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Particulate organic matter flux and planktonic new production in the deep ocean

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Primary production in the oceans results from allochthonous nutrient inputs to the euphotic zone (new production) and from nutrient recycling in the surface waters (regenerated production). Global new production is of the order of $3.4-4.7 \times 10^9$ tons of carbon per year and approximates the sinking flux of particulate organic matter to the deep ocean.

The sinking flux of particulate organic carbon (POC) to the deep sea has been estimated from a geochemical, two-layer box model of the global ocean to be 10% of the surface ocean production. If surface production is in the range $20-45 \times 10^9$ tons C yr$^{-1}$ (ref. 2), then the sinking flux would be about $2.0-4.5 \times 10^7$ tons C yr$^{-1}$. We estimate the sinking flux of POC in the deep ocean by assuming that new production, as defined by Dugdale and Goering, is quantitatively equivalent to the organic matter that can be exported from the total production in the euphotic zone without the production system running down. Regenerated production constitutes the remaining production and is based on nutrients recycled through the food web of the surface ocean. The principal source of nutrients for new production is the upwelling and diffusion of nutrients from deeper water into the euphotic zone. Secondary sources are terrestrial (rivers, runoff, sewage), atmospheric (nitrate in rain, for example), and nitrogen fixation. Export fates of new production, other than sinking (and with a lower flux rate), include the fish and shellfish catch, deposition of guano on land by marine birds and the like.

Nature of the sinking POC

All the ocean contains sinking particulate matter which is the source of food for the microorganisms and animals of the deep waters and the sea floor. Most of the suspended material in seawater is in very small particles. Marine 'snow', consisting of macroscopically visible particles has been seen, however, wherever submersibles have explored. The abundance of deep-sea animals that feed on large food items is much greater than was realised before baited deep-sea cameras were used, suggesting that some of the sinking particles are large.

The herbivorous zooplankton of upwelling areas and of temperate waters are typically calanoid copepods. Copepods and certain other taxonomic groups of herbivorous zooplankton, by producing faecal pellets make a major contribution to the sinking flux of POC. About 20-30% of the organic carbon of the phytoplankton ingested by such creatures is passed in the faeces of the animals and the faeces are encapsulated in durable, fast-sinking packets which can rapidly transport organic carbon to a great depth. This mechanism was first discovered by radioecologists studying the vertical flux of radionuclides in the ocean. Typical sinking rates of faecal pellets in laboratory experiments are 50-300 m d$^{-1}$ (ref. 9).

In coastal temperate waters, traps for intercepting particles have caught largely intact phytoplankton during the spring bloom and largely animal faecal material as the zooplankton assemblage developed to graze down the phytoplankton bloom. Trap catches in the Peru upwelling have been dominated either by intact phytoplankton, by zooplankton faecal pellets and moults, or by the faecal material of the anchoveta, Engraulis ringens. Catches with faecal pellets are also reported for oligotrophic, deep ocean situations. The total flux seems to be approximately proportional to the plankton production in the overlying water. Because of the differential sinking and decomposition rates of large and small particles, the relative importance of faecal pellets as mediators of particulate carbon transport may increase with depth.

New production and carbon flux

Primary production in the illuminated surface layer of the ocean—the euphotic zone—can be viewed as depending on two different sources of nitrogenous nutrient supply. One is the supply of ammonia, urea and to a lesser extent amino acids and other dissolved organic nitrogen compounds derived from the excretory activities of animals and the metabolism of heterotrophic microorganisms. The food or substrate that fuels these activities, including the source of nitrogen, derives from phytoplankton via the food web. The phytoplankton production resulting from this recycled nitrogen is called regenerated production (Fig. 1). In an ideal closed system the cycling of nutrients through an enclosed food web could continue indefinitely with steady-state standing stocks and fluxes. In the real ocean, however, there are losses such as the flux of sinking faecal material and cast off exoskeletons out of the euphotic
Estimation of global new production

The geographical and seasonal data on new production estimates, including measurements of nitrate assimilation and nitrogen fixation, are insufficient to assess global new production directly. Total primary production, however, is quantitatively related to new production (Fig. 2) so that the measurements of total production, based on the photosynthetic assimilation of $^{14}$C-labelled CO$_2$, can be used to provide preliminary estimates of global new production.

In Fig. 2, the ratio of new production to total production was calculated in terms of nitrogen from the rate of nitrate incorporation (new production) and the sum of nitrate plus ammonium plus an estimate of the incorporation of urea and other organic nitrogen used by phytoplankton (total production). McCarthy found urea-N incorporation averaged 28% of the total N incorporation measured as nitrate + ammonium plus urea-N in southern California coastal waters. In the central North Pacific, urea-N incorporation averaged about one-half of that of ammonium-N. The line of Fig. 2 was not very sensitive to the estimate of organic-N incorporation. Total N incorporation was similar when calculated either as 1.3 (nitrate plus ammonium incorporation, Fig. 2a) or as (nitrate + 1.5 ammonium incorporation, Fig. 2b). Figure 2b shows values for individual stations in the offshore (depth >300 m) portion of the Southern California Bight, and provides a measure of the station–station variability; it also reveals some interesting exceptions to the expected values.

Data for shallow (<200 m) inshore waters of the Southern California Bight are not shown in Fig. 2b and they often fall below the line drawn in Fig. 2. This is probably because of the increased supply rate of ammonium from sediments and benthos in the shallow waters. The generality of Fig. 2a is applied here only for deep waters not under the influence of terrestrial runoff or the bottom—for waters where the vertical flux of nitrate is the principal driving force for new production.

Most of the recent estimates of the total ocean primary production are between 20 and 45 x $10^{10}$ tons C yr$^{-1}$. To estimate global new production we have used two estimates of total production which distinguish between production over deep water where Fig. 2 might be valid and production in shallow waters where it would not. New production was calculated from these, using Fig. 2a to judge what fraction of total production might be new production. The initial slope of the line of Fig. 2a, for total production <200 g C m$^{-2}$ yr$^{-1}$, is described by

$$\text{New}/\text{Total} = 0.0025 \text{ (Total)}$$

(1)

Tables 1 and 2 offer different regional groupings of the production data. New production from the Koblenz-Mishke et al. compilation and excluding their “neritic water” category (Table 1) is 18% of total production or 3.4 x $10^{10}$ tons C yr$^{-1}$. Estimates of Table 2 are based on the most recent measurements of total primary production in the oceans. The estimate of total and new production for waters of depth >200 m, is the highest of those considered and suggests new production is nearly 20% of total production or about 4.7 x $10^{10}$ tons C yr$^{-1}$.

### Table 1: Ocean primary production by water type

<table>
<thead>
<tr>
<th>Area ($\times 10^6$ km$^2$)</th>
<th>Primary production ($g$ C m$^{-2}$ yr$^{-1}$)</th>
<th>New production ($\times 10^6$ tons C yr$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oligotrophic waters of the central parts of sub-tropical halostatic areas</td>
<td>148</td>
<td>25.6</td>
</tr>
<tr>
<td>Transitional waters between sub-tropical and sub-polar zones; extremity of the area of equatorial divergences</td>
<td>83</td>
<td>51</td>
</tr>
<tr>
<td>Waters of equatorial divergence and oceanic regions of subpolar zones</td>
<td>86</td>
<td>73</td>
</tr>
<tr>
<td>Inshore waters</td>
<td>39</td>
<td>124</td>
</tr>
<tr>
<td>Neritic waters</td>
<td>11</td>
<td>365</td>
</tr>
<tr>
<td>Totals</td>
<td>356</td>
<td></td>
</tr>
</tbody>
</table>

* From ref. 27.
Table 2 Ocean primary production in offshore ocean areas* and estimates of new production based on Fig. 2

<table>
<thead>
<tr>
<th>Ocean</th>
<th>Offshore area (&lt;10^6 km^2)</th>
<th>Primary production (&lt;10^9 g C m^-2 yr^-1)</th>
<th>New production (&lt;10^9 C yr^-1)</th>
<th>Total C yr^-1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Indian</td>
<td>71.0</td>
<td>84</td>
<td>5.96</td>
<td>21</td>
</tr>
<tr>
<td>Atlantic</td>
<td>83.9</td>
<td>102</td>
<td>8.56</td>
<td>26</td>
</tr>
<tr>
<td>Pacific</td>
<td>167</td>
<td>55</td>
<td>9.14</td>
<td>14</td>
</tr>
<tr>
<td>Antarctic</td>
<td>11.8--23.8</td>
<td>325</td>
<td>(3.30)</td>
<td>45</td>
</tr>
<tr>
<td>Arctic</td>
<td>13.1</td>
<td>1</td>
<td>(0.13)</td>
<td>0</td>
</tr>
<tr>
<td>Totals</td>
<td>347-359</td>
<td></td>
<td>23.7</td>
<td>4.7</td>
</tr>
</tbody>
</table>

* From ref. 28.

Production over continental shelves and in other areas of water depth <200 m, including coastal upwelling areas, is omitted. Values in parentheses were considered under the <200 m category by Platt and Subba Rao and are omitted from the total estimates.

The polar oceans were not included in the calculations as equation (1) may not apply where growing seasons are short while ambient nutrients are high as in the Antarctic.

The large variation between the estimates of both total and new production for the global ocean leads to the conclusion that new production over the deep ocean may be between 3 and 5 x 10^8 tons C yr^-1, excluding the polar oceans. The lower estimate seems more reasonable in view of estimated rates of the decomposition of organic matter and the attendant oxygen consumption and nutrient regeneration rates in the deep water column. For example, if 18% of total production sinks to the deep ocean (Table 1), and 3.0% reaches the sediments, then about 15% or about 2.8 x 10^8 tons C yr^-1 would be decomposed in the water column. This decomposition would, in a homogeneous ocean, require about 10 μl O₂ 1^-1 yr^-1 on average. Menzel's30 oxygen consumption rates are 9.2--13.4 at 500 m depth and 2.1 μl O₂ 1^-1 yr^-1 at 4,000 m. The regeneration of nitrate from organic nitrogen from such a flux would be about 26 x 10^-6 mol m^-2 yr^-1 based on Redfield's elemental ratios for particulate organic matter25 and ignoring losses that could result from the formation of N₂ and N₂O. If the average nitrate concentration of the deep ocean is 30 mmol m^-3, its regeneration or formation time would be ~1,200 yr, a value similar to other estimates of the average residence time of the deep water1; Table 2 gives 800 yr for this time. If only 1% of the production reached the sediments this time would be decreased to about 1,000 and 720 yr, respectively. Thus the new production estimates of the sinking of particulate organic matter to the deep sea are not inconsistent with other estimates of the rate of decomposition of organic matter. However, this would incorporate1,29 a fairly wide range of estimates of such rates and for the flux of particulate organic carbon.

New: total production and nutrient recycling

Figure 2a implies that the extent of nutrient recycling within the euphotic zone varies regionally with the total production rate. If f is the new: total production ratio, then f is the probability that a nitrogen atom is assimilated by phytoplankton via new production and (1 -- f) is the probability of assimilation via regenerated production. The number of times a nutrient element is recycled in the euphotic zone before sinking out in particulate form (r) is given by (1 -- f)/f. For the central North Pacific (Fig. 2a), f = 0.05 and r = 19. If f = 0.5 (the asymptote of Fig. 2a), r = 1. Maximum observed values of f are about 0.8 implying that r = 0.25, and only one-quarter of the nutrient is recycled while three-quarters sinks out after being assimilated by phytoplankton. This could occur only if intact phytoplankton accounted for a major fraction of the sinking POC, as observed at the end of a spring bloom30,31, and transiently in the Peru upwelling32. The ratio f thus provides qualitative information on the nature of the sinking POC as well as quantitative information on the extent of nutrient recycling within the euphotic zone.

Broecker's geochemical model for the global ocean1 suggests that an element such as nitrogen is recycled about 10 times in the surface layer before sinking out. Thus r = 10, fm = 0.1 and new production is ~10% of the total primary production. Slightly higher values are suggested in Tables 1 and 2 where new production may be about 18 or 20% of total production, respectively.

Checking the validity of the approach

Broecker et al.31 estimated a mean upwelling rate of 27 m yr^-1 for the equatorial Atlantic between 15°S and 15°N latitude. No measurements of the new:total production ratio have been made there to our knowledge. If the deep-water nitrate concentration is ~15 mmol m^-3 the nitrate flux to surface waters would be 405 mmol m^-2 yr^-1. From the Redfield ratio, this would support a photosynthetic new production rate of 32.2 g C m^-2 yr^-1; from equation (1) the total primary production would then be (32.2/0.0025) x 113 g C m^-2 yr^-1. Suschenya and Finenko's32 earlier measurements with the 14C method of primary production in this area gave for the (Northern Hemisphere) fall season an average of 201 g C m^-2 yr^-1. Earlier data for the spring season averaged 88 g C m^-2. If annual production were the mean of these values, 145 g C m^-2 yr^-1, this would give fair agreement between the calculated and measured values. Although the result is encouraging, the spatial and temporal variation in the total production measurements suggests that care should be taken in estimating regional averages from a few scattered stations.

Conclusions

New production depends on mixing and vertical advective processes associated with the circulation. Total production also depends on new production and is roughly proportional to it at low to moderate production rates.26 Thus over geological time climatic changes that reduced vertical mixing and advection must have greatly affected the planktonic production process.
Molecular structure of a left-handed double helical DNA fragment at atomic resolution

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The DNA fragment d(CpGpCpGpCpG) crystallises as a left-handed double helical molecule with Watson–Crick base pairs and an anti-parallel organisation of the sugar phosphate chains. The helix has two nucleotides in the asymmetric unit and contains twelve base pairs per turn. It differs significantly from right-handed B-DNA.

Crystallisation and structure solution

The ammonium salt of the deoxy hexamer d(CG), was prepared by a slight modification of the recently developed® phosphotriester approach. The crystals were grown from a solution containing 30 mM sodium cacodylate buffer (pH 7.0), 10 mM spermine tetrachloride, 15 mM MgCl₂ and 2 mM d(CG), using the vapour diffusion method as developed for tRNA crystallisation. The precipitating agent was 5% isopropanol. Crystals grew in the form of truncated rectangular plates over a period of 3 weeks and crystals measuring up to 0.7 × 0.7 × 0.5 mm were obtained for X-ray diffraction analysis. Crystals were mounted in a sealed glass capillary together with a droplet of mother liquor. The crystal was orthorhombic with space group P2₁2₁2₁, and cell dimensions a = 17.88, b = 31.55 and c = 44.58 Å. The h0l projection photograph revealed strong reflections in the region 3.4–3.7 Å along the c axis which suggested that the molecules were aligned with their bases perpendicular to the c axis. From the unit cell dimensions, we estimated that there would be one duplex containing 12 nucleotides in the asymmetric unit. The crystals were highly ordered and complete three-dimensional data were collected to a resolution of 0.9 Å using a Picker diffractometer.

The structure was solved by the method of multiple isomorphous replacement using three different heavy atom derivatives, Ba²⁺, Co²⁺ and Cu²⁺. Phase determination was carried out using the method of Blow and Crick, yielding a mean figure of merit m = 0.76 to 2 Å resolution and the "best" Fourier map was calculated. The electron density map and rough atomic coordinates were measured directly from the map. The structure was refined using the Konnert-Hendrickson refinement procedures. Several cycles of difference Fourier and sum function Fourier (2Fo–Fo) maps were calculated in order to locate all the atoms of the molecule as well as 62 water molecules, 1 hydrated Mg⁺⁺ ion and 2 spermine molecules. The mass of the asymmetric unit is

future plankton production and fisheries harvests is not clear.

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