

The productive oceans

from P. M. Holligan

PHOTOSYNTHETIC phytoplankton are the primary producers in the oceans with around 80% of the total photosynthetic carbon fixation occurring in the open ocean, the remainder probably in upwelling areas and shallow seas (Ryther *Science* **166**, 72; 1969). In the nutrient-poor tropical and subtropical waters nutrients rather than light are considered to limit primary production, as levels of dissolved organic phosphate and nitrate in the surface layers of the ocean are generally close to or below the limits of detection. In this issue of *Nature* on page 210, J. C. Goldman, J. J. McCarthy and D. G. Peavey draw together much recent information on phytoplankton growth rates in the oceans and from this synthesis propose the simple concept that although in oligotrophic waters the supply of nutrients, nitrogen in particular, determines the biomass or standing crop of phytoplankton, and therefore productivity, the growth rate of the individual plant cells remains close to the maximum despite an apparent shortage of nitrate and inorganic phosphate.

Phytoplankton growth in oligotrophic waters has only been understood in detail since the institution of formal analysis of the concepts of nutrient uptake and regeneration (Dugdale *Limnol. Oceanogr.* **12**, 655; 1967). Subsequent research on this topic has been mainly concerned with the dynamics of algal growth in continuous culture systems and interpretation of such experiments in relation to field observations on nutrient distributions and the physiological characteristics of natural phytoplankton populations.

Goldman *et al.*'s important conclusion stems from two basic observations: first, that measurements of the carbon, nitrogen and phosphorus content of natural populations of marine phytoplankton consistently give ratios close to 106 : 15 : 1 for the three elements and, second, that in their own experiments with continuous cultures of different species of algae these ratios are only attained at maximal growth rates. The central theme in the interpretation of the data is the analogy of steady state growth both in the continuous cultures and in surface oceanic waters. For the latter it is assumed that regenerative processes are the principal source of nutrients, providing a continuous supply of ammonium, urea and other organic forms of both nitrogen and phosphorus, and also that

the spatial and temporal distributions of phytoplankton biomass are effectively uniform.

The basis for this approach to phytoplankton growth has been established over the past few years by several research groups. For example, Thomas (*Limnol. Oceanogr.* **15**, 380; 1970) and Morris *et al.* (*Limnol. Oceanogr.* **16**, 859; 1971) provided evidence to suggest that phytoplankton in nutrient-poor waters is not nitrogen deficient; the similarity between the oligotrophic oceanic environment and steady-state culture systems was first pointed out by Eppley *et al.* (*Limnol. Oceanogr.* **18**, 534; 1973); and the possibility that grazing stress influences nutrient utilisation by phytoplankton was evaluated by Walsh (*Limnol. Oceanogr.* **21**, 1; 1976). But, as Goldman, McCarthy and Peavey indicate, acceptance of their simple concept of primary production in the oceans will depend on further investigation both of the ways in which nutrients are made available in the euphotic zone and of the physiological responses of plant cells to changes in the nutrient regime.

Although there are uncertainties about the details of nutrient recycling in surface oceanic waters, the general principles, in terms of the role of zooplankton and bacteria and also the relative time scales for the regeneration of nitrogen and phosphorus, are probably fairly well understood. This does not seem to be true, however, for the processes determining the transfer of nutrients into the surface layer. Thus, the influence of small-scale, vertical mixing across the thermocline on primary production has been recognised only recently (McGowan & Hayward *Deep-Sea Res.* **25**, 771; 1978), and considerable horizontal heterogeneity of biological as well as physical properties has now been described by Wiebe *et al.* (*Deep-Sea Res.* **23**, 695; 1976) and Shulenberger (*Deep-Sea Res.* **25**, 1193; 1978). Short-term variations in the concentrations of regenerated nutrients, that have been related to the vertical migration of zooplankton (Beers & Kelley *Deep-Sea Res.* **12**, 21; 1965), may also be produced by the combination of physical and biological processes at the level of the deep chlorophyll maximum which is a characteristic feature of tropical oceanic waters (Yentsch *Deep-Sea Res.* **12**, 653; 1965; Venrick *et al. Fish. Bull.* **71**, 41; 1973; Gieskes *et al. Neth. J. Sea Res.* **12**, 195; 1978).

Any fluctuation in the supply of nutrients raises the question of how phytoplankton cells and populations adapt to such changes. This complex problem is now attracting a great deal of attention, and the types of response shown by stressed cells to increased levels of nutrients range from the rapid stimulation of uptake rates (McCarthy

& Goldman *Science* **203**, 670; 1979) to more gradual 'shift-up' phenomena which lead to higher maximal growth rates (see Dugdale *The Sea* Vol. 6 (ed. Goldberg) 789; 1977).

One aspect of the ecology of oceanic phytoplankton that has been very neglected is their taxonomy. Apart from coccolithophorids (Okada & McIntyre *Micropaleontology* **23**, 1; 1977) the dominant forms are probably small (< 10 µm diameter), naked flagellates. These are difficult to culture or to preserve for direct microscopic and, as a result, little is known about the physiology of growth or of the distribution of the important species in the ocean. Furthermore, investigations of nutrient utilisation by mixed populations (Tett *et al. J. mar. biol. Assoc. U.K.* **58**, 923; 1978) or of nutrient competition between species (Tilman *Ecology* **58**, 338; 1977) have only been carried out for coastal and freshwater phytoplankton communities. The need for information about the biology of individual organisms is emphasised by the recent discovery by Waterbury *et al.* (*Nature* **277**, 293; 1979) that unicellular cyanobacteria (blue-green algae), 1–2 µm in diameter, are widespread in the sea.

It remains to be seen whether the hypothesis proposed by Goldman *et al.* is an accurate description of phytoplankton growth in the tropical oceans within the scales of variability that are known to exist, and whether the same ideas can also be applied to stratified continental shelf and temperate oceanic waters. □

Carbon in the sea

from Egon T. Degens

THE chief goal of a recent conference on Carbon in the Sea* was the evaluation of recent base-line studies in the Atlantic and the Pacific in respect to their contribution to understanding the global carbon cycle.

In the sea, carbon is partitioned into an oxidised and a reduced carbon pool. Bicarbonate ion is the principal species in the oxidised pools, dissolved organic matter in the reduced pool. The sizes of the two reservoirs are 35×10^{18} and 1×10^{18} g C, respectively. These figures

*A Conference on Carbon in the Sea was held in Hamburg on 14–16 March, 1979. It was organised by the staff of the SCOPE International Carbon Unit at Hamburg University, 2000 Hamburg 13, FRG, from whom further details may be obtained. SCOPE is the Scientific Committee on Problems of the Environment of the International Council of Scientific Unions (ICSU). SCOPE's project on Biogeochemical Cycles includes studies on the cycles of carbon, nitrogen, sulphur and phosphorus and is gradually being directed towards the interactions of these cycles. It is carried out with support from UNEP, Unesco and several national and international organisations. Further information can be obtained from the SCOPE secretariat, 51 Boulevard de Montmorency, 75016 Paris, France.

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