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*The Use of  $p\text{CO}_2$  for the Calculation of  
Biological Production, with Examples  
from Waters Off Massachusetts*<sup>1</sup>

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ABSTRACT

The use of  $p\text{CO}_2$  for the study of biological production in natural waters has advantages over the use of oxygen related to the persistence of changes in  $p\text{CO}_2$ , the magnitude of the changes, and the possibility of making continuous recordings of surface-water  $p\text{CO}_2$  from a ship underway. The method of calculating biological production is discussed and illustrated with data from coastal waters off Massachusetts.

*Introduction.* Photosynthesis in the oceans is estimated either by determining the changes in an essential nutrient or by measuring the chlorophyll concentrations and light intensity. Carbon dioxide is an essential nutrient, and production is often expressed in terms of the amount of carbon fixed. However, changes in carbon-dioxide concentration, aside from changes in  $\text{C}^{14}$ , have rarely been used to estimate production. The availability of the infrared gas analyzer has made it possible to measure and record accurately and continuously the partial pressure of carbon dioxide in seawater. Such a measurement can be converted into additions and subtractions of carbon dioxide to and from the water (Kanwisher 1960). From data on the seasonal changes in  $p\text{CO}_2$ , the rate of equilibration between air and ocean, and the temperature of the water, it is possible to calculate the seasonal changes in the balance between photosynthesis and respiration or the net production of the water in question.

We have made measurements of the  $p\text{CO}_2$  in waters of the Gulf of Maine (western basin), Georges Bank, Nantucket Sound, and the Vineyard Sound-Woods Hole region. With one exception, the measurements outside of the

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Woods Hole region were made on cruises designed for other purposes; although the data are limited, they are adequate to illustrate the method and type of results and to provide some information on the productivity of these four areas.

Carbon dioxide dissolves in water and then reacts to form an acid that dissociates to bicarbonate and carbonate. In seawater, carbonate reacts with sodium and magnesium to form complexes (Garrells et al. 1961). The total carbon dioxide that can be obtained from seawater by acidification and vacuum extraction amounts to about 45 ml/l. The partial pressure of carbon dioxide in air is about 0.0003 atm. The gas is very soluble (1 ml/l/atm), but, because of the low partial pressure, only 0.3 ml of the 45 ml is in true solution. Most of the remainder (99.9%) is present in ionic form, since the undissociated acid is present only in traces. In distilled water at 20°C, 96% of the total carbon dioxide is in dissolved form. In brackish waters, the alkalinity will determine the state of the carbon dioxide.

Atmospheric gases equilibrate with a water mass through a surface film that acts as the primary barrier to diffusion (Kanwisher 1963). The reactivity of carbon dioxide does not affect its rate of diffusion under normally windy conditions in nature. The flux ( $f$ ) through the film depends on: the diffusivity ( $D$ ) of the gas in water; the thickness ( $h$ ) of the film; and the solubility of the gas ( $S$ ) times the partial-pressure difference across the film ( $\Delta p\text{CO}_2$ ) which is the concentration difference:

$$f = \frac{S \times p\text{CO}_2 \times D}{h}$$

In this paper, the diffusivities of oxygen and carbon dioxide are taken to be identical and equal to  $2 \times 10^{-5}$  cm<sup>2</sup>/sec. To illustrate the advantages of using  $p\text{CO}_2$  (compared with  $p\text{O}_2$ ) as a measure of biological activity in the water, consider the following examples. Assume an oceanic water mass at 20°C in equilibrium with the air—i.e., the oxygen pressure is 0.21 atm and the water contains 5 ml  $\text{O}_2$ /l; the carbon-dioxide pressure is  $330 \times 10^{-6}$  atm (330 ppm) and the water contains about 45 ml  $\text{CO}_2$ /l. Now, assume that in this water mass there is an amount of respiration that removes 1 ml  $\text{O}_2$ /l from the water and adds an equal amount of carbon dioxide. The oxygen will be reduced by 20%, and an oxygen gradient of 0.042 atm (20% of 0.21) will be established between the water and the air. The  $p\text{CO}_2$  will be increased to 390 ppm—an increase of 18% of the equilibrium value—and the gradient between the air and the water will be 60 ppm (Kanwisher 1960; see Fig. 1). Since the measurable amount of each gas is changed by nearly the same per cent, the changes will be equally easy to detect. However, the oxygen gradient between the air and water is 700 times larger than the carbon-dioxide gradient. Therefore, even though carbon dioxide is 29 times more soluble and thus moves through

the surface 29 times faster than oxygen, it will require  $700/29$  or 24 times longer than oxygen to return to equilibrium.

In a lake of very low alkalinity—the condition most different from that in the sea—the same respiration at the same temperature would reduce the oxygen by 16.7% and increase the carbon dioxide by 390%, establishing respective gradients of 0.035 atm and 960 ppm between air and water. The time required for equilibration of carbon dioxide would be only 1.3 times longer than that for oxygen, but a much smaller change in total carbon dioxide could be detected. Should the above respiratory gas change have occurred in a mixed water column of seawater 2 m deep, with a wind such that the average thickness of the surface film was  $10^{-2}$ /cm, the half-time for oxygen equilibration would be 19 hours while the half-time for carbon-dioxide equilibration would be nearly 15 days. We can expect that the  $p\text{CO}_2$  changes in seawater as a result of biological activity will persist and be detectable for weeks or months, thus providing a means of measuring the amount and distribution of that biological activity.

The surface-film thickness in the flux equation depends upon wind velocity. Measurements in a tank, with wind velocities of up to 24 knots (12 m/sec), were made by Kanwisher (1963). These measurements can be fitted by the following relation, where  $h$  is the surface-film thickness in centimeters and  $V$  the wind velocity in meters per second:

$$h = \frac{1}{5.75V^2 + 18}.$$

The occurrence of higher winds over oceanic waters and the associated effects of breaking waves made it advisable to seek confirmation of the tank measurements under natural conditions. The  $p\text{CO}_2$  was 240 ppm in Buzzards Bay on 30 November 1963 just prior to a gale that blew directly up the bay unaccompanied by rain. Twenty-four hours later, the  $p\text{CO}_2$  had increased to 285 ppm. The air value was 320 ppm. This flux, spread over 24 hours, corresponds to a surface film of  $2.6\mu$  from which the calculated wind was 26 m/sec. The root-mean-square velocity measured with an anemometer about one mile from the bay was 22 m/sec.

Redfield (1948) derived values for the exit coefficient for oxygen from the Gulf of Maine. His data, recalculated in terms of surface film and wind velocity with the above equation, gave root-mean-square winds of 12, 7, 7, 15, 5, 5, and 6 m/sec for the first seven months of the year. The arithmetic mean velocities obtained by the Great Blue Hill, Massachusetts, Weather Station for the first seven months of 1962 were 8, 7, 8, 8, 6, and 6 m/sec, which are reasonably close, considering that the arithmetical averages must be less than the root mean squares. Apparently the linear relation between  $1/h$  and  $V^2$  from Kanwisher (1963) holds under natural conditions up to the

velocities included in his measurements but cannot be extended to velocities twice that great. At high velocities, the surface film will not only be thinned but will be continually broken and reformed by breaking waves.

*Methods.* Because of the complex nature of the carbonate equilibria, we measured directly the relation between  $p\text{CO}_2$  and total carbon dioxide in water of various salinities obtained from either Vineyard Sound or the Sargasso Sea. Salinities below 30‰ were prepared by diluting Vineyard Sound water with distilled water. Most of the carbon dioxide was driven off by bubbling with  $\text{CO}_2$ -free air overnight. Two liters of this seawater were then continuously equilibrated with about 200 ml of air that was circulated through one path of an infrared analyzer. Successive additions of 1 ml of carbon dioxide were made with a 1-ml syringe, and the resulting changes in  $p\text{CO}_2$  were recorded.

Determinations of  $p\text{CO}_2$  at sea were made by pumping water continuously from an opening below the ship's waterline into a chamber in which the water was sprayed into, and thoroughly mixed with, a small volume of air. The air was dried with silica gel and recirculated through one path of the infrared analyzer. Outside air circulated through the other path was used as a standard.

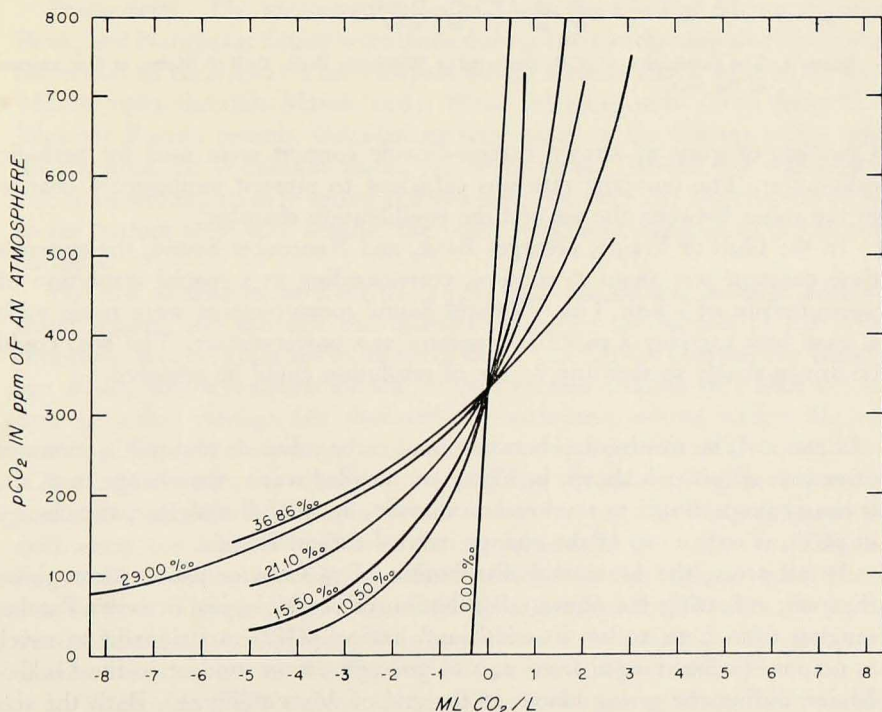


Figure 1. The measured relationship between parts per million (ppm)  $\text{CO}_2$  and changes in total carbon dioxide from the value in equilibrium with air.

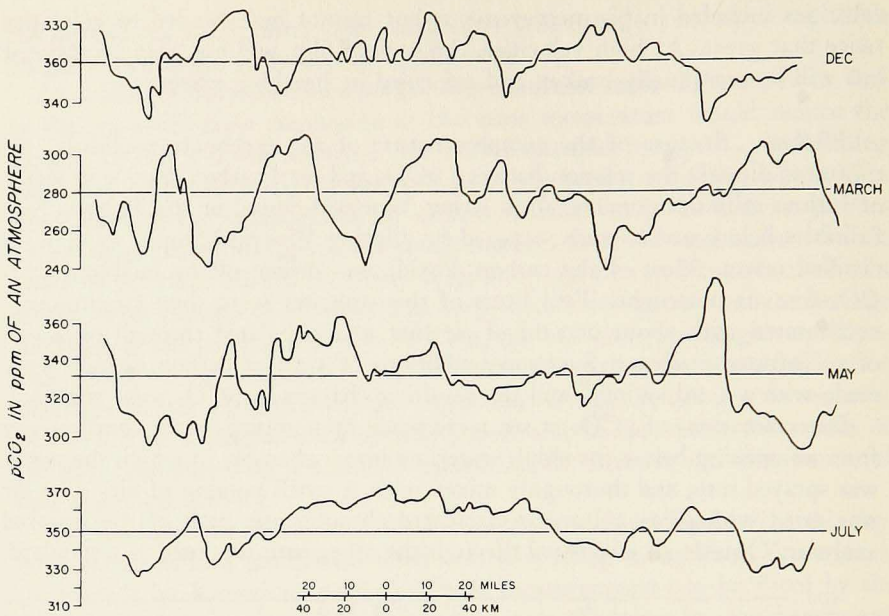


Figure 2. The distribution of  $p\text{CO}_2$  measured in Wilkinson Basin, Gulf of Maine, at four seasons of the year.

Cylinders of gases of known carbon-dioxide content were used for periodic calibration. The pumping rate was sufficient to prevent temperature change in the water between the sea and the equilibration chamber.

In the Gulf of Maine, Georges Bank, and Nantucket Sound, the system's time constant was about 5 minutes, corresponding to a spatial resolution of measurement of 1 km. The Vineyard Sound measurements were made with a small boat carrying a portable generator as a power source. The boat could be driven slowly so that any degree of resolution could be achieved.

*Results.* The relationship between total carbon dioxide and  $p\text{CO}_2$  in water of various salinities is shown in Fig. 1. In distilled water, the change in  $p\text{CO}_2$  is nearly proportional to total carbon dioxide, but in full seawater, the change in  $p\text{CO}_2$  is only 1:16 of the change in total carbon dioxide.

In all areas, the horizontal distribution of  $p\text{CO}_2$  was patchy throughout the year, reflecting the uneven distribution of the biological activity. Patches ranging from 2 to 20 km in width and having  $p\text{CO}_2$  variations of as much as 60 ppm (values ranged from 240 to 300 ppm) were evident in the Gulf of Maine during the spring bloom at the end of March (Fig. 2). Both the size of the patches and the  $p\text{CO}_2$  variations declined as the year progressed. Small-scale patchiness measured in Vineyard Sound in January showed horizontal

variations in  $p\text{CO}_2$  of 2 to 10 ppm around a value of 205 ppm on a spatial scale of 5 to 15 m.

Chlorophyll concentrations in the water, determined according to Creitz and Richards (1955), showed a strong, inverse correlation with  $p\text{CO}_2$  in March (probability of chance correlation  $P = 0.005$ , correlation coefficient,  $r_s = 0.85$ ). By May, the relationship had degenerated ( $P = 0.05$ ,  $r = 0.54$ ), and in July and December it was absent. From changes in  $p\text{CO}_2$ , we assume that the following sequence of events occurred.

The phytoplankton reduced the  $p\text{CO}_2$  during the spring bloom in proportion to the amount of photosynthesis that occurred in that particular mass of water. As the season progressed,  $p\text{CO}_2$  rose due to equilibration with the air and to the excess of respiration over photosynthesis. At the same time, horizontal mixing smoothed the patchiness of the  $p\text{CO}_2$  distribution. The patches became somewhat more accentuated in December, but, since they were totally uncorrelated with chlorophyll, they were not caused by photosynthesis. Perhaps they were associated with uneven distribution of consumer organisms.

*Productivity.* The measurements of  $p\text{CO}_2$  in the Gulf of Maine, Georges Bank, and Nantucket Sound were made during 1962 as the ship moved through the center of each area. The Vineyard Sound measurements were made from March 1962 through March 1964. Wind velocities were taken from U. S. Weather Bureau records. Calculations were based on the average  $p\text{CO}_2$  value for the area. In Wilkinson Basin, the depth to the thermocline was used—100 m in winter, 20 m in spring and summer. For the other regions, the depths to the bottom were used because the water is shallow and well mixed by tidal currents.

We had to assume, as Redfield (1948) did, that mixing between adjacent water masses and through the thermocline—i.e., the bottom of the water column—was insignificant in its effect on  $p\text{CO}_2$ . This is justified for Wilkinson Basin, where temperature and oxygen profiles indicate that little vertical mixing occurs through the thermocline; horizontal mixing within the area is unimportant, because the average  $p\text{CO}_2$  was used in the calculations. There is less justification for assuming insignificant lateral mixing in Nantucket Sound and off Woods Hole, where there exists a net nontidal southeastward drift along the coast. We allowed for the large tidal excursions by excluding from the calculations the regions where mixing between adjacent water masses was evident. This assumption is certainly unjustified for Georges Bank, but the calculations are included without any attempt to correct for the admixture of water flowing out of the Gulf of Maine across Georges Bank.

In Wilkinson Basin and on Georges Bank, the spring bloom begins sometime in March when the water column becomes stable due to warming. It has been assumed that this occurred on March 1 when there was equilibrium

between the air and the sea for  $\text{CO}_2$ . If the bloom began appreciably later, then the daily rates of production are underestimated.

Production was calculated by using the equation

$$P = f - 10^{-3} Z \frac{d \varepsilon \text{CO}_2}{d p \text{CO}_2} (\Delta - \Delta_t) \frac{12 \times 10}{22.3},$$

where  $f$  is flux calculated as above and positive as carbon dioxide enters the water;  $Z$  is the depth of the mixed layer in centimeters;  $d \varepsilon \text{CO}_2/d p \text{CO}_2$  is taken from the curve for the appropriate salinity in Fig. 1;  $\Delta$  is the change in  $p \text{CO}_2$ , and  $\Delta_t$  the change in  $p \text{CO}_2$  due to temperature change, 4.5 per cent per degrees Centigrade. The final constant converts from  $\text{ml}/\text{cm}^2$  to  $\text{g}/\text{m}^2$ .

In Wilkinson Basin and on Georges Bank, the  $p \text{CO}_2$  was above atmospheric values in early winter. During the winter, in spite of biological production of carbon dioxide, the  $p \text{CO}_2$  decreased because of declining temperature and equilibration with the air. When stability of the water column and the spring bloom occurred in March, the  $p \text{CO}_2$  decreased rapidly to values far below atmospheric values and remained low for several months. Net biological production (Table I), as estimated from the uptake of carbon dioxide, declined to low values in late spring. The rise in water temperature and also the flux from the air helped to raise the  $p \text{CO}_2$  in the water. The  $p \text{CO}_2$  rose to above atmospheric values by July in spite of a second increase in net production during early summer.

A similar sequence probably occurred in Nantucket Sound, but the spring bloom began earlier and our sampling times do not provide as clear a picture.

Table I. Data on  $p \text{CO}_2$  and temperature changes and calculated production for three areas off Massachusetts.

	Av. $p \text{CO}_2$ (ppm)	Temp. (°C)	h* ( $10^{-4}$ cm)	Productivity	
				( $\text{gC}/\text{m}^2$ )	( $\text{gC}/\text{m}^2/\text{day}$ )
Wilkinson Basin					
15 Dec.-1 Mar. . . .	345	-3	40	-16	-0.2
1 Mar.-1 Apr. . . . .	305	1	30	15	0.5
1 Apr.-15 May ..	305	4	45	3.5	0.08
15 May-1 July . . .	340	6	60	13	0.3
Georges Bank					
15 Dec.-1 Mar. . . .	330	-3	20	-12	-0.2
1 Mar.-1 Apr. . . .	280	1	15	50	1.6
1 Apr.-15 May ..	280	4	30	21	0.5
15 May-1 July . . .	322	6	50	35	0.8
Nantucket Sound					
15 Dec.-30 Mar. . .	220	-3 $\frac{1}{2}$	35	58	0.6
30 Mar.-18 May ..	270	7	40	17	0.4
18 May-3 July . . .	445	8	60	-1.6	-0.04

\* h = thickness of surface film calculated from wind velocity.



Table II. Production calculation for Vineyard Sound waters from  $p\text{CO}_2$  data. Monthly intervals for 1961 and 1962, two-week intervals for 1963 and 1964.

	Av. $p\text{CO}_2$ (ppm)	h* ( $10^{-4}$ cm)	flux (ml/cm <sup>2</sup> )	$\Delta p\text{CO}_2$ (ppm)	$\Delta p\text{CO}_2$ due to Temp.	Prod. (gC/m <sup>2</sup> /day)
Oct. 1961....	425	38	-1.24	-95	-95	-6.7
Nov. ....	360	38	-0.55	-70	-75	-2.7
Dec. ....	275	40	0.68	-100	-64	5.2
Jan. 1962....	225	38	1.87	30	-41	6.2
Feb. ....	260	39	1.15	45	0	4.4
Mar. ....	290	29	0.63	15	68	5.2
Apr. ....	335	37	-0.21	70	70	-1.1
May ....	410	62	-0.65	70	90	-3.1
June ....	480	61	-1.03	70	105	-4.9
July ....	520	70	-1.06	15	60	-4.7
Aug. ....	535	70	-1.05	15	65	-5.1
Sept. ....	525	-	-	-	-	-
Nov. 1963....	270	-	-	-	-	-
Dec. ....	290	56	0.14	25	0	1.7
	240	26	0.40	55	0	5.4
Jan. 1964....	220	36	0.72	0	0	5.6
	205	56	0.30	30	0	4.3
Feb. ....	190	31	1.09	0	0	8.4
	170	31	1.26	30	0	11.9

\* h = thickness of surface film calculated from wind velocity.

The results for Wilkinson Basin are about one-half of those calculated by Redfield (1948) for the same region on the basis of changes in phosphate in the water column. There is no reason to suppose that the production in different years should be the same, but the difference in the two calculations may indicate an error in our calculations, because we had no data on the vertical distribution of  $p\text{CO}_2$  and had no way to correct for the addition to the photic zone of water high in  $p\text{CO}_2$  from deeper layers. The results for Georges Bank are about four times higher than those for Wilkinson Basin. The Georges Bank results would also be greater if corrected for the addition of the deep water that flows out of the Gulf of Maine over Georges Bank.

For Vineyard Sound (Table II) we have a better year-round picture. Values of  $p\text{CO}_2$  reached nearly twice the equilibrium values with the air in late summer, when the production in the previous spring and summer was respired. Biological activity decreased in the fall, and concurrent temperature decline and flux through the surface reduced the  $p\text{CO}_2$  toward atmospheric levels. By early winter, the water had lost much of its suspended material, and with the lengthening days the winter bloom began. The highest net production occurred as the days became longer and the cloudy weather was less frequent. Values of  $p\text{CO}_2$  as low as 120 ppm, corresponding to a deficit

Table III. Photosynthesis in Vineyard Sound calculated from light and chlorophyll data. Respiration is difference between net production and photosynthesis.

	Chl. <i>a</i> (mg/m <sup>3</sup> )	light (g-cal/ cm <sup>2</sup> /day)	Photosyn. (gC/m <sup>2</sup> /mo.)	Net. Prod. (gC/m <sup>2</sup> /mo.)	Resp. (gC/m <sup>2</sup> /mo.)	Resp. Photosyn.
Oct. 1961....	3.0	240	5.0	-6.7	11.7	2.3
Nov. ....	3.6	165	4.5	-2.7	7.2	1.6
Dec. ....	5.0	139	5.6	5.2	0.4	0.07
Jan. 1962....	2.8	174	7.6	6.2	1.4	0.18
Feb. ....	2.0	203	5.8	4.4	1.4	0.24
Mar. ....	1.0	377	4.4	5.2	-0.8	-
Apr. ....	1.0	431	2.3	-1.1	3.4	1.5
May ....	1.3	491	3.2	-3.1	6.3	2.0
June 1963....	4.4	477	10.7	-4.9	15.6	1.5
July ....	4.8	421	11.0	-4.7	15.7	1.4
Aug. ....	4.6	376	10.0	-5.1	15.1	1.5
Sept. ....	4.4	317	10.4	-	-	-
Oct. ....	3.2	235	5.3	-	-	-
Nov. ....	3.6	153	4.6	-	-	-
Dec. ....	4.0	135	4.4	1.7	2.7	-
	4.4	120	4.6	5.4	-0.8	-
Jan. 1964....	4.7	130	5.1	5.6	-0.5	av. 0.02
	4.6	140	5.3	4.3	1.0	-
Feb. ....	4.7	180	6.5	8.4	-1.9	-

of 6 ml CO<sub>2</sub>/l, were observed. Warming and increase in consumer activity again raised the pCO<sub>2</sub> above air levels in late spring.

Chlorophyll determinations on water collected at the dock at Woods Hole were made available by Charles Yentsch. The samples were collected at the same hour each day rather than at the same state of current flow, so we attempted to exclude samples that might represent water other than that from Vineyard Sound. Radiation values were taken from U. S. Weather Bureau records for Newport, R. I. The extinction coefficient, on the basis of Secchi disc measurements, was taken to be 0.5/m during winter and 1/m for the rest of the year. Production was calculated by the method of Ryther and Yentsch (1957); see Table III. Chlorophyll was high in winter and summer. Calculated photosynthesis was highest in summer, with a smaller peak in winter (Fig. 3).

Respiration, calculated by subtracting net production from calculated photosynthesis, ranged from a few per cent of photosynthesis during the winter bloom to 2.3 times photosynthesis in early fall. Calculated photosynthesis totaled 70 gC/m<sup>2</sup> for the October-to-August interval, and respiration totaled 77 gC/m<sup>2</sup> for the same interval—a reasonably close agreement.

The data, while subject to uncertainties due to infrequent sampling and lack of vertical sampling, illustrate the value of the use of pCO<sub>2</sub> for studies

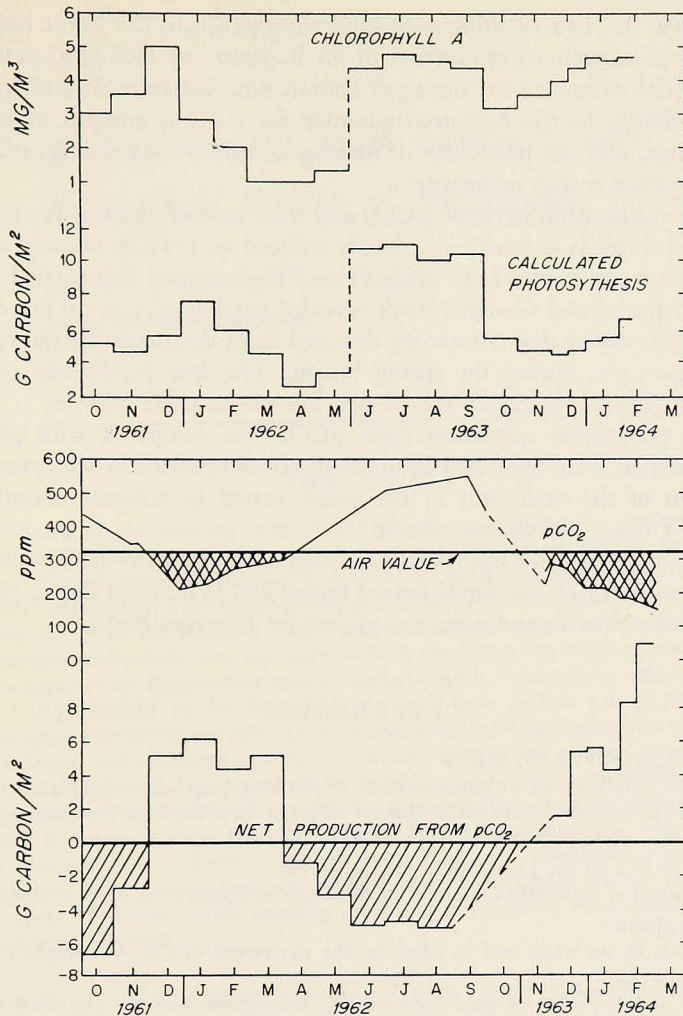


Figure 3. Changes in  $p\text{CO}_2$  and chlorophyll *a* in the waters of Vineyard Sound and the net production and total photosynthesis calculated from them.

of biological production. The measurement of  $p\text{CO}_2$  is more sensitive to biological activity in the water than is the measurement of oxygen, and it can be done in a continuous manner from a moving vessel, thereby avoiding errors caused by spot sampling in a patchy ocean. The results indicate that, for the six months after the beginning of the spring or winter bloom, the net production of the water column, i.e., the photosynthesis less the respiration of animals and plants, was about 17  $\text{gC}/\text{m}^2$  for Vineyard Sound and Wilkinson Basin, at least 70  $\text{gC}/\text{m}^2$  for Nantucket Sound, and over 100  $\text{gC}/\text{m}^2$  for Georges Bank.

*Summary.* 1. The advantages of measuring  $p\text{CO}_2$  in the water rather than the dissolved-oxygen concentration as an indicator of biological activity are discussed with reference to: the equilibration time between air and water, the per cent change in the measured quantity for a given amount of biological gas exchange, and the possibility of making continuous recordings of surface-water data from a ship underway.

2. The relationship between  $p\text{CO}_2$  and total carbon dioxide was measured. In distilled water it is nearly 1:1 but is reduced to 1:16 in oceanic water.

3. Measurements on four cruises in Vineyard and Nantucket sounds, Wilkinson Basin, and Georges Bank revealed patches of 2 to 20 km diameter having  $p\text{CO}_2$  values that commonly deviated from the mean for the region by as much as 14% during the spring bloom. The low  $p\text{CO}_2$  was correlated with high chlorophyll during the bloom, but not at other seasons.

4. Net production calculated from  $p\text{CO}_2$  was compared with photosynthesis calculated from light and chlorophyll concentrations in Vineyard Sound. Respiration of the organisms in the water varied in different months from 0.02 to 0.3 times the photosynthesis.

5. Net production for the six months beginning with the spring bloom was calculated to be 17  $\text{gC}/\text{m}^2$  for Vineyard Sound and Wilkinson Basin, 70  $\text{gC}/\text{m}^2$  for Nantucket Sound, and over 100  $\text{gC}/\text{m}^2$  for Georges Bank.

#### REFERENCES

CREITZ, G. I., and F. A. RICHARDS

1955. The estimation and characterization of plankton populations by pigment analysis. III. A note on the use of "Millipore" filters in the estimation of plankton pigments. *J. Mar. Res.*, 14: 211-216.

GARRELLS, R. M., M. E. THOMPSON, and R. SIEVER

1961. Control of carbonate solubility by carbonate complexes. *Amer. J. Sci.*, 259: 24-45.

KANWISHER, JOHN

1960.  $p\text{CO}_2$  in sea water and its effect on the movement of  $\text{CO}_2$  in nature. *Tellus*, 12: 209-215.

1963. On the exchange of gases between the atmosphere and the sea. *Deep-sea Res.*, 10: 195-217.

REDFIELD, A. C.

1948. The exchange of oxygen across the sea surface. *J. Mar. Res.*, 7: 347-361.

RYTHER, J. H., and C. S. YENTSCH

1957. The estimation of phytoplankton production in the ocean from chlorophyll and light data. *Limnol. Oceanogr.*, 2: 281-286.