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**THE EFFECT OF OXYGEN TENSION ON THE RATE OF  
OXIDATION OF ORGANIC MATTER IN SEA  
WATER BY BACTERIA<sup>1</sup>**

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It is generally recognized that the oxygen consuming capacity of heterotrophic bacteria in water serves as a good criterion of the amount of respirable or oxidizable organic matter in the water. However, the fragmentary literature on the subject records contradictory observations on the effect of oxygen tension upon the rate of bacterial oxidations. For example, Pomeroy (1938) found the amount of oxygen consumed by diluted sewage containing from 0.7 to 17.5 cc. of oxygen per liter to be independent of the oxygen tension but Heukelekian (1936) noted the maximum consumption of oxygen in such sewage mixtures containing around 10.5 cc. of oxygen per liter. According to Waksman and Carey (1935a) organic matter in sea water is oxidized more and more slowly as the oxygen tension is reduced. Conversely ZoBell and Stadler (1940a) report that the rate of bacterial oxidation of organic matter in lake water is not influenced by the oxygen tension within the examined ranges of 0.21 to 25.5 cc. of oxygen per liter.

In order to standardize procedures for the determination of the respirable organic matter content of sea water as well as to estimate the amount of oxygen being consumed by bacteria *in situ* it is necessary to have information on the effect of oxygen tension on bacterial respiration. The far-reaching significance of such determinations is emphasized by Sverdrup (1938) who points out that a rational explanation of the distribution of oxygen in the oceans awaits information on the "amount of oxygen-consuming organic matter" at different depths and the effect of oxygen content of the water on oxygen consumption.

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## EXPERIMENTAL

Sea water was collected in 5-gallon carboys from Buzzards Bay or Vineyard Sound and brought into the laboratory. It was filtered through No. 25 bolting silk and thoroughly shaken to insure uniformity in its bacterial and chemical composition. The water was warmed to 22° C. and distributed in 4 l. quantities in gallon bottles. Tank nitrogen, or oxygen as required, was bubbled through the water until the dissolved oxygen of the water was adjusted to the desired concentration. By using flow meters it became possible to admit almost exactly the required amount of nitrogen or oxygen. The water was siphoned into 140 ml. glass-stoppered bottles under an atmosphere of nitrogen and oxygen which was in equilibrium with the partial gas pressure of the water being bottled. The oxygen content of the first two bottles filled with water and the last two was determined at once, these being used as controls to show the initial dissolved oxygen content of the water. The remaining bottles of water were placed in a water bath at 22° C. and the oxygen content determined after different periods of incubation.

The oxygen tension of the water was determined by the Winkler technique (Thompson and Robinson, 1939) using a microburette and N/100 sodium thiosulphate for titrations. In most cases the initial quadruplicate determinations agreed to within 0.03 cc./l. and the series was discarded if the divergence of duplicates exceeded 0.10 cc./l.

The bottles, siphons and other glassware used in the experiments were cleaned with sulphuric-acid dichromate solution and thoroughly rinsed. These precautions were exercised because of the known tendency of organic matter and bacteria to accumulate on glass immersed in water (Stark et al., 1938).

Adjusting the oxygen tension of sea water by the procedures outlined above has a slight effect on the carbon dioxide tension and may alter other properties of the water but the following experiment demonstrated that neither the rate nor the amount of oxygen-consumption was influenced by such treatment. Part of a sample of sea water was transferred to each of several glass-stoppered bottles without treatment. The oxygen tension of the second portion of the water sample was reduced to 0.64 cc./l. by bubbling nitrogen through it. Part of this was then bottled and to the remainder oxygen was admitted until it approximated the oxygen content of the original sample. Oxygen was bubbled through another portion of the water sample until it contained 12.74 cc./l. Part of this was bottled and to the remainder nitrogen was admitted until the oxygen tension was reduced to approximately that of the original sample after which it was bottled. Duplicate

bottles of water receiving each treatment were analyzed after different periods of incubation in the water bath at 22° C. The results which are summarized in Table I show that within the limits of experimental error the same amount of oxygen is consumed by the respiring bacteria in sea water regardless of the treatment of the samples with nitrogen or oxygen.

The effect of oxygen tension on the rate of bacterial respiration in sea water was studied by adjusting the oxygen tension of different lots of a large sample of water collected from Buzzards Bay (6/23/39) at concentrations ranging from 0.41 to 18.04 cc./l. by treating with either

TABLE I  
OXYGEN CONSUMED AFTER DIFFERENT PERIODS OF TIME AT 22° C. BY BACTERIA IN SEA WATER THE GAS TENSION OF WHICH HAD BEEN ALTERED BY BUBBLING EITHER NITROGEN OR OXYGEN OR BOTH GASES ALTERNATELY THROUGH THE WATER

Gaseous treatment	Initial dissolved oxygen cc./l.	Oxygen consumed after			
		2 days cc./l.	5 days cc./l.	10 days cc./l.	20 days cc./l.
None	5.46	0.24	0.39	0.87	1.26
Nitrogen	0.64	0.25	0.34	0.62	—
Nitrogen + oxygen	5.72	0.28	0.43	0.95	1.21
Oxygen	12.74	0.21	0.41	0.97	1.32
Oxygen + nitrogen	5.30	0.25	0.36	0.84	1.24

nitrogen or oxygen. Quadruplicates were analyzed for oxygen content at once and duplicates after different periods of incubation in the water bath at 22° C. Prior to the addition of the Winkler reagents 1.0 cc. of water from each bottle was withdrawn for estimating the bacterial populations. Appropriate dilutions were plated with nutrient sea water agar and the colonies were counted after 10 days incubation at room temperature. From these data the amount of oxygen consumed per bacterial cell was calculated by applying the formula of Buchanan and

Fulmer (1930): 
$$m = \frac{2.303 S \log b/B}{t(b - B)}$$
 where  $m$  is the amount of oxygen consumed per cell per hour,  $S$  the total amount of oxygen consumed in time  $t$ ,  $B$  the number of bacteria at the beginning of the experiment and  $b$  the number after time  $t$ . Table II records the amount of oxygen which was consumed by the bacteria after different periods of incubation in water containing different concentrations of oxygen and the amount of oxygen which was consumed per cell per hour during the first two days of the experiment. Although all of the requisite conditions do not prevail to make the application of the

formula of Buchanan and Fulmer strictly valid, it is noteworthy that for each oxygen tension the rate of respiration of the bacteria is found to be of the same order of magnitude.

The rate of oxygen consumption was virtually the same for water of all oxygen concentrations until the concentration of oxygen was reduced to less than 0.2 cc./l. The rate of oxygen consumption decreased after two days incubation at 22° C. Excluding the first two series in Table II which initially contained the least dissolved oxygen and in which the

TABLE II.

OXYGEN CONSUMED BY MULTIPLYING BACTERIA IN SEA WATER CONTAINING DIFFERENT CONCENTRATIONS OF DISSOLVED OXYGEN AT 22° C. AND THE AMOUNT OF OXYGEN CONSUMED PER CELL PER HOUR DURING THE FIRST TWO DAYS OF THE EXPERIMENT AS CALCULATED FROM DATA ON THE BACTERIAL POPULATIONS AND THE OXYGEN TENSION

<i>Initial dissolved oxygen</i>	<i>Oxygen consumed after</i>				<i>Oxygen consumed per cell per hour during first two days</i>
	<i>1 day</i>	<i>2 days</i>	<i>5 days</i>	<i>10 days</i>	
cc./l.	cc./l.	cc./l.	cc./l.	cc./l.	cc.
0.41	0.07	0.20	0.37	0.39	$13.9 \times 10^{-12}$
0.77	0.06	0.24	0.55	0.72	$9.2 \times 10^{-12}$
1.19	0.06	0.21	0.62	0.95	$12.5 \times 10^{-12}$
2.36	0.08	0.26	0.56	0.91	$16.1 \times 10^{-12}$
5.10	0.07	0.28	0.59	0.98	$15.0 \times 10^{-12}$
8.26	0.09	0.25	0.61	0.92	$14.3 \times 10^{-12}$
12.74	0.05	0.23	0.67	0.91	$16.4 \times 10^{-12}$

total oxygen consumption was limited after two to five days by the amount of oxygen present, the bacteria consumed an average of  $14.9 \times 10^{-12}$  cc. of oxygen per cell per hour during the first two days of the experiment. The average rate had dropped to  $9.5 \times 10^{-12}$  cc. per cell per hour for five days and to  $4.7 \times 10^{-12}$  cc. for ten days. In fact, from the fifth to the tenth day of the experiment the bacteria were consuming an average of only  $2.6 \times 10^{-12}$  cc. of oxygen per cell per hour. The decreasing respiratory rate is attributed to the progressive utilization of the more readily oxidizable fractions of organic matter occurring in the sea water, although it may also be influenced by the age of the cells. It has been shown by Clifton and Logan (1939) and others that young cells in the logarithmic phase of growth use more oxygen than older cells. The tendency of the bacteria to adhere tenaciously to the glass walls of the bottle causing many respiring bacteria to escape detection by plating procedures is another complicating factor (ZoBell, 1936). For this reason the rate of respiration

after several days incubation may be considerably less than  $2.6 \times 10^{-12}$  cc. per cell per hour as estimated because there are probably as many or even more respiring bacteria which are tenaciously attached to the walls of the glass bottles than the number which are detected in the water by the conventional plate count procedure.

The enrichment of sea water with readily oxidizable substances accelerates the rate of oxygen consumption by bacteria. As has been shown by Waksman and Carey (1935b) the addition of utilizable organic matter to sea water causes a large increase in the bacterial population and oxygen consumption. According to Johnson (1936) the enrichment of sea water with 0.04 per cent of glucose increased the rate of respiration of marine bacteria 10 to 378 per cent. Similar results have been reported by ZoBell (1940) for both "resting" cells and multiplying cultures from lake water. In order to ascertain if the effect of oxygen tension on the rate of oxidation of organic matter is more pronounced in the presence of larger concentrations of readily utilizable organic matter, sea water was enriched with 0.05 per cent each of glucose and asparagine. The water was inoculated with mixed cultures of marine bacteria to give an initial bacterial population of approximately two million viable cells per cc. and the oxygen tension of different lots of the water was adjusted to range from 0.48 to 7.43 cc./l. The oxygen content of the water was determined from hour to hour and the amount of oxygen consumed was calculated. The results which are summarized in Table III show that the oxygen tension has

TABLE III

EFFECT OF OXYGEN TENSION ON THE OXYGEN UPTAKE OF BACTERIA IN SEA WATER ENRICHED WITH 0.05 PER CENT EACH OF GLUCOSE AND ASPARAGINE

<i>Initial dissolved oxygen</i>	<i>Oxygen consumed after</i>				
	<i>2 hours</i>	<i>4 hours</i>	<i>6 hours</i>	<i>10 hours</i>	<i>16 hours</i>
cc./l.	cc./l.	cc./l.	cc./l.	cc./l.	cc./l.
0.48	0.05	0.15	0.31	0.48	0.48
1.14	0.06	0.14	0.34	0.91	1.14
1.97	0.07	0.18	0.38	1.01	1.46
4.15	0.04	0.12	0.35	0.95	1.53
7.43	0.03	0.17	0.40	1.04	1.61

no influence on the rate of respiration of bacteria in sea water enriched with organic matter until the oxygen tension is reduced to a very low level.

Waksman and Renn (1936) suggest that the effect of oxygen tension may be more pronounced when refractory substrates are being oxidized.

Therefore the experiment was repeated using aged sea water enriched with 0.05 per cent of ferric lignoprotein, a compound which is not readily oxidized by bacteria. The lignoprotein was obtained from Dr. Waksman. The "aged" sea water had been stored in the laboratory for several weeks to permit bacterial activity to oxidize the respirable organic matter. Controls run with this water revealed that it consumed only 0.26 cc. of oxygen per liter in 20 days at 22° C. The lignoprotein was slowly oxidized by the bacteria as indicated by bacterial multiplication and oxygen consumption but the rate of oxidation was found to be independent of the oxygen tension within the examined range of 0.41 to 8.93 cc. of oxygen per liter. The results of the experiment which has been repeated with similar findings are presented in Table IV.

TABLE IV  
EFFECT OF OXYGEN TENSION ON THE OXYGEN UPTAKE OF BACTERIA INCUBATED AT 22° C. IN AGED SEA WATER ENRICHED WITH 0.05 PER CENT OF FERRIC LIGNOPROTEIN

<i>Initial dissolved oxygen</i>	<i>Oxygen consumed after</i>				
	<i>1 day</i>	<i>2 days</i>	<i>3 days</i>	<i>5 days</i>	<i>10 days</i>
cc./l.	cc./l.	cc./l.	cc./l.	cc./l.	cc./l.
0.42	0.30	0.41	—	—	—
0.99	0.37	0.61	0.82	0.92	—
2.00	0.39	0.70	0.87	1.21	1.54
4.76	0.37	0.58	0.80	1.04	1.53
8.93	0.34	0.59	0.76	0.96	1.34

The lignoprotein was oxidized much more slowly than glucose or asparagine. A sample of isolated lignin purified by Bartlett and Norman (1938) was also found to be slowly oxidized by bacteria in sea water. From water enriched with 0.05 per cent of the lignin and which initially contained 0.78, 2.19, 5.30 and 9.04 cc. of oxygen per liter there was consumed an average of 0.54, 0.65, 0.57 and 0.61 cc. of oxygen respectively in 58 days at 22° C. ZoBell and Stadler (1940b) found that each of eleven different samples of purified or isolated lignins was slowly oxidized by bacteria in lake water and the rate of oxidation was independent of the oxygen tension until the latter was reduced to less than 0.3 cc. of oxygen per liter.

Waksman and Renn (1936) showed that the filtration of sea water removes an appreciable quantity of the oxygen consuming constituents and in so doing the effect of oxygen tension on the rate of oxygen consumption is amplified. The former observation has been confirmed by testing the oxygen consuming capacity of sea water treated in different

ways. Large samples of surface water were divided into three lots. The first was siphoned into glass-stoppered bottles without any treatment. The second lot was filtered through No. 25 bolting silk and then bottled. The third lot was filtered through a No. 4 sintered-glass filter and shaken to equilibrate it with air after which it was bottled. An unfiltered sample of surface water collected from Buzzards Bay (6/24/39) was found to consume 0.86 cc. of oxygen per liter in 20 days at 22° C. That which was filtered through bolting silk consumed 0.60 cc. of oxygen per liter while the sintered-glass filtered water consumed only 0.49 cc. of oxygen per liter. Unfiltered, silk-filtered and sintered-glass filtered water collected from Vineyard Sound (8/4/39) consumed 1.09, 0.75 and 0.53 cc. of oxygen per liter respectively in 20 days at 22° C.

Using the method suggested by Dr. C. E. Renn a large volume of sintered-glass filtered sea water was obtained by immersing 2-liter bottles fitted with No. 4 sintered-glass filters to a depth of ten or twelve fathoms where the hydrostatic pressure forced water into the bottles. This water from which much of the particulate and readily utilizable organic matter had been removed by the filters was tested for its oxygen consuming capacity in the presence of different concentration of dissolved oxygen. The oxygen tension of aliquot parts of the water was adjusted at different levels ranging from 0.49 to 9.05 cc./l. and the amount of oxygen consumed after different periods of incubation at 22° C. was determined. Corroborating previous findings it was found that the rate of oxygen consumption was appreciably slower in the sintered-glass filtered water than in unfiltered water collected from the same station and secondly, it was found that regardless of the more refractory characteristic and smaller concentration of the organic matter in the sintered-glass filtered water, the rate of oxidation

TABLE V  
EFFECT OF OXYGEN TENSION ON THE OXYGEN UPTAKE OF BACTERIA IN SEA WATER  
INCUBATED AT 22° C. WHICH HAD BEEN FILTERED *in situ* THROUGH A No. 4  
SINTERED-GLASS FILTER

Initial dissolved oxygen cc./l.	2 days cc./l.	Oxygen consumed after		
		5 days cc./l.	10 days cc./l.	20 days cc./l.
0.49	0.09	0.28	0.37	0.46
0.94	0.12	0.25	0.45	0.61
1.87	0.08	0.32	0.51	0.59
3.70	0.08	0.29	0.46	0.64
5.24	0.10	0.28	0.52	0.70
9.05	0.11	0.30	0.49	0.58

of the organic matter was independent of the oxygen tension over a wide range. The results are summarized in Table V.

In the foregoing experiments it was noted that the rate at which bacteria oxidize organic matter is not influenced by the oxygen tension of sea water until the latter is reduced to 0.2 to 0.3 cc. of oxygen per liter (see Tables II and V). Below this concentration of dissolved oxygen the rate of oxygen consumption decreases with decreasing oxygen tension. However, when corrections were made for the minute amounts of oxygen introduced by the Winkler reagents it was found that respiring bacteria are able to remove the last detectable trace of oxygen from sea water provided other conditions including utilizable organic matter do not become limiting factors.

### DISCUSSION

The rate of oxidation of organic matter by bacteria in sea water does not seem to be influenced by the concentration of oxygen within the examined range of 0.3 to 12.74 cc./l. although it is influenced by the concentration of oxidizable organic matter. Apparently dissolved oxygen in sea water becomes a limiting factor in the bacterial oxidation of organic matter only when the concentration of oxygen is reduced to less than 0.3 cc. per liter. However, oxygen might become a limiting factor in localized microspheres rich in oxidizable matter such as, for example, the bodies of decomposing plankton organisms, if oxygen is consumed more rapidly than it can be replaced by diffusion from the surrounding water. Under these conditions a high oxygen tension in the surrounding water might be beneficial because it would increase the oxygen gradient and hence expedite the diffusion of oxygen to the oxygen-deficient microsphere.

According to Rashevsky (1933) the rate of oxygen consumption by protoplasm is independent of the oxygen tension except in so far as the latter might influence the diffusion or penetration rate of oxygen. Similarly Shoup (1929) concludes that "a constant and maximum rate of oxygen consumption occurs in small cells when the oxygen concentration becomes sufficient to entirely saturate the surface of the oxidative catalyst of the cell." He found that light production by photo-genic bacteria, an oxidative reaction, was not dimmed until the oxygen was reduced to less than 0.1 cc. per liter.

Although most workers (Amberson, 1928, Harvey, 1928, Hyman, 1929, Shapiro, 1934, ZoBell and Stadler, 1940a) find that the respiratory rate of aquatic unicellular organisms is independent of oxygen tension over a wide range, there seem to be certain exceptions. Different bacteria may have different types of respiratory metabolism as

indicated by Schlayer's (1936) observation that 20 to 30 per cent of oxygen is optimum for the respiration of *Pneumococci* while the respiration of certain other bacteria he studied is unaffected by the concentration of oxygen until the latter is reduced to less than one per cent (about 0.2 cc. per liter). The difference may be related to the membrane permeability of the bacteria or it might be related to the e.m.f. or other peculiarities of the biological system. It is noteworthy that certain bacteria whose respiration is reported to be favored by a high concentration of oxygen, namely, *Pneumococci* (Schlayer, 1936), *Azotobacter* (Burk, 1930) and *Rhizobia* (Georgi and Wilson, 1933), are surrounded by capsular membranes which might tend to retard the diffusion of oxygen. Taylor (1935) has shown that there is a relationship between the respiratory rate and the e.m.f. of certain cells, and the e.m.f. in turn is influenced by the oxygen tension. Kempner (1937) reports that at low temperatures or with old cells the respiration of *Escherichia coli* is independent of the oxygen tension, but near the optimum temperature or with young cells the rate of respiration is a function of the oxygen tension.

The observations reported above as well as the work of Waksman and associates show that the concentration as well as the quality of the organic matter influences the rate at which it is oxidized. In general, the rate of bacterial respiration increases as the concentration of oxidizable organic matter increases but additional experiments must ascertain the range within which this generalization maintains. Working with lake bacteria ZoBell (1940) found that the optimum concentration of glucose for the respiration of lake bacteria was between 100 and 1000 mgm./l. and similar results were obtained with glycerol, asparagine and lactic acid. With this concentration of organic matter the rate of bacterial respiration independent of the favorable influence on bacterial multiplication was appreciably faster than in the presence of only 5 to 10 mgm. of organic matter per liter, the concentration which occurs in sea water. Considering that most of the organic content of sea water is highly refractory to bacterial oxidation, it appears that the concentration of organic matter is near the threshold of the requirements for bacteria which probably accounts for the paucity of bacteria in the ocean. There is no direct evidence that a lack of either utilizable nitrogen or phosphorus limits bacterial activity in the ocean although it has been demonstrated by Waksman and Carey (1935b) and Waksman and Renn (1936) that nitrogen limits bacterial activity when glucose is added to sea water.

Whereas the bacteria in sea water incubated at 22° C. consumed only  $14.9 \times 10^{-12}$  cc. of oxygen per cell per hour, they consumed

nearly four times as much or  $54.1 \times 10^{-12}$  cc. of oxygen per cell per hour at this temperature when the sea water was enriched with 0.05 per cent each of asparagine and glucose. Considering that the bacteria approximate spheres having a mean diameter of  $1.0 \mu$  and a density near that of sea water, it is estimated that in the sea they use about 30 cc. of oxygen per hour per gram of living cells and nearly four times as much (around 110 cc. per hour per gram) in the presence of an abundance of oxidizable organic matter. Heilbrunn (1937) has compiled data which show that various marine animals consume only from 0.002 to around 1.0 cc. of oxygen per hour per gram of fresh living material under comparable conditions. However, in spite of the relatively large oxygen consuming capacity of respiring bacteria, it would require a bacterial population of more than seven thousand per cc. to consume 1.00 cc. of oxygen from a liter of sea water in a year at  $22^\circ \text{C}$ ., and proportionately more at lower temperatures. According to Johnson (1936) the  $Q_{10}$  of marine bacteria is 2.3 between  $5^\circ$  and  $15^\circ \text{C}$ . and 2.18 between  $15^\circ$  and  $25^\circ \text{C}$ .

If the results of this paper are applicable to conditions in the ocean, they have an important bearing on the explanation of the distribution of dissolved oxygen. It follows that where the concentration of oxygen is more than 0.3 cc./l. there exists no relation between the amount of oxygen consumed by bacteria and the amount present. Assuming that the bacterial oxidation of organic matter is the principal cause of oxygen consumption at depths well below the photosynthetic zone, say below 300 meters, no conclusions can be drawn concerning the rate of oxygen consumption from observations on the amount of oxygen present or vice versa because the two quantities are independent of each other. This is contrary to Sverdrup's (1938) suggested explanation of the oxygen minimum in the ocean. However, in fairness it should be added that Sverdrup emphasized the speculative character of his suggestion which was made to arouse interest in the problem. Moreover, at that time upon being consulted the author expressed the opinion that judging from reports in the literature, oxygen consumption by marine bacteria might be directly proportional to the oxygen tension, an opinion which is contradicted by the present findings.

Going a step further it appears that the distribution of oxygen in the ocean cannot be explained by considering only processes *in situ* but it is also necessary as Seiwel (1937) has done to consider the "history" of the water masses. In order to do so properly the factors which influence oxygen consumption must be studied further.

## SUMMARY

The rate of oxidation of organic matter in sea water as indicated by oxygen consumption by bacteria is independent of the oxygen tension within the examined range of 0.31 to 12.74 cc. of oxygen per liter.

As the concentration of oxygen is reduced below 0.3 cc. per liter the respiratory rate decreases, although if oxidizable organic matter is present bacteria can remove the last detectable trace of dissolved oxygen from sea water.

During the first two days of incubation at 22° C. bacteria in sea water were found to consume an average of  $14.9 \times 10^{-12}$  cc. of oxygen per cell per hour; progressively less thereafter as the more readily oxidizable fractions of organic matter were utilized.

Although the enrichment of sea water with 0.05 per cent each of glucose and asparagine accelerates the rate of respiration, the rate in the enriched sea water is not influenced by the oxygen tension within the stated limits.

Filtering sea water through silk plankton netting or sintered-glass removes much of the more readily oxidizable matter from sea water but the rate of oxygen consumption by bacteria in the filtered water is independent of the oxygen tension.

Lignoprotein as well as a sample of purified lignin was found to be slowly oxidized by marine bacteria, the rate being independent of the oxygen tension.

The probable rôle of bacteria in influencing the distribution of dissolved oxygen in the sea is discussed.

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