## The hidden half: marine primary productivity

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alf of the photosynthetic primary productivity on Learth occurs in the ocean. 98% of marine primary production is carried out by phytoplankton. These are photosynthetic organisms, almost all less than one mm long, in the upper few tens or hundreds of metres where sufficient light penetrates to allow rates of photosynthesis in excess of the rates of processes that remove the organic matter produced. The remaining 2% of marine primary productivity involves seaweeds and other photosynthetic organisms attached to the small illuminated fraction of the ocean floor. The marine primary producers are very diverse, in terms of the higher taxonomic levels (Phyla, Kingdoms). By contrast, terrestrial photosynthetic organisms are almost all so-called 'higher plants' (Embryophyta) from the Kingdom Plantae. Fig. 1 shows the number of formally described species, and the range of higher taxonomic levels involved, in primary productivity in the ocean, in freshwaters and on land. Fig. 2 shows examples of some of the major eukaryotic groups represented in the marine phytoplankton. This great diversity of higher taxa represented in the marine phytoplankton is a challenge to those of us who seek to understand the co-existence of these organisms with their different evolved approaches to living in what, at first glance from land-based observers, seems to be a rather homogeneous environment. Complete genome sequences are helping such mechanistic investigations, but so far only a handful of cyanobacterial sequences and one diatom sequence have been formally published.

Much of the senior author's work on marine (and freshwater) photosynthetic organisms has centred on the means by which they acquire inorganic carbon in photosynthesis, and the interactions of carbon acquisition processes with the supply of resources such as light and other nutrient elements. This may seem to be an arcane pursuit in view of the high concentration of inorganic carbon (carbon dioxide and the ionic compounds with which it equilibrates in solution) in seawater relative to that of other nutrients, and the stoichiometry in which the various elements are required by the organisms. However, the concentration and diffusivity of carbon dioxide in water are relatively low, and the general absence of limitation of marine primary productivity by inorganic carbon supply involves the operation of a range of 'carbon concentrating mechanisms'. Some of the research in our laboratory and with co-workers in the University of Sheffield addresses the possibility of a mechanism of inorganic carbon acquisition in marine phytoplankton resembling that of C4 land plants such as maize and sugarcane. Work in our laboratory, and elsewhere, shows that the operation of these carbon concentrating mechanisms is changed by the supply of other resources. A low light supply for growth decreases the engagement of these concentrating mechanisms, while a restricted supply of other nutrient elements usually increases their engagement. Many of these effects can be rationalised in terms of models developed here on resource costs of building, and operating, the photosynthetic apparatus. However, such rationalisation is not the same as showing the significance of these effects in natural selection. Several publications, with collaborators elsewhere, from our laboratory in 2005 present new data on carbon concentrating mechanisms and their interaction with environmental influences





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**Figure 2** Examples of eukaryotic marine phytoplankton: light micrographs (Nomarski differential interference microscopy) of living cells, and scanning electron micrographs of dried and coated cells. (a) A chain of the diatom *Stephanopyxis nipponica*. (b) A single valve (half of the silicified cell wall) of the diatom *Thalassiosira pacifica*. (c) The large, tropical coccolithophore *Scyphosphaera apsteinii*. (d) An overlapping pair of phycomas of the prasinophyte *Pterosperma moebii*. (e) A clump of cocco-spheres of *Gephyrocapsa oceanica*. (f) The athecate ('naked') dinoflagellate *Karlodinium micrum* (= *Gyrodinium galatheanum*). (g) The thecate dinoflagellate *Lingulodinium polyedra* (flagella missing). Scale bars: (a,c,e.f) 10  $\mu$ m; (b,g) 2  $\mu$ m; (d) 25  $\mu$ m.<sup>1</sup>

on the time scale of both evolutionary adaptation and short-term acclimation. Other publications synthesise the available information in this area in the context of the wider questions of determinants of marine primary productivity. One publication in which the senior author was involved was the Royal Society report on Ocean Acidification due to Increasing Atmospheric Carbon Dioxide.

Man's activities have released a large amount of carbon dioxide to the atmosphere over the last two centuries. A third of this carbon dioxide remains in the atmosphere as a contributor to the greenhouse effect, a third has been accumulated in terrestrial ecosystems, and the remaining third is now in the ocean. The ocean is thus responsible for the removal of half of the anthropogenic carbon dioxide that is not found in the atmosphere. Most of the carbon dioxide dissolving in the ocean remains in the form of inorganic carbon, but this does not mean that it has no biological effects. In particular, the changes to the equilibrium among the various chemical species of the inorganic carbon system and the associated lowering of pH decreases the degree of super-saturation of the surface ocean with respect to solid phases of calcium carbonate. This in turn decreases the potential for calcification of organisms; among the phytoplankton these calcified organisms are essentially all coccolithophores (Fig. 2), which are members of the Prymnesiophyceae (Fig. 1). Coccolithophores are quantitatively important members of the phytoplankton; while increased surface ocean carbon dioxide can reduce calcification by coccolithophores, it can increase the production of organic carbon in photosynthesis by these organisms. Work is continuing, here and in other laboratories, on the generality of the previously reported effects of increased carbon dioxide on coccolithophores.

## References

<sup>1</sup> Falkowski, P.G., Katz, M.E., Knoll, A.H., Quigg, A., Raven, J.A., Schofield, O. & Taylor, F.J.R. (2004). *Science* **305**, 354-360.