

any portion of the Greenland record over the last 700 years. If anything, the simulation puts the next minimum farther into the future than would estimates based strictly on analogies with previous "cycles." Thus, whereas the exact date of the minimum shown in the extended natural climate curve (Fig. 1) is uncertain, its occurrence in the next decade is probable. The rate of warming beyond the minimum is also open to question. As the CO₂ effect will dominate, the uncertainty here lies mainly in the estimates of future chemical fuel use and in the magnitude of the warming per unit of excess atmospheric CO₂. The major point of the argument is that over the past 30 years the warming trend due to CO₂ has been more than countered by a natural cooling. This compensation cannot long continue both because of the rapid growth of the CO₂ effect and because the natural cooling will almost certainly soon bottom out. We may be in for a climatic surprise. The onset of the era of CO₂-induced warming may be much more dramatic than in the absence of natural climatic variations.

The agricultural consequences of this ensuing warming are not obvious (neither are the implications to global sea level). A knowledge of the mean global temperature tells us little about the rainfall patterns in the chief grain-producing regions. There is little doubt, however, that this gradual warming will lead to changes in the pattern of global precipitation. Our efforts to understand and eventually to predict these changes must be redoubled.

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Chlorinated Hydrocarbon Pollutants and Photosynthesis of Marine Phytoplankton: A Reassessment

Abstract. *The chlorinated hydrocarbons DDT and PCB's (polychlorinated biphenyls), ubiquitous pollutants of the marine environment, have been observed to reduce the cell division rate of marine phytoplankton, thereby indirectly reducing the total photosynthetic carbon fixation in treated cultures. The photosynthetic capacity of each cell was not affected. Total marine photosynthesis will likely remain undiminished by these compounds, although alterations in phytoplankton communities through selective toxicity could affect herbivore populations.*

Several persistent and ubiquitous chlorinated hydrocarbon pollutants of the marine environment, most notably PCB's (polychlorinated biphenyls) and DDT [1,1,1-trichloro-2,2-bis(p-chlorophenyl)ethane], can reduce the growth rate (1, 2) and have been reported to reduce photosynthesis (2-4) in some marine phytoplankton cultures. The decrease in carbon fixation observed in treated cultures (2-4), as measured by the incorporation of ¹⁴C-labeled bicarbonate, could have resulted from an inhibition of the photosynthetic process itself, or it may have been due to a depressed growth rate, that is, fewer cells photosynthesizing in treated than in control cultures.

I conducted an experiment to determine whether algal photosynthesis on a per cell basis, as well as on a per culture basis, was affected by PCB's or DDT. The organochlorine concentrations used were above those found in natural waters (5); no attempt was made to determine the toxicity of environmentally realistic concentrations of these compounds, as was done elsewhere (6). The purpose of this study was to establish whether, in algae, photosynthetic carbon fixation itself is inhibited or whether just growth is affected by these chemicals.

The three algal species studied (7) were selected on the basis of their sensitivity to chlorinated hydrocarbons: the growth of *Thalassiosira pseudonana* and *Skeletonema costatum*, common marine diatoms, is affected by PCB's and DDT (1), and photosynthetic carbon fixation in cultures

of *Coccolithus huxleyi* and the two diatoms is reportedly reduced by DDT (2, 3). Culture conditions and procedures have been described elsewhere (8). Methanolic solutions of PCB's (Aroclor 1254) or DDT were injected (1) into the cell suspensions at time zero to give initial PCB concentrations of 10 µg/liter (parts per billion) and DDT concentrations of 50 ppb in the medium. Equal volumes of methanol were added to the control cultures (9). These organochlorine compounds, at similar concentrations (or doses per cell), have been reported to substantially depress the net carbon fixation in monocultures of these algal species (2, 3). At 48 hours, 1 ml of medium was removed from each tube so that cell counts could be determined (10), 0.2 µC of [¹⁴C]NaHCO₃ was added (11), and the cultures were incubated as before for about 5 hours. The same procedure was also carried out for dark controls. The cells were then gently filtered through 0.8-µm Millipore filters and washed with filtered seawater; the radioactivity of the filters was counted in a liquid scintillation counter (Tri-Carb, Packard). The entire experiment was repeated with the two diatom species.

Table 1 presents the 48-hour cell counts, photosynthetic carbon fixation per culture, and carbon uptake per cell (α). The dark uptake of ¹⁴C, which varied with each species (being 2 percent of the illuminated *T. pseudonana* ¹⁴C uptake, less than 1 percent with *S. costatum*, and 10 percent with *C. huxleyi*), was subtracted from the raw

Table 1. Effects of PCB's (10 ppb) and DDT (50 ppb) on three species of marine algae: growth was measured in terms of cell density at 48 hours, the carbon uptake per culture was measured after 5 hours of incubation, and the carbon uptake (α) has the units cpm per 190,000 cells per hour. Numbers are the means of four replicate cultures and are shown with their 95 percent confidence intervals (16). Single classification analysis of variance (16) indicated that growth and carbon uptake per culture by treated cells differed from control cultures for *T. pseudonana* ($P < .025$) and for *S. costatum* ($P < .001$), but uptake per cell in treated cultures did not significantly differ from control culture values for either species. Control *C. huxleyi* cultures did not significantly differ from treated cultures for growth, carbon uptake per culture, or carbon uptake per cell.

Species	Treatment	Cells per milliliter ($\times 10^4$)		^{14}C uptake per culture (cpm/19 ml)		^{14}C uptake per cell (α)		^{14}C uptake per cell (repeat) (% control)
		Mean	% Control	Mean	% Control	Mean	% Control	
<i>T. pseudonana</i>	Control	10.76 $\pm$ 0.89	100	1034 $\pm$ 226	100	15.71 $\pm$ 3.73	100	100
<i>T. pseudonana</i>	PCB's	6.77 $\pm$ 1.94	63	538 $\pm$ 180	52	13.49 $\pm$ 1.43	86	109
<i>T. pseudonana</i>	DDT	3.18 $\pm$ 1.74	30	295 $\pm$ 106	28	16.37 $\pm$ 3.63	104	102
<i>S. costatum</i>	Control	22.78 $\pm$ 4.13	100	6584 $\pm$ 1494	100	44.39 $\pm$ 4.38	100	100
<i>S. costatum</i>	DDT	4.17 $\pm$ 0.52	18	1074 $\pm$ 347	16	45.86 $\pm$ 14.26	103	94
<i>C. huxleyi</i>	Control	3.28 $\pm$ 1.30	100	404 $\pm$ 93	100	23.22 $\pm$ 8.09	100	
<i>C. huxleyi</i>	PCB's	3.17 $\pm$ 0.64	97	403 $\pm$ 187	100	23.10 $\pm$ 5.44	99	
<i>C. huxleyi</i>	DDT	2.88 $\pm$ 1.04	88	376 $\pm$ 76	93	24.55 $\pm$ 5.18	106	

counts to give the net values shown in Table 1. Because differential growth rates during incubation could cause inaccurate estimates of carbon fixation per cell, α was determined by considering the specific exponential growth rate of each culture:

$$\alpha = \frac{C}{[(N/r)(e^{rt'} - 1)]} \quad (1)$$

where C denotes the radioactive counts per minute (cpm) per 19 ml of culture, N is the cell density at 48 hours, r is the growth rate in cell divisions per hour (12), t' denotes the incubation time with the ^{14}C -labeled bicarbonate, and α is the carbon uptake rate per cell (in units of cpm per cell per hour) (13).

The total photosynthesis in cultures of *T. pseudonana* and *S. costatum* was reduced by the chlorinated hydrocarbons, confirming earlier results (2, 3). Carbon fixation per *T. pseudonana* culture was diminished 48 percent by the PCB's and 72 percent by the DDT, but growth was also diminished in the treated cultures. The ^{14}C uptake per cell (Table 1), a direct assessment of the photosynthetic response of the cells to the organochlorine compounds, was unaffected by the chemicals. Thus, what appears to be 72 percent inhibition of *T. pseudonana*'s photosynthesis and 84 percent of *S. costatum*'s photosynthesis by DDT is merely a reflection of growth inhibition by this compound, rather than of photosynthetic inhibition per se. These results, confirmed in the repeat experiment (Table 1), might explain earlier work (2-4) which showed a reduction in the incorporation of ^{14}C -labeled bicarbonate per culture by these compounds. The growth and photosynthesis of *C. huxleyi* were not affected by either chemical, in contrast with past findings (3). *Skeletonema costatum* was killed by the PCB's; both growth and photosynthesis stopped, and the integrity of the cells was completely disrupted. No other morphological differences between treated and control culture cells were observed under the light microscope.

The photosynthetic decline in treated cultures was thus due to reduced cell division rates. The mechanism by which the chlorinated hydrocarbons affect diatom growth is as yet unclear, although recent studies with *T. pseudonana* suggest that PCB's may inhibit membrane-bound enzymes involved in nitrogen metabolism (14).

Although total photosynthesis in the diatom monocultures was reduced by the PCB's and DDT, photosynthetic carbon fixation in nature would likely remain unaffected by these compounds, even if present at concentrations many times the current environmental levels. Resistant autotrophs would probably replace sensitive species, as demonstrated in mixed cultures of marine phytoplankton with low (6) and high (15) concentrations of PCB's and DDT. Alterations in the species composition of phytoplankton communities, caused by persistent pollutants, such as the chlorinated hydrocarbons, could result in deleterious effects on marine ecosystems if the resistant species that become dominant were an inferior food source for the resident herbivores. The most likely consequences of chlorinated hydrocarbon pollution for the lower marine food web would therefore stem from qualitative, not quantitative, changes in the herbivores' food supply.

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7. Clones "3H" of *T. pseudonana*, "Skel" of *S. costa-*

tum, and "BT-6" of *C. huxleyi* were obtained from R. R. L. Guillard, Woods Hole Oceanographic Institution culture collection. All cultures were axenic and were in their exponential phase of growth.

8. N. S. Fisher, L. B. Graham, E. J. Carpenter, C. F. Wurster, *Nature (Lond.)* **241**, 548 (1973). Equal cell densities ($10^4/\text{ml}$) were assured at time zero for each culture tube by first inoculating the medium in a sterile flask, vigorously stirring to form a uniform cell suspension, and aseptically dispensing 20 ml per tube (25-ml capacity). There were four replicate tubes per treatment.
9. Methanol was shown in preliminary experiments to have no effect on photosynthesis or growth. The concentrations and purity of the chlorinated hydrocarbon stocks were checked by electron-capture gas chromatography (5). The PCB concentration was lower than its reported solubility limit—1 to 2 mg/liter—in seawater [V. Zitko, *Bull. Environ. Contam. Toxicol.* **5**, 279 (1970)], whereas the DDT concentration exceeded 1.2 ppb, its solubility in water [F. Acree, M. Beroza, M. C. Bowman, *Agric. Food Chem.* **11**, 278 (1963)]. However, DDT at concentrations exceeding its solubility in water can affect algal growth in a dose-response manner (1, 2), either by influencing growth in the undissolved state or by being rapidly and virtually completely incorporated into the cells, in which case it would not crystallize in the medium. Experimental evidence supports the latter explanation [A. Södergren, *Oikos* **19**, 126 (1968)].
10. A Speirs-Levy eosinophil counter (hemacytometer) was used.
11. The ^{14}C NaHCO₃ was dissolved in sterile distilled water, pH 9.5, and filtered through a 0.22- μm Millipore filter before use. A syringe was used to add 0.2 ml per culture.
12. The value of r was calculated according to the method of R. W. Eppley and J. D. H. Strickland [in *Advances in Microbiology of the Sea*, M. R. Droop and E. J. F. Wood, Eds. (Academic Press, London, 1968), vol. 1, p. 23].
13. In Eq. 1 it is assumed that in each culture, ^{14}C uptake is dependent on the number of cells, that the uptake rate per cell remained constant, and that growth proceeded at a constant rate, r . [The elapsed time of the entire experiment was shorter than the exponential growth phase of these algae, given the same initial conditions (1).] Under these assumptions,

$$dC/dt = \alpha Ne^{r(t-48)}dt$$

for $t > 48$; integrating, we obtain

$$C = \alpha N \int_{48}^T e^{r(t-48)} dt = (\alpha N/r) (e^{rt'} - 1)$$

where T is the time at the end of the experiment for each replicate and $t' = T - 48$.

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