Rethinking the critical depth: Nonlinear mortality required to model wintertime phytoplankton growth

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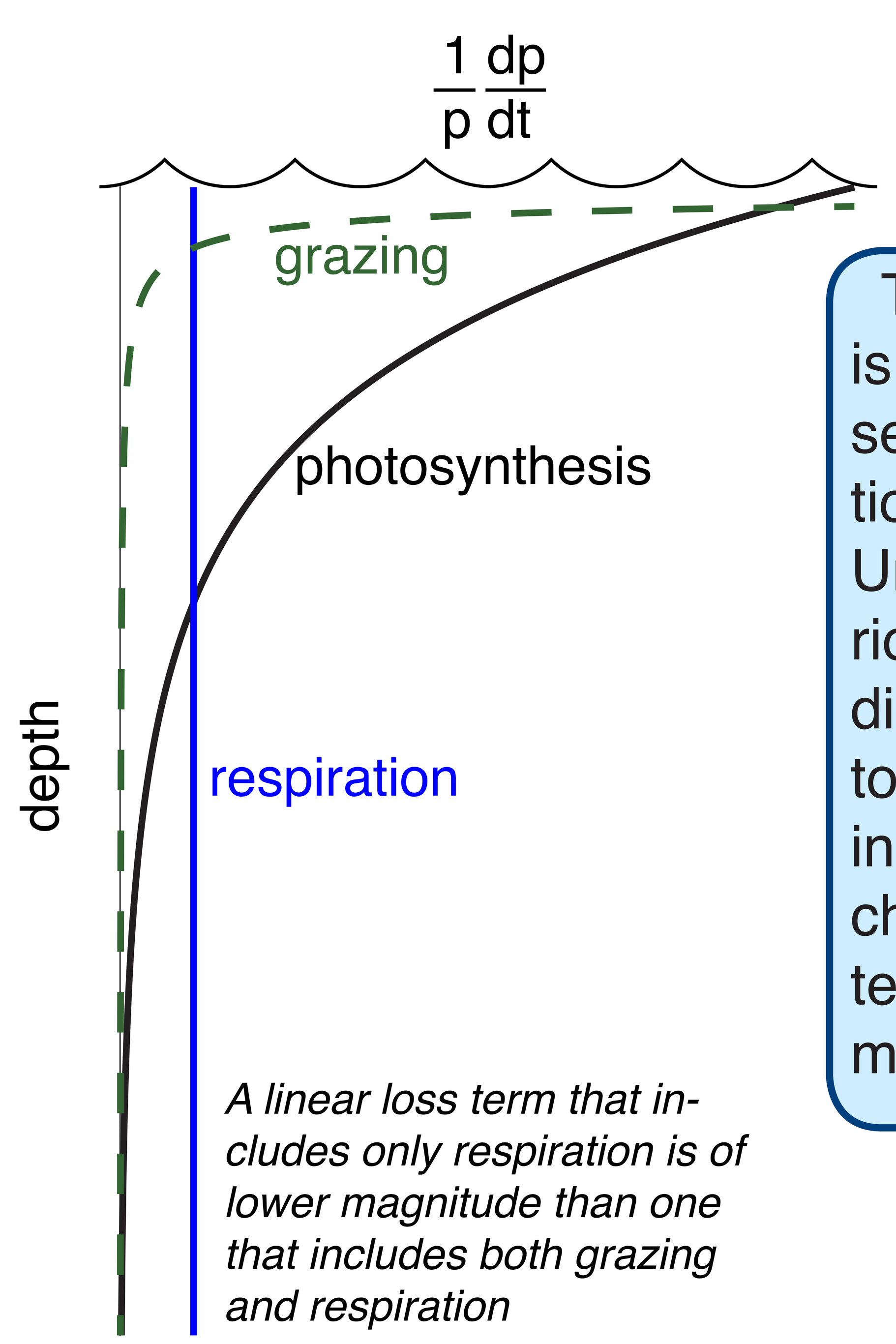
North Atlantic bloom initiation

Traditional theory (Sverdrup 1953) assumes constant loss rates so phytoplankton stocks begin to increase in the spring when the mixed layer shoals

Recent observations (Behrenfeld 2010, Mignot et al 2018) show increasing phytoplankton stocks in the wintertime.

One hypothesized mechanism for biomass accumulation is decreasing loss rates as the mixed layer deepens due to a reduction in grazing rates at low prey concentration ("dilution-recoupling hypothesis"). The mathematical model proposed here confirms that this is a plausible mechanism.

Both the traditional theory and the dilution-recoupling hypothesis posit that loss terms are dominant in the wintertime. What can we learn about phytoplankton loss terms through modeling wintertime phytoplankton stocks?

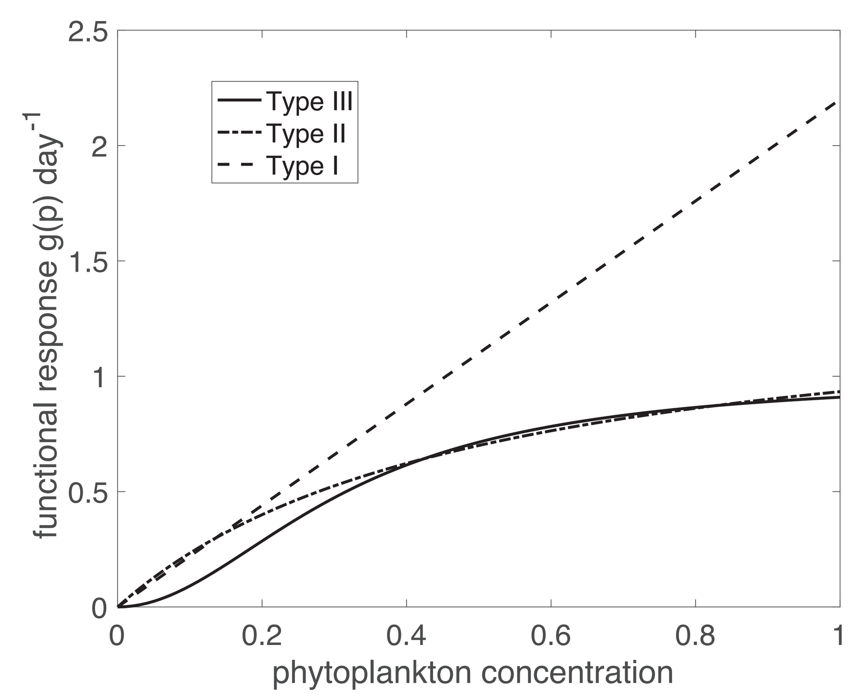


A linear loss term that includes only respiration is of lower magnitude than one that includes both grazing and respiration

The wintertime period is important because it sets the biological conditions for the spring bloom. Understanding this period is important for predicting how phytoplankton blooms might change in response to climate change (e.g. increased temperatures, shallower mixed layer).

Nonlinear mortality

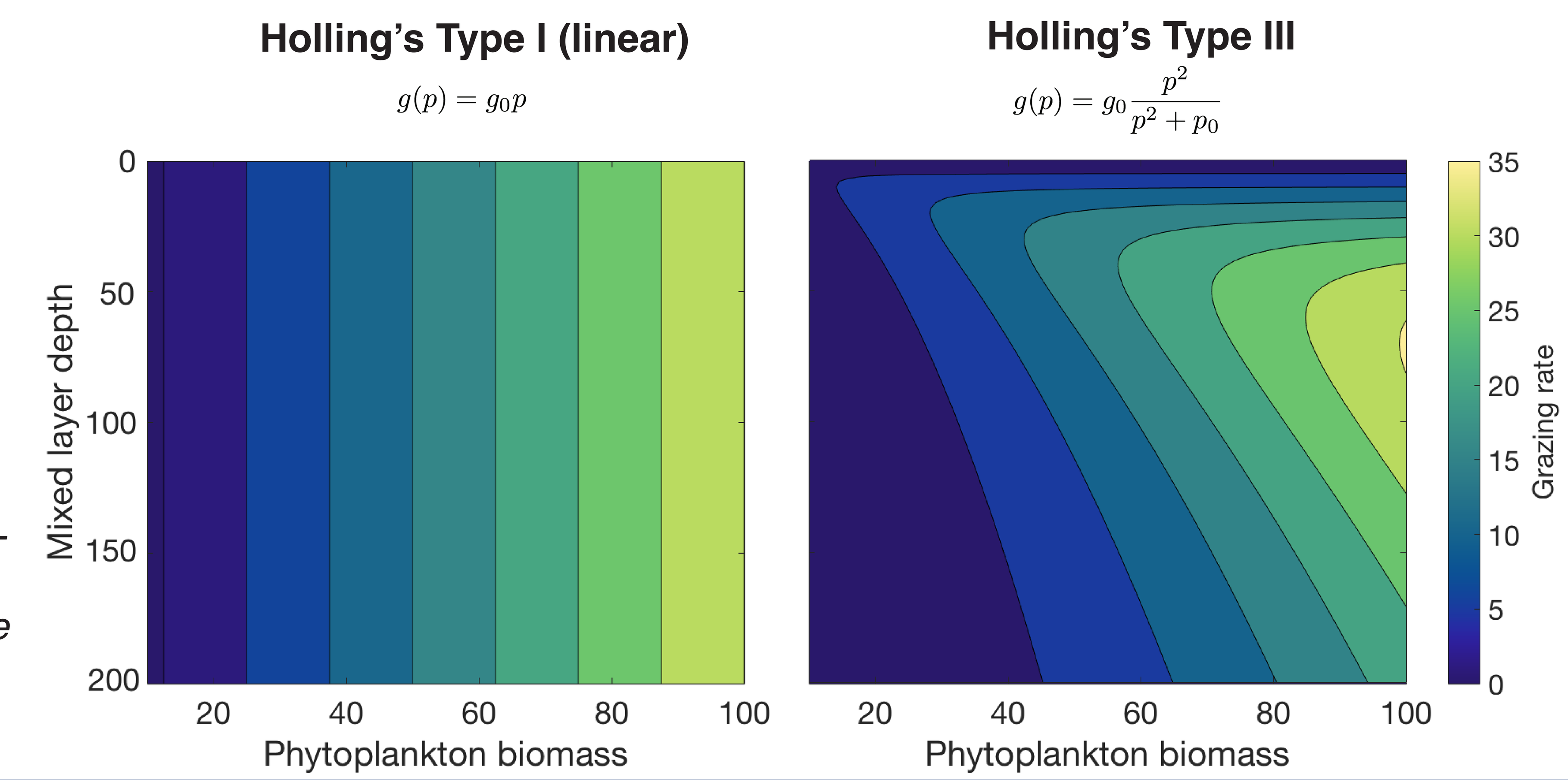
- Dilution alone does not necessarily decrease phytoplankton loss rates.
- With a linear functional response, assuming that the natural phytoplankton mortality is small, if zooplankton and phytoplankton stocks are in equilibrium, they will remain in equilibrium even as the mixed layer deepens.



- With a type III functional response, the grazing rate decreases as the mixed layer deepens.

Grazing rate g(p) as a function of phytoplankton concentration for Holling's Type I, II, and III functional responses.

Grazing rate as a function of phytoplankton biomass and mixed layer depth for Holling's type I (linear) functional response (left) and Holling's type III (inflection at low concentrations). Only in the case of Holling's type III functional response is there a decrease in the grazing rate as the mixed layer increases. This occurs at low values of phytoplankton biomass and deep mixed layers, as required for the dilution-recoupling hypothesis. The grazing rates with Holling's type I functional response is independent of mixed layer depth.



Modeling the winter-spring transition

Parameter	Significance	Value
u_0	maximum growth rate	0.75
g_0	maximum grazing rate	1
d_z	zooplankton mortality rate	1
d_p	phytoplankton mortality rate	0.05
a	zooplankton assimilation efficiency	0.4
p_0	grazing saturation factor	0.1
h	light decay scale	20
n_0	nutrient uptake saturation factor	0.3
n_{max}	nutrient concentration below mixed layer	10

Dilution decreases the concentration of both phytoplankton and zooplankton while the mixed layer is deepening

$$s^+ = \begin{cases} \frac{1}{H}\frac{dH}{dt} & \frac{dH}{dt} > 0 \\ 0 & \frac{dH}{dt} \leq 0 \end{cases}$$

$$\frac{\partial n}{\partial t} = -\mu(t,n)p + d_p p + s^+(n_{max} - n)$$
$$\frac{\partial p}{\partial t} = \mu(t,n)p - g(p)z - d_p p - s^+ p$$
$$\frac{\partial z}{\partial t} = a g(p) z - d_z z^2 - s^+ z$$

Time dependent growth rate

$$\mu(t,n) = l(t) u_0 \frac{n}{n_0 + n} \frac{h}{H(t)} (1 - e^{-H(t)/h})$$

When implemented in a full NPZ model, a grazing function with an inflection at low phytoplankton concentration is sufficient to reproduce both wintertime biomass accumulation and a spring bloom.