PRODUCTIVITY OF THE OCEANS

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Contents

Summary

Plants, by their growth, produce about the same quantity of organic material (40-60 GtC per year) in the oceans as on land, but it does not accumulate because it is consumed as fast as produced on a time-scale of weeks. Nor are the photosynthetic organisms similar in the two environments: at sea, bacteria and single-celled algae dominate. There are regional and latitudinal differences in the seasonal cycle and kinds of plant production in the sea, as on land, and these differences are dominated by the effects of differing solar irradiance and vertical stability of oceanic water masses, the latter controlling the supply of nutrient salts (nitrate, phosphate) to the lighted, surface waters..

For these reasons, the carbon cycle in the oceans is intimately linked to the atmospheric carbon dioxide level and will respond to the changes that are anticipated in ocean physics, as forcing by rising levels of anthropogenic CO2 intensifies. Whether these changes in the oceanic carbon cycle will result in positive or negative feedback cannot be predicted with confidence until concensus is reached on the nature of the changes that will occur in oceanic circulation.

1. Introduction

The annual production of organic material by plants is approximately similar both on land and in the sea. The mechanism of photosynthesis is well known: briefly, chlorophyll-containing plant cells use hydrogen ions to reduce carbon dioxide to carbohydrates, the energy required for the reaction being captured from sunlight. In the terrestrial biosphere, this reaction occurs principally in the leaves of higher plants - grasses, herbs and trees - but in the sea, photosynthesis is dominated by the activity of single, free-living plant cells of the phytoplankton. Only an insignificant proportion of the total marine productivity is contributed by the more familiar macro-algae, or seaweeds, that occur in a narrow strip only a few hundred meters wide along the coastline. The activity of the phytoplankton of the seas and oceans, thousands of kilometers wide, dominates marine primary production of organic matter. This Article is principally concerned with the productivity of the marine phytoplankton..

In extreme habitats, such as anoxic coastal basins and hydrothermal vents at deep-sea floor spreading zones, organic material may be produced by chemosynthetic bacteria which transform naturally-occurring inorganic molecules (e.g. methane, nitrite), or elements (e.g. sulphur, ferrous iron) into organic material. Chemosynthesis is not a major contribution to global energy budgets, and it will not be considered further here.

Phytoplankton are restricted taxonomically compared with land plants, and comprise only a few thousand Linnean species. In earlier years, it was customary to recognise geographically-distinct groups of species within each major taxonomic category. We now find it now more useful to recognise three universal groups of photosynthetic organisms: (a) a very small pico-fraction (0.5-2.0 μm of photosynthetic bacteria and eukaryotes, mostly small flagellates, (b) a nano-fraction (2-20 μm) of larger flagellates and small diatoms, and (c) a 'net' fraction (>20 μm), so called because caught in nets, of larger diatoms and dinoflagellates. The ecology of each group is singular, but the three groups are complementary in contributing to production of organic material in different regions of the oceans.

All photosynthetic cells face a similar set of problems. They require a sufficiently-illuminated aqueous medium with access to free carbon dioxide and to a range of other molecules that will supply the elements required for their metabolism (nitrogen, phosphorous, iron, and many others) together with those needed, like silica and calcium, for protecting their cellular structure. They must be able to release the waste products of their metabolism, including oxygen. And they must, as a population, multiply at least as fast as their rate of loss.

These problems present themselves very differently to oceanic phytoplankton cells and to the photosynthetic cells in the columnar epithelium of an oak leaf, for example. While CO_2 and H_2O are superabundant in the aqueous medium, both irradiance and nutrient supply are unreliable. If the cells are carried too deep by turbulence, they will encounter insufficient light for photosynthesis, though nutrients may be in high concentration; within the lighted layer, nutrients may become depleted by the activity of algal cells to below threshold concentrations and renewal is constrained by seasonal or episodic oceanographic processes. Finally, phytoplankton cells are lost to the active population quite differently from the way in which oak leaves are eaten by caterpillars: mostly, they either sink below the illuminated surface zone, or are individually consumed by filter-feeding herbivores (see Virus and Heterotrophic Microplankton). It will be necessary to review each of these processes in some detail to understand the control of the production of organic material by plants in the ocean.

It will also be necessary to consider how, and why, oceanic primary productivity differs regionally. As for terrestrial vegetation, it would be unreasonable to expect that plants in polar environments should grow according to the same rules as those in the tropics, though the principles will be similar. In the ocean, it is evident that regional oceanographic processes shall exert important control on the ecology of phytoplankton and that polar and tropical seas each have characteristic oceanographic regimes. Until recently, the available information on the relative distribution of plants in the oceans was far less complete than for the terrestrial flora, easily accessible to our own eyes and hands. Maps of the distribution of phytoplankton biomass, usually indicated by chlorophyll concentration per unit area of sea surface, and of estimates of its productivity, were perforce based on the very limited numbers of observations that had been made from oceanographic research ships

The data available for such mapping until very recently were strongly biassed towards coastal regions and certain oceans, the North Atlantic in particular, and some whole ocean basins, like the South Atlantic, still remain essentially *mare incognita*. For the tasks at hand, such a small data base is barely adequate though matters have improved enormously during the last few years as data from the Joint Global Ocean Flux Study become more generally available.

From 1979-1986, the passive radiometers carried aboard the Coastal Zone Colour Scanner (CZCS) satellite of NASA returned the first global images, pixel by pixel, representing sea surface chlorophyll biomass. This was a 'proof-of-concept' mission, so the sensors were only activated intermittently, and there remain serious doubts concerning their calibration, but the images were a revelation to biological oceanographers who were able to visualise for the first time the mesoscale distribution of plant material in all oceans. The intimacy of the relationship between physical oceanographic processes and the biomass and productivity of phytoplankton was confirmed dramatically. It was from these images that several research groups independently computed global productivity from the oceans, concluding that it was of the same order as terrestrial productivity.

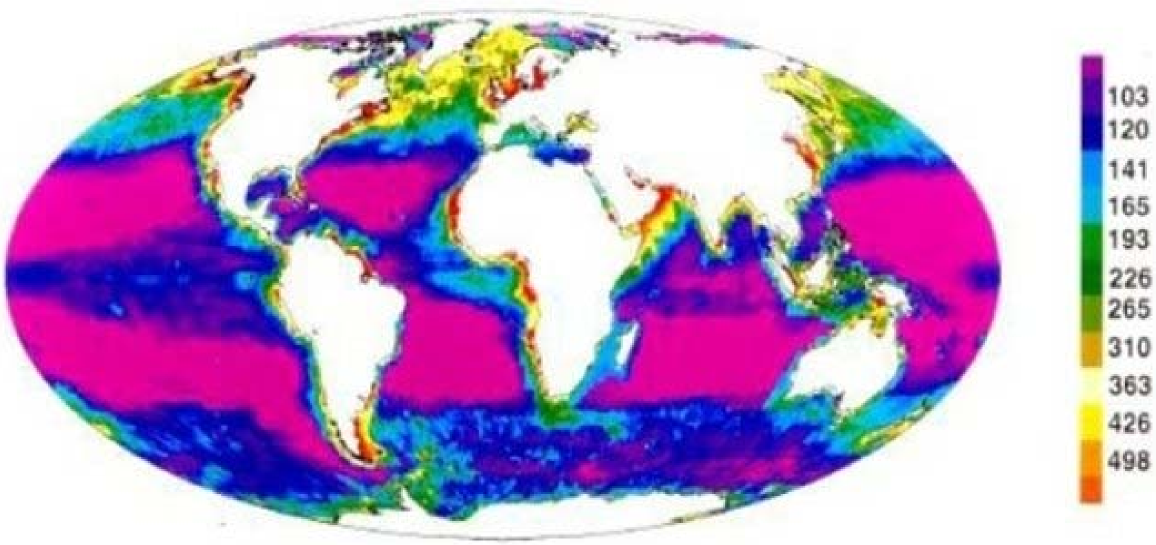

Figure 1: Global annual primary production of phytoplankton calculated from seas-surface chlorophyll field revealed by the coastal zone colour scanner (gC.m^{-2}.y^{-1})

These images also suggested a way in which the nature of the oceanic biomes, comparable to the terrestrial biomes of woodland, grassland, tundra and desert, could be inferred from oceanographic processes. To each could be assigned characteristic cycles of production and loss of plant material and a characteristic rate of primary production appropriate to each season.

Since 1996, other passive radiometer satellites have been flown, of which NASA's SeaWiFS is the most successful, at least in terms of data-flow. High-quality, high-resolution images (Figure 1) and data are freely available to any research group requiring them and many research teams themselves generate even higher resolution images of their own region of immediate interest by downloading data directly from the satellite. This is providing the substance for a revolution in biological oceanography.

Finally, it will be useful to note that marine productivity is, or should be, a matter of concern to those who are seriously attempting to assay the consequences of the release of carbon dioxide gas into the atmosphere from the combustion of fossil hydrocarbons. The activity of phytoplankton mediates, to an extent still debated, the flux of this gas across the sea surface.

This flux is controlled by complex and closely inter-related processes involving wind stress at the sea surface, differential partial pressure between sea and atmosphere, itself controlled by temperature, the uptake of the gas by active phytoplankton and its release by the heterotrophic metabolism of bacteria by their consumtion of dead algal cells and other organic debris.

Closure of this balance is difficult to achieve because the oceans themselves are an open system. That is, part of the organic material respired by bacteria and other heterotrophs is of terrestrial origin, delivered by rivers, and part of the organic material produced by algae sinks to the deep-sea sediments, there to be conserved unrespired for millenia.

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Biographical Sketch

Alan Longhurst is a biological oceanographer who began work in the mid-1950s in a fisheries research station in Freetown, Sierra Leone, and later in Lagos, Nigeria. He then directed the NOAA Southwest Fishery Center in La Jolla, California, and the Marine Ecology Laboratory in Nova Scotia. After ten years as Director-General of the Bedford Institute of Oceanography also in Dartmouth, Nova Scotia, he returned to full-time reasearch within that instutute, using satellite imagery in the study of biological processes in the sea. He retired at age 70 in 1995.

He has published more than 100 research papers in the field of fish biology and population dynamics, the ecology of tropical benthos and of oceanic plankton, and has worked at sea from New Zealand to the Canadian arctic, but more especially in the tropical Atlantic and Pacific. He has published three books, the most recent being "Ecological Geography of the Sea" (Academic Press, 1998) which summarises his views on the global relationship between physical oceanography and the production of phytoplankton, and the general productivity of the oceans at higher trophic levels.

He now lives in France, where he and his wife run a small gallery of contemporary art, and where he continues to write.