

Oceanography

Plankton in a warmer world

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Satellite data show that phytoplankton biomass and growth generally decline as the oceans' surface waters warm up. Is this trend, seen over the past decade, a harbinger of the future for marine ecosystems?

Oranges in Florida, wildfires in Indonesia, plankton in the North Pacific — what links these seemingly disparate items is that they are all affected by year-to-year fluctuations in global-scale climate. On page XXX of this issue, Behrenfeld *et al.*¹ describe their connection of such fluctuations, especially in temperature, with the productivity of phytoplankton in the world's oceans. Their analyses are based on nearly a decade of satellite data, and for much of the oceans they find that recent warmer surface temperatures correspond to lower oceanic biomass and productivity. Behrenfeld *et al.* argue that these patterns arise because climate-induced changes in ocean circulation reduce the supply of nutrients needed for photosynthesis.

Small photosynthetic phytoplankton grow in the well-illuminated upper ocean, forming the base of the marine food web, supporting the fish stocks we harvest, and underlying the biogeochemical cycling of carbon and many other elements in the sea. Phytoplankton growth depends upon temperature and the availability of light and nutrients, including nitrogen, phosphorus, silicon and iron. Most of this nutrient supply to the surface ocean

comes from the mixing and upwelling of cold, nutrient-rich water from below, with an additional source of iron from mineral dust swept off the continental deserts. Phytoplankton biomass can vary by a factor of a hundred in surface waters; the geographical distribution is determined largely by ocean circulation and upwelling, with the highest levels being found along the Equator, in temperate and polar latitudes, and along the western boundaries of continents.

Although **the broad spatial patterns of phytoplankton biomass and productivity are well** documented², large-scale temporal variations have only recently become quantifiable with the advent of satellite ocean-colour sensors³. The ocean is vast, and the limited number of research ships move at about the speed of a bicycle, too slow to map the ocean routinely on ocean-basin to global scales. By contrast, a satellite can observe the entire globe, at least the cloud-free areas, in a few days. Phytoplankton biomass and growth rates can be estimated remotely from space because chlorophyll, the main photosynthetic pigment in phytoplankton, absorbs blue and red sunlight more readily than green sunlight. Ocean-colour sensors measure, by wavelength band, the small fraction of sunlight scattered back to space from below the surface. The resulting surface-chlorophyll data can be combined with empirical relationships to estimate phytoplankton growth rates or net primary production⁴.

Not that this procedure is straightforward: other constituents of sea water absorb light; many photons reaching the satellite sensor come from atmospheric aerosols or reflection at the water surface; and optical detectors on satellites degrade with time. But with

careful calibration, high-quality, long-term records of ocean-colour data can be constructed for detecting climate-driven trends. The best such record at present is from GeoEYE and NASA's Sea-Viewing Wide Field-of-View Sensor (SeaWiFS)³, launched in the autumn of 1997. In the SeaWiFS time-series, global chlorophyll and productivity increase sharply during 1997–1998 and then decline gradually through 2005.

Behrenfeld *et al.*¹ show that these trends closely follow changes in climate. The phytoplankton increase in early part of the satellite record (1997-1998) matches a negative (cold) phase of the El Niño-Southern Oscillation (ENSO) while the subsequent slow drop in marine productivity occurred as the planet moved into an extended warm ENSO period. ENSO is a dominant mode of interannual climate variability, and involves large-scale reorganizations of atmosphere and ocean circulation that originate in the equatorial Pacific and extend across the globe. Decreases in productivity are equally well related to increases in sea-surface temperatures and vertical temperature gradients in the upper-ocean. The climate–plankton link is found primarily in the tropics and mid-latitudes where there is limited vertical mixing because the water column is stabilized by thermal stratification (that is, when light, warm waters overlies dense, cold waters). In these areas, the typically low levels of surface nutrients limit phytoplankton growth. Climate warming further inhibits mixing, reducing the upward nutrient supply and lowering productivity (Fig. 1a). At higher latitudes, phytoplankton are often light-limited because intense vertical mixing carries plankton hundreds of meters down into darkness where surface sunlight does not penetrate. In these regions, future warming and a greater

influx of freshwater, mostly from elevated precipitation and melting sea-ice, will contribute to reduced mixing that may actually increase productivity⁵ (Fig. 1b).

The recent observed surface ocean warming (about 0.2 °C per decade) is expected to accelerate in coming decades as we continue to release excess carbon dioxide into the atmosphere. In fact, the planet may soon be warmer than at any time in the past one million years⁶. Extrapolating the satellite observations into the future suggests that marine biological productivity in the tropics and mid-latitudes will decline substantially, in agreement with climate model simulations⁷⁻⁹. In those simulations, the geographical boundaries that separate specific marine ecosystems (the ocean equivalents of forests, grasslands, etc.) migrate towards the poles, and productivity increases at high latitudes because of surface warming, enhanced freshwater input, and reduced deep mixing. Ecosystem dynamics are complex and non-linear, however, and unexpected phenomena may arise as we push the planet into this unknown climate state. For example, oceanic fixation of atmospheric nitrogen into biologically available forms is concentrated in warm, nutrient-poor surface waters; under more stratified conditions, fixation might increase and enhance overall productivity^{8,10}.

Detecting the impact of climate change requires more, and more-sophisticated, monitoring of ocean biology and environmental change, both from space and with instruments in the water. Ideally, we need measures not only of such parameters as chlorophyll concentration and productivity, but also of plankton taxonomy (what is

there?) and physiology (how healthy are they?). New remote-sensing technologies may help meet these challenges¹¹.

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1. Behrenfeld, M. J. *et al. Nature* **000**, 000–000 (2006).
2. Longhurst, A. *Ecological Geography of the Sea*, 2nd edn (Academic, 2006).
3. McClain, C. R., Feldman, G. C. & Hooker, S. B. *Deep-Sea Res. II* **51**, 5–42 (2004).
4. Carr, M.-E. *et al. Deep-Sea Res. II*, **53**, 741–770 (2006).
5. Polovina, J. J., Mitchum, G. T. & Evans, G. T. *Deep-Sea Res.*, **42**, 1701–1716 (1995).
6. Hansen, J. *et al. Proc. Natl Acad. Sci. USA* **103**, 14288–14293 (2006).
7. Bopp, L. *et al. Global Biogeochem. Cycles* **15**, 81–99 (2001).
8. Boyd, P.W. & Doney, S. C. *Geophys. Res. Lett.* **29**, 1806 (2002).
9. Sarmiento, J. L. *et al. Glob. Biogeochem. Cycles* **18**, GB3003; doi:10.1029/2003GB002134 (2004).
10. Karl, D. *et al. Nature* **388**, 533–538 (1997).
11. NASA OBB Advanced Planning Team *Plan for Earth's Living Ocean: The Unseen World to Set NASA's Ocean Biology and Biogeochemistry Agenda* (NASA, in the press).

Figure 1 Phytoplankton response to increased temperature in ocean surface waters¹. a, In the tropics and at mid-latitudes, phytoplankton are typically nutrient-limited, and satellite data tie reduced biological productivity to upper-ocean warming and reduced nutrient supply. b, The opposite response to warming and freshening occurs at higher latitudes, where phytoplankton are often light-limited.

