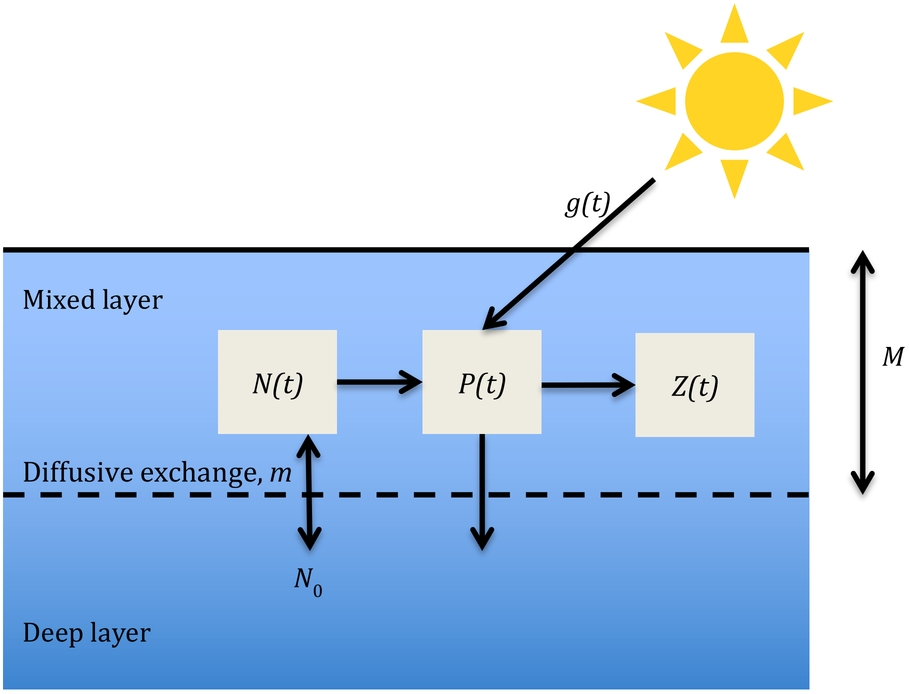
## Seasonal succession

The aim of this exercise is to study seasonal succession in a plankton system. The seasonal succession is driven by changes in light. Mathematically, this is an example of a forced dynamical system.




The equations follow largely Evans & Parslow's model ($N$ is nutrients, $P$ is phytoplankton and $Z$ is zooplankton, all measured in units of nutrients per volume):

Uptake of nutrients by $P$      Exchange with deep layer

$$\frac{\partial N}{\partial t} = -\left[g(t,\phi,M)\left(\frac{N}{H_P+N}\right)-r\right]P+\frac{m}{M}(N_0-N)$$

$$\frac{\partial P}{\partial t} = +\left[g(t,\phi,M)\left(\frac{N}{H_P+N}\right)-r\right]P-\max\left\{0,C_{\max}\frac{P-P_0}{H_Z+P-P_0}\right\}Z$$

$$-\frac{m}{M}P$$

$$\frac{\partial Z}{\partial t} = \epsilon\max\left\{0,C_{\max}\frac{P-P_0}{H_Z+P-P_0}\right\}Z-dZ,$$

Grazing on $P$ by $Z$

with the maximum growth rate of phytoplankton $g(t,\phi,M)$ given as

$$g(t,\phi,M)=\exp(-0.025\ \mathrm{m}^{-1}\cdot M)\left[1-0.8\sin\left(\frac{\pi\phi}{180^\circ}\right)\cos\left(2\,\pi\frac{t}{365\ \text{days}}\right)\right]$$

*New parameters:*
$P_0$ is the concentration of phytoplankton (the consumers) below which grazing by zooplankton (the predators) stops. This parameter, and the maximum function, changes the functional response slightly. It makes the simulations more stable.

$H_P$ and $H_Z$ are "half-saturation" coefficients. They describe the concentration where the grazers feed at half their maximum rate. To see this, you can try to plot the functional response. We normally use the clearance rate, $b$, to describe the functional response. The half-saturation coefficients and the clearance rates are related as: $H = C_{\max}/b$.

where $t$ is time (in days), $\phi$ is the latitude (in degrees) and $M$ the depth of the mixed layer (in meters). The other parameters are given in the paper but note that I have changed the lettering of some symbols to increase readability.

1. Plot the maximum growth rate of phytoplankton as a function of time.
2. Implement the model and simulate a seasonal succession at 47 degrees north with a depth of the mixed layer of $M = 60$ meter and a mixing rate constant of $m = 0.3$ day$^{-1}$ (note: less than in the paper).
3. What is the seasonal succession between nutrients (resource), phytoplankton (prey), and zooplankton (predators)?

Consider other questions of your choice, e.g.:
- How does the seasonal succession vary with latitude?
- How does the seasonal succession vary with depth of the mixed layer?
- How does the seasonal succession and the production depend on the amount of nutrients in the deep layer?
- What are the equilibria of the model? How can the succession be explained by reference to the equilibria?
- How does the model change if we use functional responses type I instead of type II?
- How would productivity and succession be influenced by climate change?
- What if we introduce two competing phytoplankton species?
- What happens if we introduce fish?
- …