# MAR 650-Lecture 1: Influences of Light on Biological Production

## 1) Photosynthesis and Primary Production

$$CO_2 + H_2O \underset{\text{respiration}}{\overset{\text{photosynthesis}}{\rightleftharpoons}} \text{Carbohydrate} + O_2$$

Importance:

**Photosynthesis requires lights, which only occurs during the daytime, but respiration could happen during the daytime and night.**

In the ocean:

**$CO_2$: 90 mg $CO_2$/L >> $CO_2$ concentration required for photosynthesis in the ocean, so in general, $CO_2$ is not a limiting factor to restrict photosynthesis process!**

## Primary Production:

**Phytoplankton biomass produced by a photosynthesis process over a unit time**.

## Total Primary Production:

**The primary production produced only by the photosynthesis process**.

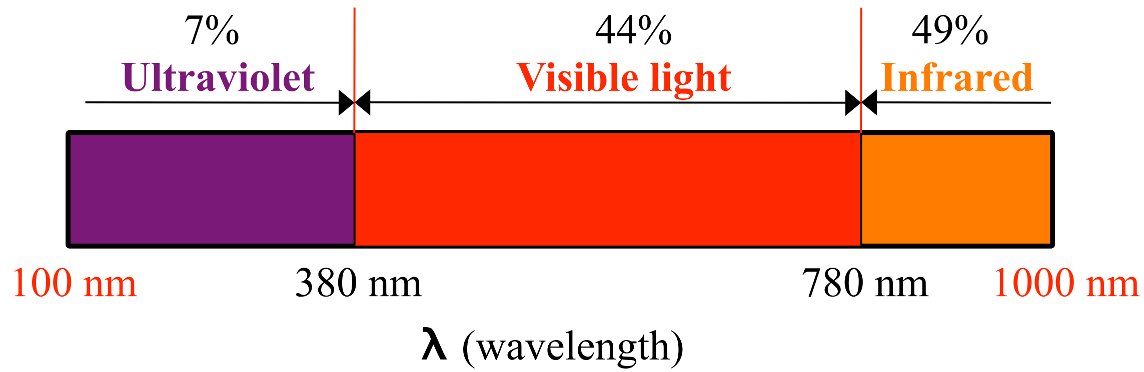
## Net Primary Production:

**The primary production produced by the photosynthesis process minus respiration process.**

## Question 1:

Could all lights absorbed by the ocean be used for photosynthesis process?

Wavelengths of the solar radiation into the ocean: 100 nm (nanometer) to 1000 nm




Unit: nm: nanometer

1 nm = $10^{-9}$ m
= $3.281 \times 10^{-9}$ ft

- 7%: Ultraviolet, λ < 380 nm. These radiations are quickly scattered and then absorbed by the water in a thin layer near the sea surface, which are not able to penetrate deeply;

- 49%: Infrared, λ > 780 nm. These radiations are quickly absorbed by the water in a thin layer near the sea surface and transferred into heat energy;

- 44%: Visible lights: 380 nm < λ < 780 nm. This part of solar radiation could penetrate into a deeper region.

**The only radiation with a wavelength between 400 nm and 700 nm can be used to the photosynthesis process.**

**Radiations between 400 nm and 700 nm is also called "Photosynthetically Active Radiation" (PAR).**

PAR: Einstein/$m^2$/second (E/$m^2$/s) or μE/$m^2$/s or μmoles/$m^2$/s

$1E = 1$ mole of photons $= 6.022\times10^{23}$ photons; $1\mu E = 1.0\times10^{-6}$ E

Radiation flux: Radiant power defined as the flow rate of radiant energy. It is measured in term of the power unit called "watts"

$1W = 1$ Joule/second $= 1$ J/s

Radiance: The radiant flux density per unit solid angle in unit " watts/$m^2$/steradian".

Irradiance: The radiant flux density per unit area at a point on the surface in unit "watts/$m^2$ (W/$m^2$)" (the light falling onto a source from all direction no matter which light's direction is)

QS. 1: How could we convert PAR unit to Irradiance unit?

PAR: $E/m^2/s$ ⟷ Irradiance: $W/m^2$ ; $1W = 1\ J/s$

$1\ E = 6.022\times10^{23}$ photons

Energy of a photon $E_p = hc/\lambda$,
where
$h$ is Planck's constant ($h = 6.626\times10^{-34}$ J s)
c is the speed of light ($c = 2.998 \times 10^{8}$ m/s)
$\lambda$ is the wavelength (an averaged value over a broad spectrum PAR sensor is 550 nm)

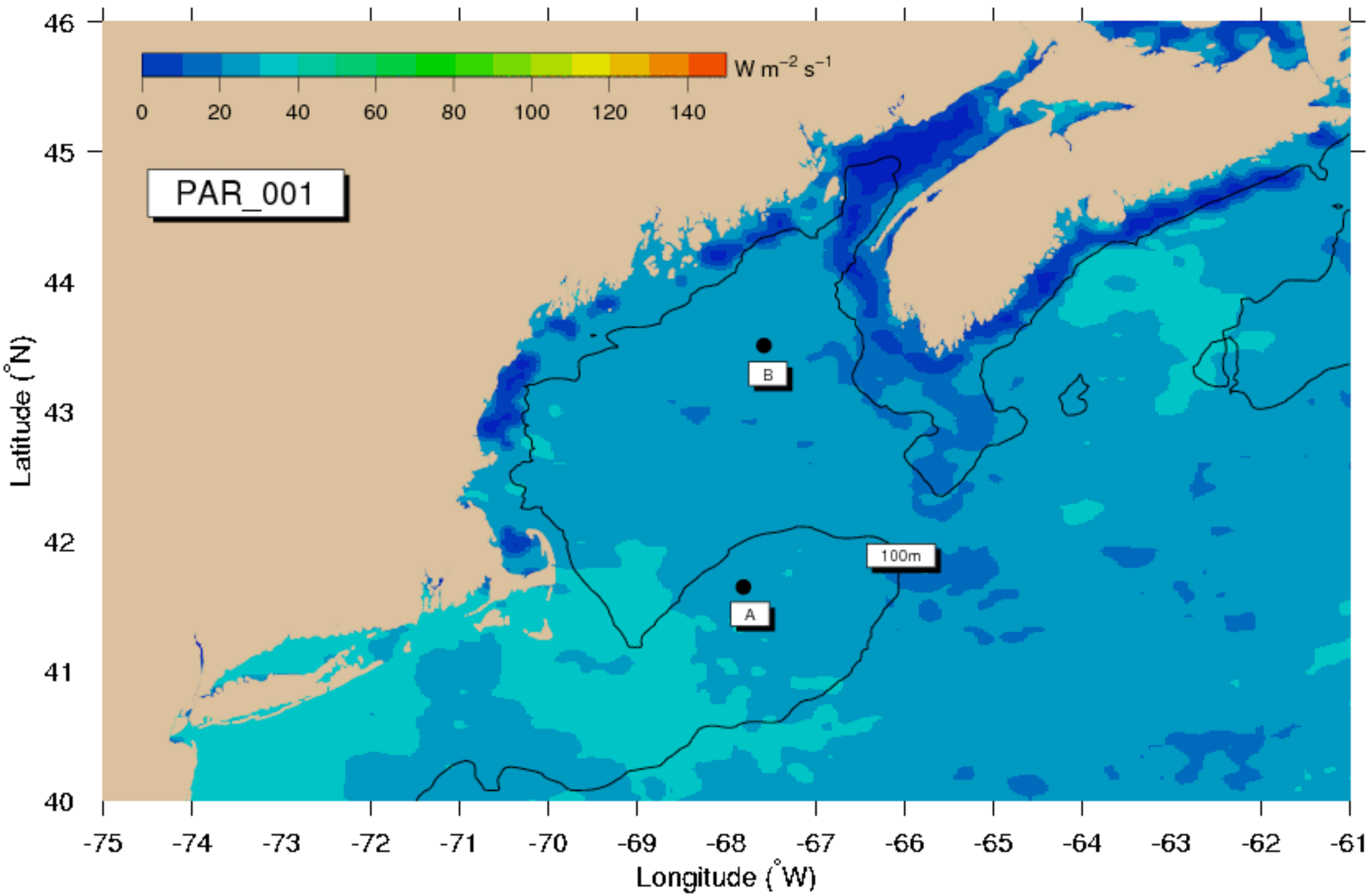
$$E_p = hc/\lambda = 6.626\times10^{-34}\ \text{J s}\times2.998\times 10^{8}\ \text{m/s} /(550\times 10^{-9}\ \text{m})$$
$$= 3.61\times 10^{-19}\ \text{J}$$

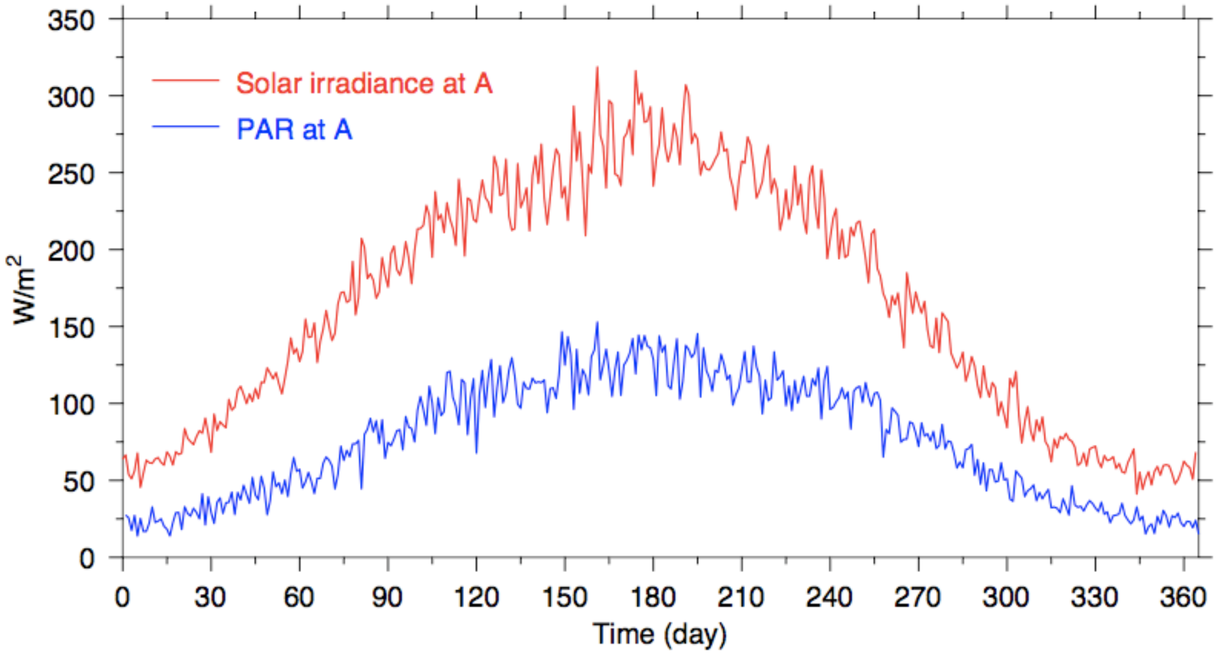
$E_p$ is the energy/photon. Assume that N photons are required to create 1 J of energy, then we have

$$N\times E = 1\ \text{J},\ \text{so}\ N = 1\ \text{J}/E = 1\ \text{J}/ (3.61\times 10^{-19}\ \text{J}) = 2.77 \times 10^{18}\ \text{photons}$$

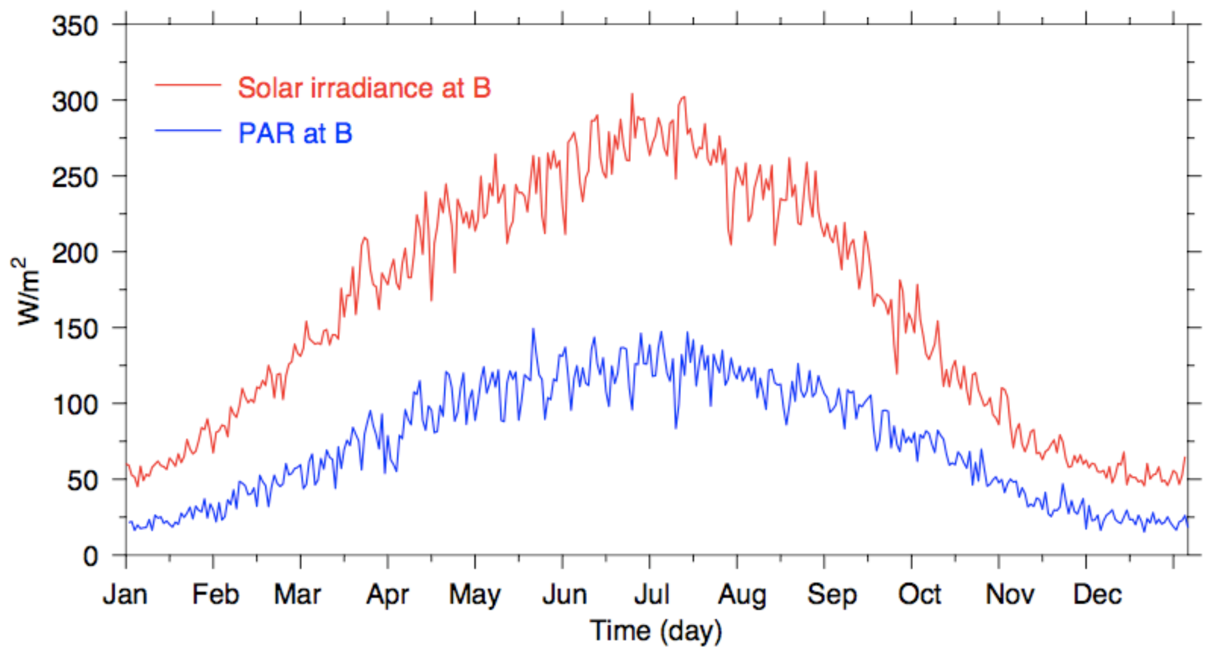
$$1\ E/s = 6.022\times10^{23}\ \text{photons/s} = (6.022\times10^{23}/2.77 \times 10^{18})\ \text{J/s} = 2.174 \times 10^{5}\ \text{J/s}$$

PAR ⟷ Irradiance: $E/m^2/s = 2.174\times 10^{5}\ W/m^2$


W m^-2 s^-1
0
20
40
60
80
100
120
140
PAR_001
B
A
100m
46
45
44
43
42
41
40
Latitude (°N)
-75
-74
-73
-72
-71
-70
-69
-68
-67
-66
-65
-64
-63
-62
-61
Longitude (°W)




Georges Bank




Gulf of Maine Interior

Question 2: Does photosynthesis reaction always increase with increase of light intensity? Does it exist a critical light intensity for photosynthesis process?

**Primary production rate due to photosynthesis increases with light intensity in a light range lower than critical light intensity, and then reduces with light intensity in a light range exceeding critical light intensity.**

**Let $P_g$: total primary production; $P_{max}$: the maximal primary production; $K_I$: the half-saturation constant of photosynthesis, we get**

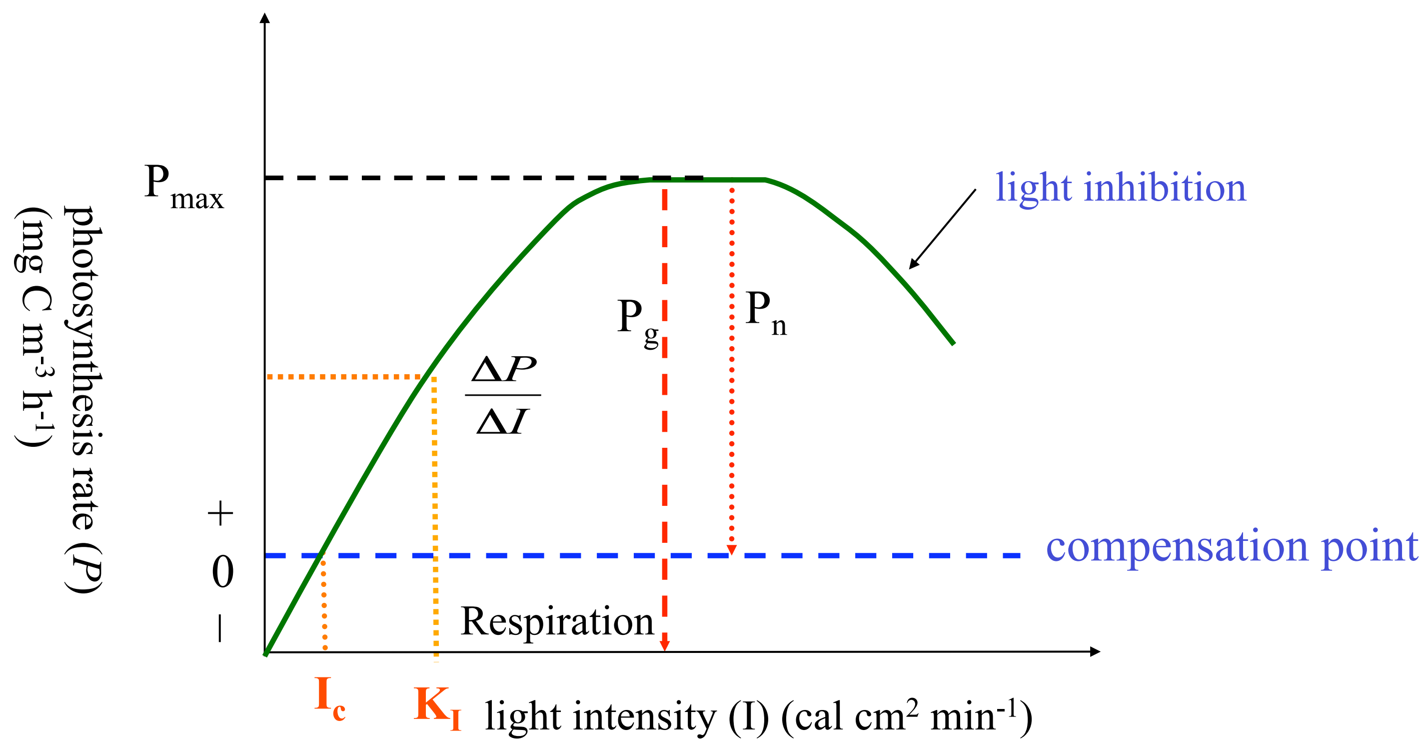
**In a light range lowered than critical light intensity:**

$$P_g = \frac{P_{\max} I}{K_I + I} \qquad (1)$$

**Considering the reduction due to phytoplankton respiration, we get**

$$P_n = \frac{P_{\max}(I - I_c)}{K_I + (I - I_c)} \qquad (2)$$

**$I_c$ is defined as the compensation light intensity at which photosynthesis rate is balanced by respiration rate.**



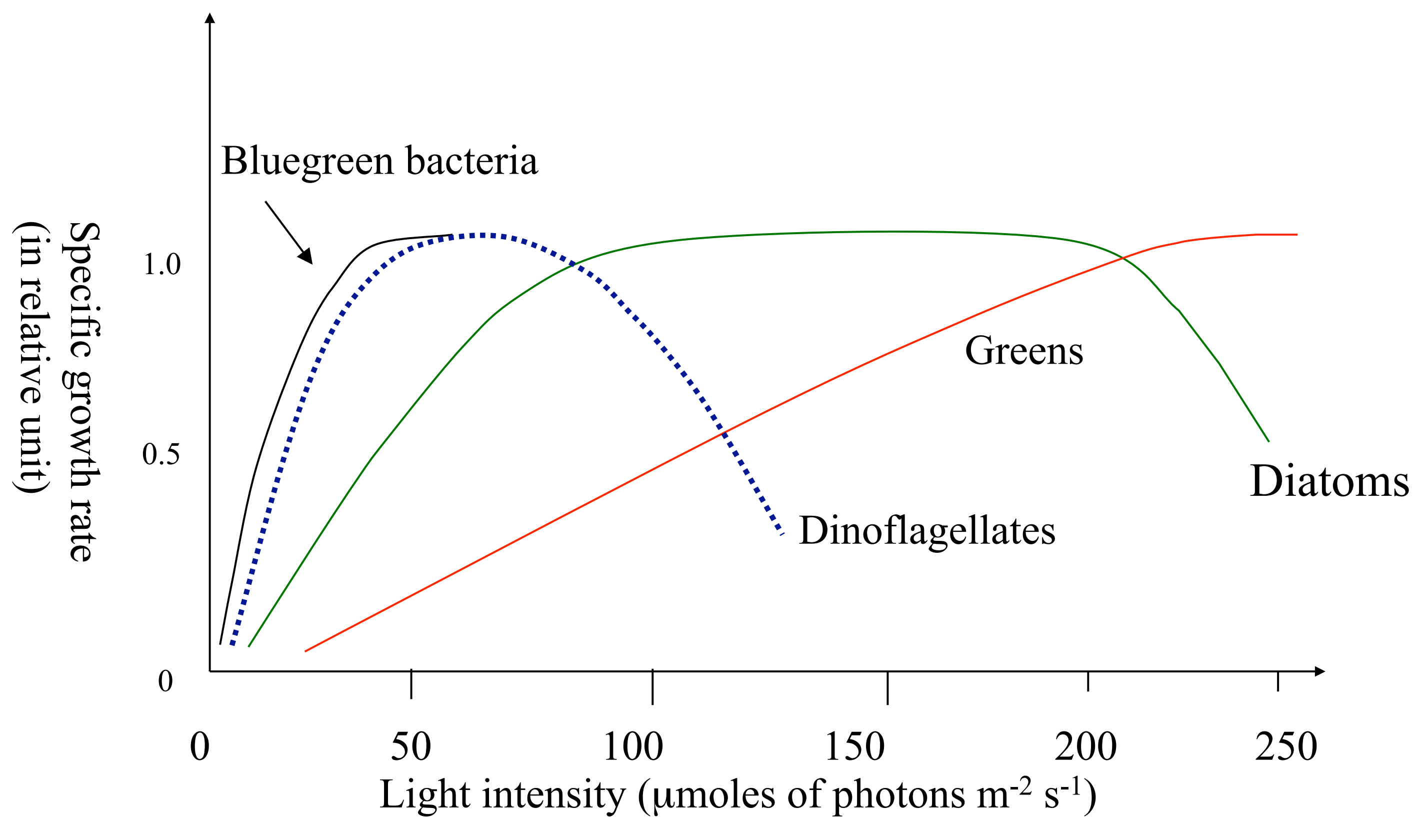

Question 3: What is the physical meaning of $I_c$ ?

**It is the minimum critical light intensity required for a positive net primary production.**

**Looking at (1) and (2), when *I* is known, $P_g$ and $P_n$ depend only on $P_{max}$ and $K_I$.**

In general

**For a given light intensity, different phytoplankton have different $P_{max}$ and $K_I$**



## The Vertical Profile of PAR:

$$I(x,y,z,t) = I_o(x,y,t)e^{-k|z|} \qquad (3)$$

where $I$: light intensity, $I_o$: the surface light intensity, $k$: the light attenuation coefficient

k usually is not a constant, which varies with location and time, also depends on radiation wavelength and phytoplankton concentration.

$\frac{1}{k}$: the vertical *e*-folding scale of the light penetration

In the shallow water, large turbulent mixing, water is turbid, large $k$, smaller $1/k$

In spring and summer, phytoplankton bloom occurs, light penetration reduces, large k.

**According to vertical profile of light intensity, the ocean life cycles can be divided into three biological layers in the vertical :**

1) **Euphotic layer**

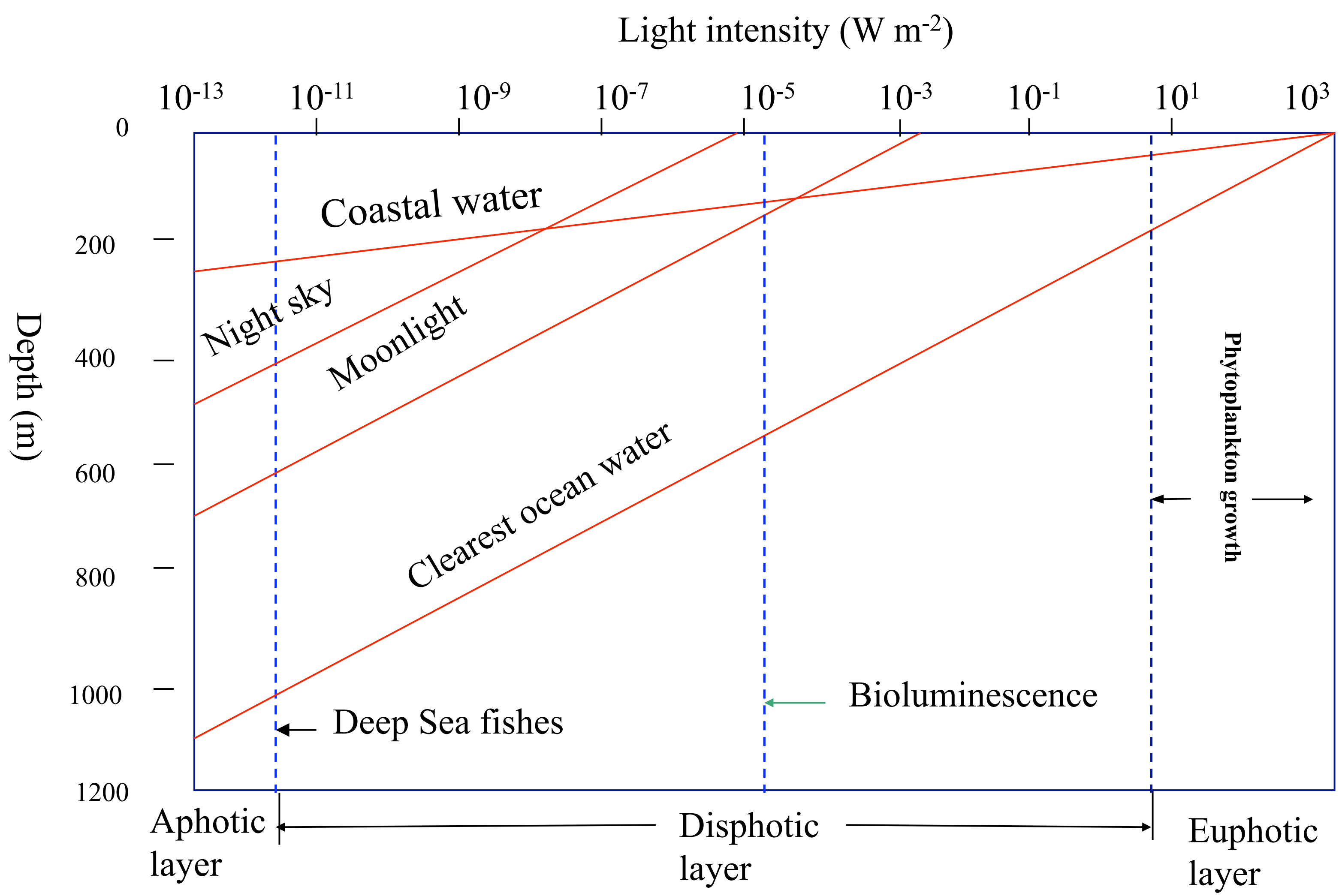
   **A positive photosynthesis layer. In this layer lights are strong enough to provide the needs for phytoplankton production. Also photosynthesis rate decreases with depth due to decrease of light intensity with depth.**

2) **Disphotic layer**

   **A layer in which light intensity is too weak to produce a positive photosynthesis production. However, fishes and zooplanktons, and other marine life still exist, and also phytoplankton from euphotic layer still be able to survive.**

3) **Aphotic layer**

   **A layer with no lights, a black world. Since most of marine life requires lights to survive, in this layer, no many marine animals could be found.**



Light intensity (W m-2)
10-13
10-11
10-9
10-7
10-5
10-3
10-1
101
103
0
200
400
600
800
1000
1200
Depth (m)
Coastal water
Night sky
Moonlight
Clearest ocean water
Phytoplankton growth
Bioluminescence
Deep Sea fishes
Aphotic layer
Disphotic layer
Euphotic layer

**Euphotic layer :**

**Varies with the water depth, it becomes smaller as the water becomes shallower**

**~ a few meter over the inner shelf close to the coast;**
**~ 200 m in a clean open ocean**

**Reasons:**

Water quality and turbulence mixing

In the shallow water, light penetration depth decreases with increase of vertical mixing of nutrients, suspended sediments, and phytoplankton blooms, so that euphotic layer could reduce to a few meters.

In the open ocean, turbulence mixing is usually much smaller, light could penetrate into a deeper region, so that euphotic layer could be deeper than 100 m.

## Compensation depth $D_c$:

**In the euphotic layer, primary production decreases with depth due to the decrease of light intensity with depth. The bottom of an euphotic layer is defined as a depth at which light intensity equals to compensation light intensity, i.e., at this depth the primary production produced by photosynthesis process is completely cancelled by loss of the production due to phytoplankton respiration.**

**The compensation depth $D_c$ is defined as a depth at which net primary production equals to zero.**

$$D_c = \frac{\ln I_o - \ln I_c}{k} \qquad (4)$$

**Since the compensation light intensity is different for different phytoplankton, for a given light intensity, the depth of the euphotic layer may be different.**

Note: $I_c = I_o e^{-kD_c} \Rightarrow \ln I_c = \ln(I_o e^{-kD_c}) = \ln I_o - kD_c \Rightarrow kD_c = \ln I_o - \ln I_c \Rightarrow D_c = \frac{\ln I_o - \ln I_c}{k}$

## Roles of Nutrients in Primary Production

Phytoplankton growth needs inorganic nutrients (nitrate, phosphorus, ammonia, and silicates, etc). In most coastal and open oceans, nutrients are limited. The phytoplankton growth is directly limited by nutrients.

**Assuming that light is sufficient, then the relationship between phytoplankton growth and nutrient concentrations can be expressed using Michaelis-Menten's formula as follows:**

$$\mu = \frac{\mu_{\max} N}{K_N + N} \qquad (5)$$

**$\mu$: the phytoplankton growth rate at $N$ under sufficient light condition;**
**$N$: the nutrient concentration;**
**$K_N$: the half-saturation constant of nutrients;**
**$\mu_{max}$: the maximum phytoplankton growth rate.**

**Questions 4: What is a relationship between the phytoplankton growth rate and nutrient concentrations if the growth is limited by multiple nutrient sources?**

**Key points:**

**Relationship between the phytoplankton growth rate and multiple nutrient concentrations is not linear!**

**Two popular methods:**

**1) Assume that the contribution of multiple nutrients to the phytoplankton growth rate is equal to a product of individual contribution described by Michaelis-Menten's formula.**

For example, consider nitrate, phosphorus, and silicates, we have

$$\mu = \mu_{\max} \frac{NO_3}{K_{NO_3} + NO_3} \cdot \frac{PO_4}{K_{PO_4} + PO_4} \cdot \frac{S_i}{K_{S_i} + S_i} \qquad (6)$$

a) **Relative contribution of individual nutrient depends on its own saturation rate;**
b) **Total contribution of multiple nutrients depends on a linear factor of individuals. When all nutrients are at a saturation level, their product is equal to 1.**

However, in a real application, it is difficult to make the product equal to 1.

**For example**:

**Contribution of each individual is 0.98,**

**a product of 3 nutrients is 0.94**
**a product of 10 nutrients is 0.82**

How do we know that product is correct?

**2) By competition, select one of multiple nutrients as a key control factor.**

For example, for three nutrients shown above:

$$\mu = \mu_{\max} \min\left(\frac{NO_3}{K_{NO_3} + NO_3}, \frac{PO_4}{K_{PO_4} + PO_4}, \frac{S_i}{K_{S_i} + S_i}\right) \qquad (7)$$

**Key assumption of the second method is :**

**Phytoplankton growth is mainly limited by one of the most important nutrient factors and the contribution of nonlinear interactions among multiple nutrients is generally one order of magnitude smaller than that key factor.**

This assumption is also difficult to be proved correct for the real ocean, since the interaction of multiple nutrients factors is not only a nonlinear process, but also varies with locations and times.

**In addition, in most of the ocean, the phytoplankton growth is directly controlled by nitrogen concentration (such as nitrate $NO_3$ and ammonia $NH_4$).**

$NO_3$: directly related to physical process, and it is one of main sources for primary production of phytoplankton;

$NH_4$: related to recycling of nutrients within food web, and it is one of main sources for regenerated production of phytoplankton.

In the case with available $NH_4$, phytoplankton tends to take $NH_4$ first, therefore, $NH_4$ acts like a factor inhibiting the uptake of nitrate by phytoplankton

**In this case,**

New production

$$\mu = \mu_{\max}\left(\frac{NO_3}{K_{NO_3} + NO_3} \cdot \frac{1}{1 + \frac{NH_4}{K_n}} + \frac{NH_4}{K_{NH_4} + NH_4}\right) \qquad (8)$$

Regenerated production

$K_n$ is the efficient coefficient of nitrate inhibited by ammonia.

**Advantages:**

1) **Physically separate the new and regenerated production processes. This allows us to identify the relative contribution of the environmental processes and internal recycling processes to the phytoplankton growth;**

2) **Introduce the inhibition role of ammonia to nitrate in the photosynthesis process.**

## Light Limiting and Water Temperature Factors

**Observational evidence**:

Uptake rate of nutrients by phytoplankton could be couple when water temperature change up to $10^{o}$ C.

$$\mu = \mu_{\max} \frac{N}{K_N + N} f(I) f(T) \qquad (9)$$

Where $f(I)$ and $f(T)$ are light intensity and water temperature controlling functions.

$f(I) = e^{kz}$ The photosynthesis rate has a maximum at the sea surface and decrease exponentially with depth. It is probably not correct during the summer when light intensity is very strong. In this case, the optimal condition for photosynthesis occurs at a subsurface due to light inhibition at the sea surface

$$f(I) = \frac{I}{I_S} e^{(1-\frac{I}{I_S})}$$

Where $I_s$ is a light intensity at the maximum photosynthesis rate

$$I = I_o e^{kz}$$

(Steele, 1962)

When light intensity is smaller than $I_s$ , photosynthesis rate increases exponentially with light intensity, but when light intensity is larger than $I_s$ , the photosynthesis rate decreases exponentially with increase of light intensity.

$$f(T) = e^{\alpha(T-T_o)}$$

$T_o$ is a temperature at which $\mu_{\max}$ is measured;

$\alpha$ is a factor related to an increase rate of phytoplankton uptake due to change of water temperature. $\alpha$ could be significantly different for different species of phytoplankton.

**In real ocean, the annual change of the water temperature is about $10^o \sim 20^o$ C, so there should no any infinite value issue by using an exponential form for temperature limiting factor.**

## Influences of Surface Mixed Layer on the Seasonal Variation of Phytoplankton Biomass → Sverdrup Theory (Sverdrup, 1942)

**Question 5:**

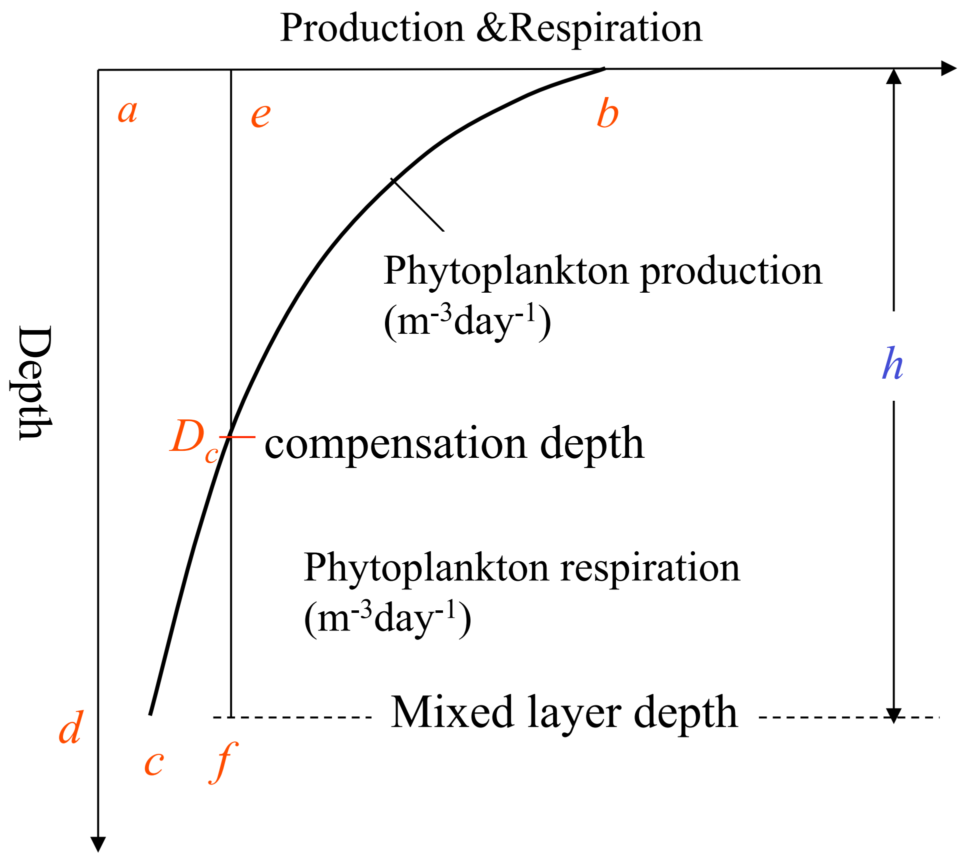
**What is the physical mechanism causing the springtime phytoplankton bloom?**

Guess: Atkin (1928): Solar radiation is couple in spring.

**Wrong! Because in many regions there exist an optimal light condition around a year, but the phytoplankton bloom only occur during spring.**

**Additional observational evidences:**

The seasonal variation of primary production in moderate climate region (at mid-latitude) is related to the seasonal change of water temperature. In fall and winter, surface cooling and strong winds tend to cause the surface mixed layer deeper than euphotic layer, the phytoplankton can not stay in the euphotic zone due to strong downwelling. Large part of these sinked phytoplankton stayed at the bottom of mixed layer, and then go back to the enphotic layer during spring time when the mixed layer become thinner due to stratification.




1) Line *bc* represents the vertical profile of primary production;

2) Line *ef* represents the daily respiration rate that is independent of light intensity;

3) $D_c$ is the compensation depth at this depth daily primary production gain is equal to daily respiration loss;

4) Individual phytoplankton cells randomly move in the vertical. When they move into the upper region above $D_c$, they grow, otherwise, when they move into a lower region below Dc, they can not grow due to limited lights.

**Therefore, if a net growth of phytoplankton exists in a mixed layer, then**

**Area of abcd > Area of aefd**

**Two more evidences:**

1) **When the mixed layer depth increases, the daily respiration loss area of aefd enlarges, but the daily primary production area of abcd does not changes!**

2) **When the mixed layer depth decreases, the daily respiration loss area of aefd decreases at a faster rate than the daily primary production loss area of abcd.**

**Therefore:**

**There must be a critical mixed layer depth $D_{cr}$, at which the total daily primary production generated by photosynthesis process equals to the total daily loss due to respiration.**

Phytoplankton grows as $h < D_{cr}$, otherwise, no phytoplankton grows.

**Question 7**: **How do to find $D_{cr}$?**

Assuming that the phytoplankton production rate at a depth is proportional to averaged light intensity at that depth,

the curvature line *bc* also represents not only the vertical profile of light intensity but also the vertical profile of phytoplankton production;

the straight line *df* or *ae* equals the light intensity $I_c$ at the compensation depth $D_c$. $I_c$ should be proportional to the respiration loss at any depth in the mixed layer:

$$I_c = I_o e^{-kD_C}$$

When the mixed layer depth equals to $D_{cr}$, the total loss due to phytoplankton respiration is

$$I_c D_{cr}$$

and the total phytoplankton production should be

$$I_o \int_{-D_{cr}}^{0} e^{kz} dz = \frac{I_o}{k}(1 - e^{-kD_{cr}})$$

**According to the definition of $D_{cr}$, the area of *aefd* and *abcd* must equal each other, i.e.,**

$$I_c D_{cr} = \frac{I_o}{k}(1 - e^{kD_{cr}})$$

**For given $I_o$, $k$ and $I_c$, $D_{cr}$ could be determined by using graphic approach (find the cross point of the right and left sides of the above equation).**

**Note: Sverdrup theory is derived by assuming that nutrients are not a limiting factor. In many real cases, it probably is not always true.**

For example, the diatom bloom is limited by silicate concentration. The diatom bloom could drop rapidly as thermoclines develop to restrict an upward supply of silicates from the deep stratified region to the mixed layer.