creased phytoplankton productivity may therefore not be reflected in increased phytoplankton biomass levels, but may instead be rapidly transferred to higher trophic levels. Changes in phytoplankton community structure could also result in higher rates of production per unit biomass. Such changes could happen if, for example, the mean generation time of phytoplankton decreased as different groups of phytoplankton become more abundant; population growth rates, and therefore production, are directly proportional to generation time[3].

Several lines of evidence point to a change in North Pacific productivity, particularly at higher trophic levels. As well as the doubling of chlorophyll in the central North Pacific gyre between 1965 and 1985 (ref. 4) mentioned by Falkowski and Wilson, zooplankton biomass in the Gulf of Alaska also doubled between the 1950s and 1980s (ref. 5). A similar trend in zooplankton abundance is apparent in the western North Pacific[6] — although perhaps not in the central North Pacific[7]. The productivity of many fish populations in the northeast Pacific has also shown sharp increases, beginning in the late 1970s (ref. 8). Similar changes in a wide range of physical oceanographic variables have also occurred in the eastern Pacific[9]. These changes may be associated with the intensification of the Aleutian Low[10], a major meteorological system which dominates the weather of the North Pacific region.

The detailed reasons for these increases in productivity at higher trophic levels are unknown. They could involve increased levels of wind-driven mixing of sub-surface nutrients through the thermocline, shifts in phytoplankton community structure towards more intrinsically productive species, or increased insolation.

However, the assumption that productivity must be directly related to biomass or chlorophyll is a fallacy. Particularly in tightly coupled systems such as the North Pacific, increased phytoplankton production may not be reflected in increased phytoplankton biomass levels; production may instead be rapidly exported to higher trophic levels not readily indexed by Secchi disk measurements. There have been striking changes in biological productivity at higher trophic levels in the North Pacific, the mechanisms for which have yet to be fully explained. Nevertheless, the existence of these changes strongly suggests that Falkowski and Wilson's inference that open ocean phytoplankton productivity has remained roughly constant since the industrial revolution is premature, and may even be false. The potential for the oceans to act as an enhanced sink for anthropogenic CO_2 remains, although the absolute increase in the rate of oceanic CO_2 sequestering possible may still be small relative to the global carbon budget[11].

David W. Welch
Pacific Biological Station,
Department of Fisheries and Oceans,
Nanaimo, British Columbia,
Canada V9R 5K6

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FALKOWSKI AND WILSON REPLY — Welch objects to our application[1] of a simple algorithm[2] relating phytoplankton chlorophyll to productivity, calling it a "fallacy" in the North Pacific because of rapid export of production to higher trophic levels. In doing so he is confusing carbon fixation with the fate of phytoplankton[3]. Obviously chlorophyll is a pool and primary production is a flux, but primary production (carbon fixation) can be quantitatively related to chlorophyll through light, nutrients and temperature[4–6], independent of the fate of the production.

We agree that the specific algorithm we used would have been inappropriate if we were interested in examining seasonal or short-term changes in primary production, not because the algorithm does not include a grazing term but because it does not include terms for irradiance and quantum efficiency. But unless there have been marked changes over the past 30 years in insolation, the quantum efficiency of phytoplankton photosynthesis, or rates of nutrient supply, interannual changes or lack thereof, in chlorophyll (which we inferred from interannual changes in Secchi depths) will reflect interannual variations in primary production in the North Pacific or any other ocean basin.

Welch implies that to account for the apparent increases in zooplankton biomass over the past 30 years in the North Pacific without a marked concomitant increase in phytoplankton biomass (as reflected by chlorophyll), phytoplankton productivity must have increased. This would require that for the same amount of light energy (measured incident solar radiation has not varied by more than 0.5% since the beginning of the twentieth century[7]) more carbon is fixed per unit chlorophyll (the quantum yield has changed). Although the quantum yield of photosynthesis can vary in the ocean[8], a systematic, multi-decadal change in the quantum yield of twofold is highly implausible. Moreover, if such an increase in chlorophyll-specific production had occurred and was responsible for the changes in zooplankton biomass, the hypothesized increase in primary productivity would have to reflect an increase in new production[9] which, in turn, must be fuelled by a systematic increase in nutrient supply to the region. If, for example, primary productivity in the region is limited by iron[10], and iron is becoming increasingly available, the iron stimulation would have to lead to a reduction in upper ocean nitrate and phosphate in the summer over the past 30 years. There is no evidence of a systematic decrease in nutrients in the region[11]. Examination of the data showing the interannual variability in zooplankton biomass at Ocean Weather Station P (ref. 12) suggests there are decadal cycles, but the long-term, systematic changes are not clear.

Finally, as we discussed previously[1], even if primary productivity were to have increased, unless the increase was supported by nutrients external to the ocean, or led to depletion of the excess nutrients in the upper ocean, the effect on the drawdown of anthropogenic CO_2 would be insignificant[13]. We stand by our conclusion that the effect of open ocean primary production on the drawdown of anthropogenic CO_2 appears to be extremely small in comparison with other sinks.

Paul G. Falkowski
Cara Wilson*
Oceanographic and Atmospheric Sciences Division,
Brookhaven National Laboratory,
Upton, New York 11973, USA

* Present address: College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, Oregon 97331, USA.

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