ON THE PHOTOSYNTHETIC POTENTIAL IN THE OPEN OCEANS

SOBRE EL POTENCIAL FOTOSINTÉTICO EN EL OCÉANO MUNDIAL

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The photosynthetic potential of the main primary producers in open oceans (phytoplankton) is quantitatively assessed using Jerlov's optical classification for ocean waters. To consider more accurately the inhibitory effect of ultraviolet radiation on photosynthesis, two biological weighting functions were used, one for equatorial and tropical phytoplankton, and the other for the subarctic one. Results show similar photosynthetic potentials in equatorial and tropical regions, and smaller photosynthesis rates for the subarctic zones. On the other hand, for the same latitude, there were considerable differences in the photosynthetic potential between the clearest open ocean waters (optical type I) and the darkest (optical type III), being around five times greater in the clearest open ocean waters. Se estima cuantitativamente el potencial fotosintético de los principales productores primarios (fitoplancton) en las cuencas oceánicas, utilizando la clasificación óptica de Jerlov para las aguas oceánicas. Para considerar con mayor exactitud el efecto inhibitorio de la radiación ultravioleta sobre la fotosíntesis, se usaron dos espectros de acción biológica, uno para el fitoplancton ecuatorial y tropical, y el otro para el subártico. Los resultados muestran similares potenciales fotosintéticos para las regiones ecuatorial y tropical, y menor para las subárticas. Por otro lado, para la misma latitud, hubo considerable diferencias de potencial fotosintético entre las aguas más claras (tipo óptico I) y las más oscuras (tipo óptico III), en todos los casos el potencial fue alrededor de cinco veces mayor en las aguas más claras.

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INTRODUCTION

Photosynthesis is the most basic process of Earth's biosphere. It transforms the energy of (solar) electromagnetic radiation in the approximate wavelength range 400–700 nm (photosynthetically active radiation, PAR) into biochemical energy. On the other hand, this process is inhibited by (solar) ultraviolet radiation (UVR). Therefore, in open oceans the maximum potential for photosynthesis in general is achieved at depths where the compromise UVR–PAR has some sort of optimum: where UVR has been sufficiently attenuated by water absorption and scattering, while still important amounts of PAR get there. This is the result of a stronger attenuation of UVR in ocean water (as compared to PAR).

In this work we use an optical classification of ocean water to assess, in a generic way, the potential for the photosynthesis of phytoplankton in the open oceans of our planet. Photosynthesis by phytoplankton cells in aquatic environments contributes to more than 40% of the global primary production [1]. Being phytoplankton the starting points in aquatic food assemblages, it is crucial to quantitatively assess the photosynthesis potential of ocean waters. Phytoplankton also has an important role in the regulation of climate in our planet, as it absorbs considerable amounts of carbon dioxide (a greenhouse gas) and releases oxygen to the biosphere.

MATERIALS AND METHODS

The solar radiation To make the quantitative assessment on the role of UVR on ocean phytoplankton productivity, we quantify the photosynthetic potential for phytoplankton for three representative (proxy) latitudes: equatorial (0°), tropical (30°) and subarctic (60°). Annual average solar spectral irradiances at these latitudes for photosynthetically active radiation (400-700 nm) and inhibitory ultraviolet radiation (280-400 nm) were used. In all cases cloudless skies were assumed.

The oceanic radiative transfer model It was used Jerlov's optical ocean water classification [2], selecting the ocean water types I and III (clearest and darkest).

The spectral irradiances just below sea surface $(z = 0^{-})$ were obtained from the corresponding ones just above sea surface $(z = 0^{+})$ through

$$E(\lambda, 0^{-}) = [1 - R]E(\lambda, 0^{+}), \qquad (1)$$

where *R* is the reflection coefficient obtained from Fresnel formulae applied to the interface air-water. The spectral irradiances $E(\lambda, z)$ at depth *z* were calculated using Lambert-Beer's law of Optics:

$$E(\lambda, z) = E(\lambda, 0^{-}) \exp[-K(\lambda)z]$$
⁽²⁾

 $K(\lambda)$ stands for the attenuation coefficient for wavelength. The set of attenuation coefficients define the optical type of ocean water. In [2] they are reported for given wavelengths, typically separated by intervals of 25 nm. For previous works some of us made a linear interpolation to have the coefficients for each wavelength in the full range 280 – 700 nm [3].

The irradiances of photosynthetically active radiation were calculated by

$$E_{PAR}(z) = \sum_{400nm}^{700nm} E(\lambda, z) \Delta \lambda, \qquad (3)$$

while those for ultraviolet radiation were weighted with a biological weighting function (BWF) $\varepsilon(\lambda)$ which gives more weight to more inhibitory wavelengths

$$E_{UVR}^{*}(z) = \sum_{222nm}^{399nm} \varepsilon(\lambda) E(\lambda, z) \Delta \lambda.$$
⁽⁴⁾

In equations (3) and (4), $\Delta \lambda = 1$ nm. To consider more accurately the inhibitory effect of UVR on photosynthesis we used two biological weighting functions (BWF) $\varepsilon(\lambda)$: one for temperate and other for Antarctic phytoplankton. These BWF's which account for both DNA damage and photosystem inhibition, resulting in whole-cell phytoplankton photosynthesis inhibition. The BWF for temperate phytoplankton was used to calculate the photosynthesis rate in equatorial an tropical zones, while the other was used for subarctic regions.

The photosynthesis model To compute the photosynthesis rates P at depth z (normalised to saturation rates P_s), we use a model for photosynthesis, typically employed with phytoplankton assemblages with good repair capabilities of solar UVR damage [4]

$$\frac{P}{P_{s}}(z) = \frac{1 - \exp\left[-E_{PAR}(z)/E_{s}\right]}{1 + E_{UV}^{*}(z)},$$
(5)

where E_{PAR} and E_{UV} are the irradiances of photosynthetically active radiation and ultraviolet radiation at depth *z*. The parameter E_s accounts for the efficiency with which the species uses PAR: the smaller its value, the greater the efficiency. The asterisk in E_{UV} means that spectral irradiances of UVR are weighted with a biological weighting function $\varepsilon(\lambda)$.

The average photosynthesis rate $\langle P/P_s \rangle$ in the first 200 meters of the oceanic water column was calculated splitting it into *N* layers. Then, the photosynthesis rate $P/P_s(n)$ inside the *n*-th layer was calculated. The average photosynthesis rate was then given by

$$\left\langle \frac{P}{P_s} \right\rangle = \frac{\sum_{n=1}^{N} \frac{P}{P_s}(n)}{N}.$$
(6)

RESULTS AND DISCUSSION

Figures 1–3 show the photosynthetic rates for optical ocean water type I (clearest).



Figure 1. Photosynthesis rates in ocean water type I in equatorial regions. Solid and dashed curves represent, respectively, high $(E_s = 2 W/m^2)$ and low $(E_e = 100 W/m^2)$ efficiency of phytoplankton in the use of PAR.



Figure 2. Photosynthesis rates in ocean water type I in tropical regions. Solid and dashed curves represent, respectively, high ($E_s = 2 W/m^2$) and low ($E_s = 100 W/m^2$) efficiency of phytoplankton in the use of PAR.



Figure 3. Photosynthesis rates in ocean water type I in subarctic regions. Solid and dashed curves represent, respectively, high ($E_s = 2 W/m^2$) and low ($E_s = 100 W/m^2$) efficiency of phytoplankton in the use of PAR.



Figure 4. Photosynthesis rates in ocean water type III in equatorial regions. Solid and dashed curves represent, respectively, high $(E_s = 2 \ W/m^2)$ and low $(E_s = 100 \ W/m^2)$ efficiency of phytoplankton in the use of PAR.

Figures 4–6 show the photosynthetic rates for optical ocean water type III (darkest).



Figure 5. Photosynthesis rates in ocean water type III in tropical regions. Solid and dashed curves represent, respectively, high ($E_s = 2 W/m^2$) and low ($E_s = 100 W/m^2$) efficiency of phytoplankton in the use of PAR.



Figure 6. Photosynthesis rates in ocean water type III in subarctic regions. Solid and dashed curves represent, respectively, high $(E_s = 2 W/m^2)$ and low $(E_s = 100 W/m^2)$ efficiency of phytoplankton in the use of PAR.

From a visual inspection of Figures 1–6, we see similar photosynthesis rates for equatorial and tropical regions. This can be explained because a more intense PAR in the Equator is accompanied by a more intense (inhibitory) UVR. In subarctic regions, the relatively low intensity of PAR determines a lower photosynthetic potential. This pattern is better seen after the application of equation (6) to obtain average photosynthetic rates in the first 200 meters of the ocean. Table 1 shows remarkable similar photosynthetic potential for equatorial and tropical regions, in the two extremes of optical ocean water (clearest and darkest) and for the two extremes of phytoplankton efficiency in the use of PAR (given by the parameter E_c).

Table I			
Average photosynthesis rates (%) in the first 200 meters of the ocean			
water column.			

Region	Water Type I		Water Type III	
	$E_s = 2 W/m^2$	$E_{s} = 100 \ W/m^{2}$	$E_s = 2 W/m^2$	$E_{s} = 100 \ W/m^{2}$
Equatorial	90	25	19	4.3
Tropical	89	23	18	4.1
Subarctic	76	12	15	2.3

As expected, in all cases species highly efficient in the use of PAR ($E_s = 2 W/m^2$) would have much higher photosynthetic rates than the very low efficient species ($E_s = 100 W/m^2$). Additionally, highly efficient species do not change their potential much when latitude changes, which would keep good

biological primary productivity in subarctic ocean regions, provided nutrients are available.

Table II Relative photosynthesis rates (the photosynthetic potential for clear waters divided by the corresponding one for darkest waters).			
Region	$\frac{P_I / P_{III}}{E_s = 2 W/m^2} \qquad \qquad E_s = 100 W/m^2$		
Tropical	4.9	5.6	
Subarctic	5.1	5.2	
Equatorial	4.7	5.8	

On the other hand, for the same latitude, there were enormous differences in the photosynthetic potential between the clearest ocean waters and the darkest ones. This is clearly seen in Table 2, where relative photosynthetic potentials are shown: in all cases the photosynthetic potential for the clearest ocean waters is around five times greater than the potentials in the darkest waters.

CONCLUSIONS

Our generic quantitative assessment of the potential for phytoplankton photosynthesis in Earth's open oceans shows that type I (clearest) ocean optical waters have a photosynthetic potential around five times greater than type III (darkest) ocean waters. Another interesting fact is that equatorial and tropical regions show quite similar potentials, caused by a similar balance PAR–UVR. This first modeling of planetary aquatic primary productivity considered only light (PAR and UVR). In the future, we shall address this issue from a more general point of view, introducing another variables such nutrients and temperature, and in general more elements of Quantitative Habitability Theory [5].

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