New and size fractionated primary production

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Work Package I - Temporal evolution of surface production and fate of organic matter

The major activity during the period of this report was the WP I cruise to the Iberian shelf - cruise *CD114* on the *Charles Darwin* in August 1998 - which was led by Ian Joint, PML-c. Measurements were made from 29 July to 24 August and 2 conditions typically found in the region were studied in Lagrangian drift experiments. These measured changes in plankton production and biomass as a body of upwelled water moved south along the shelf and similar measurements were done within a filament as it moved off-shelf.

The first experiment began on 3 August when a drifting buoy was deployed at 42° 37'N 09° 24'W. The buoy was followed for 6 days, during which time it travelled along the shelf edge to 41° 56'N 09° 09'W. The second drifting experiment began on 14 August with the deployment of 5 Argos drifting buoys at 41° 56'N 09° 51'W; these were followed for 5 days. Further information on the daily drift positions, and all measurements done by cruise participants, is given in the Cruise Report - refer to the OMEX Web Page - <u>http://www.pol.ac.uk/bodc/omex/omex.html</u>.

WP I Task I.3 Nutrient dynamics, primary production, biomass and phytoplankton

The PML-c tasks in WP I relate to primary and new production. These were measured daily during both Lagrangian experiments. There were significant daily changes during the experiment in the upwelling region. Nitrate concentration declined over the first 4 days of the experiment and strong vertical gradients in nitrate concentration were found. There was clear evidence of nitrate utilisation with a deepening of nutrient depletion with time (Fig. 1). The vertical distribution of chlorophyll concentration also changed with time. At the beginning of the experiment, most of the chlorophyll was in the upper 15 m but by day 4, surface chlorophyll concentrations were reduced and the highest concentrations were below 10 m. (Fig. 1)



Fig. 1 Changes in vertical profiles of nitrate and chlorophyll concentrations between 3 and 6 August 1998

Primary production showed a similar change in depth profile with a general deepening of the region of maximum production. Primary production was usually measured by *in situ* incubations but on two occasions, on deck incubations were done when, for logistical reasons, it was not possible to do an *in situ* incubation. During the 5 days of the first drifting experiment, primary production increased from

ca. 828 mgC m⁻² d⁻¹ (69 mmolC m⁻² d⁻¹) to a maximum value of 1176 mgC m⁻² d⁻¹ (98 mmolC m⁻² d⁻¹). At the beginning of the upwelling experiment, the picoplankton fraction (<2 μ m) was slightly more productive than the >5 μ m fraction. However, there was little change in the production of the picoplankton during the experiment and most of the additional production was by the >5 μ m phytoplankton. (Fig. 2)



Fig. 2 Size fractionate primary production during the 2 Lagrangian experiments

During the experiment in the off-shore filament, production was less than half that in the upwelling region at the shelf edge (Fig. 2). This was a region of oligotrophic conditions and nitrate concentrations were *ca*. 10 nmol kg⁻¹. Picoplankton was the most productive fraction but was about 60% of the activity measured during the upwelling experiment. The >5 μ m phytoplankton fraction was much less active in the filament than in the upwelling water, suggesting that larger cells are less well adapted to low nutrient conditions than picoplankton.



Fig. 3 Size fractionated nitrate uptake during the upwelling experiment

During the upwelling experiment, nitrate uptake by different size fractions of phytoplankton was measured by *in situ* incubations with ¹⁵N. There was good correspondence between the *in vitro* ¹⁵N uptake rate and the observed change in ambient nitrate concentration on all but the first day of the

experiment; it is possible that a different water mass was sampled on day 1. The *f*-ratio declined from *ca*. 0.6 on Day 1 to *ca*. 0.1 at the end of the second experiment.

Nitrate was the dominant nitrogen source for phytoplankton. The uptake rates measured on successive days decreased as the nitrate concentration declined (Fig. 3). The >5 μ m phytoplankton was responsible for more than 50 % of the uptake. Most of the ammonium uptake (>65%) was by the small size-fraction and, although rates also decreased each day, ammonium became increasingly more important as a nitrogen source and *f*-ratio decreased from 0.7 to 0.5. As nitrate was used in the upper 10 m, the depth profile of *f*-ratio paralleled the changes observed in chlorophyll and primary production depth profiles.

Typical oligotrophic conditions were found in the filament. Nitrate and ammonium concentrations were below the detection limits ($<0.05 \ \mu mol \ kg^{-1}$) of standard autoanalysis and more sensitive methods were required to give accurate estimates of ambient nutrient concentration. Uptake rates of both nitrate and ammonium were 5 - 10 times lower than in the upwelling region. Primary production was approximately 0.2 - 0.5 that measured in the upwelling region and was dominated by pico- and small nano-plankton. The ratio of C:N uptake rates, based on the assumption that nitrate and ammonium are the only nitrogen sources, were 13 - 44. In comparison, the Redfield ratio is *ca.*6.7. This suggests either severe nitrogen depletion or the phytoplankton were utilising an alternative source of nitrogen.

Phytoplankton cells have been known for many years to utilise urea as sole nitrogen source. Urea concentrations were determined on samples, which had been stored frozen following GF/F filtration. In the upwelling region, concentrations were generally low (<0.05 μ mol kg⁻¹), although higher values were measured at the surface and the seasonal thermocline. In contrast, concentrations of urea in the filament were high throughout the water column (max. 0.6 μ mol kg⁻¹). Since nitrate and ammonium concentrations were less than 0.05 μ mol kg⁻¹ in the upper 30 m, the high urea concentrations suggest that urea could be a dominant source of available nitrogen.



Urea uptake (µmol kg⁻¹)

F-ratio determined with and without urea uptake



Fig.4 Urea uptake during in the oligotrophic conditions of the filament.

Microbial uptake of urea was greater than that of nitrate and ammonium by factors of 5 to 30. The *f*-ratio (which is defined as nitrate uptake \div uptake of all other nitrogen sources) is 10 times lower if urea uptake is included. This raises several questions regarding the source of nitrogenous nutrients for phytoplankton, particularly during times of severe inorganic nitrogen depletion. The first question is, are the urea concentrations correct? Even if these are reduced by a factor of 100, uptake rates were still *ca*. 3 times greater than NO₃⁻ and NH₄⁺ uptake. The measured urea uptake would remove all urea in the upper 10 m in one day. Therefore, if these data are correct, there must be a very large flux of urea. The second question is, what is this large source? Support for the hypothesis that urea is an important nitrogen source comes from the C:N uptake ratios. If urea uptake is exclude, the C:N uptake ratio was *ca*. 30; including urea uptake reduces the C:N ratio to *ca*. 4, which is much closer to the Redfield ratio. Therefore, it is probable that urea is an important nitrogen source for phytoplankton growth in the oligotrophic waters of the filaments. However, more research is required to understand the flux, and particularly the sources, of urea in these very oligotrophic regions.

Work Package II - Spatial, seasonal fluxes and biogeochemical processes in the water column

WP II Task II.4.1 Nutrient oceanography

Nutrient concentrations were measured throughout *CD114* in August 1998. Nitrate, nitrite, phosphate, silicate and ammonium were measured by standard autoanalyser methods during both Lagrangian experiments. In addition, in the offshore filament, the concentrations of nitrate and ammonium were measured by sensitive chemiluminescent and fluorescent methods. In these oligotrophic waters, nitrate concentrations were *ca*. 10 nmol kg⁻¹ and ammonium *ca*. 30 nmol kg⁻¹; these concentrations are close to the limits of detection of even these sensitive methods and emphasise that phytoplankton are extremely efficient at taking up nutrient at very low concentrations.

WP II Task II.4.4 Nitrate remote sensing algorithms

One major objective of OMEX II is to develop algorithms which will allow satellite remote sensing to estimate parameters over large spatial scales. In OMEX I, a relationship was found between sea surface temperature and nitrate concentration. Figure 5 shows that, although the region sampled during *CD114* was very heterogeneous, it is possible to develop algorithms to estimate nitrate concentration from SST. The r^2 of a fitted line to the data in Fig. 5 is 0.78.



Fig. 5 Relationship between sea surface temperature and nitrate concentration at 5-m depth on a transect along the Iberian shelf.

WP II Task II.5.4 Pigment biomarker

Chlorophyll concentrations if different size fractions of phytoplankton were measured during *CD114* as part of this task.

WP II Task II.7.1 CO₂ partial pressures and upper ocean biogeochemistry

PML-c is a minor partner in this task and activities have been limited to providing primary production estimates to the partners involved in pCO₂ measurements.

WP II Task II.8.2 Intercalibration of primary and new production

During the first Lagrangian experiment on *CD114*, primary production was measured by two independent groups. PML-c made measurements by *in situ* incubations for 24 h and IIM estimated primary production from the photosynthetic parameters determined from short-term incubations within an artificial light gradient. This was a major intercalibration since simultaneous measurements were done over the whole of the first Lagrangian experiment. Results were compared at the OMEX Annual meeting in Plymouth and it is clear that there is a large discrepancy between the methods (Fig.6).



Fig. 6 Primary production estimated by in situ incubations (PML) and modelled from photosynthesis/irradiance measurements (IIM).

Another intercalibration experiment will be carried out in Plymouth on 19-21 July 1999 to resolve this discrepancy.

WP II Task II.8.3 Parameterisation of primary production

Completion of the parameterisation is not possible until the problem outline above is resolved.

WP II Task II.8.4 New production

Another algorithm developed during OMEX I linked *f*-ratio with nitrate concentration. Fig. 7 shows the relationship between *f*-ratio and nitrate concentration in the upper 10 m of the water column obtained during *CD114*. The nitrate concentrations were much lower than those measured in OMEX I and so these data help to better define the shape of this curve.

We believe that we now have a robust understanding of the relationship between *f*-ratio and ambient nitrate concentration and that this algorithm can be applied to the OMEX region to obtain estimates of new production from satellite remote sensing.



Fig. 7 Relationship between ambient nitrate concentration and f-ratio determined during CD114

WP II Task II.8.5 Assimilation of phosphorus

Phosphorus uptake by phytoplankton and bacteria was measured during cruise *CD114*. Most of the uptake was by cells smaller than 2 μ m and there was significant uptake in the dark. These data indicate that a significant proportion of the uptake may have been by bacteria.

WP II Task II.8.6 Spatial and seasonal distribution of primary and new production

Primary production has now been measured by *in situ* incubations on 3 cruises; *CD105* in June 1997, a *Poseidon* cruise in February/March 1998 and *CD114* in August 1998. This is a substantial data set, which describes the activities of different size fractions of phytoplankton throughout the year.



Fig. 8. Proportion of ^{14}C fixed by phytoplankton cells >5 μ m, 5-2 μ m and <2 μ m in late winter and early summer.

The data from all three cruises (Fig. 2 and 8) emphasise the importance of the picophytoplankton to the productivity of this region. Even in winter, picoplankton can account for more than 50% of the production at certain stations/

WP II Task II.12.2 Algorithm development and validation

Primary production data have been supplied to NSS and collaboration is continuing to produce algorithms for remote sensing of primary production (see NSS report).

Work Package IV - Integrated margin exchange product

WP IV Task IV.2 Carbon sources, cycling and fates

As outline above, a ¹⁴C intercalibration experiment will be done in Plymouth in July 1999 to resolve the different estimates, which derive from the two methodologies in use. In addition, there will be an intercalibration of ¹⁵N methods with VUB and of phosphate uptake determinations with ULB.

WP IV Task IV.3 Nutrients, trophodynamics and fertility

A number of nutrient determinations have now been completed which give confidence in the methods being used by the different partners. In addition, PML-c is part of the QUASIMEME Quality Control Programme and fully achieves the standards set in that programme.