

Life in the Ocean – Primary Productivity and Respiration

الحياة في المحيط - الإنتاجية الأساسية والتنفس

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Life determines ocean chemistry and responds to it. It is not possible to understand the composition of seawater (or marine sediments) without understanding life processes. Organic matter in the ocean is produced by photosynthesis (and chemosynthesis to a lesser extent) and destructed by respiration.

Much of this material is covered in biological oceanography but here we talk about biological oceanography from a chemical oceanography perspective, with an emphasis on chemical tracers and feedbacks.

The topic is important for three key reasons:

1. One cannot understand the chemistry of the oceans without considering biological influences.
2. To understand the limits on biological production in the oceans, we need to understand the underlying chemical constraints (especially the macro (e.g. N and P) and micro (e.g. Fe and Zn) nutrients.
3. The balance between ocean productivity and respiration is called export production. Export production is the flux of biologically produced organic carbon from the surface ocean to the deep ocean and is also referred to as the biological pump. This biological pump is a primary control on atmospheric CO₂. Changes in the magnitude of the biological pump are one of the main explanations for why atmospheric CO₂ was lower during glacial times than during interglacials. It is important for us to understand how the biological pump might change in response to increases in anthropogenic CO₂ and global warming.

Units

Many different units are used for primary production. The most common are $\text{mmol C m}^{-2} \text{d}^{-1}$, $\text{mg C m}^{-2} \text{d}^{-1}$, $\text{g C m}^{-2} \text{y}^{-1}$, and Gt C y^{-1} . Chemical Oceanographers always recommend that moles be the preferred unit, i.e. $\text{mmol C m}^{-2} \text{d}^{-1}$. Use of moles makes comparison of stoichiometric ratios between nutrients and carbon easier.

Note: $1 \text{ Gt} = 1 \text{ Pg} = 10^9 \text{ tons} = 10^{12} \text{ kg} = 10^{15} \text{ grams}$

Global view of primary production:

A map of the distribution of primary production in the global ocean is shown on the following page.

| Note the | General Patterns: | |
|----------|--------------------|--|
| | Central gyres | Low |
| | Equatorial zones | high, especially toward the eastern boundaries |
| | Coastal regions | High |
| | Arabian Sea | High |
| | Circumpolar region | mostly moderately high |

There have been many different estimates of the **total amount of primary production** in the ocean. There is general consensus that the correct value is about 50 Gt C y^{-1} .

The total (marine plus terrestrial) global annual net primary production (NPP) has recently been estimated to be 104.9 Gt of C per year (Field et al., 1998), with similar contributions from the terrestrial (56.4 Gt, 53.8%) and oceanic (48.5 Gt, 46.2%) regimes. **NPP is defined as the amount of photosynthetically fixed carbon available to the first heterotrophic level in an ecosystem.** It can be expressed as the difference between autotrophic photosynthesis and respiration. This estimate was made using satellite data and the co-called CASA-VGPM biosphere model. In general, NPP for both land and ocean models is determined from the absorbed photosynthetically active (400 to 700 nm) solar radiation (APAR) and an average light utilization efficiency (ϵ).

Even though the total amounts are about equal, the amounts per area are greater on land than in the ocean. Average NPP on non-ice covered land is $426 \text{ g C m}^{-2} \text{ yr}^{-1}$ while in the ocean it is $140 \text{ g C m}^{-2} \text{ yr}^{-1}$. The lower NPP per unit area of the ocean largely results from competition for light between phytoplankton and their strongly absorbing medium, seawater. Only about 7% of the incident radiation as photosynthetically active radiation (PAR) is absorbed by the phytoplankton, with the remainder absorbed by water and dissolved organic matter. In contrast, terrestrial plants absorb about 31% of the PAR incident on land. Even though primary producers in the ocean are responsible for nearly half the total NPP, they represent only 0.2% of the global producer biomass. Thus, the turnover time of plant organic carbon in the ocean (average 2 to 6 days) is about a thousand times faster than on land.

Important major elements in soft parts - protoplasm (except H and O)

| | C | N | P |
|---------------|-----|------|---|
| Zooplankton | 103 | 16.5 | 1 |
| Phytoplankton | 108 | 15.5 | 1 |
| Average | 106 | 16 | 1 |

The table below summarizes the elemental ratios for P:N:C:Ca:Si in different forms of particulate debris settling into the deep sea as caught in deep moored sediment traps, the average ratios for deep and warm surface seawater and the ratios in plankton tows from different ocean areas.

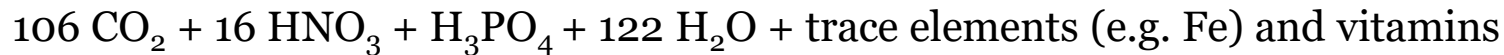
| Material | | P | N | C | Ca | Si |
|--------------------|--------------|-----|-----|------|------|-----|
| Particulate debris | Soft tissue | 1 | 16 | 106 | 0 | 0 |
| | Hard parts | 0 | 0 | 26 | 26 | 50 |
| | Composite | 1 | 16 | 132 | 26 | 50 |
| Seawater | Deep | 1 | 15 | 1000 | 5000 | 50 |
| | Warm surface | 0 | 0 | 868 | 4974 | 0 |
| Warm surface | %Removal | 100 | 100 | 13 | 0.5 | 100 |

The Redfield - Ketchum - Richards or "RKR" Equation

The data for the elemental composition of plankton were assembled to construct an equation to represent average photosynthesis and respiration. The elemental ratio in plankton is called the Redfield Ratio, after Alfred Redfield of Woods Hole. The mean elemental ratio of marine organic particles is thought to be highly conserved (Falkowski et al, 1998) and is given as:

$$P : N : C = 1 : 16 : 106$$

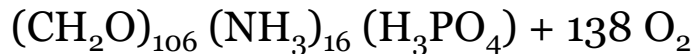
The RKR equation written for the average ocean photosynthesis and aerobic (O₂) respiration is written as:



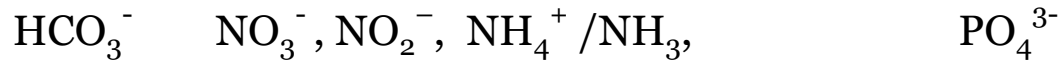
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or



The actual chemical species assimilated during this reaction are:

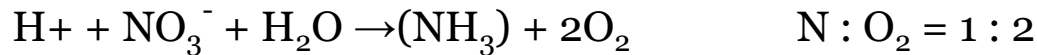
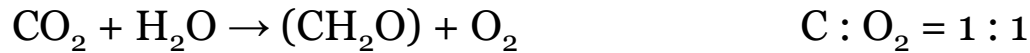


This is an organic oxidation-reduction reaction – during photosynthesis, C and N are reduced and O is oxidized. During respiration, the reverse occurs. There are no changes in the oxidation state of P.

Photosynthesis is endothermic. This means it requires energy from an outside source. In this case the energy source is the sun. Essentially plants convert the photo energy from the sun into high-energy C-C bonds. This is a non-equilibrium reaction whose slow kinetics are enzymatically facilitated.

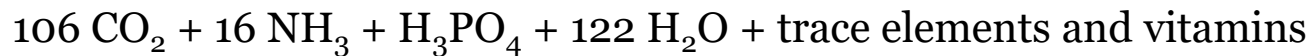
Respiration is exothermic. This means it could occur spontaneously and release energy.

Stoichiometry breakdown of oxygen production (theoretically calculated)

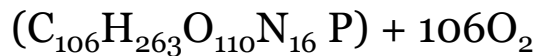


Total oxygen production: $106\text{C} + 16\text{N} \times 2 = 138\text{O}_2$

If ammonia is available it is preferentially taken up by phytoplankton. If NH_3 is used as the N source then less O_2 is produced during photosynthesis



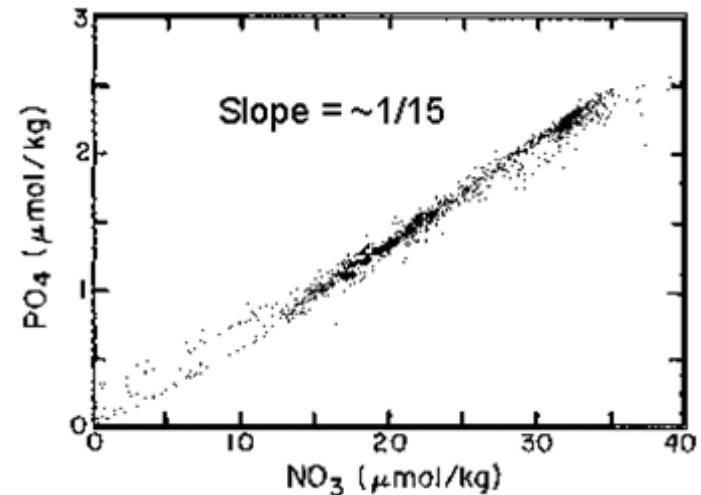
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Dissolved seawater N:P ratios are also close to the Redfield ratios. The slope is close to 15 (see figure). Falkowski et al (1998) point out that below the upper 500m, the average N/P ratio for the world's oceans is ~14.7, which corresponds to a small deficit in N. This deficiency corresponds to fixed inorganic nitrogen losses mediated by anaerobic denitrifying bacteria.

Shortcomings of the RKR paradigm:

- 1- The elemental composition of plankton varies with nutrient availability.
- 2- Plankton compositions vary regionally, as indicated by varying respiration ratios.

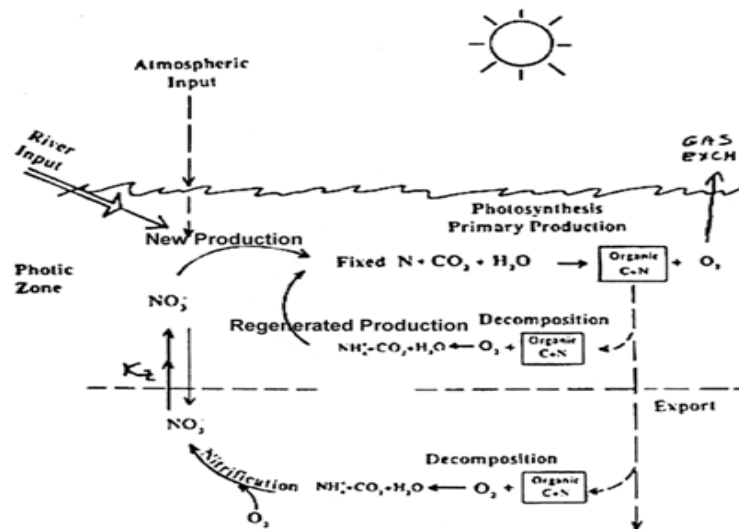


Dissolved Element Availability versus Plankton Demand:

- 1- Both N and P are in short supply (limiting) relative to plankton needs.
- 2- Inorganic C is present in seawater in ten times excess of that needed for photosynthetic use of all available N and P.
- 3- O₂-saturated seawater contains only a slight excess of oxygen versus the amount required to respire all the organic matter that can be photosynthesized from the available N and P.
- 4- Biogenic tests (“hard body parts”) also have global average compositions.
- 5- Si is limiting for diatom production.

New Production and Regenerated Production:

New Production is defined as the primary production that is based on NO_3^- as N source (from diffusion/upwelling from below and from the atmosphere via nitrogen fixation or nitrification) *Regenerated Production* is the production based on NH_4^+ and urea as N sources.



The **f-ratio**:

$f = \text{NO}_3 \text{ uptake} / \text{NO}_3 + \text{NH}_4 \text{ uptake}$ (the original definition by Dugdale and Goering, 1969).

If we write P = gross production and R = respiration then we can also approximate f as:

$f = (P - R)/P$ also called the ratio of **Net to gross production**.

At steady state NO_3 uptake should equal particulate and dissolved organic N flux exported out of the euphotic zone and the O_2 flux to the atmosphere (in equivalent units).

This is a schematic diagram of the new and regenerated production cycle (based on N source).

Magnitude of New Production

A global synthesis of new production was compiled by Chavez and Toggweiler (1995). These estimates were obtained by first estimating the rate of upwelling in the different ocean areas. The units are Sverdrups ($10^6 \text{ m}^3 \text{ sec}^{-1}$). The upwelling rate was multiplied by the nitrate concentration upwelled.

Assuming all the NO_3 is consumed and converted to carbon in the ratio $\text{C/N} = 106/16 = 6.6$ gives the estimate of new production. The calculation yields a total oceanic new production of $7.2 \times 10^{15} \text{ g C y}^{-1}$.

Predicting New Production

Eppley and Peterson (1979) wrote a classic paper in which they summarized existing data to suggest that new production should vary regionally in relation to the primary production rate.

They suggested the relation: $\text{New/Total} = 0.0025 \text{ Total}$; or $f = 0.0025 \text{ Total Production}$

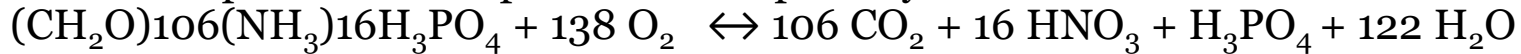
Other suggested relations include a relation based on sediment traps that indicates that the flux of C to depth for ocean depths bigger than 1000m is: $J(z) = 0.17 \text{ PP}/z + 0.01 \text{ PP}$; where PP is the primary productivity and Z the water column depth. Eppley gives a comprehensive summary of new production estimates and methods in the book *Productivity of the Ocean: Present and Past* (Wiley and Sons 1989).

Calculations by Falkowski et al (1998) of annual mean export (e.g. new production) using

CZCS chlorophyll distributions, the conversion of the chlorophyll data to primary production and the Eppley and Peterson conversion to new production yielded total global new production of 16 Gt C y^{-1} . This is about twice the value of 7.2 Gt C y^{-1} estimated by Chavex and Toggweiler. If NPP equals 50 Gt C y^{-1} then the corresponding global f-ratios are 0.32 and 0.14, respectively. Most field observations support the lower estimate.

Respiration

Aerobic respiration corresponds to RKR photosynthesis run backwards:



This means that the dissolved oxygen concentration is a tracer for respiration.

Respiration is:

- 1- An exothermic, enzymatically mediated reaction.
- 2- Theoretical stoichiometries closely match RKR values
 - a. $\Delta P = 1/138$ $\Delta \text{O}_2 = 1/138$ AOU
 - b. $\Delta N = 16/138$ $\Delta \text{O}_2 = 1/8.6$ AOU

Apparent Oxygen Utilization (AOU)

We can calculate the extent of respiration by calculating a parameter called the Apparent Oxygen Utilization or AOU. AOU is defined as: $\text{AOU} = \text{O}_2' - \text{O}_2$

Where: O_2' = value of O_2 the water would have if it was in equilibrium with the atmosphere at the temperature and salinity of the water. This is called saturation. This implies that all waters are in equilibrium with the atmosphere (100% saturated) when they sink to become the deep ocean water. O_2 in the above equation is the dissolved oxygen actually measured in the same water sample.

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Regenerated Nutrients

This term refers to the nutrients released to the water column as a result of respiration, these can be determined from RKR stoichiometries using a calculated AOU. Once you've calculated the AOU in a water sample, you can calculate the CO_2 , HNO_3 and H_3PO_4 released by respiration.

$$\begin{aligned} 1 \text{ mol O}_2 \text{ consumed} &= 106/138 \text{ mol CO}_2 + 16/138 \text{ mol HNO}_3 \\ &+ 1/138 \text{ mol H}_3\text{PO}_4 = \\ &= 0.77 \text{ CO}_2 + 0.12 \text{ HNO}_3 + 0.0072 \text{ H}_3\text{PO}_4 \end{aligned}$$