Phytoplankton productivity in the North Pacific ocean since 1900 and implications for absorption of anthropogenic CO$_2$

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THE world's carbon budget has not been in steady state since the beginning of the Industrial Revolution[1]. At present, carbon dioxide released by anthropogenic activities adds about 7 ± 1.2 gigatonnes (Gt) C yr^{-1} to the atmosphere, of which about 2 Gt C yr^{-1} is thought to be sequestered in the oceans[2]. In the steady state, phytoplankton fix about 35–50 Gt C yr^{-1}, representing a significant component of the natural carbon cycle[1]. If ocean productivity were changing, these biological processes could have a significant influence on anthropogenic CO$_2$ levels by drawing down the CO$_2$ concentration in surface waters and increasing the concentration gradient across the air–sea interface[1,3,4]. The question of productivity changes is unresolved, however[2,5,6]. Venrick et al.[7] reported that phytoplankton chlorophyll concentrations had roughly doubled in the central North Pacific gyre between 1965 and 1985. Here we use historical records of Secchi depth data to investigate whether such dramatic changes in phytoplankton biomass have occurred throughout the North Pacific ocean during this century. We find that, although very minor changes may have occurred in this basin over the past 70 years, they are too small to have a significant effect on the rise in atmospheric CO$_2$ concentrations.

Introduced to oceanography in the nineteenth century by a Jesuit astronomer[8], the white Secchi disk, between 0.25 and 0.50 m in diameter, is lowered into the ocean and an observer measures the depth (Z_D) at which the disk disappears from view. This simple device is relatively insensitive to changes in observer technique and is still used by oceanographers. The Secchi depth (Z_D) can be related to optical coefficients of sea water through

$$Z_D = \ln[(A - R_{ZD})/R_0 C]/(c + K) \qquad (1)$$

where A is the disk albedo, R_{ZD} and R_0 are the reflectance functions at depths Z_D and the surface, C is a function of observer variability, c is the average beam attenuation coefficient (m^{-1}) and K is the average diffuse attenuation coefficient (m^{-1}) for downwelling irradiance.

Gordon and Wouters[9] and Preisendorfer[10] analysed the errors associated with different terms. Most of these are small, contributing to random, non-systematic errors of less than 10%. The primary source of variability in Secchi disk readings is in the $(c + K)$ term, which covaries with the amount of attenuating material in the water. In open ocean waters, with the exception of small amounts of atmospheric dust, all particles suspended in the water column have a biotic origin. Most of the variability in the absorption of visible light in the open ocean is related to the abundance of phytoplankton, which contain pigments such as chlorophyll[11], and Secchi depths can be empirically related to the variability in phytoplankton chlorophyll (Chl)[12-15] by the equation

$$\text{Chl} = 457 Z_D^{-2.37} \qquad (2)$$

(where Chl is in mg m^{-3} and Z_D in m) which is significant at the 99.9% level.

Nolton[14] compared chlorophyll values derived from Secchi depths with those calculated from the ratio of water-leaving radiances at 440 and 550 nm. The latter forms the basis of satellite-derived chlorophyll estimates[16] in open-ocean (case I[17]) waters. The comparison revealed that 89.7% of the variance in surface chlorophyll could be explained using the water-leaving radiance ratios, and 88.2% of the variance could be explained by Secchi depths. Thus, there is statistically only about 1.5% more uncertainty in estimating chlorophyll in the upper open ocean from Secchi depth measurements than from radiance ratio measurements at the sea surface. In fact, global maps of chlorophyll derived from Secchi data are closely comparable to those inferred from satellite measurements of ocean colour[13].

Secchi depths are the earliest oceanographic measurements of ocean transparency, and the global data set is one of the few historical measurements that can be analysed in biological oceanography from the beginning of the twentieth century. More than 116,000 Secchi depth observations, spanning the years 1900 to 1981, are archived by the National Oceanic Data Center (NODC); most observations are for coastal waters. The data analysed here, for the central ocean, consist of 10,733 observations made since 1907 and were primarily confined to the North Pacific, where the data set is richer both spatially and temporally
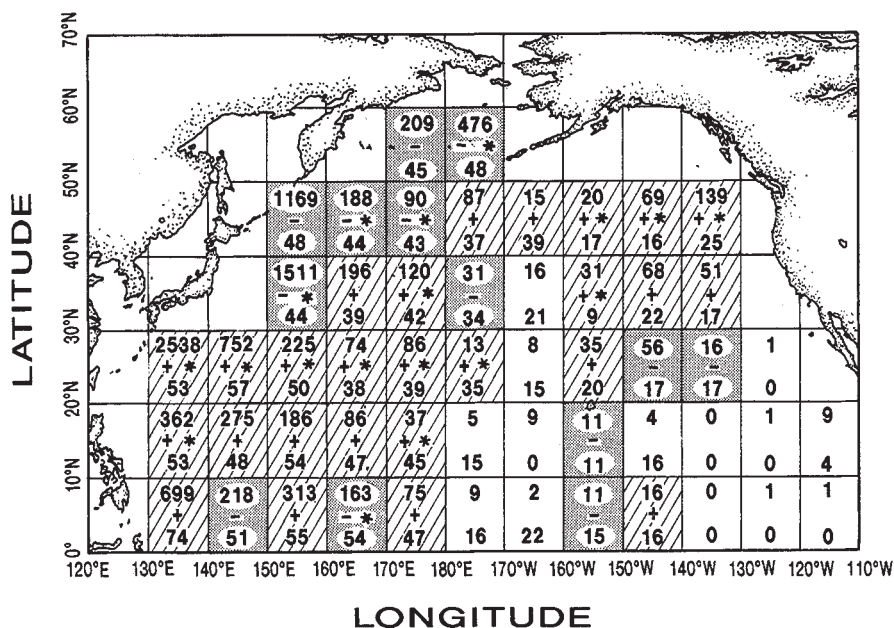

FIG. 1 Spatial distribution of the time-series analysis of Secchi disc data for the North Pacific. Each box corresponds to a 10°×10° grid. Grids with increasing Secchi depths are dark grey and marked '+', light grey grids correspond to areas with decreasing Secchi depths and are marked '−'. Grids with significant slopes ($P < 0.05$) are marked with an asterisk. The top number in each grid corresponds to the total number of reported observations, and the bottom number corresponds to the years spanned by the data.

TABLE 1 Annual changes in North Pacific Ocean

	Number of 10°×10° grids	Total number of observations	Average Secchi depth (m)	Average annual change in Secchi depth (m yr^{-1})	Average chlorophyll (mg m^{-3})	Average annual change in chlorophyll (mg m^{-3} yr^{-1})	Average primary production (g C m^{-2} yr^{-1})	Average annual change in primary production (g C m^{-2} yr^{-1})
All grids	40	10,733	26.1 ± 10.23	0.06 ± 0.29	0.328 ± 0.306	−0.002 ± 0.010	188.7 ± 84.6	−0.59 ± 2.69
Mean and s.d. of all positively sloped grids	26	6,568	30.8 ± 8.30	0.20 ± 0.19	0.25 ± 0.22	−0.006 ± 0.010	166.5 ± 66.2	−1.82 ± 2.31
Mean and s.d. of all negatively sloped grids	13	4,049	18.93 ± 8.53	−0.21 ± 0.27	0.49 ± 0.39	0.006 ± 0.005	233.7 ± 101.3	1.82 ± 1.64

Calculated annual changes in Secchi depths, chlorophyll concentration and primary production for the North Pacific Ocean since the early twentieth century. The grids with increasing and decreasing Secchi depths are shown in Fig. 1. Data from each grid were analysed and the mean and s.d. for each grid were individually calculated.

than other main ocean basins. The data were grouped into 10° square grids and a linear regression of the time-dependent variation in Secchi depths was done individually for each grid with more than 10 observations (Fig. 1). A subset of the grids was tested for assumptions of normality, linearity, homogeneity of variance and independence[18]. The results showed that the variance is homogeneously distributed, and that transformations of the data did not improve the normality of the error terms. It should be emphasized that this approach only reveals overall long-term trends; although there could be several increases and decreases within a time span, the number of observations and their distribution in time do not allow for analysis of that resolution. For example, no differences could be discerned between average and El Niño years.

Of the 40 grids with sufficient data for analyses, 26 had an increase in Secchi depth over time, 13 a decrease, and one grid was unchanged (Fig. 1). Thirteen of the 26 linear regressions yielding positive slopes were statistically significant (F-test) at the 95% level, whereas five of the 13 negatively sloped grids were significant. The analyses suggest that throughout much of the central North Pacific basin, upper ocean transparency has increased slightly since the beginning of the twentieth century. In grids corresponding to the Kuroshio current and the equatorial Pacific, upper-ocean transparency seems, on average, to have decreased.

Using both the Moran–Geary[18] and Mantel[19] tests, we examined whether the spatial pattern of the changes in the Secchi depths presented in Fig. 1 is random. The results of both tests suggested that although the magnitudes of the slopes are not spatially autocorrelated, the signs of the slopes are, implying that the spatial pattern shown in Fig. 1 is nonrandom. We therefore assume that the differences in the sign of the change in the Secchi depths between different grids are not due to systematic changes in the measurement procedures (such as changes in disk albedo or correction for line angle), but may be due to subtle changes in physical or chemical forcing in the open ocean. In the North Atlantic, changes in Secchi depths are randomly distributed, but the paucity of reported observations from the eastern portion of the North Atlantic Ocean precludes rigorous spatial analysis.

In the North Pacific Ocean, the average Secchi depth is 26.2 ± 10.23 m (mean ± s.d.). The linear regression analyses of the data with time suggest that the average depth is increasing by 0.06 ± 0.29 m per annum (Table 1). This increase in ocean transparency corresponds to an average annual decrease in chlorophyll of 0.002 mg m^{-3} and is not significantly different from zero ($P < 0.05$). Analysing only those grids with significant positive slopes, we find that the average change in the Secchi depth is 0.20 ± 0.19 m, which corresponds to a decrease in chlorophyll of 0.006 ± 0.010 mg m^{-3} yr^{-1}. Such small changes are at the limit of more modern chlorophyll analysis methods, which have been in common use only since the mid-1960s.

Although the calculated changes in chlorophyll are only representative of the upper portion of the water column and are less than 2% of the mean, the surface chlorophyll concentrations can be used statistically to derive integrated values and primary production[20].

We calculated primary production rates by converting the Secchi depths values to chlorophyll through equation (2), and converting the chlorophyll to primary production (PP) rates using the relationship described by Eppley et al.[21]

$$PP\ (\text{mg C m}^{-2}\ \text{d}^{-1}) = 1,000\,[\text{Chl}\,(\text{mg m}^{-3})]^{1/2} \qquad (3)$$

where Chl is the concentration of chlorophyll in the near surface ocean. As equations (2) and (3) are both nonlinear, chlorophyll and primary production values were calculated for the initial and final date recorded in each grid. The difference, divided by the years spanned by the data, yields an average annual value. The calculated annual mean primary production in the North Pacific is 188.7 g C m^{-2} and the average annual rate of change is −0.59 g C m^{-2}. Regions with increasing Secchi depths have an average productivity of 166.5 g C m^{-2} yr^{-1}, and regions with decreasing Secchi depths average 233.7 g C m^{-2} yr^{-1} (Table 1). The mean values of primary production calculated from Secchi depths are surprisingly comparable to recent radiocarbon measurements in the North Pacific[22,23], but because of inherent variance, the calculated annual rates of change are much too small to be reliably measured with any known oceanographic technique, even over decadal timescales. Our calculations suggest that the average total primary production for the North Pacific, representing an area of 4.94 × 10^{13} m^2, is 9.3 Gt C yr^{-1}, and is decreasing at an average annual rate of 0.03 Gt C, which is not significantly different from zero.

It might not be surprising that phytoplankton biomass and primary production in a principal central ocean basin have not changed significantly in this century; CO_2 is not limiting carbon fixation in marine systems, and there is no obvious fertilization of the open oceans. Venrick et al.[7] suggested that the apparent doubling of chlorophyll they reported for the central North Pacific gyre might be due to increased storm activity or intensity, which effectively increased the flux of essential plant nutrients from below the pycnocline to the euphotic zone. Our analysis indicates that although phytoplankton biomass and productivity may have changed in parts of the North Pacific Ocean, the changes are much smaller and of opposite sign in the region studied by Venrick et al.

Does phytoplankton carbon fixation contribute significantly to the flux of excess atmospheric CO_2 into the ocean? To account for all of the estimated ocean uptake of 2 Gt C yr^{-1}, net phytoplankton productivity would have to increase exponentially by about 4% each year (assuming that total global production is about 50 Gt C yr^{-1}), and the fixed carbon would have to be sequestered either below the main pycnocline or in the sediments (export production[23]). An increase in production would require

either the addition of nutrients external to the ocean[24], or an increase in the efficiency of their use in areas where nutrients are in excess. Throughout most of the central ocean basins, inorganic fixed nitrogen and phosphate are vanishingly small in the euphotic zone. In these areas, increased turbulent mixing within the ocean could lead to increased upwelling of nutrients from below the pycnocline, but such an upwelling flux would include inorganic carbon. The potential stimulation of primary production induced by such forcing would have no significant effect on the atmospheric concentration of CO_2; the ratio of inorganic carbon to other essential inorganic nutrients (the Redfield ratio) below the pycnocline is virtually identical to the elemental composition of phytoplankton[2].

There are three main open-ocean regions where inorganic nutrients are in excess in the euphotic zone: the equatorial and subarctic Pacific, and the Southern Ocean[25,26]. In these three regions it has been argued that phytoplankton productivity is limited by iron, which is supplied to the upper ocean primarily from atmospheric deposition[25,26]. In principle, the spread of deserts and/or increase of wind speeds could promote the transport of iron-rich particles seawards, and on geological timescales this seems to have stimulated primary production enough to affect atmospheric CO_2 (ref. 26). The spatial pattern of minute changes in Secchi depths in the North Pacific suggests there has been an increase in phytoplankton biomass in the subarctic and equatorial Pacific in this century. This spatial pattern of temporal changes (and lack thereof in the North Atlantic) is consistent with a hypothetical stimulation of phytoplankton biomass resulting from an increased deposition of aeolian iron. Our analysis shows, however, that even if this enhancement occurred, it has had relatively little impact on phytoplankton productivity. Moreover, model calculations suggest that even if all of the excess nutrients in these two areas were consumed by phytoplankton, the net invasion of atmospheric CO_2 would be small[27]. Because proxy historical data bases, such as Secchi depths, are extremely sparse or non-existent for other main ocean basins (such as the Southern Ocean), we cannot preclude the possibility that changes in primary production have occurred elsewhere. But if our analysis is representative of other ocean basins, it seems reasonable to assume that open-ocean phytoplankton biomass and production have not changed significantly since the beginning of the Industrial Revolution. Consequently, for the purposes of modelling the sources and sinks of excess atmospheric CO_2, open-ocean biological processes can be considered to be in a steady state[2,5,27].

In contrast to the open ocean, coastal ocean regions have experienced large increases in nutrient supply correlated with increases in human population levels in coastal areas[28], and it has been suggested that this enrichment is large enough significantly to affect anthropogenic CO_2 levels[29]. If that were the case, we would expect to see changes in phytoplankton biomass on continental shelves and a carbon sink amounting to ~2 Gt C yr^{-1} in either the interior ocean or the sediments of the continental margins. Unfortunately, although there are abundant Secchi depth data for continental margins, the data are difficult to interpret using equation (2) because of the interference of terrigenous particles and other absorbing materials. Nonetheless, there is compelling evidence that phytoplankton biomass and, presumably, productivity, have been increasing on continental shelves throughout the twentieth century[30]. As yet there is no conclusive evidence for a significant sink of recently produced carbon in the coastal oceans[31]; nearly all organic matter seems to be efficiently reoxidized in the upper 500 m of the ocean[32,33]. ☐

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Experimentally produced oscillatory zoning in the (Ba, Sr)SO₄ solid solution

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WHEN crystals grow from a multicomponent fluid phase under conditions where ionic diffusion in the solid is negligible compared to that in the liquid, any compositional gradients in the crystal record the evolution of the solid/liquid interface composition during growth. For the particular case of oscillatory zoning[1-3], a relatively common feature of natural crystal growth[4], there has been considerable theoretical interest[4-6], but the specific question of whether high or low supersaturations are required to explain the development of the zoning remains unanswered. Experimentally produced compositional oscillations have been observed[7,8], but the role of supersaturation had to be inferred, rather than measured directly. Here we describe major-element oscillatory zoning in $(Ba, Sr)SO_4$ solid solutions grown by the counter-diffusion of (Ba^{2+}, Sr^{2+}) and SO_4^{2-} ions through a porous silica-gel transport medium. We demonstrate how the different solubilities of the two pure phases determine the threshold supersaturation for nucleation, and show how coupling between the compositional gradients in the solid and the liquid results in the observed oscillatory behaviour.

In the experiment (Fig. 1), the silica gel acts as a transport medium, allowing counter-diffusion of the anionic and cationic reactants, and effectively supressing convective transport. Diffusion-controlled concentration profiles of Ba, Sr and S and