Modelling Plankton Dynamics in the Oceanic Mixed Layer

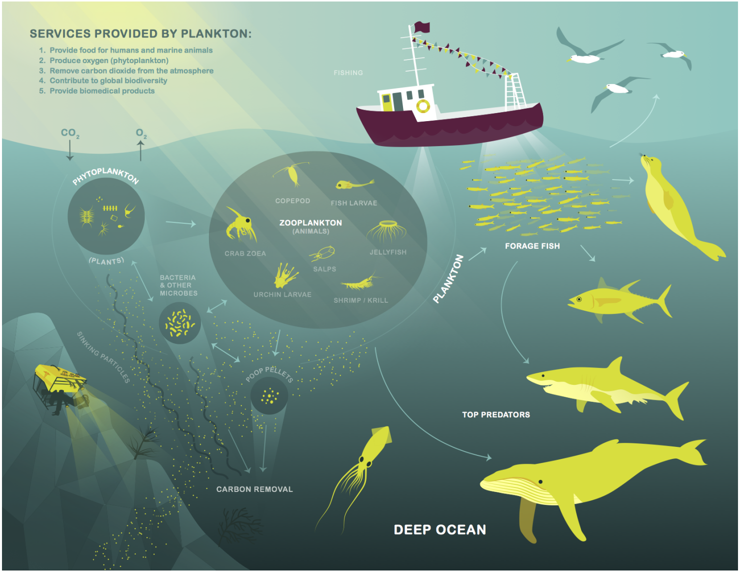
Lecture 5

Ago Merico

29 January 2020

Part 1 – Main concepts and NPZ model

Part 2 – Physical dynamics and NPZD model



SERVICES PROVIDED BY PLANKTON:
1. Provide food for humans and marine animals
2. Produce oxygen (phytoplankton)
3. Remove carbon dioxide from the atmosphere
4. Contribute to global biodiversity
5. Provide biomedical products
FISHING
CO_2
O_2
PHYTOPLANKTON
(PLANTS)
COPEPOD
FISH LARVAE
ZOOPLANKTON
(ANIMALS)
CRAB ZOEA
JELLYFISH
SALPS
URCHIN LARVAE
SHRIMP / KRILL
BACTERIA
& OTHER
MICROBES
PLANKTON
FORAGE FISH
SINKING PARTICLES
POOP PELLETS
TOP PREDATORS
CARBON REMOVAL
DEEP OCEAN

Nutrients

The fundaments of life...

Inorganic: Macro-	Inorganic: Micro-	Organic
Carbon (C)	Iron (Fe)	Carbohydrates
Nitrogen (N)	Cobalt (Co)	Lipids
Phosphorus (P)	Manganese (Mn)	Proteins
Silicon (Si)	Copper (Cu)	Vitamins
...	Zinc (Zn)	...
	...	

Photosynthesis: uses inorganic nutrients and light to synthesise biomass

$$\underbrace{106\,CO_2}_{\text{carbon dioxide}} + \underbrace{16\,HNO_3 + H_3PO_4}_{\text{nutrients}} + \underbrace{122\,H_2O}_{\text{water}} \rightleftarrows \underbrace{1(CH_2O)_{106}\,(NH_3)_{16}\,(H_3PO_4)}_{\text{organic matter}} + \underbrace{138\,O_2}_{\text{oxygen}}$$

Bacteria

- Most diverse groups of organisms in the marine realm;
  - many are free-living, others form symbiotic associations;
  - many thrive within dead organic substrates;
  - important recycling role.
- Can live under extreme conditions;
  - e.g. high salinity, high temperature, anoxic waters.
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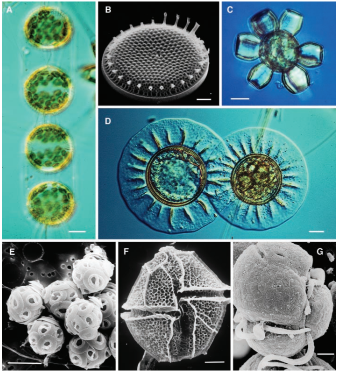
Phytoplankton

- Phytoplankton is a diverse group of microscopic, mostly single-celled, photosynthetic organisms that drift with the currents in marine and fresh waters.
- Although accounting for less than 1 % of Earth's photosynthetic biomass, phytoplankton are responsible for more than 45 % of our planet's annual net primary production.
- They are agents for primary production, the creation of organic compounds from CO_2 dissolved in the water, a process that sustains the aquatic food web and life in general.
- Phytoplankton depend on inorganic nutrients, primarily nitrate, phosphate, and silicic acid, whose availability is governed by a balance between the biological pump and upwelling of deep, nutrient-rich waters. Across large regions of the World Ocean phytoplankton are also limited by lack of iron.



Examples of representative marine phytoplankton. (A) Diatom chain; (B) single valve diatom; (C) coccolithophore; (D) overlapping pair of phycomas; (E) clump of coccospheres; (F) dinoflagellate; (G) dinoflagellate. Scale bars: (A, C, E, F) 10 μm; (B and G) 2 μm; and (D) 25 μm.

Zooplankton

- Grazers: dominant consumers of phytoplankton;
- Transporters: eat at one depth, extrete at another;
- Through their consumption and processing of phytoplankton and other food sources, zooplankton play a key role in aquatic food webs, as a resource for consumers on higher trophic levels (e.g. fish).

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- a standard problem in marine ecology is the causal explanation of the phytoplankton spring bloom in temperate regions;
- there are benthic models, fishery models, population-dynamical models for whales, and many more...

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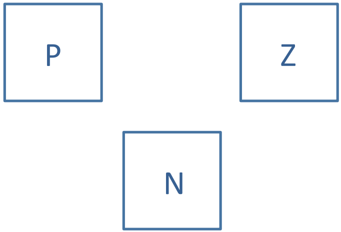
5. the fall bloom is mixed away by the storms of early winter, which also resupply the surface with nutrients; the cycle begins again.

A simple pelagic ecosystem model

The basic goals in marine ecology are to understand the interactions among nutrient avialability, phytoplankton growth, phytoplankton stock size and zooplankton stock size.

The most basic models are called Nutrient-Phytoplankton-Zooplankton, or NPZ, models.



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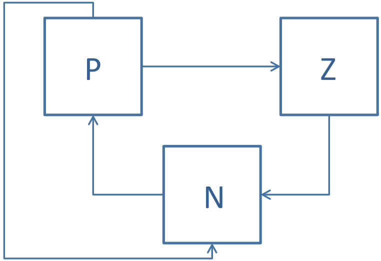

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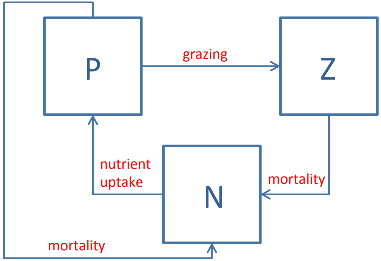

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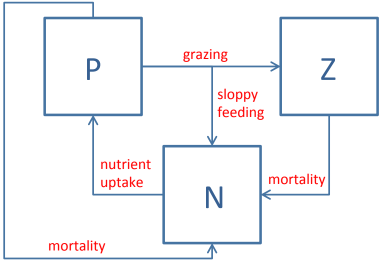


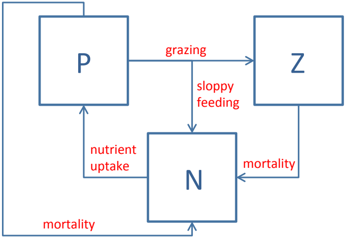
A simple pelagic ecosystem model

The differential equations can be written in words as follows:

$$\frac{dP(t)}{dt} = +Nutrient\ Uptake - Mortality_P - Grazing\ ,$$

$$\frac{dZ(t)}{dt} = +(Assimilation\ Efficiency) * Grazing - Mortality_Z\ ,$$

$$\frac{dN(t)}{dt} = -Nutrient\ Uptake + (1 - Assimilation\ Efficiency) * Grazing + Mortality_P + Mortality_Z\ .$$



Processes

The processes involved in the interactions among the different dynamic variables (also called compartments) can be spelled out as follows:

$$
\begin{aligned}
Nutrient\ Uptake &= \mu(N)\,P = \mu_{max}\left(\frac{N}{N+K_N}\right)\,P\,,\\
Grazing &= g(P)\,Z = g_{max}(1-e^{\Lambda P})\,Z\,,\\
Mortality_P &= m_P\,P\,,\\
Mortality_Z &= m_Z\,Z\,,\\
Assimilation\ Efficiency &= \gamma\,.
\end{aligned}
$$

with: $m_p = 0.1\,\mathrm{d}^{-1}$; $m_Z = 0.2\,\mathrm{d}^{-1}$; $\gamma = 0.3\,(\text{i.e. } 30\,\%)$

Nutrient uptake

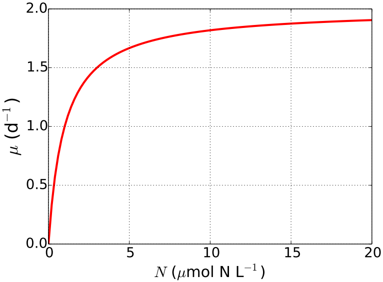
Nutrient uptake is simulated with a Monod-type function:

$$\mu(N) \; = \; \mu_{max}\left(\frac{N}{N+K_N}\right)$$

with:

$\mu_{max} = 2.0\ \mathrm{d}^{-1}$ (maximum growth rate)

$K_N = 1.0\ \mu\mathrm{mol\,N\,L}^{-1}$ (half-saturation constant)



Grazing

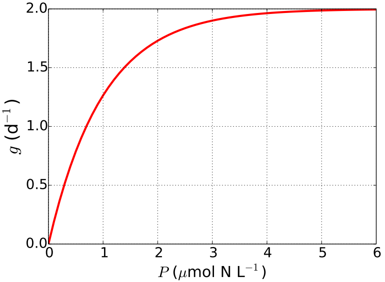
Grazing is simulated using the Ivlev's formulation:

$$g(P) \;=\; g_{max}(1 - e^{-\Lambda\, P})$$

with:

$g_{max} = 2.0.5\ \mathrm{d}^{-1}$ (maximum ingestion rate)

$\Lambda = 1.0\ \mu\mathrm{mol\,N\,L}^{-1}$ (Ivlev constant)



Grazing

Grazing is simulated using the Ivlev's formulation:

$$g(P) \; = \; g_{max}(1 - e^{-\Lambda\,(P - P_0)})$$

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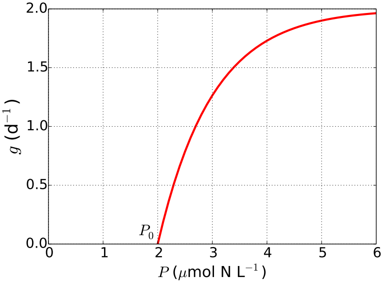

Complete model equations

This model was developed by Franks et al. (1986), the complete equations are:

$$\frac{dP(t)}{dt} = \mu_{max} \left(\frac{N}{N + K_N} \right) P - m_P \, P - g_{max} \left[1 - e^{-\Lambda\,(P - P_0)} \right] \, Z \, ,$$

$$\frac{dZ(t)}{dt} = \gamma \, g_{max} \left[1 - e^{-\Lambda\,(P - P_0)} \right] \, Z - m_Z \, Z \, ,$$

$$\frac{dN(t)}{dt} = -\mu_{max} \left(\frac{N}{N + K_N} \right) P + m_P \, P + m_Z \, Z + (1 - \gamma) \, g_{max} \left[1 - e^{-\Lambda\,(P - P_0)} \right] \, Z \, .$$

Complete model parameters

Symbol	Description	Value	Unit
μ_{max}	maximum growth rate (P)	2.0	d^{-1}
K_N	half-saturation constant	1.0	$\mu\mathrm{mol\,N\,L}^{-1}$
g_{max}	maximum ingestion rate (Z)	1.5	d^{-1}
Λ	Ivlev constant	1.0	$\mu\mathrm{mol\,N\,L}^{-1}$
P_0	minimum grazing threshold	0.0	$\mu\mathrm{mol\,N\,L}^{-1}$
m_P	mortality rate (P)	0.1	d^{-1}
m_Z	mortality rate (Z)	0.2	d^{-1}
γ	assimilation efficiency	0.3	fraction

with: $P(0) = 0.3\,\mu\mathrm{mol\,N\,L}^{-1}$, $Z(0) = 0.1\,\mu\mathrm{mol\,N\,L}^{-1}$, $N(0) = 1.6\,\mu\mathrm{mol\,N\,L}^{-1}$

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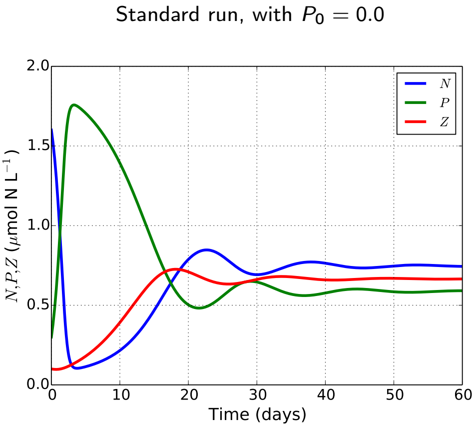
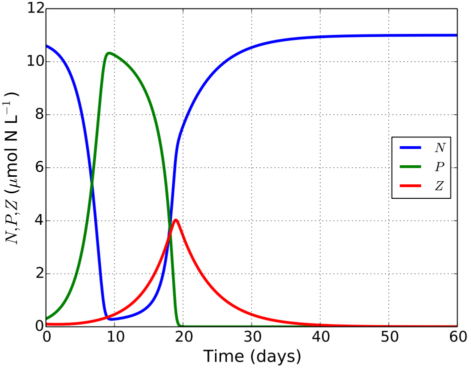
In this way nitrogen is said to represent the *currency* of the model.

Results of the NPZ model



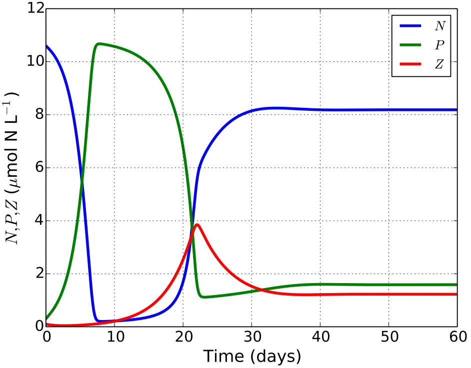
Results of the NPZ model

Run with $N(0) = 10.6$, $\mu_{max} = 0.69$, and $P_0 = 0.0$



Results of the NPZ model

Run with $N(0) = 10.6$, $\mu_{max} = 0.69$, and $P_0 = 1.0$



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- Thus a more realistic model would simulate control of primary production by seasonally varying sunlight and include the decrease of light with depth, at least to the bottom of a mixing layer;
- Phytoplankton growth varies non-linearly with irradiance (P-I relationship), and irradiance decreases exponentially downward, so one should integrate production down through the water column; variations in mixing should be also included (at least in a simplified fashion) for example by varying the mixed-layer depth through the simulated season.

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- Zooplankton can be taken to sustain their stock within the mixed layer by swimming;
- We add another dynamic variable, 'detritus' (D), to reflect the fact that organic matter (fecal materials and dead organisms) is temporarily stored in this compartment where it gets decomposed by bacteria and then transferred to restock the inorganic nutrient pool.

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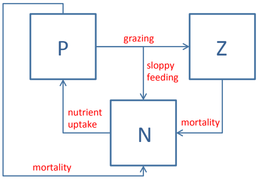
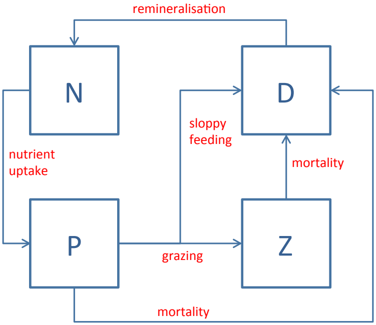


$\Rightarrow$



Adding the detritus pool implies that (1) all dead material pass by this compartment before reaching the inorganic nutrient pool and (2) a new process must be added, *remineralisation*, which represents the decomposition (or break down) of organic materials into inorganic minerals by bacteria.

End of part 1

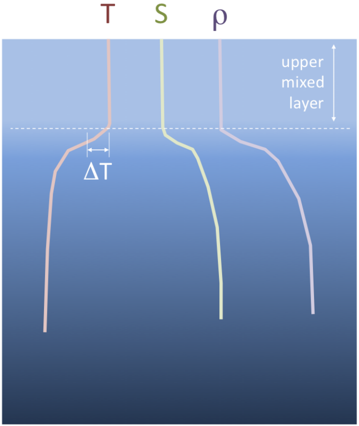
Part 2

Ocean upper mixed layer

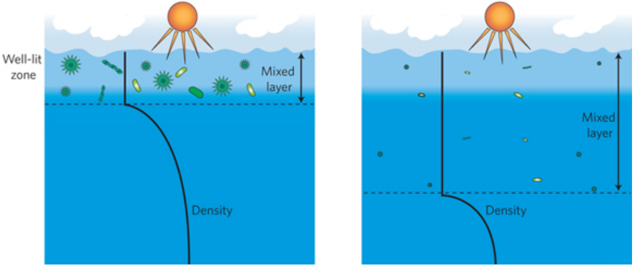
Turbulence create a well mixed surface layer where temperature (T) salinity (S) and density (ρ) are nearly uniform with depth;

The depth of this mixed layer is measured by the depth at which T is some value less than SST (e.g. ΔT$=0.5$);

Undergoes large seasonal changes;



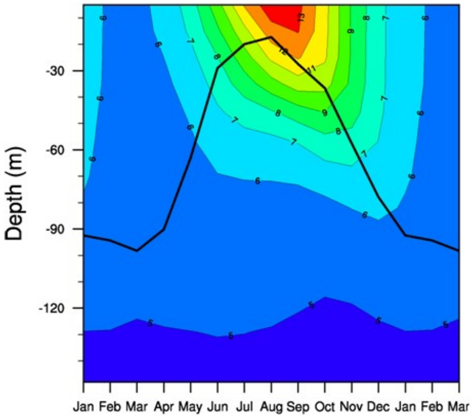
Upper mixed layer depth dynamics



When the mixed layer is shallow, phytoplankton mostly stay within the well-lit zone, where they thrive. When the mixed layer deepens, phytoplankton are distributed over a larger volume of water, and sink more easily to depths too dark to sustain them.

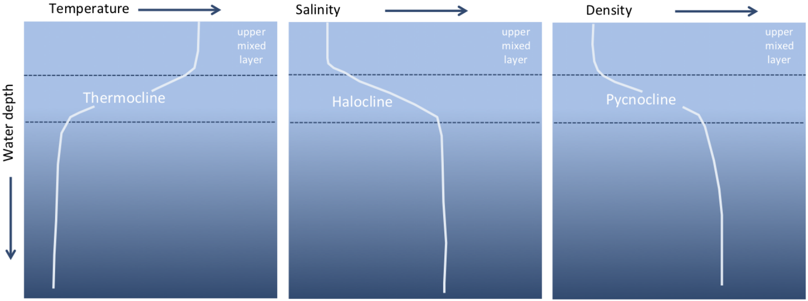
Seasonal cycle of MLD and T

Northeast Pacific (50 °N, 145 °W)



Below upper mixed layer

Just below the upper mixed layer, there is another water layer where temperature, salinity, and density change rapidly; these layers are called, respectively, thermocline, halocline and pycnocline.



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- Such slab models can be run quickly and straightforwardly, enabling both a multitude of runs and ease of analysing results;
- Despite the simplicity of the two-layer slab physics, these models are sufficiently well formulated to permit realistic and insightful simulations of marine ecosystems.

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We assume that some data is available (e.g. vertical profiles of temperature, salinity, or density) to define the seasonal change in the mixed layer depth (M) as a function of time (t), mathematically:

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$$\frac{dM}{dt} = h(t)$$

An NPZD model of the oceanic mixed layer

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In the case of non-motile entities, a deepening of the mixed layer (i.e. when the rate of change of M is positive, $dM/dt > 0$) will dilute the concentration (thus decreasing P). In contrast, when the mixed layer shallows, material is left behind, or detrained, but the concentration in the mixed layer will remain unchanged because the loss due to detrainment is balanced by the increased phytoplankton density due to the decreased volume (thus detrainment, i.e. negative rate changes of M, $dM/dt < 0$, will not alter the concentration of P).

An NPZD model of the oceanic mixed layer

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The asymmetry between motile and non-motile entities can be accounted for by defining the variable $h^{+}(t) = max(h(t)\,,0)$, and using $h^{+}(t)$ rather than $h(t)$ in equations representing non-motile entities.

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Diffusive mixing across the thermocline is parameterised with a constant factor (κ).

For non-motile entities, the whole diffusion term is, thus, written as

$$K = \frac{\kappa + h^+}{M(t)}$$

For motile entities (i.e. zooplankton), the diffusion term is simply

$$\frac{h(t)}{M(t)}$$

An NPZD model of the oceanic mixed layer

Light limitation:

Light limitation:

Phytoplankton growth is limited by light availability. This requires the consideration of (1) photosynthetically active radiation (PAR) on the surface of the ocean (i.e. I at $z = 0$, I_0), (2) attenuation of PAR with depth z, and (3) photosynthesis as a function of light. PAR is attenuated with depth according to the Beer-Lambert law with attenuation coefficient k_{PAR}:

$$I(z) = I_0 \, e^{-k_{PAR} \, z}$$

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The daily depth-average photosynthetic rate is calculated considering a P-I curve and then integrating through the mixed layer depth. We will use the Smith function:

$$P(I) = \frac{\alpha \, I(z) \, P_{max}}{\sqrt{(P_{max})^2 + \alpha^2 \, I(z)^2}}$$

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thus the light limiting term is given by:

$$\Psi(I) = \frac{1}{M(t)} \int_0^M P(I) \, dz$$

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Instead of solving the integral numerically at each model time step, we will use the following analytical solution (according to Anderson et al. 2015):

$$\Psi(I) = \frac{1}{M(t)} \int_0^M P(I)\, dz = \frac{P_{max}}{k_{PAR}\, M} \ln \left(\frac{\alpha\, I_0 + \sqrt{P_{max}^2 + (\alpha\, I_0)^2}}{\alpha\, I_M + \sqrt{P_{max}^2 + (\alpha\, I_M)^2}} \right)$$

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with α initial slope of the P-I curve, P_{max} maximum photosynthetic rate (i.e. the phytosynthetic rate at $I \to \infty$), I_0 irradiance on the top surface (i.e. at $z = 0$), and I_M irradiance at $z = M$ (i.e. $I_M = I_0\, e^{-k_{PAR}\, M}$) with M mixed layer depth.

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k_{PAR} is the sum of attenuation due to water and phytoplankton, parameters k_w and k_p, respectively:

$$k_{PAR} = k_w + k_p\, P$$

An NPZD model of the oceanic mixed layer

Temperature dependence:

Temperature dependence:

Phytoplankton growth depends on temperature according to the Eppley's formulation:

$$f(T) = e^{0.063\,T}$$

with T = Sea Surface Temperature or SST.

An NPZD model of the oceanic mixed layer

Phytoplankton gross growth:

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Phytoplankton gross growth is the product of light-dependent growth with different limiting terms (varing between 0 and 1):

$$\text{Gross growth} \quad = \quad \underbrace{e^{0.063\,T}}_{\text{temp dependence}} \quad \cdot \quad \underbrace{\left(\frac{N}{N+K_N}\right)}_{\text{nutrient limitation}} \quad \cdot \quad \underbrace{\Psi(I)}_{\text{light limitation}}$$

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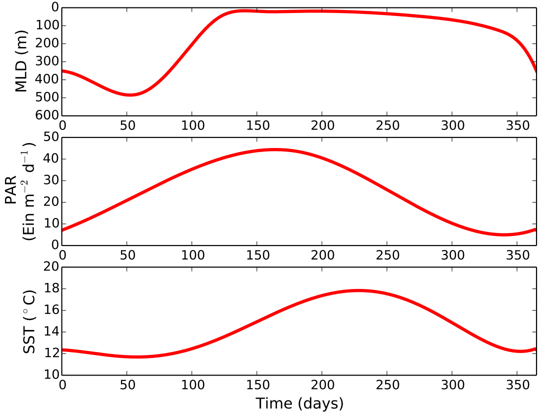
Temporal changes in temperature (T), irradiance at the top of the ocean surface (I_0), and mixed layer depth (M) drive the seasonal changes in the plankton ecosystem model.

These environmental data are external input to the model and represent the *physical forcing* to the model. Thus data files for T, I_0, and M are required; these files are called SST (seas surface temperature), PAR (irradiance at $z=0$), and MLD (mixed layer depth), respectively.

Physical forcing

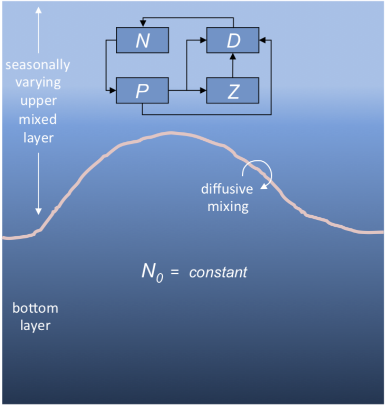
Environmental data typical of a temperate region of the North Atlantic:



Physical scheme – summary

Zero-dimensional "slab" model:

1. The water column is devided into two layers, which are assumed to be homogeneously mixed;
2. Lateral advection is not considered;
3. Environmetal data are external inputs and used as physical forcing to the model;
4. Biological and ecological processes occur only in the upper mixed layer;
5. Nutrient concentration is assumed constant in the bottom layer.



An NPZD model of the oceanic mixed layer

Grazing by zooplankton:

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Grazing by zooplankton is assumed to be on both phytoplantkon and detritus. This choice illustrates how to implement ingestion on multiple prey types. Our grazing functions reflect a passive switching response (according to Anderson et al. 2015) and are formulated as follows:

$$G_P = \left(\frac{g_{max}\, \varphi_P\, P^2}{K_Z^2 + \varphi_P\, P^2 + \varphi_D\, D^2} \right)$$

$$G_D = \left(\frac{g_{max}\, \varphi_D\, D^2}{K_Z^2 + \varphi_P\, P^2 + \varphi_D\, D^2} \right)$$

An NPZD model of the oceanic mixed layer

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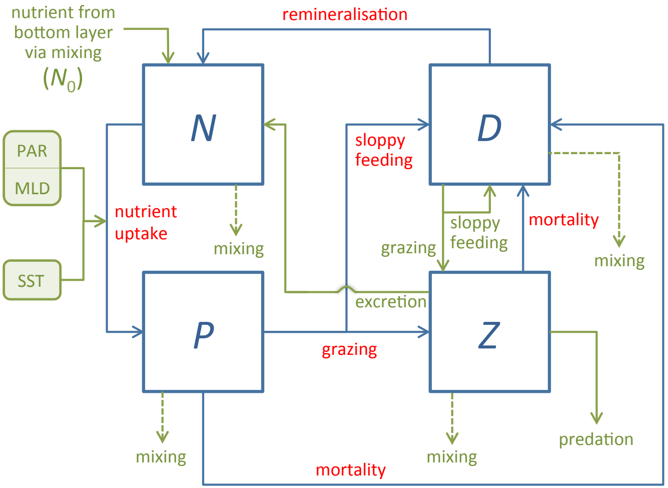
These are sigmoidal functions and the terms g_{max}, K_Z, φ_P, and φ_D are parameters indicating, respectively, maximum grazing (or ingestion) rate, half-saturation constant for intake, preference for phyotplankton, and preference for detritus.

NPZD model – flow diagram



NPZD model – equations

$$\frac{dN(t)}{dt} = -f(T)\,U(N)\,\Psi(I)\,P + m_D\,D + \underbrace{\beta\,(1-K_{NZ})\,(G_P+G_D)\,Z}_{\text{excretion}} + K\,(N_0 - N)\,;$$

$$\frac{dP(t)}{dt} = f(T)\,U(N)\,\Psi(I)\,P - m_P\,P - G_P\,Z - K\,P\,;$$

$$\frac{dZ(t)}{dt} = \beta\,K_{NZ}\,(G_P+G_D)\,Z - m_Z\,Z - m_Z^*\,Z^2 - \frac{h(t)}{M}\,Z\,;$$

$$\frac{dD(t)}{dt} = m_P\,P + m_Z\,Z + \underbrace{(1-\beta)\,(G_P+G_D)\,Z}_{\text{sloppy feeding}} - G_D\,Z - m_D\,D - K\,D\,.$$

with:

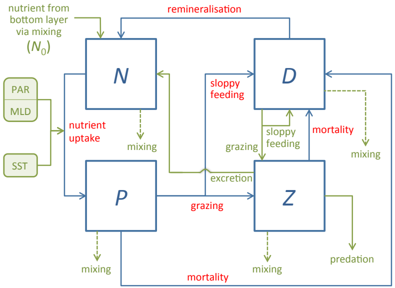
$$f(T) = e^{0.063\,T}, \quad U(N) = \frac{N}{N+K_N}, \quad \text{and} \quad T = \text{sst.dat}$$

$$\Psi(I) = \frac{P_{max}}{(k_w + k_p P)\,M}\,\ln\left(\frac{\alpha\,I_0 + \sqrt{P_{max}^2 + (\alpha\,I_0)^2}}{\alpha\,I_M + \sqrt{P_{max}^2 + (\alpha\,I_M)^2}}\right), \quad I_M = I_0\,e^{-(k_w + k_p P)M}, \quad \text{and} \quad I_0 = \text{par.dat}$$

$$K = \frac{\kappa + h^+}{M(t)}, \quad h^+ = max(h, 0), \quad h = \frac{dM}{dt}, \quad \text{and} \quad M = \text{mld.dat}$$

$$G_P = \left(\frac{g_{max}\,\varphi_P\,P^2}{K_Z^2 + \varphi_P\,P^2 + \varphi_D\,D^2}\right) \quad \text{and} \quad G_D = \left(\frac{g_{max}\,\varphi_D\,D^2}{K_Z^2 + \varphi_P\,P^2 + \varphi_D\,D^2}\right).$$

NPZD model – flow diagram and equations



$$\frac{dN(t)}{dt} = -f(T)\,U(N)\,\Psi(I)\,P + m_D\,D + \underbrace{\beta\,(1 - K_{NZ})\,(G_P + G_D)\,Z}_{\textbf{excretion}} + K\,(N_0 - N)\,;$$

$$\frac{dP(t)}{dt} = f(T)\,U(N)\,\Psi(I)\,P - m_P\,P - G_P\,Z - K\,P\,;$$

$$\frac{dZ(t)}{dt} = \beta\,K_{NZ}\,(G_P + G_D)\,Z - m_Z\,Z - m_Z^*\,Z^2 - \frac{h(t)}{M}\,Z\,;$$

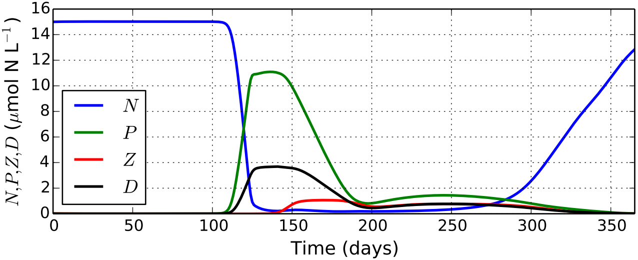
$$\frac{dD(t)}{dt} = m_P\,P + m_Z\,Z + \underbrace{(1 - \beta)\,(G_P + G_D)\,Z}_{\textbf{sloppy feeding}} - G_D\,Z - m_D\,D - K\,D\,.$$

NPZD model – parameters and initial conditions

Symbol	Description	Value	Unit
N_0	nitrogen in bottom layer	15.0	μmol/L
P_{max}	maximum photosynthetic rate	1.1	d^{-1}
g_{max}	maximum ingestion rate	0.9	d^{-1}
K_N	half saturation constant (P)	0.85	μmol/L
K_Z	half saturation constant (Z)	0.6	μmol/L
m_P	mortality rate (P)	0.2	d^{-1}
m_Z	mortality rate (Z)	0.1	d^{-1}
m_D	remineralisation rate (D)	0.6	d^{-1}
β	zooplankton ingestion efficiency	0.69	fraction
K_{NZ}	zooplankton assimilation efficiency	0.75	fraction
k_w	light extinction due to water	0.05	m^{-1}
k_p	light extinction due to P	0.03	$m^{-1}\,(\mu mol/L)^{-1}$
α	initial slope of P-I curve	0.15	$(Ein\,m^{-2})^{-1}\,d^{-1}$
κ	cross thermocline mixing	0.1	$m\,d^{-1}$
m_Z^*	mortality due to higher predators (Z)	0.34	$(\mu mol\,/\,L)^{-1}\,d^{-1}$
φ_P	grazing preference for P	0.67	%
φ_D	grazing preference for D	0.33	%

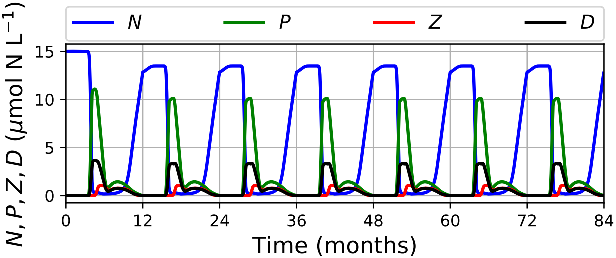
with: $N(0) = 15.0\,\mu mol\,L^{-1}$, $P(0) = 0.01\,\mu mol\,L^{-1}$, $Z(0) = 0.01\,\mu mol\,L^{-1}$, $D(0) = 0.01\,\mu mol\,L^{-1}$.

NPZD model – results



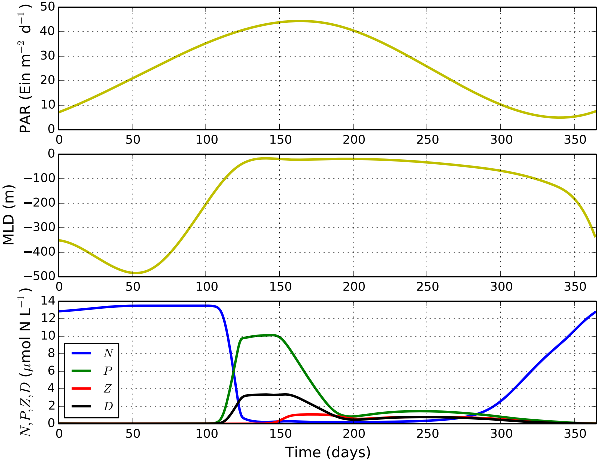
NPZD model – results

Run the model over several years by forcing it every year with the same environmental variables to reach a stable solution after an initial spin-up phase.



NPZD model – results

Stable solutions (4th year after spin-up phase of 3 years) plotted along with forcing variables (PAR and MLD).



Suggestions and hints

Upload the external forcing files as follows:

```
mld = np.loadtxt("/Users/ago/CompLifeSci/mld.dat") # mixed layer depth (M)
par = np.loadtxt("/Users/ago/CompLifeSci/par.dat") # irradiance at z=0 (Io)
sst = np.loadtxt("/Users/ago/CompLifeSci/sst.dat") # sea surface temperature (T)
```

Calculate the derivative of the MLD as follows:

```
mld = mld[1,:]
ldiff = mld[365]-mld[364]
dt = 1.0                                # 1.0 is the time interval (1 day)
dMdt = np.ediff1d(mld,to_end=ldiff)/dt  # calculates rate of change of M
# ediff1d calculates the differences between consecutive elements of mld
```

Create functions for the various processes as follows:

```
def uptake(n):
    u = n/(n+K_N)
    return u

def grazeP(p,d):
    g = (g_max*pP*p*p/(K_Z**2 + pP*p*p + pD*d*d))
    return g
```

Call these functions as appropriate when defining the differential equations:

```
def npzd(y, t):
    N, P, Z, D = y
    dPdt = (temp(sst[t])*uptake(N)*light(t,P))*P - mP*P - grazeP(P,D)*Z - mix(t)*P
    ...
    return dydt
```

Further reading

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