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STUDIES ON THE PHYSIOLOGY OF CORALS

VI. THE RELATIONSHIP BETWEEN RESPIRATION IN CORALS AND THE PRODUCTION OF OXYGEN BY THEIR ZOOXANTHELLAE

BY

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WITH FOUR TEXT-FIGURES

CONTENTS

1. INTRODUCTION AND LITERATURE.

In the two preceding papers in this series accounts have been given of the structure, distribution in the tissues of the corals, and physiology of the zooxanthellae, and of experiments conducted to determine the nature of their relationship with the animals in which they live, especially in connection with the theory that the zooxanthellae provide an accessory source of food for the corals. In the present paper the study of this relationship is continued by the description of investigations into the conditions controlling the production of oxygen by the zooxanthellae as a result of photosynthesis and the consumption of oxygen by the corals due to respiration. By this means the elucidation of the relationship between the two processes has been attempted. The results of extensive series of experiments are here recorded, and certain conclusions deduced from these

results are briefly discussed. The full discussion of these results in their broader aspects will be contained in the final, seventh, paper in this series, where the results of the whole series of papers dealing with the physiology of corals and of the zooxanthellae will be reviewed and compared, and general conclusions drawn from the great body of evidence which has been accumulated.

The literature on oxygen exchange between coelenterates containing zooxanthellae and the surrounding water is not extensive. Brandt (1883) was the first to investigate the matter in any detail, and the results he obtained for actinians were later confirmed and extended by Trendelenburg (1908), who worked on *Anemonia sulcata*, and by Pütter (1911), who worked on *Anemonia* and *Aiptasia diaphana*, both of which contain zooxanthellae. Both workers found that during the daytime the zooxanthellae produced more oxygen than the actinians used for respiration. Gardiner (1898, 1899) was apparently the first to point out that similar conditions prevailed in the reef-building corals. Mayor (1918) states that if corals are kept in sunlight the water soon becomes supersaturated with oxygen owing to the photosynthetic activity of the zooxanthellae, but he did not carry out any oxygen determinations. Cary (1918) notes the same fact for Alcyonaria containing zooxanthellae, but also gives no figures. McClendon (1918) states that on coral reefs the zooxanthellae of corals and actinians have a great effect upon the oxygen content of the sea-water, while he found that a specimen of *Cassiopea xamachana* (a bottom-living scyphozoan which contains zooxanthellae) 11 cm. in diameter and weighing about 117 grammes, gave out 1·9 c.c. of oxygen per hour in the sunlight, but absorbed 2·8 c.c. per hour in darkness. Verwey (1930, 1931) gives definite figures for the oxygen exchange of *Acropora hebes* in light and darkness, and shows that under the former conditions the oxygen content of the water increases and under the latter it decreases. He concludes from his experiments that " in shallow water the production of oxygen by coral zooxanthellae during the day is about 2·5–5 times as great as the consumption of oxygen through corals and zooxanthellae together " (1931, p. 177).

This excess of oxygen production over consumption during the daytime naturally gives rise to great diurnal changes in oxygen content of the water over coral reefs. This appears first to have been investigated quantitatively by McClendon (1918), who found that the water which washes the reefs of the Florida keys varied in oxygen content from a minimum of between 3 and 4·5 c.c. per litre at dawn to a maximum of between 4·5 and 7 c.c. at 3 p.m. Verwey (1930, 1931) found a similar change throughout the day in the lagoon of the coral island of Hoorn in the Bay of Batavia, the minimum oxygen content occurring between 6 and 8 a.m., and the maximum between 12 noon and 3 p.m. or between 3 p.m. and 6 p.m. He found similar conditions in the water close to the shore and above the reef, but water taken from the open sea at a depth of 3 metres showed little change in oxygen content throughout the day.

Mayor (1918*b*, 1924), by finding the oxygen consumption of various species of corals in the dark and then estimating the amount of living tissue in each specimen, obtained figures for the oxygen consumption of equivalent amounts of living tissue for the different corals. His results, which Verwey and Vaughan (1930) have not unreasonably criticized, show differences for the oxygen consumption of a gramme of living tissue in one hour, from 0·0256 c.c. for *Siderastrea radians* to 0·48772—18·7 times as much—for *Acropora muricata* (1918), and from 0·085 c.c. for *Porites andrewsi* to 0·468 c.c. for *Pocillopora damicornis* (1924). As Verwey notes, the figures for *Acropora* and *Pocillopora* are as high as those for fish,

and inherently improbable for a sessile animal. Mayor's results, however, do indicate that different genera of corals may have very different oxygen needs, and this matter needs further and more accurate investigation. Mayor also found that, of a number of corals studied, only one, *Acropora muricata*, was unable to survive for eleven hours in water deprived of oxygen under an air-pump, while even that species survived for six hours. But the value of these observations is greatly reduced owing to his failure to furnish figures as to the actual oxygen content of the water.

Various authors, *e.g.* Gardiner, Boschma (1924, 1925, 1926), Hickson (1924), Vaughan (1919) and Verwey, consider that the vertical distribution of reef-building corals is determined by the ability of the zooxanthellae to flourish, and so is dependent on the amount of light which can penetrate through the water. Verwey (1931) has shown that in the Bay of Batavia the depth to which living coral extends increases with increasing distance from the shore, and this he correlates with diminishing quantities of silt and so increased penetration of light. The reason for the dependence of corals on zooxanthellae is another matter. As stated in Paper V of this series, a number of workers, notably Boschma, consider that the zooxanthellae form an accessory source of food for the corals—a view which our own experimental results did not in any way confirm. But others, Vaughan and Verwey in particular, think that the oxygen which the zooxanthellae produce may be of vital importance to the corals. Vaughan (1919, p. 204) says that the zooxanthellae, " set free oxygen which is intimately available for use by the corals, as it is in immediate contact with the animal tissues. Since these plants, while in the dark, cease to set free oxygen, and the corals under such circumstances are deprived of oxygen from that source, it may be that the poverty of coral growth in dark places is due to the suppression of the activities of these plants." Verwey (1931), from the figures he obtained for the oxygen consumption of *Acropora hebes*, calculated that a large colony of this species would consume, over a tropical night of twelve hours, 250 c.c. of oxygen for every kilogramme that it weighs. Since a reef will contain many thousand kilogrammes of living coral (the skeleton is included in these weights), it will consume several hundred litres of oxygen every night. The water itself only contains about 5 c.c. of oxygen per litre, diffusion and convection are slow, and Verwey concludes that without the excess of oxygen produced daily by the zooxanthellae the corals would be unable, growing as they do in such immense numbers together, to obtain enough oxygen to support themselves and to exist in sufficient numbers to form a reef. These conclusions will be considered in more detail in the discussion at the end of this paper after our own results have been described.

2. EXPERIMENTAL PROCEDURE.

The purpose of the series of researches described in this paper was essentially to elucidate as far as possible the conditions of oxygen exchange between corals and the surrounding water as these occur *in nature*. Accordingly the great majority of the experiments were carried out in the waters of the anchorage, and at depths where coral growth was about at its maximum. A certain number of experiments, on specially treated corals and on the influence of low oxygen content of the water on respiration and powers of survival of corals, were conducted in the aquarium at the back of the laboratory, where the temperature—no means of controlling which were available—was more constant than elsewhere on the island. It is not claimed that these researches

compare in absolute accuracy with similar experiments carried on under properly controlled conditions. It *is* claimed that the results obtained are relatively accurate, and that they *do* present a true picture of the conditions controlling oxygen consumption in corals and oxygen production by the zooxanthellae, from which valid conclusions may be drawn as to nature of the relationship, if any, between the two.

Small coral colonies, seldom exceeding 150 c.c. in volume, were selected for experimentation. The greatest care was taken first to remove any animals which might be commensal on or burrowing into the corals, while the bases of all the solid colonies, such as *Favia*, were thoroughly excavated by means of bone-forceps until all decaying matter, a certain amount of which was almost invariably present, had been removed. The experiments were all carried out in 7 lb. " Kilner " jars of glass, the tops of which were secured by metal screw bands. The external dimensions of these were, roughly, 21 cm. high and 15 cm. wide, with a mouth opening of 10 cm. in diamter. These jars were always filled and the tops secured under water in large buckets in which the water was brought up from the sea. In almost no case did any air subsequently enter the jars, although they had frequently to be carried in from the sea in baskets.

After filling, the jars were placed in wooden crates specially constructed by one of us (A. G. N.). Two of these consisted of a framework only, one of them holding six jars and the other eight, while the third consisted of a light-tight box with a sliding lid secured by a peg, the whole being painted black inside and out. These were known as the light and dark crates. The jars fitted easily but securely into compartments, those in the light crates being also secured from above by means of a wooden bar, which rested on the inner shoulders of the jars and passed through slots at either end of the crate, through which it could be drawn out when the jars were removed. To the bottom of all three crates very heavy metal weights were fastened, so that they sank immediately when placed in the sea, and rested securely on the bottom. Bridles of strong manilla rope were attached to the ends of the crates. These were tied together over the centre of the crates, and a length of rope attached to them by means of which the crates were lowered into the sea and subsequently drawn up again. A wooden float, consisting of a piece of deal $2\frac{1}{2}$ ft. long, was fastened to the free end of rope, and this served to show the position of the crates after they had been placed in the sea.

After some preliminary investigations a suitable site for the experiments was selected, and here all experiments, unless otherwise stated, were carried out. It lay on the inner side of Wishart's reef (see map of Low Isles in Vol. III, No. 2), where a narrow gully with a clean sandy bottom separated that reef from the reefs which projected out from the shore of the island, as shown in the map. The gully was sheltered and easily accessible, while conditions there were more uniform and corresponded more to those on the exposed surfaces of reefs than they did in the pools on the reef flat which were originally used. The crates rested on the flat, sandy bottom some 7 ft. below datum, and therefore 11·8 ft. below mean sea-level. This was probably about the optimum depth for coral growth around Low Isles. It must be borne in mind that the results of all experiments carried out here are for corals living at an average depth of about 2 fathoms (4 metres) and *not* at the surface.

The oxygen content in c.c. per litre, the temperature and, in some cases, the pH of the water were estimated at the beginning and again at the end of each experiment. Except when deemed unnecessary owing to the short experimental period,

controls were invariably carried out with jars containing water only. This was very important, because in an experiment of any considerable duration at the high temperatures prevailing, the large quantities of organic matter in the water caused, by their oxidation, a considerable fall in oxygen content. Oxygen was estimated by Winkler's method, duplicates being taken and the results (which seldom exceeded experimental error) being averaged. The jars were thoroughly shaken before the water was siphoned off into the oxygen bottles. Practically all the very many hundred titrations involved were carried out by one of us (M. J. Y.), while our thanks are due to Mr. A. P. Orr for his initial instruction in the method and for his constant help and advice. We are, likewise, indebted to Miss S. M. Marshall for much practical help, and to Mr. G. W. Otter for further help.

The capacity of the jars was approximately 2800 c.c. In a few experiments smaller jars of the same type with a capacity round about 820 c.c. were used. The majority of experiments were comparative, however, and the same corals were subjected to different conditions, times, etc., in the same jars throughout, so that the actual capacity of the jars, though recorded in most cases, is of minor importance. Owing to the essentially comparative nature of the experiments, oxygen is expressed in terms of c.c. per litre and not of total content. The volumes of the corals were determined by the amount of water they displaced, and are recorded. This also means little, because the amount of living tissue in a branching coral, *e. g. Pocillopora*, and in a solid coral such as *Porites*, of the same volume, is very different. The amount of oxygen consumed in a definite period in the dark is some indication of the amount of living matter, and is a safe guide when specimens of the same species are compared, but, as the results of Mayor's work show, different corals vary greatly in their oxygen requirements. Although the dark crate was probably light-tight, practically all experiments in darkness were carried on at night, so as to reduce all risk of light penetration to the minimum. The temperatures given are, unless otherwise stated, the average between the initial and final readings.

This work was carried out under the direction of the senior author, who is alone responsible for the actual writing of this paper, for the presentation of the data collected, and, with the concurrence of his colleagues, for the conclusions drawn from these.

3. OXYGEN EXCHANGE OF CORALS IN LIGHT AND DARKNESS.

A series of experiments was carried out with a representative sample of Madreporaria, and also with the Alcyonarian *Heliopora*, the Hydrozoan *Millepora*, and the Zoanthid *Palythoa*, all of which contain zooxanthellae, in order to determine the relation between the consumption of oxygen by the animals and the production of oxygen by the plants as a result of photosynthesis. Experiments were run for nine hours in the daytime, from about 8.30 a.m. to 5.30 p.m., in the light crates, and then overnight, from about 11 p.m. to 8 a.m., in the dark crate. The results of a selected series of such experiments are given in Table I. The figures in column 7 represent in terms of c.c. of oxygen per litre the difference between the final oxygen content of the jars containing the animals in the light and the control jar, *i. e.* the *total* oxygen exchange of the organisms which is the outcome of the balance between oxygen consumption by the corals and oxygen production by the

TABLE I.—*Oxygen Exchange of Corals after Exposure to Light and to Darkness for 9 Hours. Oxygen in terms of c.c. per litre. Experiments in Open Sea in usual position.*

Coral.	Volume in c.c.	Volume of jar in c.c.	Light.				Darkness.				O_2 produced by zooxanthellae.
			Average temperature.	O_2, initial.	O_2, final.	Difference from control.	Average temperature.	O_2, initial.	O_2, final.	Difference from control.	
Hydnophora microconus	53	2830	22·1° C.	4·47	8·20	+3·88	22·2° C.	4·47	2·85	−1·60	5·48
Psammocora gonagra	190	2820	,,	,,	3·39	−0·93	,,	,,	1·72	−2·73	1·80
Lobophyllia corymbosa	150	2920	,,	,,	4·78	+0·46	,,	,,	1·86	−2·59	3·05
Pavona danai	45	2910	,,	,,	4·91	+0·59	,,	,,	2·53	−1·92	2·51
Cyphastrea chalcidicum	200	2775	,,	,,	4·87	+0·55	,,	,,	2·37	−2·08	2·63
Control	..	820	,,	4·47	4·32	..	,,	4·47	4·45	..	..
Porites, sp.	145	2815	29·65° C.	4·39	5·90	+1·54	28·9° C.	4·08	1·78	−2·13	3·67
,,	130	2830	,,	,,	7·65	+3·29	,,	,,	1·20	−2·71	6·00
Favia, sp.	157	2880	,,	,,	7·32	+2·96	,,	,,	0·93	−2·98	5·94
,,	120	2830	,,	,,	8·15	+3·79	,,	,,	1·45	−2·46	6·25
Galaxea fascicularis	45	2830	,,	,,	5·25	+0·89	,,	,,	2·82	−1·09	1·98
,, ,,	43	2830	,,	,,	6·03	+1·67	,,	,,	2·18	−1·73	3·40
Fungia danai	31	2790	,,	,,	6·89	+2·53	,,	,,	2·02	−1·89	4·42
,, ,,	32	2820	,,	,,	8·97	+4·61	,,	,,	1·64	−2·27	6·88
Pocillopora bulbosa	28	2810	,,	,,	10·21	+5·85	,,	,,	1·08	−2·83	8·68
,, ,,	45	2815	,,	,,	12·23	+7·87	,,	,,	0·76	−3·15	11·02
Control	..	2790	,,	4·39	4·36	..	,,	4·08	3·91	..	..
Flabellum rubrum (2)	6	810	26·15° C.	4·65	4·96	+0·43	25·3° C.	5·36	4·72	−0·49	0·92
Control	..	830	,,	4·65	4·53	..	,,	5·36	5·21	..	..
Millepora	23	2825	29·5° C.	3·03	3·86	+0·83	29·65° C.	4·56	3·32	−1·14	1·97
,,	30	2880	,,	,,	3·71	+0·68	,,	,,	2·78	−1·68	2·36
Heliopora	35	2780	,,	,,	3·85	+0·82	,,	,,	3·27	−1·19	2·01
,,	90	2810	,,	,,	4·29	+1·26	,,	,,	2·16	−2·30	3·56
Palythoa	28	2760	,,	,,	3·07	+0·04	,,	,,	3·65	−0·81	0·85
,,	24	2830	,,	,,	3·15	+0·12	,,	,,	3·42	−1·04	1·16
Control	..	2810	,,	3·03	3·03	..	,,	4·56	4·46	..	..

zooxanthellae. It will be noted that, with the solitary exception of *Psammocora*, oxygen production invariably exceeds oxygen consumption—to a remarkable extent in the case of *Pocillopora*, a coral with thin tissues and a large surface. The figures in column 11 represent a similar difference for the experiments run in darkness, and since photosynthesis is cut out, indicate the *oxygen consumption* only of the organisms (animals and plants). The last column, giving the difference between the two former series of figures, represents the amount of oxygen, in c.c. per litre, produced by the zooxanthellae in nine hours at the particular temperature indicated and at the degree of illumination which prevailed on the day the particular experiment was carried out. There was no means of estimating this, but care was taken to conduct these experiments only on clear, sunny days and when the sea was calm.

The second series of experiments recorded in Table I (*Porites* to *Pocillopora*) formed part of a regular monthly series, which were continued for the first six months the expedition was at work. It was hoped originally to test out by this means the validity of Boschma's statement that corals feed on their zooxanthellae when plankton is scarce. But, as already indicated in Paper V of this series, the results of starvation and other experiments indicated clearly that corals do *not* under any circumstances obtain nourishment from their zooxanthellae, while, as will be shown in the papers on zooplankton by Russell and Colman in Vol. II of these reports, the zooplankton in these waters, unlike that of temperate seas, shows no seasonal variations except of a very minor character.

In addition to the above, a second series of experiments was carried out, using *Dendrophyllia* and *Balanophyllia*, neither of which contain zooxanthellae. The results of these experiments are shown in Table II.

In the case of *Dendrophyllia* and *Balanophyllia* it will be seen that, so far from there being an excess of oxygen produced in the light, there is actually, in all cases, a greater utilization of oxygen in the light than in the dark. This is probably explained by the higher temperatures which prevailed in the daytime. It should be noted in this connection, moreover, that both of these corals expand equally in light and in darkness, unlike the great majority of reef-building corals (see Paper I of this series). These experiments provide yet another confirmation of the fact, already discussed in Paper IV, that these two Eupsammiid corals possess neither true zooxanthellae nor, as Boschma (1924, 1925, 1926), has suggested, any other form of symbiotic algae.

These preliminary experiments show that in corals containing zooxanthellae a significant amount of oxygen is produced in light by the algae, an amount which, in all cases but one, which is possibly not typical, is in excess of the consumption of oxygen by the corals during this period. The figures for oxygen consumption by the corals, shown in the penultimate column in Table I, do not correspond in their variations with the figures for oxygen production by the zooxanthellae which are given in the last column. This may be due to one of two causes, or, more probably, a combination of the two. Different corals may possess, at maximum capacity, different proportions of zooxanthellae as compared to bulk of animal tissue. Thus the corals with deep, comparatively fleshy tissues, such as *Lobophyllia* (see Plate I, fig. 2, of Paper I of this series for an illustration of this coral), will probably have fewer zooxanthellae in comparison with their bulk than corals with thin tissues, such as *Pocillopora*. Perforate corals also probably have generally a lower content of zooxanthellae than imperforate corals owing to the inability of much light to penetrate into the internal canals. But the work of Mayor (1918 *b*, 1924) indicates that individual

TABLE II.—*Oxygen Exchange of Corals without Zooxanthellae after Exposure to Light and Darkness. Procedure as in Table I.*

Coral.	Volume in c.c.	Capacity of jar in c.c.	Light.				Darkness.			
			Average temperature.	O_2, initial.	O_2, final.	Difference from control.	Average temperature.	O_2, initial.	O_2, final.	Difference from control.
Dendrophyllia	40	2780	30·35° C.	4·46	2·86	−1·49	29·1° C.	4·10	2·79	−1·14
,,	30	2815	,,	,,	2·86	−1·49	,,	,,	2·57	−1·36
,,	28	2830	,,	,,	3·09	−1·26	,,	,,	2·94	−0·99
Control	..	2810	,,	4·46	4·35	..	,,	4·10	3·93	..
Balanophyllia	12	815	26·15° C.	4·65	3·99	−0·54	25·3° C.	5·36	4·83	−0·38
,,	12	820	,,	,,	4·24	−0·29	,,	,,	4·98	−0·23
Control	..	830	,,	4·65	4·53	..	,,	5·36	5·21	..

TABLE III.—*Oxygen Exchange of Corals previously kept for* 152 *Days in Total Darkness in the Light-tight Box on the Reef Flat, after Exposure to Light and Darkness for* 6 *Hours. Oxygen in terms of c.c. per litre. Experiments Carried out in Anchorage, Crates suspended from Boom of Whale Boat, Light Crate being flush with the Surface of the Water.*

Coral.	Volume in c.c.	Capacity of jar in c.c.	Light.				Darkness.				O_2, produced by zooxanthellae.
			Average temperature.	O_2, initial.	O_2, final.	Difference from control.	Average temperature.	O_2, initial.	O_2, final.	Difference from control.	
Porites, sp.	110	2820	21·7° C.	5·87	5·48	−0·30	21·6° C.	5·53	5·08	−0·47	0·17
Cyphastrea chalcidicum	160	2830	,,	,,	5·24	−0·54	,,	,,	4·76	−0·79	0·25
Lobophyllia corymbosa	155	2850	,,	,,	5·19	−0·59	,,	,,	4·76	−0·79	0·20
Favia, sp.	95	2920	,,	,,	5·21	−0·57	,,	,,	4·91	−0·64	0·07
Fungia danai	55	2850	,,	,,	5·79	+0·01	,,	,,	5·21	−0·34	0·35
Psammocora gonagra	65	2890	,,	,,	5·99	+0·21	,,	,,	4·78	−0·77	0·98
Control	..	830	,,	5·87	5·78	..	,,	5·53	5·55	..	..

corals respire at very different rates, so that the differences in the figures for oxygen consumption in the darkness may be due to this and not to differences in the actual amount of living tissue. It is a matter of regret that this work by Mayor was overlooked and no similar work carried out.

4. INFLUENCE OF PROLONGED EXPOSURE TO DARKNESS.

An account was given in Paper IV of this series of experiments carried out on corals kept for long periods in a light-tight box cemented down on the reef flat. As a result of long exposure to complete darkness the corals lost the greater part of their zooxanthellae, as was shown by experiments on phosphate excretion and by subsequent sectioning, the results of which are described in that paper. The effect of exposure for six hours first to light and then to complete darkness was determined for a series of these corals which had been in total darkness for 152 days. The experimental procedure employed was identical with that already described, except that the light crate employed was suspended from the boom of the whale boat in the anchorage, so that the tops of the jars were flush with the surface. This was done to give maximum illumination in view of the extremely small numbers of zooxanthellae within the tissues. The dark crate was put out in the same position, but lowered to the bottom. The results of these experiments are recorded in Table III.

The low content of zooxanthellae in the tissues of these corals is clearly shown by the figures in the last column, which, however, cannot be directly compared with those of Table I, owing to the shorter period of the experiments, which were carried out only a few days before the end of the expedition. It is especially noteworthy that in the light four of the corals showed an excess of oxygen consumption, in *Fungia* there was a negligible increase within the experimental error of the method, and only in *Psammocora* was there a significant rise. It appears that only in this last coral were any significant number of zooxanthellae present. It must be remembered, moreover, that the light crate was slung level with the surface of the water, and so the maximum amount of light was available for the zooxanthellae. Had the jars been in the usual position in the anchorage the difference between the results in light and darkness would have been even less, *i. e.* the figures in the last column in Table III might have been very close to zero.

5. OXYGEN EXCHANGE OVER DAY AND NIGHT.

Although, as the experiments already described show clearly, an excess of oxygen is produced by reef-building corals containing zooxanthellae during the daylight, it is necessary also to know what are the conditions of oxygen content in the water surrounding the corals at the end of twenty-four hours, *i. e.* after exposure to day and night, dusk and dawn. To this end a large number of corals were put out in the light crates for this period, details of a selected number of cases, experiments and of the results obtained being given in Table IV.

An examination of Table IV shows that at the end of 24 hours the oxygen content of the water in the jars containing the corals varied from 1·6% (no. 2) to 114·3% (no. 14) of that in the control jars. The latter jar, which contained a colony of *Favia*, is, however, the only case where there was an increase in oxygen at the end of the experimental period.

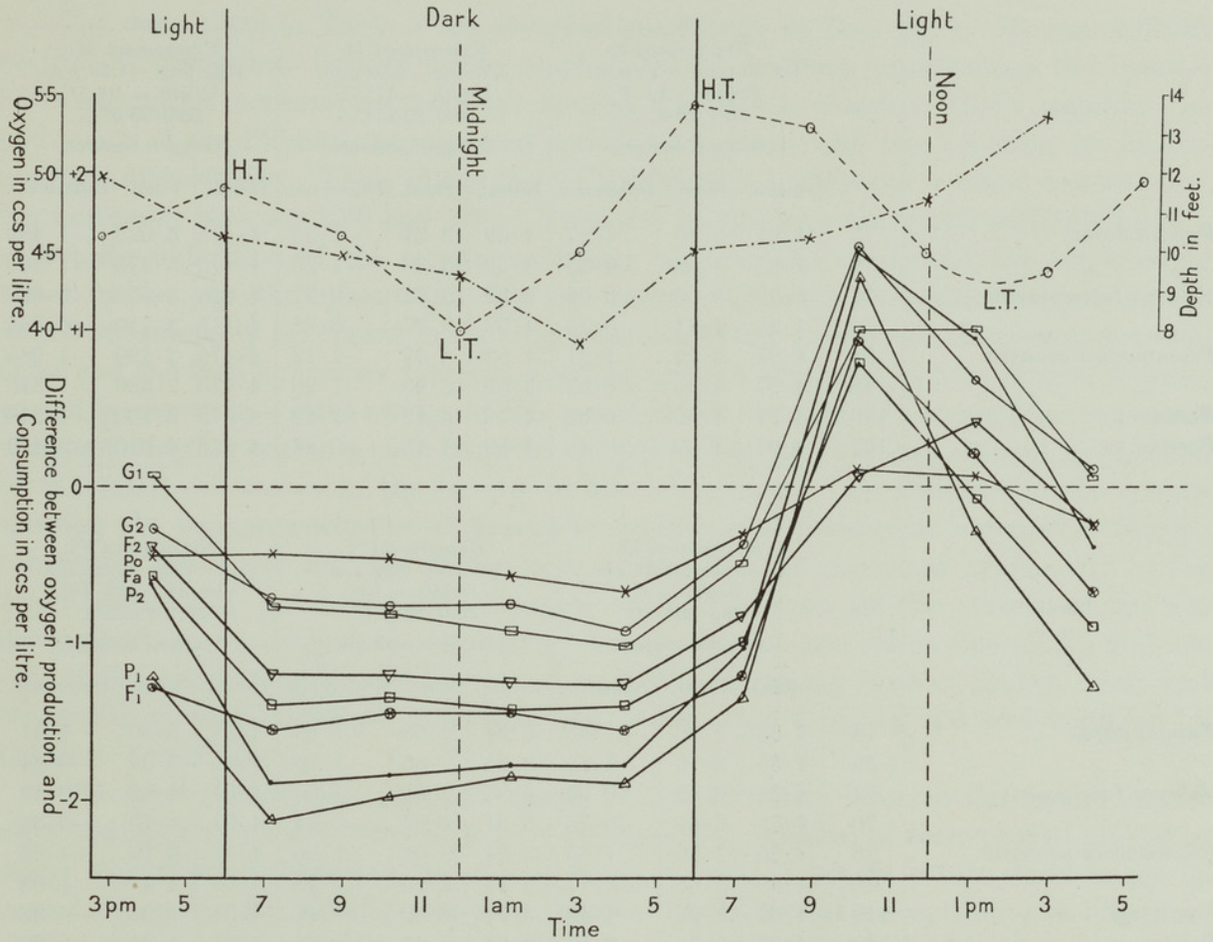
TABLE IV.—*Change in Oxygen Content, in c.c. per litre, of Water in Sealed Jars containing Corals after Exposure for 24 Hours in Light Crates in the Usual Position. Exposed about 2 p.m.*

No.	Coral.	Volume in c.c.	Capacity of jar in c.c.	Average temperature.	O_2, initial.	O_2, final.	Difference from control.	Percentage of O_2 in control.
1	*Fungia danai*	40	2810	28·95° C.	6·46	2·88	−3·58	44·6
2	,, *actiniformis*	80	2840	,,	,,	0·10	−6·36	1·6
3	*Galaxea fascicularis*	75	2760	,,	,,	4·17	−2·29	64·5
4	*Porites*, sp.	140	2830	,,	,,	1·24	−5·22	19·2
5	*Lobophyllia corymbosa*	110	2880	,,	,,	1·30	−5·16	20·1
6	*Tridacophyllia lactuca*	45	2810	,,	,,	4·21	−2·25	65·2
7	*Caulastrea furcata*	15	2810	,,	,,	5·42	−1·04	84·0
8	*Dendrophyllia*	15	2850	,,	,,	4·28	−2·18	66·3
	Control	..	830	,,	6·46	6·46	..	..
9	*Fungia danai*	75	2830	26·25° C.	4·88	3·54	−1·34	72·5
10	*Galaxea fascicularis*	65	2900	,,	,,	3·22	−1·66	65·6
11	*Psammocora gonagra*	48	2870	,,	,,	4·01	−0·87	82·2
12	,, ,,	26	2890	,,	,,	1·07	−3·81	22·0
13	*Porites*, sp.	140	2890	,,	,,	3·00	−1·88	61·5
14	*Favia*, sp.	180	2870	,,	,,	5·58	+0·70	114·3
	Control	..	830	,,	4·88	4·88	..	..
15	*Caulastrea furcata*	20	2900	26·25° C.	5·37	4·92	−0·14	97·2
16	*Lobophyllia corymbosa*	95	2890	,,	,,	2·16	−2·90	42·7
17	*Cyphastrea chalcidicum*	240	2920	,,	,,	3·08	−1·98	60·0
18	*Coeloria*, sp.	90	2870	,,	,,	2·45	−2·61	48·6
19	*Pavona danai*	90	2870	,,	,,	3·30	−1·76	65·2
	Control	..	830	,,	5·37	5·06	..	..
20	*Psammocora gonagra*	53	2820	22·95° C.	5·63	4·73	−0·87	84·5
21	*Favia*, sp.	95	2850	,,	,,	4·33	−1·27	77·3
22	*Pavona danai*	45	2910	,,	,,	3·39	−2·21	60·5
23	*Pocillopora bulbosa*	50	2775	,,	,,	2·85	−2·75	51·0
24	*Dendrophyllia*	35	2870	,,	,,	4·59	−1·01	81·9
	Control	..	830	,,	5·63	5·60	..	..
25	*Hydnophora microconus*	190	2830	22·65° C.	6·10	3·39	−2·51	57·5
26	*Cyphastrea chalcidicum*	200	2910	,,	,,	2·65	−2·25	44·9
27	*Millepora*	25	2850	,,	,,	4·29	−1·61	72·7
28	*Heliopora*	110	2775	,,	,,	5·65	−0·25	95·8
29	*Palythoa*	70	2920	,,	,,	4·02	−1·88	68·1
	Control	..	830	,,	6·10	5·90	..	..

It is clear, therefore, that apart from a few exceptional cases, the oxygen produced by the zooxanthellae over night and day does not balance the amount consumed by the coral, and by the zooxanthellae themselves, over that period. There is little to be gained by analyzing the figures in Table IV, the experiments being run purely to determine whether or no the oxygen production of the zooxanthellae does balance the oxygen consumption over night and day. Attention may, however, be drawn to the difference between oxygen consumption for *Fungia actiniformis* (no. 2), where the oxygen content falls to 1·6%, and

those for *Fungia danai*, 44·6% and 72·5% (nos. 1 and 9). The former species, as described and figured in detail in Paper I of this series, differs from *F. danai* in the possession of exceptionally long, fleshy tentacles and of much thicker tissues. There is clearly a much greater bulk of tissue as compared to zooxanthellae in *F. actiniformis*, and hence the much greater fall in oxygen.

The next matter which required elucidation was the relationship between oxygen consumption and production, between respiration and photosynthesis, at different periods



TEXT-FIG. 1.—Graph showing difference between oxygen production and consumption in c.c. per litre, also oxygen content in the water and tidal changes over a period of 27 hours. See Table V. F_1, F_2, *Fungia*; Fa, *Favia*; G_1, G_2, *Galaxea*; P_1, P_2, *Psammocora*; Po, *Porites*. Vertical broken lines indicate midnight and noon, vertical unbroken lines indicate 6 p.m. and 6 a.m., *i. e.* approximate times of dusk and dawn. H.T., high tide; L.T., low tide.

over night and day. Two experiments, one carried continuously over a period of 27 hours and the other of 12 hours, were carried out.

In the 27-hour experiment eight corals were used, the large light crate being employed, no controls being considered necessary, owing to the short experimental period. The water in the jars was changed, without bringing the corals in from the sea, every three hours, as short a period as possible, 20 to 30 minutes, being allowed for sampling the water of the previous experiments and for refilling the jars. The actual experiments lasted, therefore, for between 2 hours and 30 minutes and 2 hours and 20 minutes. The same jars were used

TABLE V.—*Continuous Experiment over 27 Hours to Determine the Relationship between Respiration and Photosynthesis in the Consumption and Production, respectively, of Oxygen over that Period. The same 8 Corals employed throughout, the Jars being Re-filled with Fresh Sea-Water every 3 Hours, about 20 Minutes being allowed for this and for Sampling the Water from the Previous Experiment, Oxygen Content in c.c. per litre being Determined Before and After each Experiment. Usual Position, Light Crate employed throughout.*

Coral.	Vol.	Experiment I. 2·50 p.m.–5·30 p.m. Depth = 10′ 4″. 30·7–29·9° C. Oxygen content.			Experiment II. 5.55 p.m.–8.30 p.m. Depth = 11′ 7″. 30·0–29·8° C. Oxygen content.			Experiment III. 8.55 p.m.–11.30 p.m. Depth = 10′ 5″. 29·9–30·0° C. Oxygen content.		
		Initial.	Final.	Difference.	Initial.	Final.	Difference.	Initial.	Final.	Difference.
Fungia danai . . .	75	4·97	3·70	−1·27	4·59	3·04	−1·55	4·475	3·025	−1·450
,, ,, . . .	39	4·97	4·58	−0·39	4·59	3·39	−1·20	4·475	3·275	−1·200
Galaxea fascicularis . .	74	4·97	5·03	+0·06	4·59	3·82	−0·77	4·475	3·655	−0·820
,, ,, . .	70	4·97	4·71	−0·26	4·59	3·87	−0·72	4·475	3·710	−0·765
Psammocora gonagra .	56	4·97	3·76	−1·21	4·59	2·47	−2·12	4·475	2·490	−1·985
,, ,, .	48	4·97	4·35	−0·62	4·59	2·69	−1·90	4·475	2·630	−1·845
Favia, sp. . . .	119	4·97	4·39	−0·58	4·59	3·19	−1·40	4·475	3·130	−1·345
Porites, sp. . . .	142	4·97	4·52	−0·45	4·59	4·15	−0·44	4·475	4·010	−0·465

Coral.	Vol.	Experiment IV. 11.59 p.m.–2.32 a.m. Depth = 8′. 30·3–30·0° C. Oxygen content.			Experiment V. 3·0 a.m.–5.30 a.m. Depth = 10′. 30·0–29·6° C. Oxygen content.			Experiment VI. 6.0 a.m.–8.30 a.m. Depth = 13′ 10″. 29·7–29·75° C. Oxygen content.		
		Initial.	Final.	Difference.	Initial.	Final.	Difference.	Initial.	Final.	Difference.
Fungia danai . . .	75	4·35	2·90	−1·45	3·91	2·36	−1·55	4·51	3·30	−1·21
,, ,, . . .	39	4·35	3·10	−1·25	3·91	2·65	−1·26	4·51	3·67	−0·84
Galaxea fascicularis . .	74	4·35	3·42	−0·93	3·91	2·88	−1·03	4·51	4·02	−0·49
,, ,, . .	70	4·35	3·60	−0·75	3·91	2·97	−0·94	4·51	4·15	−0·36
Psammocora gonagra .	56	4·35	2·50	−1·85	3·91	2·01	−1·90	4·51	3·16	−1·35
,, ,, . .	48	4·35	2·58	−1·77	3·91	2·13	−1·78	4·51	3·48	−1·03
Favia, sp. . . .	119	4·35	2·92	−1·43	3·91	2·50	−1·41	4·51	2·53	−0·98
Porites, sp. . . .	142	4·35	3·78	−0·57	3·91	3·23	−0·68	4·51	4·21	−0·30

Coral.	Vol.	Experiment VII. 8.55 a.m.–11.30 a.m. Depth = 13′ 3″. 29·8–30·3° C. Oxygen content.			Experiment VIII. 11.55 a.m.–2.30 p.m. Depth = 10′. 30·6–30·7° C. Oxygen content.			Experiment IX. 2.58 p.m.–5.30 p.m. Depth at 2.58 = 9′ 7″. ,, 5.30 = 11′ 10″. 30·5–29·5° C. Oxygen content.		
		Initial.	Final.	Difference.	Initial.	Final.	Difference.	Initial.	Final.	Difference.
Fungia danai . . .	75	4·58	5·53	+0·95	4·83	5·04	+0·21	5·37	4·68	−0·68
,, ,, . . .	39	4·58	4·65	+0·07	4·83	5·26	+0·43	5·37	5·12	−0·25
Galaxea fascicularis . .	74	4·58	5·64	+1·06	4·83	5·89	+1·06	5·37	5·44	+0·07
,, ,, . .	70	4·58	6·12	+1·54	4·83	5·52	+0·69	5·37	5·48	+0·11
Psammocora gonagra .	56	4·58	5·93	+1·35	4·83	4·56	−0·27	5·37	4·10	−1·27
,, ,, .	48	4·58	6·10	+1·52	4·83	5·79	+0·96	5·37	4·98	−0·39
Favia, sp. . . .	119	4·58	5·39	+0·81	4·83	4·77	−0·06	5·37	4·47	−0·90
Porites, sp. . . .	142	4·58	4·69	+0·11	4·83	4·91	+0·08	5·37	5·13	−0·24

for each coral throughout. Nine of these experiments were conducted, one after the other, and in this way the entire period of night and day was covered, with an overlap of 3 hours. The first experiment was put out at 2.50 p.m., and the last one brought to a conclusion at 5.30 p.m. on the following day. The weather remained dead calm throughout and continuous sunshine prevailed during the day. This experiment was carried out when the sun was almost directly overhead, on 18th February, 1929. The results of the experiment, with details as to times, temperature and tidal changes, are recorded in Table V.

The data given in Table V are recorded graphically in Text-fig. 1. It was difficult at first to know how best to figure graphically the numbers representing the balance between oxygen consumption and production, but it was decided, finally, to take the mid-points of the different experimental periods to represent the time, plotting the various numbers above these. Thus, in the case of Experiment 1, the time is taken as 4.10 p.m., the mid-point between 2.50 and 5.30. Prepared in this way the graph certainly gives a very clear indication of the oxygen exchange between the corals and the surrounding water in the jars throughout the day and night. Although the initial oxygen figures varied considerably (as shown in the upper portion of the graph), the differences between these and the final figures are taken as absolute, and not expressed as percentages, because, as will be shown in a later section of this paper, corals can remove oxygen from sea-water with equal facility within a wide range of oxygen tension, nor has any account been taken of the small differences in the periods of the experiments. In addition to the graphs showing the oxygen exchange of the eight experimental corals, the changes in oxygen content of the water throughout the same period are also expressed graphically in the upper portion of the text-figure, together with the depth of the water, which was determined by sounding at the beginning of each experiment. High tide (H.T.) and low tide (L.T.) are indicated. Midnight and noon are shown by vertical broken lines, and the period of total darkness, taken as from 6 p.m. to 6 a.m., by the area bounded by the two vertical lines.

The most striking feature of the graph is the uniformity between the results for the eight corals, which were selected, it may be explained, because of their proved ability to stand experimental handling without apparent injury. (Certain corals could never be used for experiments, notably *Acropora*, because of their great susceptibility to handling, while others, such as *Pocillopora*, could not always be relied on. In this case all the corals used were as healthy and normal at the end of the experiment as they were at the beginning.)

The first experiment showed that, with the exception of *Galaxea* I, all the corals showed a preponderance of oxygen consumption over oxygen production during the afternoon of the first day. There was, with the exception this time of *Porites*, a decided increase in this utilization of oxygen in Experiment II, and remarkably parallel results were obtained for Experiments III, IV and V—*i.e.* throughout the night, when no photosynthesis could take place, not one of the graphs crossed another during this period. Experiment VI showed a marked decrease in consumption of oxygen, the result of the first appearance of light in the morning, but in no case does production exceed consumption. In Experiment VII all the corals showed an excess of oxygen production, representing the peak for all but two, *Fungia* II and *Galaxea* II, and the latter gave identical results in Experiment VIII, when the other corals, except *Fungia* II, showed a very marked decrease, though only two, *Favia* and *Fungia* I, showed a slight excess of oxygen

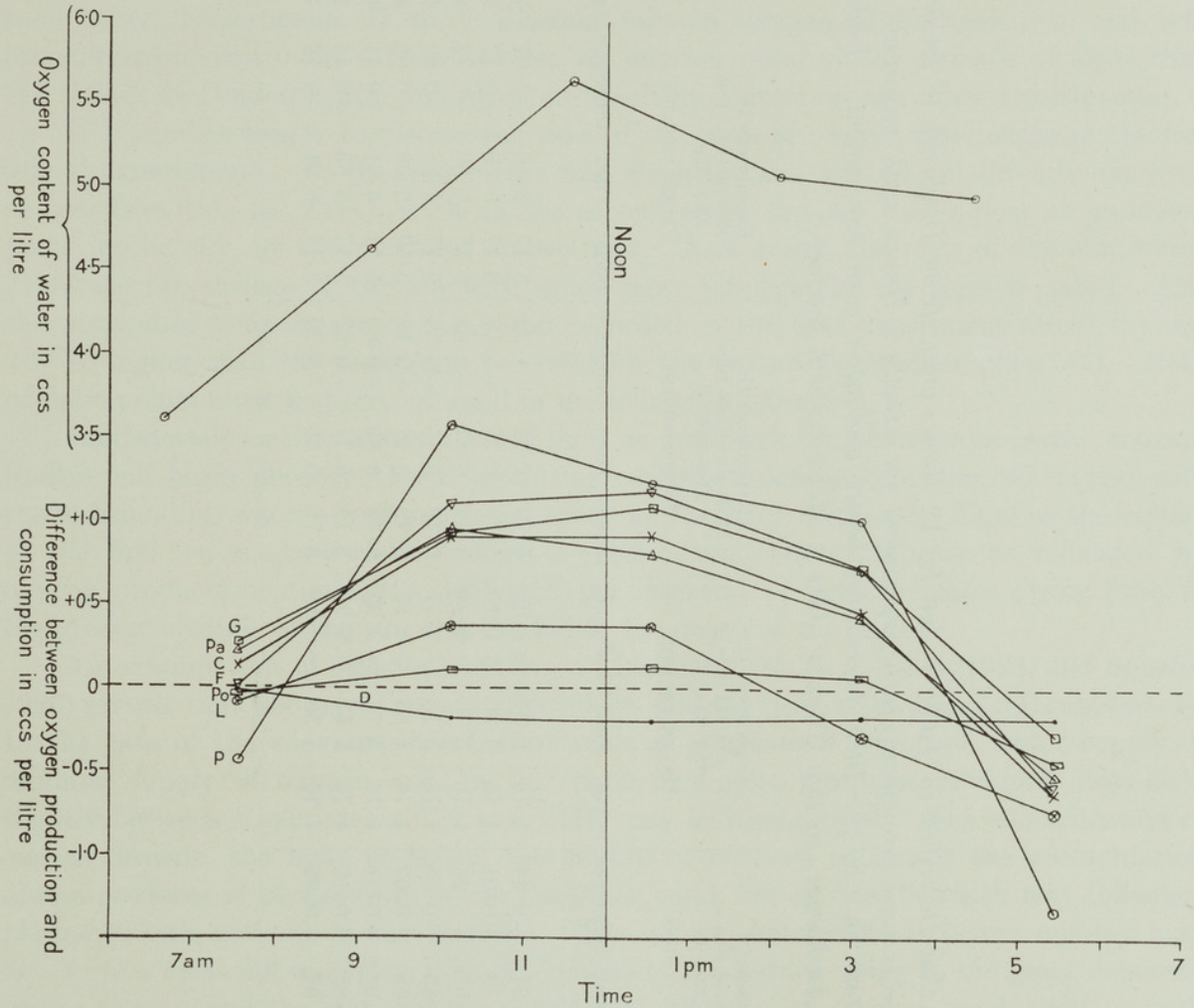
consumption over production. In the last experiment, the production of oxygen again fell off considerably, only two corals, *Galaxea* I and II, still showing an excess of oxygen production. These final figures showed a very marked resemblance to those of Experiment I, carried out over a similar period on the previous day, in two cases, *Galaxea* I and *Psammocora* I, being practically identical.

While the figures for darkness were what was expected, practically identical for each coral and gave horizontal lines on the graph, the figures for the light were somewhat unexpected and correspondingly more interesting. The peak of oxygen production, instead of appearing about noon, when the sun was highest in the sky and the penetration of light into the water at its maximum, actually came in the case of six corals at a little past 10 a.m. In *Galaxea* II the subsequent figure was identical with that for Experiment VII, while in *Fungia* II there was a decided rise. One possible explanation of these results, namely that the tide was lower in the morning and so allowed more light to penetrate to the corals then than at noon, or in the afternoon, is disproved by the graph for depth of water, which shows that precisely the opposite occurred, the water falling all the morning and low tide coming somewhere about 1 p.m. It will be better to leave the discussion of the reasons for this morning peak in oxygen production until the results of the next experiment have been described. Before leaving Text-fig. 1, however, attention must be drawn to the graph for oxygen content of the water in the anchorage. This fell steadily from 2.50 p.m., reaching its minimum at about 3 a.m.—this minimum would almost certainly have come later but for the rising tide bringing in water from further out which had not been influenced by coral respiration. After this the oxygen content rose steadily for the remainder of the experiment; unfortunately a final reading at 5.30 p.m. was not taken. Here again the peak was certainly affected by the retreating tide washing back water from nearer the shore, where supersaturation with oxygen invariably occurs to a striking extent in calm weather. This matter is dealt with at length by Mr. A. P. Orr in a forthcoming paper on " Variations in Some Physical and Chemical Factors on and near Low Isles Reef," which will appear in Vol. II of these reports. In this paper he shows that in coral pools at low tide in the day during the early summer (26th November) oxygen saturation rose as high as 230·4%. In the present case the water was fully saturated with oxygen at a concentration of 4·58 c.c. per litre, falling to a minimum of 85·5% saturation and rising to a maximum of 117·25%. These changes must almost entirely be due to the respiration of the corals—by far the most abundant animals—and the photosynthetic activities of the zooxanthellae—by far the most abundant and ubiquitous plants.

The results of this experiment were such as to justify a second experiment, carried out this time for a period of 12 hours over the period of daylight only. The experimental conditions in this case were somewhat different. The experiment was carried out in winter, on 19th June, 1929, and at a *constant depth*, the light crate being slung from the whale boat by means of a projecting boom, so that no shadow fell over it, and with the tops of the jars 1 metre beneath the surface. The weather was calm in the morning, with a slight breeze in the afternoon and sunshine was continuous. Experiments were run for exactly 2 hours in all five cases, the intervening periods being made as short as was possible in view of the extensive sampling that had to be carried out in them. The first experiment was put out at 6.40 a.m. and the last brought in at 6.27 p.m. It was light to the extent that surrounding objects could be seen plainly at about 6.35 a.m., while it was completely

dark at 6.25 p.m. As in the previous experiment, no controls were considered necessary, but on this occasion specimens of *Dendrophyllia* were available for experimentation and, as they possess no zooxanthellae, they acted as ideal controls.

Full details of the results of this experiment are given in Table VI, and are shown graphically in Text-fig. 2. The figures representing the balance between oxygen consumption and production are again recorded on the graph over the mid-point of the time of



TEXT-FIG. 2.—Graph showing difference between oxygen production and consumption in c.c. per litre, also changes in oxygen content of the water over a period of 12 hours covering daylight. See Table VI. C, *Cyphastrea*; D, *Dendrophyllia*; F, *Fungia*; G, *Galaxea*; L, *Lobophyllia*; P, *Psammocora*; Pa, *Pavona*; Po, *Porites*.

each experiment. The oxygen content of the water in the anchorage is recorded in the upper portion of the graph, but not tidal changes, since the experiment was carried out at a constant depth. At its lowest point, at 6.40 a.m. the oxygen saturation was 70·1%, and at its highest, at 11.34 a.m., it was 113·8%.

If the graphs for the 8 corals are examined and compared with those for the previous experiment, certain differences will be noted. The only two corals in which the oxygen production in Experiment II (9.07 a.m. to 11.07 a.m.) exceeds that in Experiment III (11.34 a.m. to 1.34 p.m.) by any significant amount are *Psammocora* and *Pavona*. In the

TABLE VI.—*Similar Experiment to that Described in Table V, but for* 12 *Hours only, from Daybreak to Dusk. Five Successive Experiments run, same* 8 *Corals used throughout, each experiment for exactly* 2 *Hours, with minimum period between for Sampling, etc. Oxygen content in c.c. per litre determined before and after each experiment. Light Crate used and Slung from Whale Boat in Anchorage, so that Tops of Jars* 1 *Metre beneath Surface.*

Coral.	Vol. in c.c.	Experiment I. 6.40 a.m.–8.40 a.m. 21·3–22·2° C. Oxygen content.			Experiment II. 9.07 a.m.–11.07 a.m. 22·2–23·6° C. Oxygen content.			Experiment III. 11.34 a.m.–1.34 p.m. 23·6–23·3° C. Oxygen content.			Experiment IV. 2·05 p.m.–4·05 p.m. 23·3–22·6° C. Oxygen content.			Experiment V. 4.27 p.m.–6.27 p.m. 22·6–22·3° C. Oxygen content.		
		Initial.	Final.	Difference.	Initial.	Final.	Difference.	Initial.	Final.	Difference.	Initial.	Final.	Difference.	Initial.	Final.	Difference.
Psammocora gonagra .	100	3·71	3·27	−0·44	4·76	6·34	+1·58	5·79	7·01	+1·22	5·17	6·18	+1·01	4·97	3·63	−1·34
Fungia danai . .	65	3·71	3·72	+0·01	4·76	5·86	+1·10	5·79	6·97	+1·18	5·17	5·89	+0·72	4·97	4·39	−0·58
Galaxea fascicularis .	80	3·71	3·97	+0·26	4·76	5·70	+0·94	5·79	6·87	+1·08	5·17	5·89	+0·72	4·97	4·70	−0·27
Lobophyllia corymbosa .	150	3·71	3·63	−0·08	4·76	5·13	+0·37	5·79	6·15	+0·36	5·17	4·88	−0·29	4·97	4·24	−0·73
Porites, sp. . . .	140	3·71	3·68	−0·03	4·76	4·86	+0·10	5·79	5·91	+0·12	5·17	5·23	+0·06	4·97	4·52	−0·45
Pavona danai . .	45	3·71	3·92	+0·21	4·76	5·71	+0·95	5·79	6·59	+0·80	5·17	5·61	+0·44	4·97	4·45	−0·52
Cyphastrea chalcidicum .	200	3·71	3·83	+0·12	4·76	5·67	+0·91	5·79	6·71	+0·92	5·17	5·63	+0·46	4·97	4·35	−0·62
Dendrophyllia nigrescens	35	3·71	3·69	−0·02	4·76	4·58	−0·18	5·79	5·59	−0·20	5·17	5·01	−0·16	4·97	4·80	−0·17

case of *Lobophyllia*, *Porites* and *Cyphastrea* there is no significant difference between the figures for the two experiments, while in *Galaxea* and *Fungia* there is a slight but significant rise in Experiment III. Averaging the results for the 7 corals containing zooxanthellae, the peak of oxygen production is seen to lie very close to midday. In the case of *Dendrophyllia*, where there are no zooxanthellae in the tissues, the results are very different. Here, apart from Experiment I, where some error clearly crept in, a fall of only 0·02 c.c. of oxygen being recorded, the figures are all within experimental error of each other, Experiments II to V showing falls in oxygen of between 0·16 and 0·20 (experimental error 0·05). This provides yet another proof of the absence of algae from the tissues of *Dendrophyllia*, and gives an excellent control on the other experiments.

It is now necessary to discuss the time of the peak of oxygen production in the two sets of experiments. At the time of the first series the sun was almost directly overhead at Low Isles (lat. 16° 23′S.), while in the second series the sun was almost at its lowest point in the sky, at the northern midsummer. As a result the rays of the sun would penetrate the surface of the sea with much more intensity at the former period. Also the maximum temperature of the water recorded in the first experiment (30·7° C.) was 7·1° C. higher than the maximum recorded for the second experiment (23·6° C.). Both of these points must be borne in mind in the following discussion.

Immediately on the appearance of light at daybreak the chlorophyll in the zooxanthellae will begin photosynthesis, producing carbohydrates—and giving off oxygen into the surrounding water—with increased speed as the light increases. But, as the results of the first series show clearly, after a certain time photosynthesis, as indicated by oxygen production, diminishes, although the intensity of light increases owing both to the greater altitude of the sun and the fall in the depth of the water.

An examination of standard works on photosynthesis (*e.g.* Stiles, 1925, and Spoehr, 1926) reveals that photosynthesis is affected by a variety of external and internal factors. In the case of the zooxanthellae factors such as anatomical structure, water supply, a minimal supply of oxygen and, in this particular case, temperature which rises only slightly between Experiments VII and VIII, may be disregarded. The concentration of carbon dioxide, the light intensity, the supply of nutrient salts and the accumulation of end-products of photosynthesis, on the other hand, are all factors which may influence photosynthetic activity in this instance. The fall in photosynthesis before midday may be due to a local fall in carbon dioxide content in the tissues owing to the great demands of the plants—and the fact that the corals with the highest oxygen production in both experiments have the earliest peaks supports this view—or to too great an intensity of light, which depresses photosynthesis (though this is less probable because the zooxanthellae are shielded by at least 9 ft. of water and by the superficial tissues of the corals), or else to a slowing down of the reaction owing to the accumulation of its end-products, which is possibly accentuated when fat and not starch is the reserve product. This may have as a contributory cause a temporary lack of nutrient salts containing nitrogen, phosphorus or sulphur, which enables the carbohydrate or fat to be converted into protein. It is impossible to say which of these factors, or what combination of them, is responsible for the fall in photosynthesis in spite of the increase in illumination. The important point is, however, that, under the conditions which prevailed during the 27-hour experiment, the peak in photosynthetic activity did *not* correspond with the period of greatest illumination.

Since the differences in temperature at different times and places may be neglected because the effects on photosynthesis will be largely offset by those on respiration of the corals, it follows that the time of the peak in oxygen production at any time and any depth will vary according to the intensity of the light. The results of the 27-hour experiment in midsummer and of the 12-hour experiment in midwinter can be entirely reconciled by this. Although the earlier experiments was conducted at an average depth about four times greater than that of the later ones, yet the illumination was so much greater that the maximum oxygen production (which corresponded very closely for similar species of corals in the two series of experiments, as a comparison of Tables V and VI. shows) occurred between 10 and 11 in the morning. In the second experiments, when sunshine was equally continuous but the sun was much lower in the sky and penetration of light correspondingly less, the maximum production of oxygen did not occur until about midday.

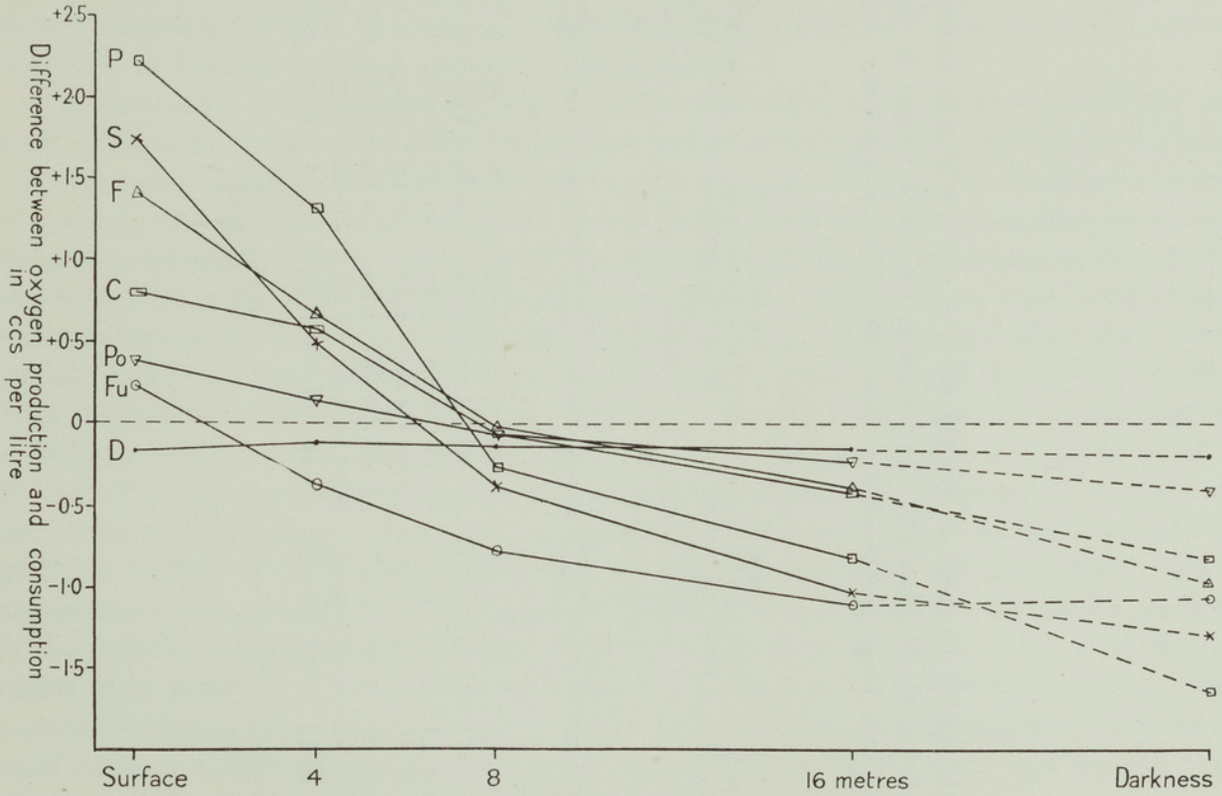
These findings have clearly a very important bearing on the vertical distribution of reef-building corals. If, as the evidence presented in Papers IV and V suggests, these animals are only able to exist in the great numbers necessary for the formation of reefs because the zooxanthellae automatically remove the end-products of their metabolism, then their distribution in depth must be dependent on the depth to which the zooxanthellae can live and increase. Now it is clear that, in the case of the first set of experiments, zooxanthellae at a considerably greater depth would photosynthesize with equal efficiency, only the peak of oxygen production would come at noon, while below that, again, their chlorophyll would definitely produce less carbohydrate than it was capable of doing. This would cause a slower rate of increase, a fact of which definite evidence was recorded in Paper IV of this series when discussing the low content of zooxanthellae in corals taken from depths of 7 to 9 fathoms off Low Isles (and so near the bottom, where visibility would be abnormally affected by the stirring up of the black mud). Nearer to the surface, on the other hand, the peak of oxygen production in the summer would be earlier and earlier in the day. In the second series, when light was much less intense, the zooxanthellae were apparently producing oxygen as a result of photosynthesis without waste of efficiency within 1 metre of the surface. This matter will be further dealt with in the discussion at the end of this paper.

6. INFLUENCE OF DEPTH.

It is clear that confirmation of the above statements can only be obtained by direct experimental evidence of the effect of depth on the oxygen exchange of reef-building corals at various times of the year. Unfortunately lack of time to analyse results at the time, owing to continuous pressure of work during the period of the Expedition, prevented this fact from being realized. Depth experiments were carried out immediately before the conclusion of the Expedition and near enough to the 12-hour experiment to make the two comparable, but there are no data for the summer months.

Experiments were carried out with seven corals, including *Dendrophyllia*, and with one control in the larger light crate. This was slung at depths of 4, 8 and 16 metres from a buoy consisting of a large, empty oil drum, which was moored about a quarter of a mile directly out from the shingle spit which, as shown in the map, formed the eastern boundary of the anchorage. The water there was about 19 metres deep at half tide. An experiment

with the crate just level with the surface and another, using the dark crate, in darkness were carried out from the whale boat in the anchorage, as in the 12-hour experiment. These five experiments were carried out between 11th and 17th July, 1929, continuous sunshine prevailing on all days, and the weather being calm except for a slight S.E. breeze. The experiments were carried on for 4 hours, being put out between 11.45 a.m. and noon. Owing to the difficulty of sampling the jars in a small boat beyond the shelter of the anchorage, this had to be done after the jars were brought on shore, and in *all* five experiments, sampling took place precisely half an hour after the conclusion of the 4 hours under the experimental conditions. Secchi disc readings were taken in connection with the experiments at 4, 8 and 16 metres, and the readings obtained, $7\frac{1}{2}$, $7\frac{1}{2}$ and 8 metres



TEXT-FIG. 3.—Graph showing difference between oxygen production and consumption in c.c. per litre at various depths and in darkness. See Table VII. C, *Cyphastrea ;* D, *Dendrophyllia ;* F, *Favia ;* Fu, *Fungia ;* P, *Psammocora ;* Po, *Porites ;* S, *Symphyllia.*

respectively, indicate that the penetration of light was approximately the same in all three cases.

The results of this experiment are given in Table VII, and are shown graphically in Text-fig. 3. With the exception of *Dendrophyllia* there is a steady fall in oxygen production from the surface to darkness, the latter being recorded on the graph as similar to 24 metres, which, in the turbid water around Low Isles, does not appear unreasonable. The broken lines connecting the figures for 16 metres and darkness indicate, however, the arbitrary nature of the position of the latter. Only one anomalous result is recorded, in *Fungia actiniformis* the oxygen production in darkness being slightly higher than it was at 16 metres, but the difference lies within the experimental error of the method.

TABLE VII.—*Experiments using* 7 *Corals and a Control at Depths of* 4, 8 *and* 16 *Metres in Light Crate Suspended from Buoy* $\frac{1}{4}$ *Mile North of the Spit, and also at the Surface and in Darkness (in Dark Crate) in the Anchorage. Experiments all for* 4 *Hours over the same Period of the Day, and Samples taken* 30 *Minutes after the Jars lifted from the Sea. Oxygen in c.c. per litre.*

Coral.	Vol.	Surface. 11.45 a.m.–3.45 p.m. Initial temperature = 21·1° C. Initial O_2 = 5·07. Final O_2 content.			4 metres. 11.57 a.m.–3.57 p.m. Initial temperature = 21·0° C. Initial O_2 = 5·21. Final O_2 content.			8 metres. 11.45 a.m.–3.45 p.m. Initial temperature = 21·6° C. Initial O_2 = 4·92. Final O_2 content.			16 metres. 11.53 a.m.–3.53 p.m. Initial temperature = 21·5 C. Initial O_2 = 4·52. Final O_2 content.			Darkness. 12 noon–4 p.m. Initial temperature = 20·9° C. Initial O_2 = 5·45. Final O_2 content.		
		Control.	Experiment.	Difference.	Control.	Experiment.	Difference.	Control.	Experiment.	Difference.	Control.	Experiment.	Difference.	Control.	Experiment.	Difference.
Fungia actiniformis .	45	4·96	5·18	+0·22	5·04	4·65	−0·39	4·88	4·09	−0·79	4·81	3·72	−1·09	5·37	4·32	−1·05
Symphyllia recta . .	55	4·96	6·70	+1·74	5·04	5·53	+0·49	4·88	4·49	−0·39	4·81	3·78	−1·03	5·37	4·09	−1·28
Psammocora gonagra .	60	4·96	7·17	+2·21	5·04	6·35	+1·31	4·88	4·61	−0·27	4·81	4·00	−0·81	5·37	3·74	−1·63
Favia, sp. . . .	100	4·96	6·36	+1·40	5·04	5·69	+0·65	4·88	4·86	−0·02	4·81	4·41	−0·40	5·37	4·41	−0·96
Porites, sp. . . .	95	4·96	5·33	+0·37	5·04	5·17	+0·13	4·88	4·82	−0·06	4·81	4·58	−0·23	5·37	4·97	−0·40
Cyphastrea chalcidicum .	180	4·96	5·76	+0·80	5·04	5·61	+0·57	4·88	4·82	−0·06	4·81	4·39	−0·42	5·37	4·56	−0·81
Dendrophyllia nigrescens	35	4·96	4·79	−0·17	5·04	4·93	−0·11	4·88	4·74	−0·14	4·81	4·66	−0·15	5·37	5·18	−0·19

All the corals, except *Dendrophyllia*, show an excess of oxygen production over consumption at the surface, and all, save *Dendrophyllia* and *Fungia actiniformis*, at 4 metres. For the remaining experiments oxygen consumption in all cases exceeds oxygen production. The low readings for *Fungia actiniformis* are in accordance with the figures given in Table IV for the oxygen consumption over 24 hours of this species and, as indicated in the discussion on those results, is the result of the exceptionally large bulk of tissue possessed by this remarkable species. In all the corals with zooxanthellae there is a continuous diminution of oxygen production from the surface to darkness, with the exception of the anomalous results already mentioned for *Fungia*. *Dendrophyllia*, as in the 12-hour experiment, provides a perfect control. The results for the five experiments range from 0·11 to 0·19, *i. e.* practically within experimental error, and again demonstrate the absence of any organisms within them possessing chlorophyll, while they also show the entire adequacy of the experimental procedure employed.

In discussing these results the experimental conditions must be borne carefully in mind. The corals were exposed to them for a period of 4 hours only, and when the sun was still exceptionally low on the horizon for this latitude. Under *these* conditions there is a steady fall in oxygen consumption for all corals possessing zooxanthellae from the surface downwards. But it must be understood that before being exposed, the corals had been kept in the relatively deep shade of the aquarium, where the zooxanthellae would certainly be unable to form carbohydrate at any great rate. Accordingly, when they were put out in the sea they would continue, for the comparatively short period of the experiment, to produce carbohydrate—and so oxygen—at the maximum speed which the degree of light permitted. Had the experiments been for a longer period, the results of the 27- and 12-hour experiments would indicate that the differences between the results of the surface and 4-metre experiment in particular would have been smaller owing to a probable falling off of oxygen production by the zooxanthellae at the surface. Had experiments been carried out in the summer, the differences between all the results, except of those of the experiment in darkness, would probably have been less. It is a matter of regret that pressure of work prevented the implications of the results of the 27-hour experiment being grasped at the time; but it is hoped that an opportunity will present itself at some future time of extending the experiments here recorded and testing the validity of the assumptions drawn from their results.

7. SURVIVAL OF CORALS IN SEALED JARS OVER LONG PERIODS.

Since reef-building corals possess zooxanthellae which, during the daytime, produce oxygen which to a large extent, though not entirely, offsets the amount of oxygen used by the corals in respiration, it follows that these organisms are, to a large extent, a closed system. Under the artificial conditions presented by their enclosure within jars containing a limited amount of water, the corals will clearly be able to survive for a much longer period than an animal with no such accessory source of oxygen as is provided by the zooxanthellae so long as light is present. The zooxanthellae, under these conditions, will not be affected so long as there is abundant light, the coral remains healthy, and there is sufficient carbon dioxide for photosynthesis and nitrogen, phosphorus and sulphur for protein synthesis.

A series of experiments was carried out in which corals containing zooxanthellae

were confined in jars which were placed in the light crates and put out in the sea at the usual place for a period of 14 days. All experiments were put out in the morning between 10.30 and 11.30. Very great care had to be taken to cleanse these corals and remove commensal worms and crustacea. When these precautions were taken considerable success attended the experiments, as the results, tabulated in Table VIII, indicate.

TABLE VIII.—*Experiments on Corals to Test the Effect of Long Confinement within Sealed Jars in the Sea. Light Crates used, in usual position. Oxygen in c.c. per litre.*

No.	Coral.	Capacity of jar in c.c.	Initial oxygen.	pH.	Period in jar.	Time removed.	Final oxygen.	pH.	Condition.
1	*Porites*, sp. . .	2775	5·17	8·26	14 days	3·30 p.m.	..	..	Coral died between 10th and 14th day.
2	,, . .	2825	,,	,,	,,	,,	3·69	8·02	Healthy.
3	*Pocillopora bulbosa*	2810	,,	,,	,,	,,	6·97	7·22	Few dead polyps.
4	,, ,,	2880	,,	,,	,,	,,	..	..	Dead after 10 days.
5	*Galaxea fascicularis*	2820	,,	,,	,,	,,	2·68	7·62	Healthy.
6	,, ,,	2815	,,	,,	,,	,,	6·06	7·37	,,
7	*Fungia danai* .	2830	4·85	8·32	14 days	10·30 a.m.	0·73	7·00	Healthy.
8	,, ,, .	2790	,,	,,	,,	,,	0·54	7·18	,,
9	*Psammocora gonagra*	2840	,,	,,	,,	,,	0·53	7·35	,,
10	*Porites*, sp. . .	2760	,,	,,	,,	,,	0·00	7·80	,,
11	*Galaxea fascicularis*	2830	,,	,,	,,	,,	0·00	7·80	,,
12	*Fungia danai* .	2775	4·46	8·32	14 days	4·10 p.m.	..	..	Dead.
13	*Psammocora gonagra*	2830	,,	,,	,,	,,	0·00	7·75	Healthy.
14	,, ,,	2820	,,	,,	,,	,,	2·11	7·89	,,
15	*Galaxea fascicularis*	2840	,,	,,	,,	,,	..	..	Dead.
16	,, ,,	2760	,,	,,	,,	,,	6·58	7·82	Healthy.
17	*Porites*, sp. . .	2830	,,	,,	,,	,,	0·00	7·79	,,
	Control . .	2900	,,	,,	,,	,,	4·76	8·32	..
18	*Fungia danai* .	2850	5·52	..	14 days	3·15 p.m.	3·69	..	Healthy.
19	,, ,, .	2900	,,	..	,,	,,	..	..	Dead.
20	*Psammocora gonagra*	2920	,,	..	,,	,,	6·24	..	Healthy.
21	,, ,,	2870	,,	..	,,	,,	1·93	..	,,
22	*Galaxea fascicularis*	2890	,,	..	,,	,,	3·25	..	,,
	Control . .	2890	,,	..	,,	,,	3·87	..	..

Out of 22 colonies, all but 5 survived at the end of 14 days. The oxygen content of the water in the jars containing the survivors was, in four cases, *Pocillopora* (3), *Galaxea* (6), *Galaxea* (16) and *Psammocora* (20), higher than it had originally been.* In the second series of experiments (7–11), where the jars were removed and the oxygen content estimated at 10.30 in the morning, this was in all cases low; in the other three experiments where sampling was done in the afternoon, between 3.15 and 4.10 p.m., the oxygen content, as was to be expected, was considerably higher. Clearly, therefore, the zooxanthellae had not suffered unduly as a result of confinement. A probable reason for this death of a proportion of the corals is revealed by the pH of the water at the end of the experiments. This averaged, for the first three experiments (by an oversight the pH was not

* See note on p. 251.

taken in the last experiment), 7·56, 7·43 and 7·81 respectively. Here, again, the figures for the second experiment when estimations were made early in the day, indicate, by their low value, the effect of photosynthesis by the zooxanthellae, which had materially reduced the amount of carbon dioxide, and so raised the pH, in the afternoon. It is clear that under these conditions carbon dioxide accumulates at a greater speed than the zooxanthellae can dispose of it, and so the pH gradually falls, until, in the course of time, it may fall below the lethal limit for corals. These results have an important bearing on the conclusions arrived at in Paper IV of this series, namely, that zooxanthellae are expelled from the tissues of corals when the metabolism of these is lowered by any means —starvation, raising of the temperature, etc.—owing to the lack of the end-products of coral metabolism, which form the inorganic food supply of the zooxanthellae. But apparently *carbon dioxide is always produced by the coral in excess of the amount which the zooxanthellae can utilize*. It follows, therefore, that the limiting factor is not this, but some material for protein synthesis, namely, nitrogen, phosphorus or sulphur, details of the utilization of the second of which are given in Papers IV and V.

In this connection the results of an experiment carried out very early in the course of the Expedition are of interest. Two specimens of *Fungia danai* were exposed in sealed jars containing twice-filtered water, prepared as described in Paper V, for one week; then the jars were removed from the sea, the oxygen content and pH of the water determined, and the state of the corals noted before they were again placed in the jars with twice-filtered sea-water, and for a second time exposed in the sea for a week. This process was repeated again at the end of the second week. The results are given in Table IX.

Unfortunately no note of the time that these corals were removed from the sea and the samples taken has been recorded. The point of particular interest is, however, the condition of the corals at the end of the various periods. As shown by the results of experiments recorded in Paper V, the twice-filtered sea-water contains no zooplankton on which the corals can feed. The results of this experiment show the progressive effects of enclosure in this water. There is a progressive fall in oxygen content, due to the ejection and subsequent death of zooxanthellae, the result of the lowered metabolism of the corals (particularly well shown at the end of the second week), while the fall in pH is progressively less, owing, it may be presumed, to the decrease in the tissues due to starvation, which was very apparent at the end of the third week. But in all cases but one there is an actual increase in carbon dioxide, indicated by a fall in pH, and so the ejection of the zooxanthellae can only be due to a lack of the other excretory products of the corals—nitrogen, phosphorus and sulphur.

Another point to which attention may be drawn is the remarkable fall in oxygen content in the controls. The water had been filtered successively through a coarse filter-paper and a fine sintered silica filter, and yet enough organic matter was left in the water for the oxidation of this to reduce the oxygen content of the water after one week, in one case almost to zero, and in others to less than half its original value. And yet, as shown in Table VIII, the oxygen content in controls which had been exposed for two weeks, though it fell in one case, actually rose considerably in the other. This water was not filtered, and the increase in the one case and the much higher figure obtained in the second than with the filtered sea-water can only be due to the presence of phytoplankton in the unfiltered water. This great reduction of the oxygen content of controls was one of the great difficulties of these experiments, and the presence of what appear to be

TABLE IX.—*Two* Fungia danai *and One Control Exposed for Three Successive Periods of One Week in Sealed Jars containing Twice-Filtered Sea-Water. Capacity of Jars* 2775, 2825 *and* 2810 *c.c. respectively, Placed in Light Crate and Exposed in Usual Position.*

Time.	Initial.		Fungia I.			Fungia II.			Control.	
	Oxygen.	pH.	Oxygen.	pH.	Condition.	Oxygen.	pH.	Condition.	Oxygen.	pH.
1 week	4·74	8·28	3·78	7·00	Healthy	1·79	7·90	Healthy	0·08	8·08
2 weeks	4·62	8·28	0·12	7·79	Healthy, but water full of mucus and zooxanthellae, majority alive	0·00	7·90	Healthy, but water full of mucus and zooxanthellae, majority alive	1·87	8·28
3 ,,	4·59	8·31	0·00	7·30	Poor condition; part of tissue away from disc	0·00	8·10	Poor condition; not quite so bad as I	2·22	8·30

exceptionally large amounts of organic matter in the water around Low Isles demands further investigation. The high temperature of the water would, of course, accentuate the reaction. Verwey (1931) found that in his experiments reduction in oxygen content in the controls did not occur after the water had been filtered through fine plankton nets, but his experiments were all for comparatively short periods.

8. SURVIVAL OF CORALS IN WATER OF LOW OXYGEN TENSION.

The results of the preceding experiments showed the need for collecting data on the length of time which corals can survive in water of low oxygen tension when kept in the dark, so that the zooxanthellae cannot produce oxygen. The limited time at our disposal only permitted of the carrying out of one experiment, of which full particulars and results are given in Table X.

The results of these experiments, though they are by no means so extensive as could have been wished, are worthy of consideration, because they do indicate that corals can survive for some considerable time in the presence of only slight traces of oxygen. The two examples taken of each of the four genera showed in all cases a remarkable similarity. *Galaxea* failed to survive one day, *Fungia* died before the end of the second day, *Cyphastrea* before the end of the fourth day, and *Porites*, although the initial oxygen content was lower than in the other cases, not until the end of the sixth day. A noteworthy occurrence was the ejection of zooxanthellae in *Cyphastrea* and, to a less degree, *Porites* before death. This is yet another proof that a lowering of the metabolism of the corals, in this case due to lack of oxygen, results in the extrusion of the zooxanthellae. Precisely the same results were obtained when corals were starved (Paper V), or subjected to high temperatures artificially or in nature (Paper IV).

9. THE UTILIZATION OF OXYGEN BY CORALS.

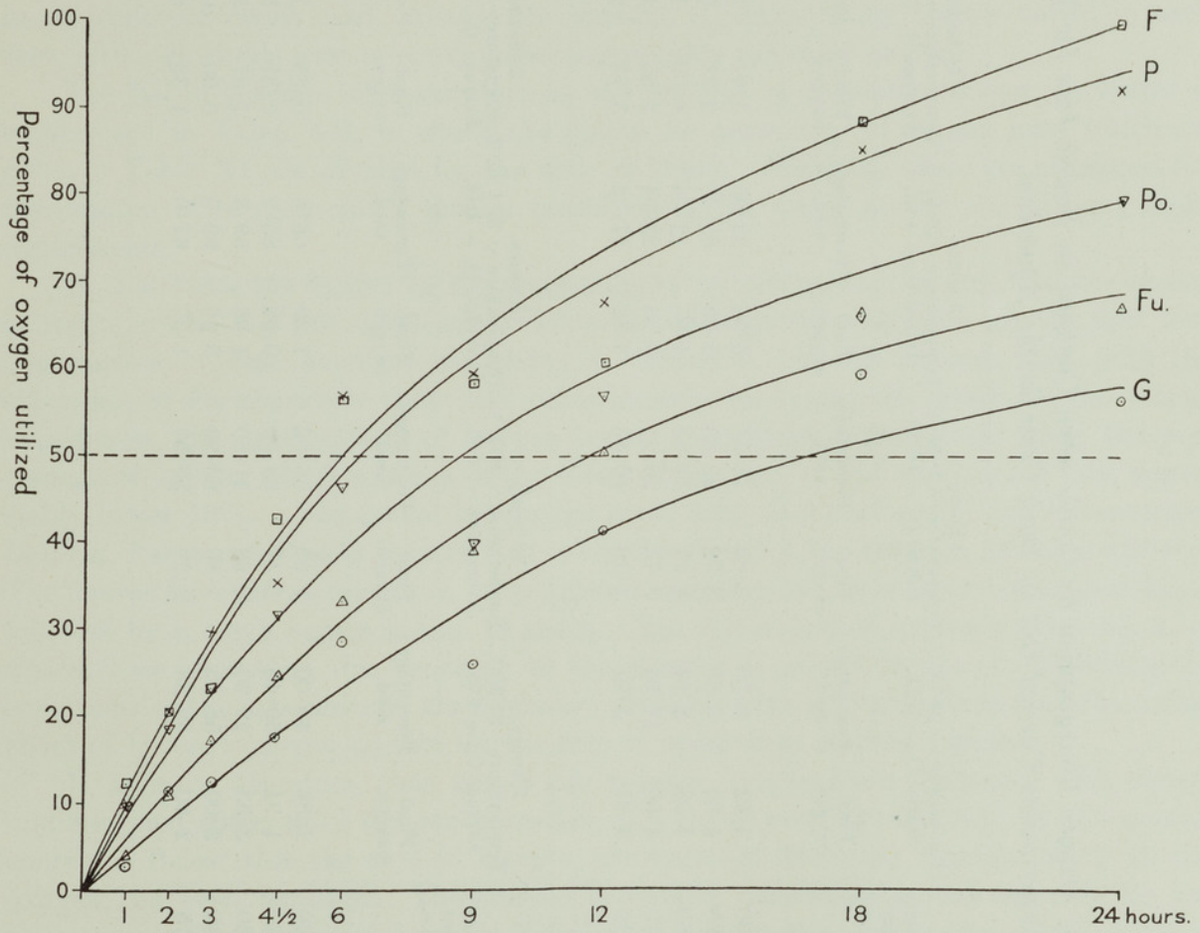
The results of the experiments described in the two preceding sections show that corals can live for a certain length of time in water of very low oxygen tension. Unlike higher animals there appears to be no lethal limit, short of complete lack of oxygen. More accurate data were clearly needed on this point, and to this end an experiment was carried out in which a series of corals were confined in jars for periods ranging between 1 and 24 hours all in total darkness, in order that some clear indication of the influence of oxygen tension upon the rate of respiration might be obtained. Five different genera of corals with a control were used and experiments were carried out in the dark crate, which was kept in the aquarium. Although the length of time of the various experiments could be controlled better in this way, the temperature naturally varied more than in the sea; and this fact must be remembered when the results are examined. Eight experiments in all were carried out with as little time between them as possible, and the corals were all in perfect health at the end of the series. Water was taken in the anchorage for each experiment, and this, for reasons already given in this paper, varied somewhat in oxygen content. It was impossible anywhere near the island to obtain water of constant oxygen content. In view of this fact the results of this experiment are given in terms of percentage amount of oxygen which remained at the end of each period. In all experiments carried on for more than 3 hours the oxygen content in the control fell significantly. In these

TABLE X.—*Experiments on the Survival of Corals in Filtered Sea-Water, the Oxygen in which has been largely Removed by Subjecting it to the Passage of a Stream of Fine Bubbles of Hydrogen for Half an Hour, shaking every Five Minutes. Experiments Carried Out in Small Jars (capacity about 800 c.c.), about Two-thirds Full of Water, with a Layer of Liquid Paraffin, about ½ in. thick, on the Surface. In Total Darkness in the Aquarium. Oxygen in c.c. per litre.*

Coral.	Volume in c.c.	Volume of water in c.c.	Initial O_2	After 1 day.		2 days. Condition.	3 days. Condition.	4 days. Condition.	5 days. Condition.	6 days.	
				O_2	Condition.					O_2	Condition.
Fungia danai . .	12	545	1·05	0·57	Poor	Dead	..	..	..	..	..
,, ,, . .	10	585	1·05	1·06	,,	,,	..	..	..	..	..
Galaxea fascicularis .	20	720	1·05	..	Dead	..	..	..	..	..	..
,, ,, .	30	575	1·25	..	,,	..	..	..	..	..	..
Cyphastrea chalcidicum .	38	600	1·25	0·44	Healthy	Healthy, extruding algae	Poor, extruding algae	Dead, many algae in water	..	0·0	..
,, ,, .	38	590	1·25	0·26	,,	Healthy, extruding algae	Poor, extruding algae	Dead, many algae in water	..	0·0	..
Porites, sp. . . .	35	585	0·51	0·51	,,	Healthy	Healthy	Healthy	Poor, some algae extruded	0·0	Dead.
,, . . .	38	600	0·51	0·58	,,	,,	,,	,,	Poor, some algae extruded	0·0	,,

cases the *average* of the initial and control figures have been taken to indicate the amount of oxygen available for the coral, because the oxygen content falls continually throughout the experiment, and more is available than is indicated by the controls, though less than the initial figures show. Full details of this experiment are given in Table XI, the results of which are also shown graphically in Text-fig. 4.

The figures for the percentage of oxygen utilized show, with two slight discrepancies (low figures for *Porites* and *Galaxea* at 9 hours), a progressive diminution as the length of



TEXT-FIG. 4.—Graph showing effect of reduction of oxygen content in the water on the rate of oxygen consumption in corals. See Table XI. F, *Favia*; FU, *Fungia*; G, *Galaxea*; P, *Psammocora*; PO, *Porites*.

the experimental period increases. In one case, *Favia*, all the oxygen in the water was used up at the end of 24 hours, and in another, *Psammocora*, 92·48%. The others varied between 79·95% and 56·9%. Thus, although there was no means of accurately controlling the conditions of the experiment, the average temperature (readings being taken at the beginning and at the end of each experiment) varying between 28·95° and 25·85° C., and the available oxygen between 5·11 c.c. per litre and 4·18, the results of this experiment are undoubtedly significant. A final 1-hour experiment was run in order to determine what effect this prolonged experimentation had had upon the corals. The results show that oxygen consumption had decreased in all cases but *Galaxea*, while the increase in

TABLE XI.—*Experiments on the Rate of Oxygen Consumption by Corals when Confined in Sealed Jars for Various Periods of Time. Experiments Carried Out in Dark Crate in the Aquarium.*

Coral.	Volume in c.c.	Capacity of jar in c.c.	1 hour. Temperature = 28·75° C. Initial O_2 = 5·11.		2 hours. Temperature = 28·95° C. Initial O_2 = 4·70.		3 hours. Temperature = 28·45° C. Initial O_2 = 4·62.		4½ hours. Temperature = 28·65° C. Average O_2 = 4·975.		6 hours. Temperature = 27·75° C. Average O_2 = 4·67.	
			Final oxygen.	Percentage used.	Final oxygen.	Percentage used.	Final oxygen.	Percentage used.	Final oxygen.	Percentage used.	Final oxygen.	Percentage used.
Porites, sp.	140	2830	4·62	9·59	3·83	18·51	3·56	22·95	3·41	31·40	2·51	46·2
Psammocora gonagra	40	2820	4·62	9·59	3·72	20·85	3·25	35·40	3·21	35·40	2·01	57·0
Galaxea fascicularis	75	2760	4·98	2·54	4·17	11·28	4·05	12·34	4·09	17·80	3·33	28·8
Favia, sp.	190	2810	4·50	11·94	3·75	20·21	3·56	22·94	2·85	42·70	2·04	56·3
Fungia danai	40	2815	4·91	3·91	4·19	10·85	3·82	17·32	3·73	24·75	3·12	33·2

Coral.	Volume in c.c.	Capacity of jar in c.c.	9 hours. Temperature = 27·95° C. Average O_2 = 4·78.		12 hours. Temperature = 27·4° C. Average O_2 = 4·60.		18 hours. Temperature = 27·1° C. Average O_2 = 4·18.		24 hours. Temperature = 25·85° C. Average O_2 = 4·24.		1 hour. Temperature = 27·05° C. Initial O_2 = 4·62.	
			Final oxygen.	Percentage used.	Final oxygen.	Percentage used.	Final oxygen.	Percentage used.	Final oxygen.	Percentage used.	Final oxygen.	Percentage used.
Porites, sp.	140	2830	2·86	40·00	1·99	56·96	1·39	66·6	0·85	79·95	4·36	5·6
Psammocora gonagra	40	2820	1·94	59·40	1·47	68·00	0·59	85·9	0·31	92·48	4·25	8·0
Galaxea fascicularis	75	2760	3·53	26·20	2·68	41·80	1·68	59·8	1·87	56·90	4·49	2·8
Favia, sp.	190	2810	2·00	58·20	1·80	60·90	0·46	89·0	0·00	100·00	4·20	9·0
Fungia danai	40	2815	2·90	39·33	2·28	50·50	1·37	67·0	1·36	67·92	4·44	3·9

the case of *Fungia* was negligible. This decrease may be attributed to the long period of starvation suffered by the corals.

In Text-fig. 4, where oxygen utilization is plotted against time, smoothed curves have been drawn through the points. These curves give a good indication of the effect of lowered oxygen tension on the rate of respiration. The early parts of the curves approximate closely to straight lines, the curvature increasing and the speed of oxygen utilization decreasing after about 50% of the oxygen has been utilized. It should be understood that these curves convey no information as to the *comparative* rate of respiration in the different corals used, because the amount of actual living matter varied in each case, although corals were selected possessing roughly the same amount.

The fall in the rate of respiration as the amount of available oxygen decreases is emphasized in Table XII, in which the figures for percentage of oxygen used which are given in Table XI are divided by the time in hours. Alongside these are tabulated the percentages of oxygen which remain *unutilized* in the water at the end of the various experiments.

In this Table the figures for the percentage of oxygen utilized in unit time are shown in italics when they fall significantly below the average for unit time for the first four experiments. These averages are given in column 9. It will be seen that, with the exception of *Porites*, where there was, unfortunately, an anomalous result for the 9-hour experiment, the consumption of oxygen begins to decrease significantly when the percentage of oxygen which remains in the water at the end of the experiment falls appreciably below 50%. The actual figures are 40·6, 40·2, 41·8 and 49·5% for *Psammocora*, *Galaxea*, *Favia* and *Fungia* respectively, while for *Porites* it lies between 53·8 and 43·04%. The figures for *Galaxea* are also a little difficult to interpret, a low figure at 9 hours being followed by a much higher one at 12 hours. But the smoothed curves in Text-fig. 4, in which these anomalies, due probably to the absence of proper means of controlling the conditions of the experiments, are neglected, probably give a good indication of the actual effect of lowered oxygen tension on the rate of respiration of these corals.

It appears, therefore, that corals can remove oxygen from sea-water with almost undiminished speed until the concentration falls to between 40 and 50% of the normal content. Below this the rate of oxygen consumption decreases steadily, until all the oxygen has been removed. The decline in oxygen consumption may actually be less than appears in the curves shown in Text-fig. 4, because the temperature of the water in the longer experiments—which had to be carried out overnight—was several degrees lower than that for the shorter experiments, all of which were conducted during the day, and this lower temperature would certainly reduce the rate of oxidation in the tissues.

It is interesting to compare these results with those obtained for other marine invertebrates. It has been found, broadly speaking, that these animals can be divided into two classes according to whether the rate of oxygen consumption varies with oxygen tension or is to a large extent independent of this. Thus, in the molluscs *Aplysia*, *Eledone* (Henze, 1910), *Loligo* (Amberson, Mayerson and Scott, 1924), *Anodonta* (Dakin and Dakin, 1925), and *Ostrea circumpicta* (Nozawa, 1929), oxygen consumption is largely independent of changes in oxygen content, down to 30%, 50% and 16% saturation respectively for the three last named. In the Crustacea, *Carcinus*, *Scyllarus* (Henze) and *Palaemonetes* (Amberson, etc.)—the last-named down to 50% oxygen saturation—conditions are similar, but in *Homarus* and *Callinectes* (Amberson, etc.) the oxygen consumption varies with

TABLE XII.—*Oxygen Utilization Expressed in Percentages per Unit Time* (1 *Hour*), *with Percentage of Unutilized Oxygen at the End of Each Experiment.*

Coral.	1 hour. Oxygen.		2 hours. Oxygen.		3 hours. Oxygen.		4½ hours. Oxygen.		Average of previous experiments.
	Percentage used per hour.	Percentage left.	Percentage used per hour.	Percentage left.	Percentage used per hour.	Percentage left.	Percentage used per hour.	Percentage left.	
Porites	9·59	90·41	9·255	81·49	7·65	77·05	6·98	68·60	8·37
Psammocora . . .	9·59	90·41	10·425	79·15	9·88	70·35	7·87	64·60	9·44
Galaxea	2·54	97·46	5·640	88·72	4·11	87·66	3·96	82·20	4·06
Favia	11·94	88·06	10·105	79·79	7·65	77·06	9·50	57·30	9·80
Fungia	3·91	96·09	5·425	89·15	5·77	82·68	5·50	75·25	5·15

Coral.	6 hours. Oxygen.		9 hours. Oxygen.		12 hours. Oxygen.		18 hours. Oxygen.		24 hours. Oxygen.	
	Percentage used per hour.	Percentage left.	Percentage used per hour.	Percentage left.	Percentage used per hour.	Percentage left.	Percentage used per hour.	Percentage left.	Percentage used per hour.	Percentage left.
Porites	7·70	53·8	*4·44*	*60·00*	4·75	43·04	3·70	33·4	3·33	20·05
Psammocora . . .	9·50	43·0	*6·60*	*40·60*	5·67	32·00	5·33	14·1	3·85	7·52
Galaxea	4·80	71·2	2·91	73·80	3·48	58·20	*3·32*	*40·2*	2·37	44·10
Favia	9·38	43·7	*6·47*	*41·80*	5·08	39·10	4·95	11·0	4·17	0·00
Fungia	5·54	66·8	4·37	60·67	*4·20*	*49·50*	3·72	33·0	2·83	32·08

the oxygen tension, as it does, according to the same authors, in the Annelid, *Nereis*. All the echinoderms which have so far been investigated from this standpoint, *Caudina* (Nomura, 1926), *Patiria* and *Strongylocentrotus* (Hyman, 1929) show complete dependence on oxygen tension. The gephyrean worms *Sipunculus* (Henze) and *Urechis* (Hall, 1931) behave in the same manner, and so do the coelenterates *Anemonia*, *Actinia* (Henze) and *Cassiopea* (McClendon, 1917), though Henze also found, on somewhat slender experimental evidence, that in *Pelagia* and *Carmarina* respiration is largely independent of the concentration of oxygen present.

Mayor (1924) conducted experiments on *Pocillopora damicornis* first in water of pH 8·24 and oxygen content of 4·1 c.c. per litre, and then in water of pH 5·85 (due to the addition of carbon dioxide) and oxygen content of 3·1 c.c. per litre. Under these conditions he found that the rate of oxygen consumption by this coral was proportional to the oxygen tension. He interpreted these results, in the light of Henze's work on *Actinia* and *Anemonia*, as showing that carbon dioxide does not affect oxygen consumption. But in the light of the results here recorded on five different genera of corals, the opposite interpretation appears the more probable, especially when the very low pH of the water is remembered.

There is as yet no unanimity as to the interpretation of these results. Henze's contention, that the more highly organized invertebrates which possess gills and respiratory pigments are independent of oxygen tension in the water, whereas the simpler animals are not, has been disproved by Amberson, Mayerson and Scott. It may be that, apart from the cephalopods, which possess a more efficient form of haemocyanin than the other molluscs or the crustaceans, the power of regulating oxygen consumption is an adaptation to life in water of variable oxygen content. It has been contended by some that the accumulation of carbon dioxide might depress oxygen consumption, but Amberson, Mayerson and Scott failed to find any appreciable effect from this cause in *Homarus* or *Nereis*. Hyman (1929) and Buchanan (1931), as a result of work on freshwater *Planaria*, have shown that this animal controls oxygen consumption over a wide range of oxygen tension. They conclude that a mechanism for oxygen regulation may be present in the bounding membrane of the body, while the work of Buchanan further indicates that the greater the water content of the tissues—and so the lower the concentration of oxidative enzymes—the greater the powers of regulation. Henze, later supported to a large extent by McClendon, considered that the dependence of oxygen consumption on oxygen tension in the more simply organized animals was due to the fall in the rate of diffusion as the oxygen tension became less. In coelenterates, for example, where there are no gills and no respiratory pigments or circulatory system, oxygen must make its way through the ectoderm and thence to the various tissues by some process such as diffusion. If the actual process of oxidation is quicker than that of diffusion, then the whole process will be controlled by the rate of diffusion, which naturally decreases with the fall in oxygen tension. On this assumption animals with the smallest volume in relation to surface should be affected least by changes in oxygen tension. This is confirmed to some extent by the work of Amberson (1928) and earlier workers therein quoted, on protozoa and echinoderm eggs (*Paramecium* and the eggs of *Arbacia* in this instance), in which the respiratory rate was found to be constant over a wide range of oxygen tensions.

The Madreporaria are characterized by the possession of large skeletons, over which the tissues are spread as an excessively thin sheet. They have thus a very large surface

compared with the volume of the tissues. This is even more strikingly the case when the animals are expanded than when they are contracted. In the former condition the transparent tissues are lifted away from the underlying skeleton, and water passes into the coelenteron and up into the hollow, greatly elongated tentacles. Under these conditions all the tissues are in very close contact with the water, and so with the oxygen it holds in solution. These facts appear a reasonable explanation of the differences between the behaviour at different oxygen tensions of the coelenterates studied by Henze and McClendon, and of the corals. In the Actiniaria and in *Cassiopea* the tissues, especially the mesogloea, are relatively thick for coelenterates, and so a fall in oxygen tension may well cause a considerable fall in diffusion. In *Pelagia* and *Carmarina*, conditions apparently approximate to those in corals, where the large body surface allows diffusion to take place with such speed that the amount of oxygen required for oxidation is available for the animal until it falls to about one-half the normal concentration. Only then does the rate of diffusion become the controlling factor in oxygen consumption. Another point to be remembered is that corals are sessile animals, which expend little energy, and so their oxygen needs will be correspondingly low. Moreover, they have a high water content, which, according to Buchanan, should make for greater powers of regulation.

But whatever the actual reason is for the ability of corals to utilize oxygen with equal ease over a wide range of oxygen tension, the obvious conclusion remains that they are especially well fitted for living in water of very variable oxygen content. The important bearing which this conclusion has upon the views of various workers, that oxygen production by the zooxanthellae is of vital importance to the corals in which they live, will be discussed in the next section of this paper.

10. DISCUSSION.

The results of the experiments recorded in this paper provide definite advances in knowledge regarding the conditions controlling respiration in corals and photosynthesis in the zooxanthellae. They also give certain indications as to the nature of the relationship between these two processes, but it is abundantly evident that much further work is necessary before the actual significance of this relationship in the life of the reef-building corals is fully understood. It is a matter for satisfaction that this paper does indicate the lines along which such future work should be conducted.

The most important result of the work on respiration in corals is the discovery that this does not diminish in rate until the oxygen content has been reduced to one-half or less of the normal, and that corals can survive in darkness for considerable periods in water with a very low initial oxygen content. The results of these last experiments, which show a much greater power of survival in *Porites* and *Cyphastrea* than in *Fungia* and *Galaxea*, indicate that this may be correlated with the normal habitat of these corals. The former corals are often exposed at low tide; the latter are never exposed. A similar gradation in the powers of survival of corals buried under mud was found by Mayor (1918*a*) at Murray Island, corals such as *Porites*, *Coeloseris* and *Goniastrea*, which live near the shore, being more resistant than others, such as *Seriatopora*, *Pocillopora* and *Acropora*, which live further off shore. It appears, therefore, that, in addition to their general power of utilizing oxygen with equal facility over a wide range of oxygen tension, individual species of corals may also develop adaptations fitting them for life under conditions where oxygen

may, on occasion, be almost or completely absent, as in small isolated pools at night (see Orr's paper in Vol. II of these reports), or when actually exposed by the falling tide. There can be no doubt that reef-building corals are exceptionally well fitted for survival in water of very variable oxygen content.

Turning now to the zooxanthellae, under the conditions which prevailed during the experiments there was a great excess of oxygen produced during the daylight, but this, with one exception in a large series, was not the case over the full period of 24 hours. It might at first be concluded that had the crates been nearer to the surface during these last experiments, the greater amount of available light would have permitted the zooxanthellae to produce more oxygen, which might have exceeded the amount used by the corals over the full period of the experiment. But the results of the series of experiments over 27 and 12 hours reveal that this would not necessarily be the case. Owing to some limiting factor, the possible nature of which has already been discussed, photosynthesis in the zooxanthellae does not increase indefinitely with increasing intensity of illumination. It attains a certain maximum, and there remains. The experiments on the effect of depth on oxygen production have also to be considered in the light of these findings. Only when a full study has been made of the effect of different intensities of light and for varying periods of time on photosynthesis in the zooxanthellae can this matter be fully decided. The statements contained in the following paragraphs are therefore *tentative only.*

Evidence was produced in Papers IV and V of this series, and is also discussed elsewhere (Yonge, 1931), indicating that the capacity of corals to exist in sufficient numbers to form reefs may be due to the presence within them of zooxanthellae. If such is indeed the case, then the vertical distribution of reef-building corals, at any rate as a community which constitutes a living coral reef, must be limited by the penetration of light, without which the zooxanthellae cannot live. The foregoing results have a fundamental bearing on this question. They indicate that corals at some considerable depth may possess as many zooxanthellae as those at or near the surface, the difference being that the zooxanthellae in deeper water will photosynthesize at maximum capacity throughout the day, whereas those nearer the surface will be very active in the morning but, unless on exceptionally dull days, will have slowed down before noon. The end-result in terms of carbohydrate formed will be the same in both cases. A coral colony can only contain a certain concentration of zooxanthellae within its tissues, dependent apparently on the quantity of nitrogen, phosphorus and sulphur produced (since the results of experiments described in this paper show that carbon dioxide, except possibly for short periods of maximum illumination, is always present in excess of the demands of the zooxanthellae). It follows, therefore, that so long as the illumination is sufficient to permit the chlorophyll to produce enough carbohydrate for the needs of the plants, and enable them to increase at the same speed as the coral grows, then the association between corals and zooxanthellae will continue under optimum conditions. Should the illumination be too low, then, as shown by the low algal content of corals dredged from between 7 and 9 fathoms in the turbid waters off Low Isles (see Paper IV), the algal content will fall below the maximum. As the light is reduced, so will the numbers of the zooxanthellae decrease, until they are no longer abundant enough to carry out their apparently essential *rôle* as excretory organs to the corals.

But above the critical minimum degree of illumination, instead of the zooxanthellae increasing indefinitely and being rejected as they certainly are when the metabolism of

the coral falls for any reason—starvation, exposure to high temperatures, or, as shown in this paper, to low oxygen tensions—the activity of the chlorophyll is checked by some limiting factor or factors, so that the concentration of zooxanthellae in the tissues remains steady at the maximum figure, any slight excess being rejected in the manner described in Papers IV and V. In this way the balance between the population of zooxanthellae and the bulk of the tissues (which probably varies for different genera of corals) is automatically controlled so long as the illumination is above the critical intensity. Other things being equal, it follows that reef-building corals will flourish with equal ease wherever the zooxanthellae occur in maximum concentration. Actually they will flourish better below the tidal zone, while the vertical migrations of the zooplankton will have an important influence. This last matter will be discussed in detail in the final paper of this series after the publication, in Vol. II, of the appropriate papers dealing with zooplankton.

In the next paper in this volume Miss S. M. Marshall gives an account of experiments, on the same lines as those described in this paper, on the oxygen exchange in coral planulae. These have an important bearing on the matter under discussion. Her experiments on the effect of depth indicate that in the planulae optimum conditions for photosynthesis in the zooxanthellae *do* occur at the surface. Moreover, experiments carried on over 24 hours at the surface showed only a slight excess of oxygen production in the daylight. Unfortunately the sunlight on that day was not continuous, so that the results cannot be compared directly with those for the 12- and 27-hour experiments. It would appear that the balance between oxygen consumption by the animal and its production by the plants is different in the planulae. Either the algal content of the planulae is lower than that of the adult, or the metabolism of the planulae is higher. Both of these alternatives may be true, but the second is probably the more important. The planulae are rapidly developing, and, as shown in Paper IV, they have large fat reserves, which will be oxidized at considerable speed during the larval period, when development is rapid and no food is taken. Since the planulae live near the surface of the water until they settle and metamorphose, Miss Marshall's results indicate no waste of efficiency on their part and are completely reconcilable with the work on adult corals.

Verwey (1930, 1931) has been able to show some correlation in the Bay of Batavia between the depth to which corals extend and the penetration of light. This is largely dependent there on the amount of silt in the water, which decreases with increasing distance from the shore. The algal content of corals dredged from between 7 and 9 fathoms off Low Isles was less than half that of corals from the surface. Clearly, therefore, the critical degree of illumination was above 7 fathoms. But it by no means follows that this figure is generally applicable. The water around Low Isles contained large quantities of silt (see paper by Marshall and Orr, No. 5 in this volume), and visibility was correspondingly poor. The great difference in the turbidity of the water within and without the Great Barrier is shown by the Secchi disc readings included in the data in the List of Stations given by Russell and Colman in Vol. II, No. 2. Whereas the readings for the regular station three miles east of Low Isles varied between 3·5 and 25 metres (the last an exceptional reading), the majority falling at about 8 or 9 metres, and the readings taken in connection with the depth experiment were $7\frac{1}{2}$ and 8 metres, those for the open water beyond Trinity Opening (see map in Vol. I, No. 1) ranged between 23 and 36 metres. The average figures for outside the Barrier were about 20 metres greater than those for inside the channel. Obviously the critical illumination will occur at a much

greater depth in the clear water outside, and this applies to the outer seaward faces of all reefs, be they fringing or barrier reefs or atolls, upon the growth of which depends the maintenance of the whole.

As Verwey points out, silt itself has been considered as a limiting factor in the vertical distribution of corals. His arguments against this view are well founded and, combined with the work of Marshall and Orr at Low Isles, appear conclusive. This matter will be further discussed in the final paper of this series.

The production of oxygen by the zooxanthellae as a result of photosynthesis is a most valuable guide to the abundance of zooxanthellae in any coral, and to the effect of any particular series of conditions on photosynthesis. It remains to be considered whether the oxygen so produced is of vital importance to the corals, or rather to the community of reef-building corals as a whole. This is a very difficult question to answer. Verwey draws attention to the immense amount of living matter represented by a living reef and to the great quantities of oxygen which this must consume. This fact, added to the slow rate of diffusion of oxygen in water and to the slowness of currents, leads him to the conclusion that the oxygen produced by the zooxanthellae during the daytime *is essential* to the maintenance of this accumulation of animal matter. The force of these arguments cannot be denied. Oxygen must be present in sufficient amounts to satisfy the needs of the corals and other animals, and this, in the absence of powerful currents, can only be maintained at a sufficiently high concentration by the aid of plants, the inorganic food materials for which will be amply supplied from the excreta of the animals. It may be accepted that in regions where there are no powerful currents an adequate amount of plant life is essential for the support of a living coral reef, although it has been shown in this paper that corals can live with unimpaired efficiency in water of very variable oxygen content. But is it also essential that this oxygen should be produced by plants which live within the tissues of the coral ? This is by no means certain. What is certain is that the great majority of reef animals (almost all Coelenterata, some Foraminifera and Tunicata, and the Tridacnidae) possess zooxanthellae, which intercept the nutrient salts which would otherwise be excreted into the water, and even (as shown in Paper IV) extract phosphorus from the surrounding sea-water, so that only a very limited phytoplankton can exist. Its place is taken by the zooxanthellae, which are essentially imprisoned phytoplankton (Yonge, 1931). But it is quite certain that did the corals and other reef animals not possess zooxanthellae within their tissues, the great quantities of nutrient salts which they would discharge into the water would permit of the growth of a very abundant phytoplankton. This would develop so rapidly in the bright light and utilize the nutrient salts at such a speed that these would probably never diffuse far from the reefs. Accordingly, there would be a very abundant phytoplankton in the waters actually washing the reefs, with a corresponding production of oxygen. It is, of course, impossible to be certain whether this would be sufficient for the needs of the corals, or be as readily available as that produced by the zooxanthellae. But the immense quantities of animal life present on artificial oyster beds (particularly in France and the United States), and on natural mussel and cockle beds, certainly obtain enough oxygen without the aid of symbiotic algae. They represent as great a concentration of living matter as a coral reef, so that there seems no reason why reefs should not obtain sufficient oxygen, even in comparatively still waters, if their excretory products were utilized by phytoplankton.

On the seaward slopes of reefs even phytoplankton might be unnecessary. The pounding of the surf ensures an adequate oxygen content in the surface waters, while an upwelling, which may well be of general occurrence, would bring a continuous supply of oxygenated water from below. But we need a great deal more information about the water movements on the exposed surfaces of reefs before these suppositions can be either substantiated or refuted.

The general conclusion to which we are led is that the oxygen produced by the zooxanthellae may be essential for the maintenance of reefs in sheltered, still waters, but may be unnecessary on the exposed, seaward faces of reefs. The actual production of the oxygen *within the tissues* of the corals may also not be essential, for there seems no reason to suppose that coral reefs would not flourish equally well if oxygen were produced in the water round about them by phytoplankton. It is clearly otherwise when we consider zooxanthellae as excretory organs which automatically remove the end-products of coral metabolism. For this purpose their presence within the tissues of the coral *is* essential. As stated elsewhere (Yonge, 1931), the exceptional powers of growth and repair possessed by reef-building corals may well be due to the high degree of efficiency bestowed on such simply organized animals by the automatic removal of the end-products of their metabolism.

Certain secondary effects of photosynthesis which may, in the opinion of various workers, be of importance in the life of the corals, call for mention here. Thiel (1929) has advanced the hypothesis that by their production of oxygen in the tissues the zooxanthellae assist the corals in the formation of their skeletons. He refers to work of his own on Lamellibranchs, in which he found that species living in well-oxygenated water have thicker shells than those living in water with less oxygen. He also points to the massive shells of *Tridacna* and the presence of zooxanthellae in these animals (of which an account will be given in a later paper in this volume). Thiel's hypothesis is interesting, but it must be remembered that zooxanthellae are just as abundant in coelenterates—actinians, alcyonarians and scyphozoans for example—which have no massive skeletons, and that the deep-water corals and also *Dendrophyllia* and *Balanophyllia* form massive skeletons and yet have no zooxanthellae. In the lamellibranchs also, genera such as *Chama* or *Spondylus* have shells as massive as those of *Tridacna* in proportion to their tissues, and yet they have no zooxanthellae. Nevertheless Thiel's views are worthy of experimental investigation. Verwey (1930) points out that an excess of carbon dioxide might cause dissolution of the skeletons of the corals. At the same time he admits that a lowering of the oxygen content which would accompany this might have the opposite effect, since the ammonia which might then accumulate would unite with the carbon dioxide to form ammonium carbonate, which, acting on calcium sulphate, would cause the precipitation of calcium carbonate. While it can be readily admitted that an excess of carbon dioxide would be injurious to the corals, there seems no reason for assuming that the presence of algae actually within the tissues would be more effective in preventing this than an equal concentration of phytoplankton in the water round about. In other words, a commensal relationship between the corals and the algae is not apparently necessary.

Finally, Gardiner (1930) has put forward the very interesting suggestion that the inability of corals to form reefs in any great numbers in the still waters of atoll lagoons or within boat channels between barrier reefs and the mainland may be due to the

influence of the photosynthetic activities of the zooxanthellae. Under conditions such as these an enormous deposit of lime has been found on the surface of corals dredged from below 10 fathoms and occasionally in shallower water. Gardiner attributes this to the action of the zooxanthellae and other plants which, by raising the pH of the water, may cause precipitation of calcium carbonate in a very fine amorphous form, which, in the absence there of water currents to assist in its removal, may kill the corals below a certain depth and so prevent the formation of reefs in sheltered waters. This attractive hypothesis also demands experimental investigation.

11. SUMMARY.

1. This paper deals with experiments on the conditions affecting oxygen production by zooxanthellae and its consumption by the corals in nature and the relationship between these.

2. Reef-building corals exposed for 9 hours over the daytime almost invariably produced considerably more oxygen than they consumed. In darkness considerable quantities of oxygen were always consumed.

3. *Dendrophyllia* and *Balanophyllia*, neither of which contain zooxanthellae, showed a slightly greater consumption of oxygen by day than by night, owing probably to the higher day temperature.

4. The actual oxygen consumption by any coral in a series bears no relation to the oxygen production in the light by its zooxanthellae. This may be due to differences in algal content or differences in the respiratory needs of different species of corals, or to a combination of these two factors.

5. Corals largely deprived of zooxanthellae by long subjection to total darkness showed, with one exception, little change between the oxygen exchange for similar periods in light and in darkness.

6. At the end of 24 hours, out of a series of corals exposed at an average depth of about 4 metres, only one showed an increase in oxygen content. The zooxanthellae do not, under these conditions, produce as much oxygen as the coral consumes.

7. Experiments carried out over 27 hours near midsummer at an average depth of between 3 and 4 metres showed a peak in oxygen production between 10 and 11 in the morning in six out of the eight corals used.

8. Similar experiments over the daylight only in midwinter and at a constant depth of 1 metre showed a maximum production of oxygen about midday.

9. The cause of these differences is discussed, and the greater intensity and penetration of light in the summer indicated as the probable explanation of the earlier peak. The importance of these findings on the vertical distribution of reef-building corals is also discussed.

10. About midwinter corals exposed for 4-hour periods over the middle of the day show a progressive diminution in oxygen production at successively greater depths. The results of the previous experiments indicate that these differences would have been less had similar experiments been carried out in the summer or for longer periods.

11. Oxygen exchange in *Dendrophyllia* is not affected by either the time of day or by depth.

12. Corals can survive for 2 weeks in sealed jars with, in some cases, an actual increase in oxygen content if the final samples are taken in the afternoon. But the pH always falls, from which it appears that more carbon dioxide is produced than the zooxanthellae can utilize, and so this substance cannot be a limiting factor in the abundance of zooxanthellae in the tissues.

13. The water immediately around Low Isles contained so much organic matter that even after filtration through a fine sintered silica filter the dissolved oxygen was, in certain cases, entirely utilized after one week in a sealed jar as a result of oxidation.

14. Different corals can survive in darkness in water containing an initial oxygen content of between 1·25 and 0·51 c.c. per litre for periods varying from under 1 to under 6 days. Those which survived longest discharged large numbers of zooxanthellae before they died, in the same manner as corals which have been starved or exposed to high temperatures.

15. Experiments on the effect of lowered oxygen tension on the rate of respiration in a series of corals show that the oxygen content can fall to between 40 and 50% saturation before respiration is affected. In lower oxygen tensions the rate of consumption steadily decreases until all the oxygen has been utilized.

16. This may possibly be due to the very high ratio of surface to volume in corals and to their extremely thin tissues. It certainly fits them for life in water of very variable oxygen content.

17. The tentative conclusion is reached that above some critical degree of illumination reef-building corals contain the maximum content of zooxanthellae, and so will function with equal efficiency, other factors being equal, anywhere above the depth at which this critical illumination occurs, which in turn is dependent on latitude, turbidity of the water and other factors.

18. Although the presence of abundant plant life in the water is probably essential, at any rate in the absence of powerful currents, for the maintenance of the necessarily large oxygen demands of a living reef, yet there seems no reason for assuming that this plant life must occur actually within the tissues of the animals. This would, however, clearly be necessary if the essential *rôle* of the zooxanthellae is the automatic removal of the end-products of coral metabolism.

19. The possible injurious effects on the skeletons of corals by an accumulation of carbon dioxide is prevented by the photosynthetic activities of the zooxanthellae. But for this purpose also a commensal relationship between the algae and the corals is not apparently essential.

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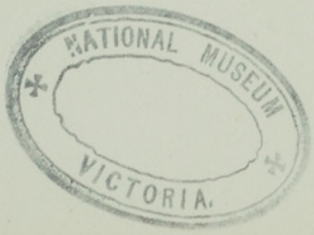
Note from p. 234.—These results are not in agreement with those recorded in Table IV. The excess of oxygen may be due to an increase of phytoplankton in these jars, the result possibly of the decomposition of material at the broken bases of the skeletons of the corals, always very difficult to cleanse. Such an effect would hardly appear in 24 hours, but easily in 14 days. The fall in pH which accompanies the rise in oxygen content may also be due to decomposition.



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