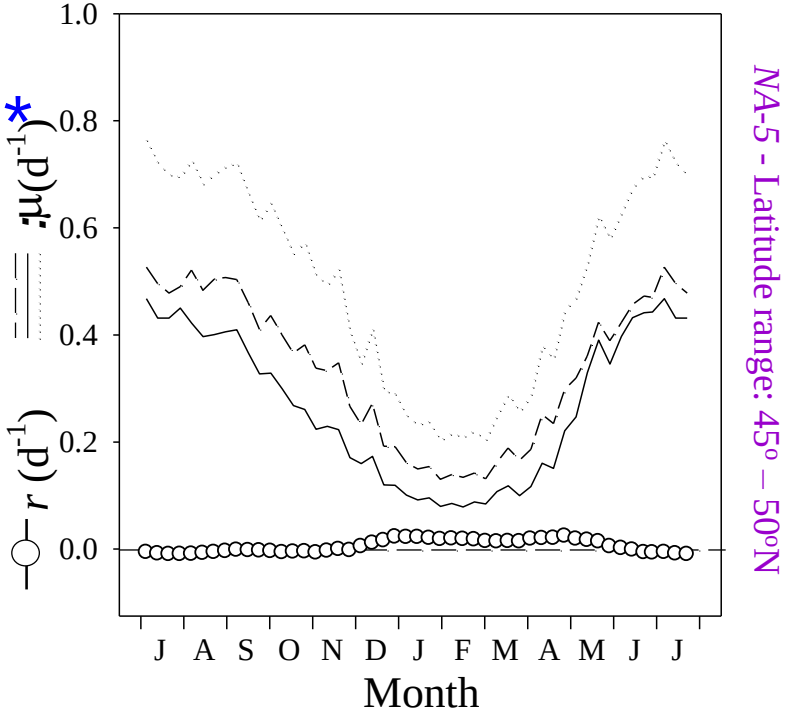
Remote sensing + MLD:
Annual average cycles of net population growth for each bin show similar patterns, with some variations in magnitude of features

* μ = NPP /(MLD<C>)



Shallow

Deep



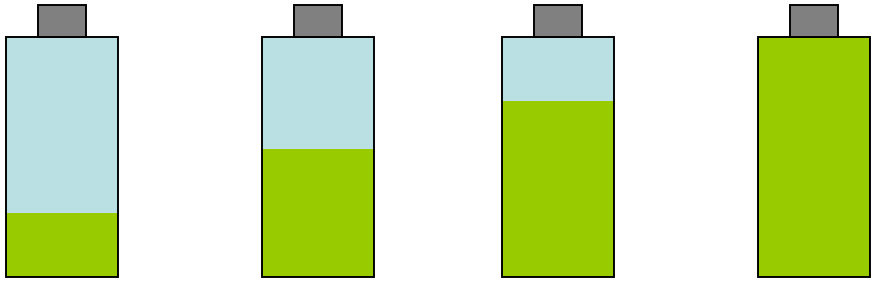
- A net specific growth rate of 0.02 implies approximately 1 division per month
- Typical winter C = 4 – 8 mg m^{-3}, Typical spring C peak = 25 – 70 mg m^{-3}
- NA bloom requires 2 – 4 doublings over 3 - 4 months, or *average r of 0.009 to 0.03 d^{-1}*

Satellite and field data show that phytoplankton biomass starts increasing when environmental conditions are going from bad to worse

And that the net population growth rate is largely inversely related with phytoplankton specific growth rate

…. How is this possible?

Digression: Dilution Experiments



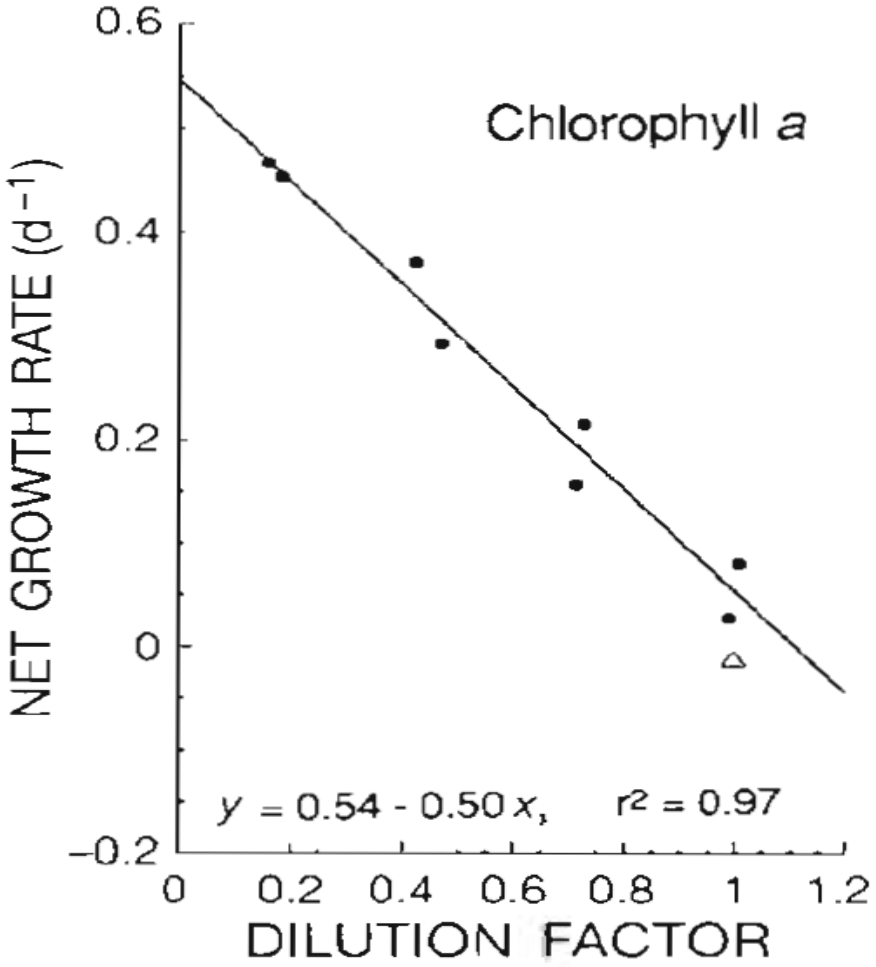
Implies that rate of loss to grazing is density dependent. Rather than Sverdrup's:

$$\frac{\partial P}{\partial t} = (m - r)P$$

Something like:

$$\frac{\partial P}{\partial t} = (m - gH)P$$

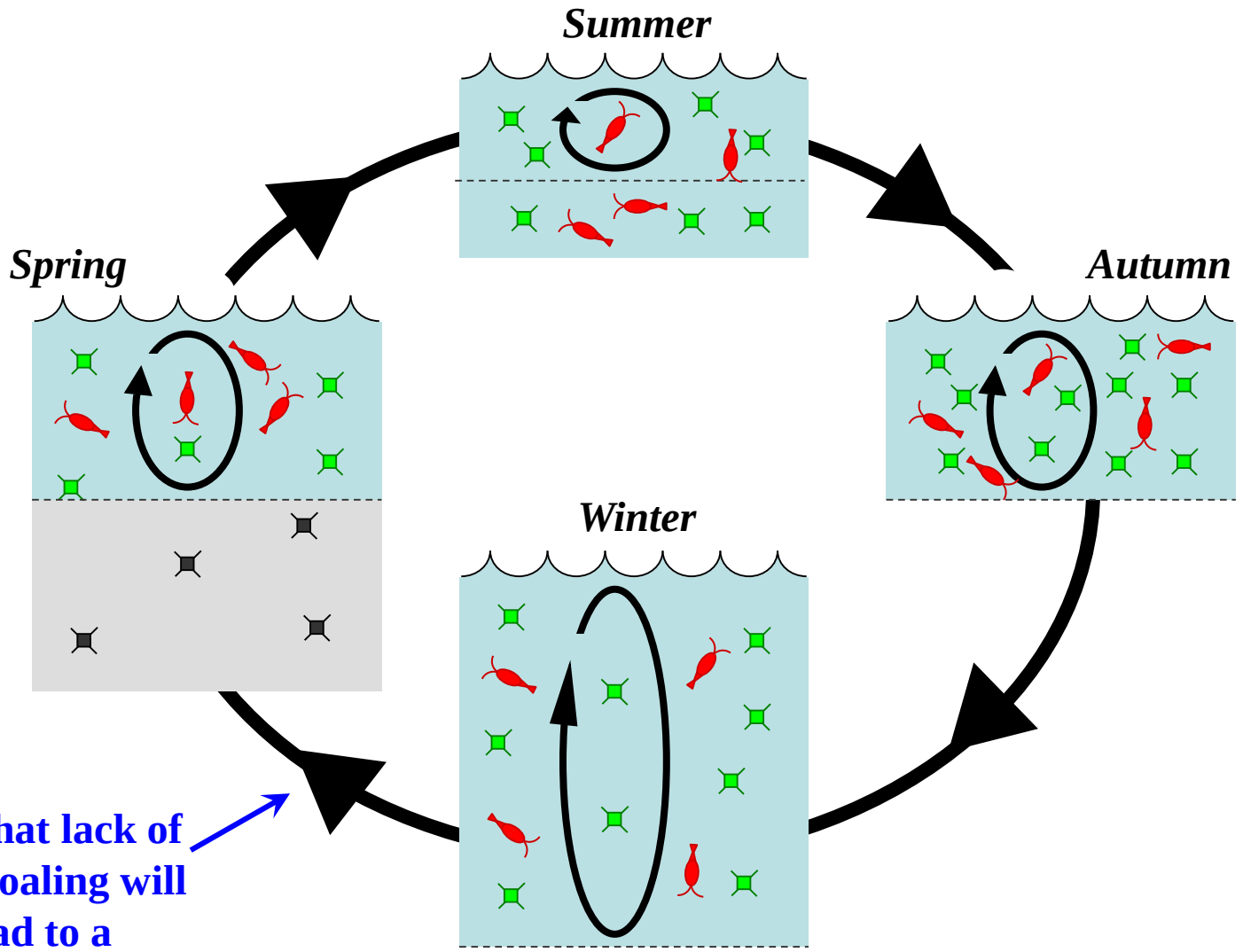
Where H = herbiovres



Landry & Hassett 1982 Mar. Biol. 67, 283-288

Landry et al. 1995 Mar. Ecol. Prog. Ser. 120, 53-63

The ‘Dilution-Recoupling Hypothesis’



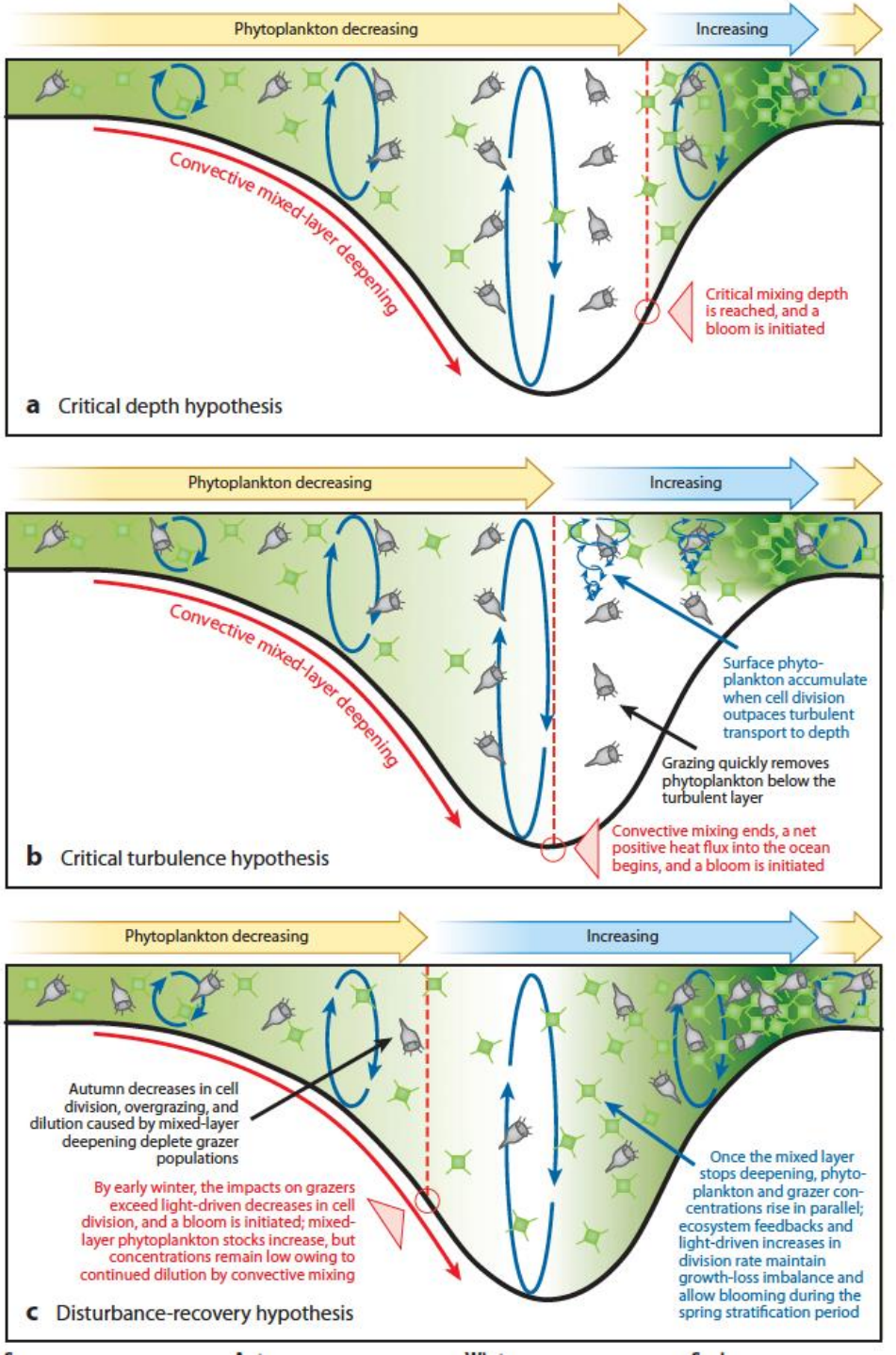
A cartoon view of the competing hypotheses

Role played by physics

Role played by phytoplankton physiology.

Role played by prey-predator interactions

Sensitivity to parametrization in models



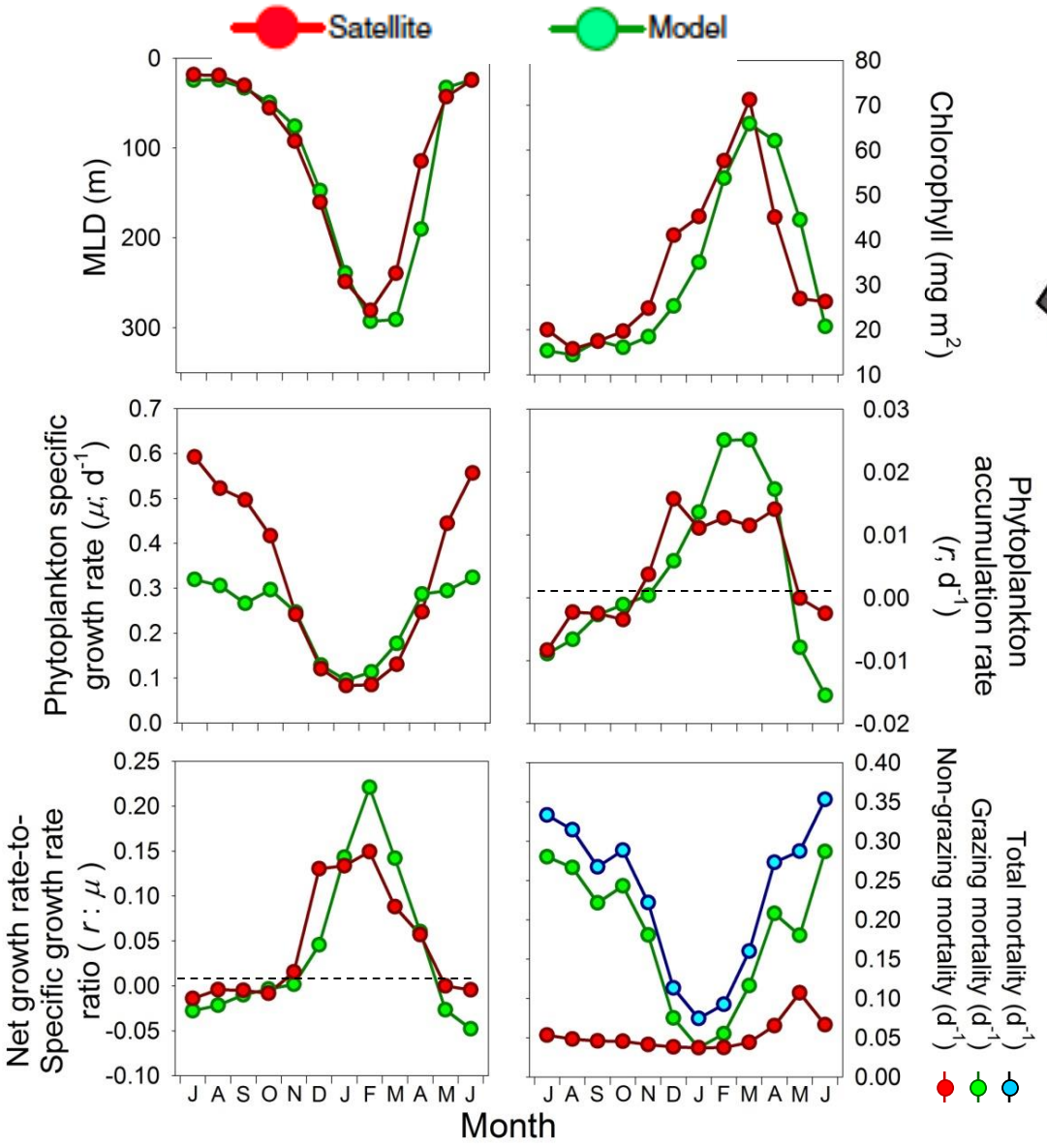
Back to the equation:

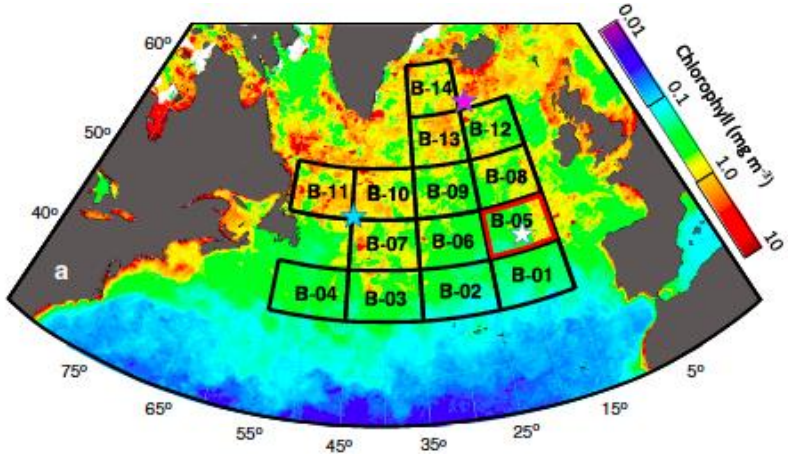
$$\frac{dP}{dt} = P\left(\bar{m} - loss\right)$$

For phytoplankton in the ML to accumulate: $\bar{m} > loss$

Mechanisms that reduce net loss (e.g. dilution, temperature) as well as those that contribute to net growth can cause blooming.

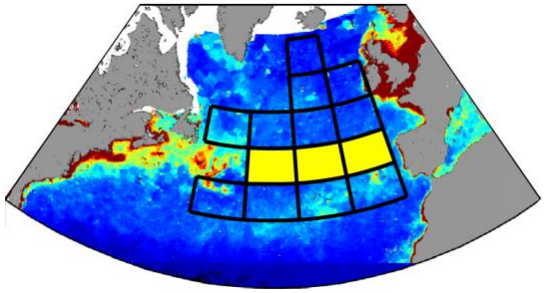
Consistent with results using a global biogeochemical model:

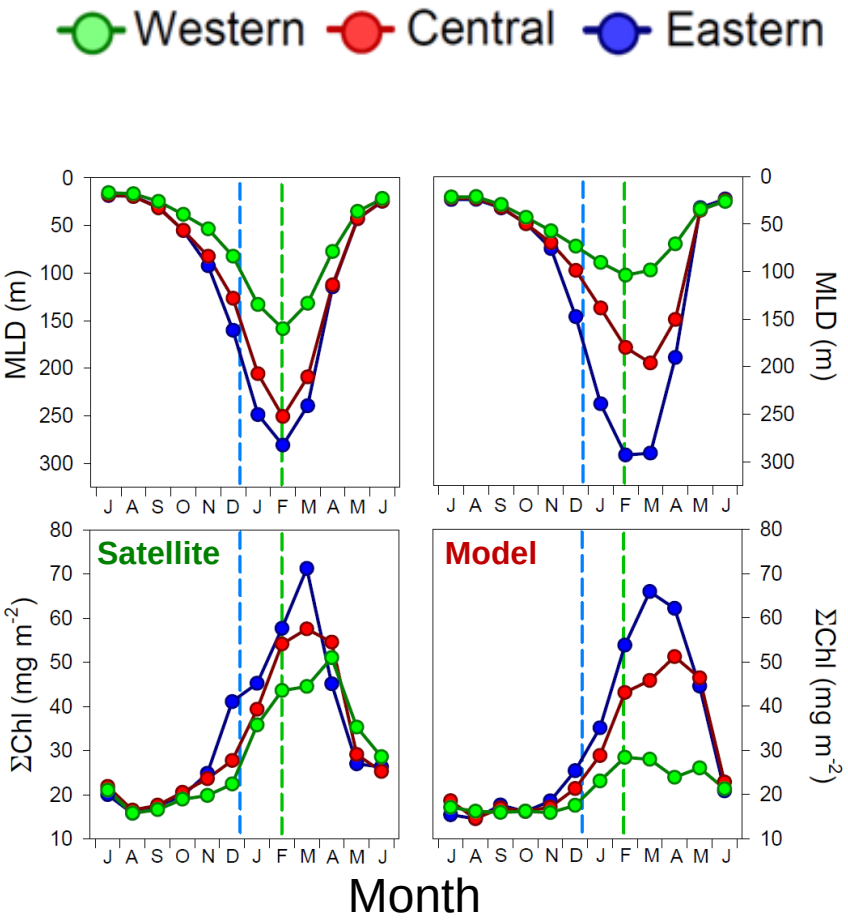


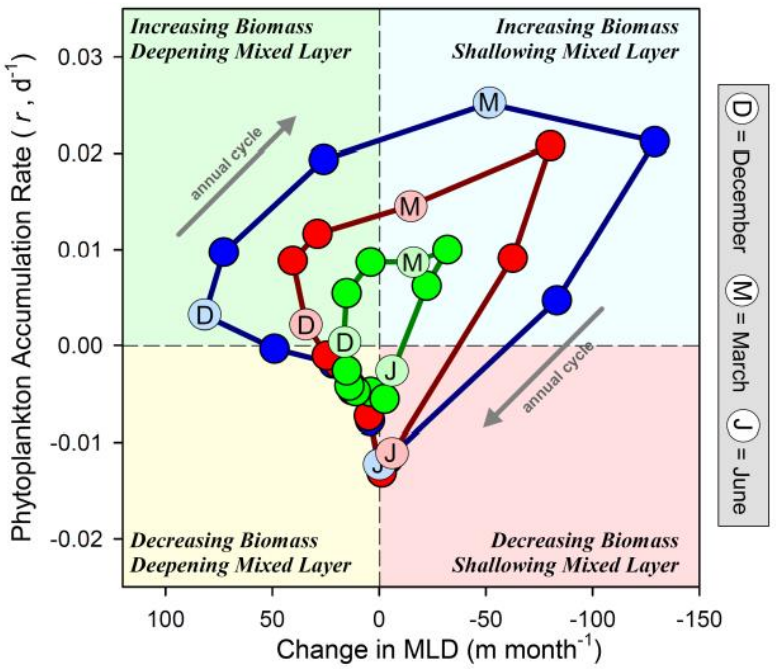


Behrenfeld et al., 2013

Greater disturbances yields greater biomass:



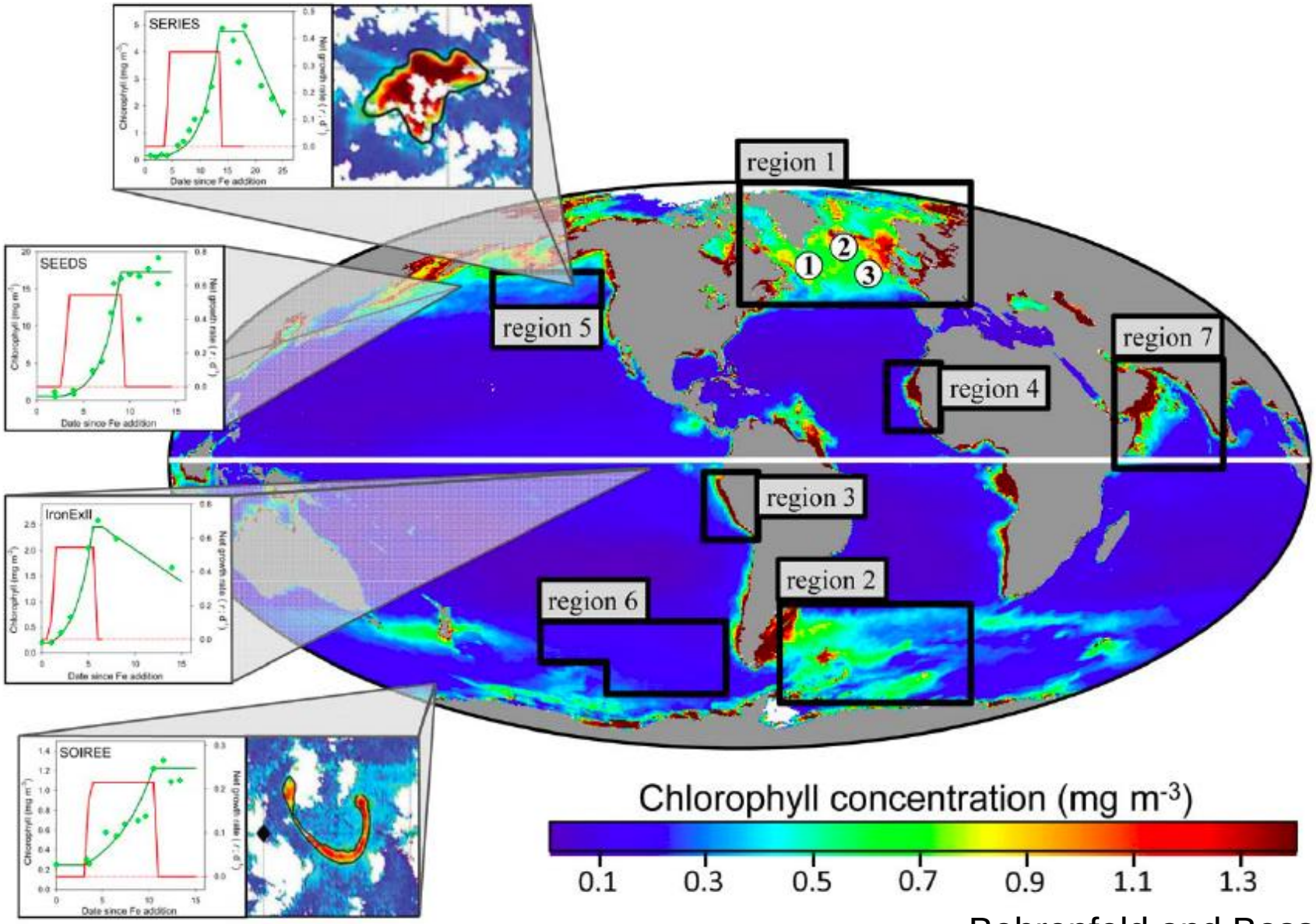




Behrenfeld et al. 2013 *GBC*

Link to climate: MLD and stratification under a warming trend.

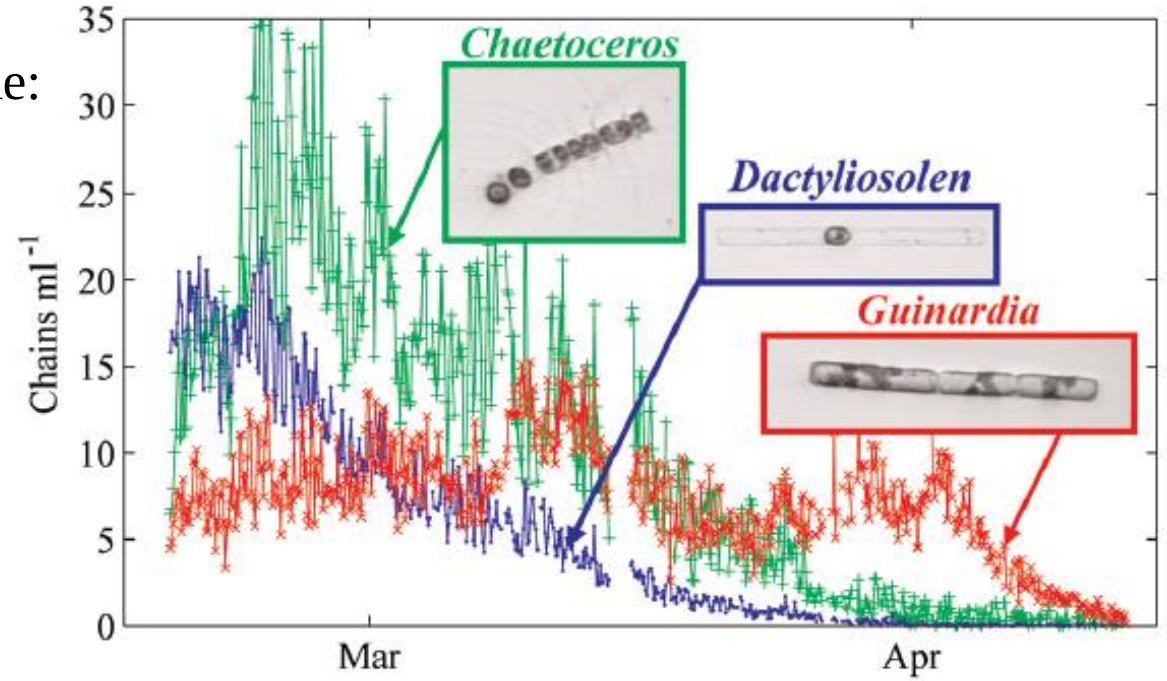
What about man made blooms?



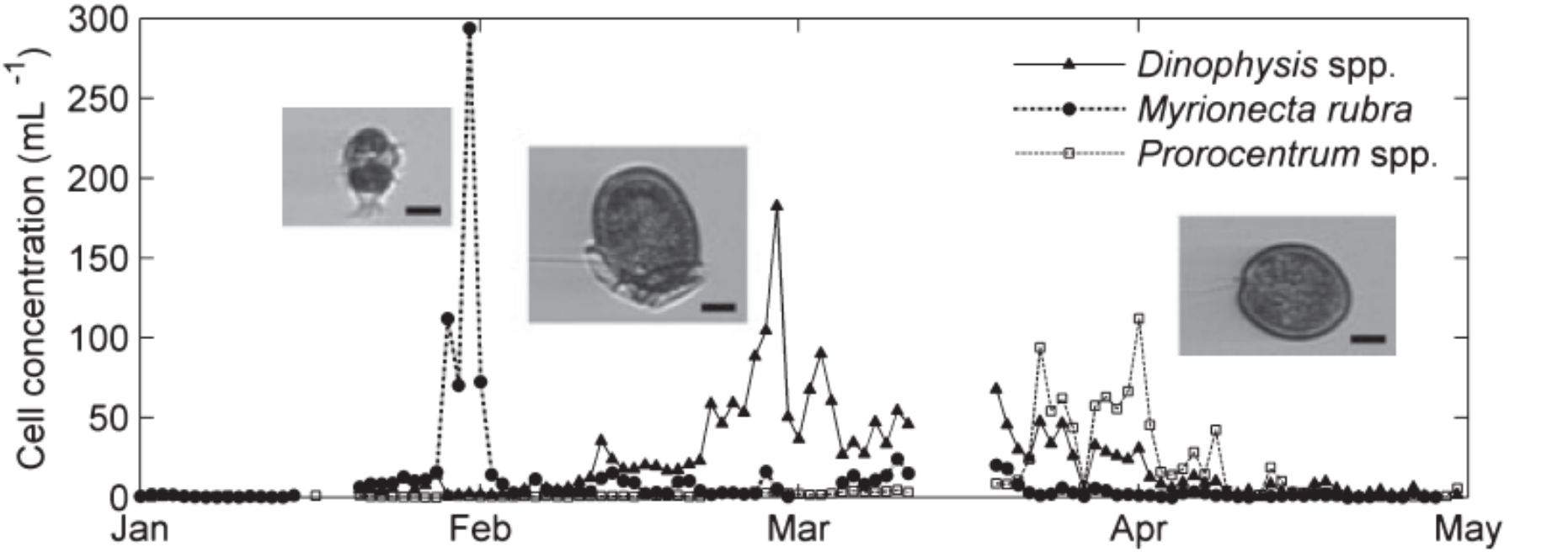
Behrenfeld and Boss, 2014

Not all phytoplankton are the same:

Species dynamics as revealed by automated in-situ microscopes.



Sosik and Olson, 2007



Campbell et al., 2010

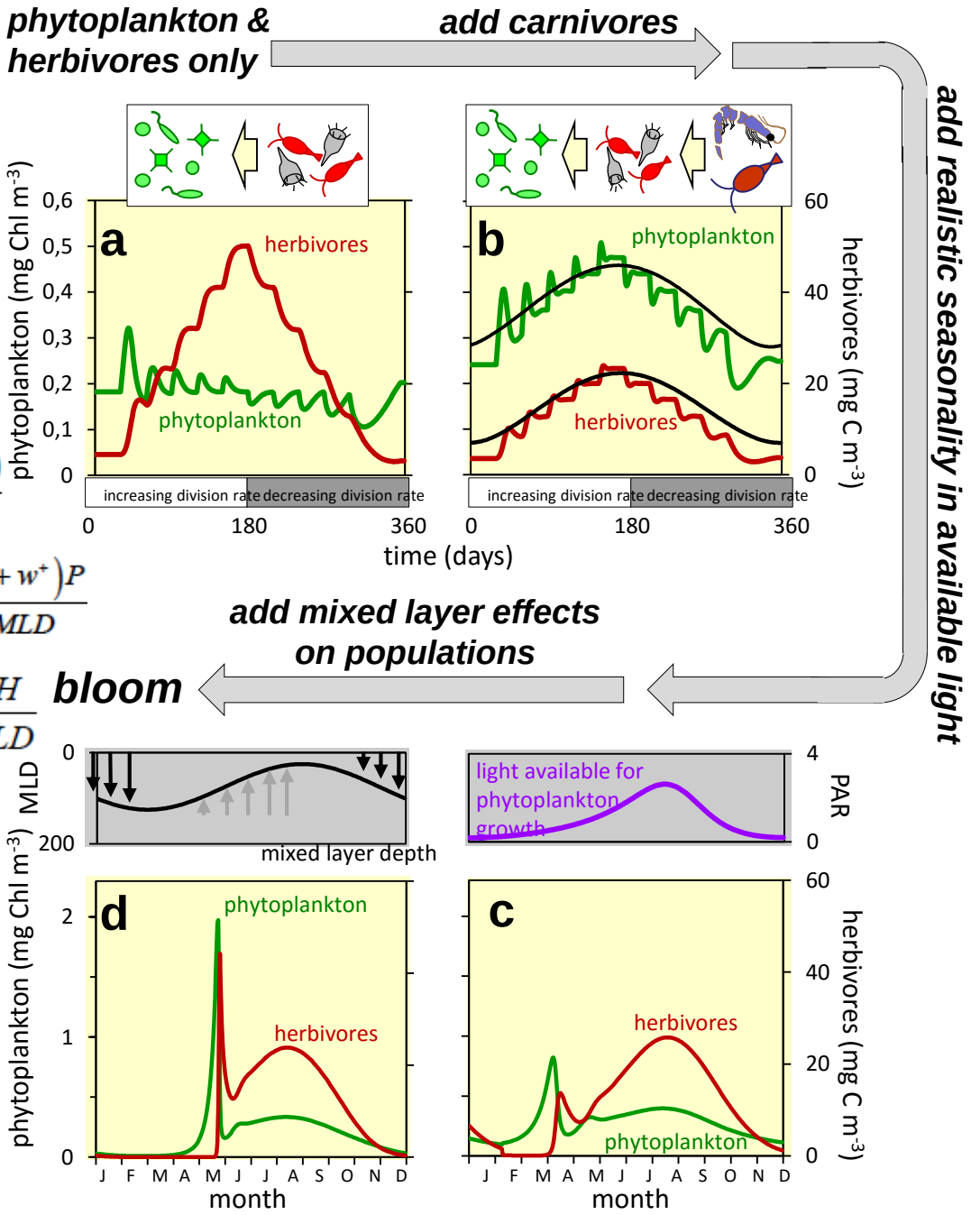
A simple ecosystem model:

A 0-D model

$$\frac{dN}{dt} = -\alpha\left(MLD, Lat, yearday\right)\frac{NP}{N+J} + \frac{\left(m+w^{+}\right)\left(N_0 - N\right)}{MLD}$$

$$\frac{dP}{dt} = \left(\alpha\left(MLD, Lat, yearday\right)\frac{N}{N+J} - b\right)P - c_1\frac{HP^2}{P^2+c_2} - \frac{\left(m+w^{+}\right)P}{MLD}$$

$$\frac{dH}{dt} = \left(c_1 c_3 \frac{P^2}{P^2+c_2}\right)H - c_4 H - c_5 H^2 - \frac{wH}{MLD}$$



Behrenfeld and Boss, 2014

Example of insight one may garner from simplistic models:

Example1 (Riley, 1946, Lotka-Volterra):

$$\frac{dP}{dt} = mP - c_1 PH$$

$$\frac{dH}{dt} = c_1 c_2 PH - c_3 H$$

Steady states:

$$(P_0, H_0) = (0, 0)$$

$$(P_0, H_0) = \left(\frac{c_3}{c_1 c_2}, \frac{m}{c_1}\right)$$

Period: $t = \frac{2\pi}{\sqrt{c_3 m}}$

Example 2:

$$\frac{dP}{dt} = mP - c_1 PH$$

$$\frac{dH}{dt} = c_1 c_2 PH - c_4 H^2$$

$$(P_0, H_0) = (0, 0)$$

$$(P_0, H_0) = \left(\frac{c_4}{c_1 c_2} m, \frac{m}{c_1}\right)$$

Convergence time: $t = \frac{c_1}{c_4 m}$

3 out of 4 unknowns…

Quasi Steady-state (QSS, Evans and Parslow, 1985)

Phytoplankton concentration trace a trajectory in time that is not far from the local steady state (as determined by intantaneous light, temperature and nutrients).

This assumption is built into some climate models (Princeton's BLING), which predicts phytoplankton biomass from its growth-rate (explaining 70% of the variance observed in surface [chl]).

Such a scheme CANNOT get the phytoplankton phenology correctly as it is not driven by growth-rate controlling parameters only.

When the QSS assumption is correct, one can use observed values of phytoplankton + growth rate to learn more about the loss processes (for which large scale observations are lacking).

In the least, we can learn how to appropriately formulate grazing losses.

Summary

- The streetlight analogy – we form our world view with the measurements we have (e.g. hydrography+chl+light) – need to measure more ecological parameters (e.g. [zooplankton], virus, grazing rates) to explain some in-situ observations.

- Periodic shifts in taxonomic dominance are another essential feature of blooms that needs to be addressed– not all the ‘chlorophyll’ is the same.

- When oceanic ecosystems are in quasi-equilibrium, there is hope to constrain their parameters with observations.

- Things I have left out: ‘eddy-correlation’ terms (e.g. small scale physics and phytoplankton patchiness, prey-predator affinity etc’).