CORAL REEF STUDIES.

II. THE DEPTH OF CORAL REEFS IN RELATION TO THEIR OXYGEN CONSUMPTION AND THE PENETRATION OF LIGHT IN THE WATER.

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INTRODUCTION.

Measurement of the oxygen content of coral reef water, which I made in connection with ecological work, showed that the oxygen consumption of a reef can be so considerable that the water around it may become deprived of a large part of its oxygen. This fact brought me to the much discussed problem of the relation existing between the development of reefs and their want for light. It occurred to me that this problem could be approached if there could be shown to exist a correlation between the depth of the living part of certain reefs and the silt content of the water around them, as the silt content must influence the penetration of light in the water. If I should succeed in proving such a relation to exist, this would be a very strong argument in favour of the dependence of coral reefs on light. The observations in question were carried out in the years 1928—1930 in the Bay of Batavia and the work had to consist of observations on:
1. the oxygen production and consumption of reef corals and coral reefs;
2. the influence of currents;
3. the silt content of the water;
4. the depth of light influence;
5. the depth of the living part of the reefs in question.

The observations were all made at or in the neighbourhood of the island Onrust in the western half of the Bay of Batavia. As already stated in a previous paper, the aquarium built on this island in 1928 for the Laboratorium voor het Onderzoek der Zee offers quite unique opportunities for the study of coral reefs. It is fed with water pumped up from the reef, receives full sunlight, and all kinds of reef animals flourish here as on the reef itself. Thus the work was in first instance made possible through the kindness of the authorities of the Medical Service, Batavia, as Onrust is their Quarantine Station for Java. For the flourishing of this aquarium, however, its construction, the care for its welfare, we are indebted in the very first place to the intense interest in scienti-

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fic work of Mrs. and Mr. Steinfurth, medical officer and administrator to the
Station, to whom no trouble was too much, each new fact a revelation. It is
largely due to their devotion that the Laboratory at Batavia now offers working
opportunities in the dutch tropics, which are hardly surpassed by those of any
other tropical marine biological station.

One will see below that I further owe many thanks to Dr. S. W. Visser
and Dr. H. P. Berlage, of the Meteorological Observatory at Batavia, for valu-
able help in connection with solar radiation and some other problems. Finally I am
indebted for help to Ir. B. Markus of the Visscherij Station, Batavia, and Dr.
Ir. C. P. Mom, director of the Proefstation voor Waterzuivering at Manggarai,
Batavia. And I thank Prof. Delsman for reading the manuscript.

1. The oxygen consumption of reef corals and coral reefs.

In June and July, 1928, in studying the small lagoon of the coral island
Hoorn in the Bay of Batavia, I made a number of oxygen measurements of the
lagoon water at different times of the day, to see whether there would be a daily
rise and nightly fall in the quantity of oxygen due to assimilation and respiration
respectively. The measurements were made during a period in which the
inrush of new seawater into the lagoon fell during late afternoon and early
evening, so that the lagoon did not receive any renewal of water either in the
morning or in the second half of the night. For that reason it was to be expected
that increase and decrease in oxygen should be considerable and the results bore
out this conclusion.

Table I.

	Time of day	Oxygen content (cc. per litre)		
		2nd lagoon	3rd lagoon	
water falling.	6—8 a.m.	2.4,2.4	1.6,1.8,2.3,2.7,3.5,3.8	Temperatures ran-
	8—10 „	4.1,4.6	3.7,3 9,4 4	ging from 27.5 to
	10 · 12 „	6.-,6.6	5.4.5.9,6.3,	30o C., giving sa-
	12—3 p.m.	4.6,6.5	6.4(9.-),7.9,8.9(9.4) [1]),	turation of seawa-
water rising			7.6(9.5)	ter (about 18⁰/₀₀ Cl)
	3—6 p.m.	7.6	5.3,6.8	with 4.8 4.5 cc. of oxygen per litre.

To make possible a comparison of these figures with those for the sea
outside the shingle wall, measurements were also made of the water above the
reef, some metres from the shingle wall. These few observations tended to show
that the water of the sea close to the shore above the reef shows the same
daily rise and nightly fall in the quantity of oxygen, though probably to a
lesser extent.

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[1])   The figures between brackets are duplo-figures, differing much from the pre-
ceding figure. In such a case one of the two or both values are false.

TABLE II.

Time of day	Oxygen content (cc. per litre)	
6 — 8 10 — 12 12 — 3	2.1,2.1,3.2 5.6.5.7 4.-(5.1)	Temperatures ranging from 27.°5 to 29.°2, giving saturation of sea water with 4.8 — 4.65 cc. oxygen per litre

To see the influence of rising water I again made a series of measurements in February, 1929, when the water was rising in early morning, falling during the afternoon. I now chose the east side of the island Onrust, where the reef is living in shallow water close to shore, but also in open communication with the sea. As it was westmonsoon now, the place represented the lee side of the island.

TABLE III.

Time of day	Oxygen content (cc. per litre)	
6 — 8 8 — 12 12 — 3 3 — 6	1.5,3.4,3.9,4.-,4.2,5.3 4.6.4.7,5.4,5.7,6.3,7.- 5.4.5 5,6.2,6 2(5.5?). 5.-,5.1,5.1,5.5	Temperatures ranging from 28.°1 — 29.°8, giving saturation of sea water with 4.8 — 4.5 cc. oxygen per litre

These measurements show that even where the water is rising in early morning (beginning from 4 to 6 o'clock during the days of the observations) there is a very important difference between the oxygen content in the early morning and during the afternoon. From the place where the water was taken to the edge of the reef, a distance of 30—60 metres only, the water is becoming very gradually deeper and though the current along the reef's edge is of little influence over the shallow reef itself, the water above the reef is in open communication with the water of the sea around.

I did not measure the oxygen content of the water around the reefs during the days of the observations. Generally spoken we certainly may assume that the water of the open sea is always more or less saturated with oxygen and does not show a distinct diurnal variation. Therefore I did not bother about oxygen measurements in the open water during those days. However, to exclude the possibility of making fault assumptions in this direction, I lateron made a small series of measurements of the open water between the reefs. I let them follow here and also mention some earlier observations, which were made in other connection.

During a trip to the Thousand Islands in the southwestern Java Sea, on 25—27 July, 1928, I made a number of measurements at different times of the day and during the night. They gave bad figures, as the controls differ much

from one another, but all 12 values show saturation or supersaturation with oxygen (water 8 m deep). The same holds good for 8 measurements (also bad figures) made in the western half of the Bay of Batavia on 25 August, 1928, 7.30 a.m.—2.30 p.m. — On 4 September, 1930, 7.15 a.m., I found 5.52 cc. oxygen p. l. for the water near Onrust. So there was supersaturation in early morning [1]). In the afternoon (2 p.m.) I found at the same place a value of 5.75 cc. p. l. (temperatures 28°.1 and 29°.5 resp.). — On 12 October 1930, between 6.30 and 8.30 a.m., I found about 5.-cc. for water between Batavia and the island Edam (eastern half of Bay of Batavia, 4 measurements), in the afternoon I found 5.2 there (3 measurements). So this water too showed slight supersaturation in early morning (temp.: 28.2—29.9). — On 17—19 October I made a series of measurements in the open water between Onrust and Purmerend. The water was 10.5—12 m deep and the samples were taken from 3 m deep. They yielded the following results.

TABLE IV.

Date	Time of day	Temperatures	Oxygen in cc. p. l.	S in %₀ [2])	Cl in %₀ [2])
17 X	5.45 a.m.	28°. 7	5.12, 5.08 = 5.10		
	9.—	29°. 6	5.13, 5.14 = 5.14		
	9.50	29°. 7	5.02, 5.02 = 5.02	32.80	18.16
	10.25	29°. 9	5.14, 5.16 = 5.15	32.61	18.05
	11.30	30°. 1	5.14, 5.14 = 5.14	32.63	18.06
	2.55 p.m.	30°. 4	5.13, 5.16 = 5.15	32.89	18.21
	3.50	30°. —	5.06, 5.08 = 5.07		
	4.40	29°. 3	5.21, 5.21,		
			5.18 = 5.20		
	5.15	29°. 5	5.37, 5.37 = 5.37		
18 X	5.30 a.m.	28°. 8	5.38, 5.34 = 5.36		
	6.50	28°. 9	5.35, 5.31 = 5.33	32.98	18.26
	8.40	29°. 2	5.34, 5.35 = 5.35		
	9.25	29°. 5	5.27, 5.28 = 5.28	32.84	18.18
	10.35	29°. 6	5.11, 5.16 = 5.14		
	11.15	29°. 5	5.21, 5.23 = 5.22	32.84	18.18
	2.— p.m.	30°. 2	5.25, 5.27 = 5.26		
	2.45	30°. —	5.10, 5.15 = 5.13	32.95	18.24
	3.20	29°. 8	5.38, 5.41 = 5.40		
19 X	10.— a.m.	29°. 5	5.51, 5.51 = 5.51		

In these same days I also made some measurements at other places round Onrust. They are not even of local interest, but again show high figures.

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[1])   Sea water of 28°-30°C. is saturated with oxygen when it contains 4.8-4.5 cc. per litre.
[2])   Calculated from areometre readings with the use of KNUDSEN's tables.

Table V.

Place of Sample	Time	Temper.	Oxygen	
South of Onrust	16 X, 3.15 p. m.	29°.9	5.18,5.20 =	5.19
East of Onrust (waves)	3.45	30°.1	4.97,5.10 = ±	5.—
South of Purmerend	4.15	29°.9	5.18,5.13 =	5.16
North of Purmerend (waves)	4.45	29°.8	5.12,5.13 =	5.13
On reef south of Kerkhof	5.15	29°.8	4.97,4.86 =	4.90
East of Onrust outside reef	17 X, 6.05 a. m.	29°.1	5.20,5.15 =	5.18
On reef east of Onrust	6.30	28°.9	3.72,3.80 =	3.76
On reef nearer to island	7.—	28°.5	4.17,4.20 =	4.19
Between Onrust and Purmerend	18 X, 5.30 a. m.	28°.8	5.38,5.34 =	5.36
Edge of Onrust-reef	6.—	28°.7	4.70,4.73 =	4.72
On reef east of Onrust	6.25	28°.9	4.80,4.79 =	4.80

I give these observations in extenso, as they reveal several peculiarities. As sea water of 28°.5—30° C. and 18⁰/₀₀ Cl is saturated with about 4.70—4.60 cc. O_2 p.l. (I use the table of Fox in Harvey, p. 60), we first of all see that the water in the shallow Bay of Batavia is supersaturated with oxygen night and day, at least during the days of the measurements. Secondly we see that there are slight but distinct variations in oxygen content of one and the same place (extremes 5.02 and 5.51 cc. p. l. in 3 days), though there is no regular diurnal variation with a maximum and minimum. Probably these variations are due to currents. Thirdly some few measurements of reef water confirm the earlier observations that the reef water may show figures different from those of the water around the reefs. The reason why these differences in this case are not greater, is to be found in the time of rising of the water: the second half of the night.

From table IV one will see that there occur slight variations in the oxygen content of the water, which are of short duration only. So, for instance, a measurement of 5.02 cc. between an earlier and a later one of 5.14 and 5.15, and so on. I think these variations are real variations, but the possibility is perhaps not wholly to be excluded that the stopping of the motorboat, stirring up the water, may cause a slight loss of oxygen of the supersaturated water, one time more than another. As I came to this assumption after the work had been finished, I made no control measurements in this direction. There is no possibility that these variations are due to fault measurements, as the controls differ very little.

These few measurements, as far as they permit such a conclusion, show that the water of the shallow Bay of Batavia is night and day supersaturated with oxygen, at least during calm weather. For when during "bad" days in the west monsoon the silt is stirred up and brought into suspension (see below), there will probably be a short of oxygen instead of too much. Whether plankton or bottom algae or both cause this supersaturation, I do not know. But it is clear that these observations are further proof of the remarkably low figures for the oxygen content of reef water in early morning.

The rule of the absence of a distinct diurnal variation in the oxygen content of water in the open tropical sea does not always hold. On 27-30 September, 1928, Ir. B. Markus made a series of observations during a trip from Java (Indramaju) to Borneo (Kumai). They were made at the request of Prof. Delsman in a period when wide patches of the alga *Trichodesmium* covered the Java Sea. All samples were taken from a depth of 3 m whereas the depth of the sea ranged from 36 to 52 m. [1]

TABLE VI.

Date	Hour	Temperature	Oxygen
27 X	8.13 a.m.	28.3	3.62
	9.20	28.6	3.94
	10.07	28.4	4.25
	10.44	28.5	4.24
	11.30	28.6	4.56
	1,24	28.5	4.67
	2.15	28.7	5.12
	3.32	28.6	5.57
	6.—	28.3	5.16
	9.30	28.2	5.11

The following day, 28 October, gave no such a low minimum in the morning, nor such a high maximum in the afternoon, the five values ranging from 4.89 to 5.— cc. p. l.

It follows from these observations that large quantities of phytoplankton may cause a distinct diurnal variation in the oxygen content of the water in the open sea, giving a rather important under- and supersaturation; that, in general, however, this diurnal variation in the oxygen content of the open water is of little importance, at least in calm periods, and that shallow water like that of the Bay of Batavia may even be continuously supersaturated with oxygen. Supersaturation seems to arise very easily, and even a rather strong wind does not succeed in causing much oxygen loss; in the same way a rather strong wind on the reef does not prevent a strong under-saturation.

These observations on supersaturation of open water show that the large variations in the oxygen content of reef water are the more important. They show that the consumption of oxygen by a coral reef, this enormous block of living matter, must be enormous. Assuming that only a body of water of 100 metres along the shore, 10 metres across and 2 metres deep shows a lowering of the oxygen content from 5 to 3 cc. p. l., whereas this water is in more or less open communication with the sea, there must be a consumption of much more than 4000 litres of oxygen during one single night.

Before proceeding, however, we first may ask whether this consumption and production of oxygen of coral reefs cannot be measured more directly.

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[1]   I have omitted the figures for the neighbourhood of the coast.

Production: It is to be expected that higher algae as well as the zoöxanthellae, which live within the coral tissues are the cause of the large production of oxygen. As to higher algae one can directly see the continuous stream of small bubbles, in smooth shallow water rising to the surface in direct sunlight. The more shallow parts of the reefs (in the Bay of Batavia down to a depth of about 5 m), in so far they are not wholly covered by corals, are covered with a silky carpet of fine green algae. Large tables of *Acropora,* turned over by the waves, die, while their undersides get covered with these algae; the same happens with broken corals, the bottom of sand or coral fragments, etc. This zone therefore becomes the home of large bands of parrotbill fishes, especially *Pseudoscarus dubius* (Benn.), *pyrrostethus* Blkr, *cantori* Blkr and *fasciatus* Valenc., which feed on these algae, scraping the coralrock covered with them with their sharp "teeth". It is especially this zone which produces large quantities of oxygen.

As to oxygen production through zoöxanthellae I made the following measurements.

On 22 February, 1929, 6.30 a.m., 4 jars, with a content of 9.3 l. each, were filled with unfiltered sea water. This was done by means of a siphon in such a way that the water was not mixed with oxygen in filling. The water was taken from one of the tanks of the Onrust Aquarium, the oxygen content of which had been measured directly before filling and found to be 3.25 cc. per litre (3.25, 3.27). The jars were put in the dark until 8 a.m. In the mean time 3 (wet) pieces of *Acropora hebes* were freshly collected and later weighed under similar conditions. At 8 a.m. the pieces of coral were put into the jars.

Jars 1 and 3 were hung in full sunlight in one of the aquarium tanks, the cover just under the water surface, in order that the temperature remained constant. The other jars, 2 and 4, were put into a dark room. The proof yielded the following results.

Table VII.

Number of jars	Weight of *Acropora hebes* in gr	Kept in light or dark	Duration of experiment	cc. O$_2$ per litre at beginning	at end	Increase in O$_2$ (cc. p.l.)
1	83.5	in the sun	8 a.m.—3 p.m.	3.25	6.04 (5.96,6.11)	2.79
2	71.3	in the dark	8 a.m.– 3.30 p.m.	3.25	2.28 (2.08,2.47)	-0.97
3	73.1	in the sun	8 a.m.—4 p.m.	3.25	5.78 (5.53,6.06)	2.53
4	no coral.	in the dark	6.30 a.m.— 4.15 p.m.	3.25	2.84 (2.82,2.86)	-0.41

Though these observations give us some insight into the matter, their value is not great. The duplo-figures found at the end of the experiment for the jars 2 and 3 differ much inter se. Moreover the decrease in oxygen of jar 4 shows

that organic matter used up 0.4 cc. of oxygen p. l. from 6.30 a.m. (when the jars were filled) until 4.15 p.m., i.e. somewhat less than 0.04 cc. p.l. per hour. — 71.3 gr *Acropora hebes* and suspended matter of jar 2 used up about 1 cc. of oxygen p.l. during the experiment. Assuming that the organic matter was about the same in all the jars, the latter may have used up about 0.36 cc. p. l. and the coral may have consumed 0.60 cc. p. l. in 7.5 hours, i.e. for the whole jar $9.3 \times 0.6 = 5.58$ cc. As 73.1 cc. of coral and the organic matter in jar 3 produced in the sun 2.53 cc. p.l. and may have used up about 1 cc. of oxygen p.l. (compare jar 2), the total production of oxygen may have been 3.5 cc. p. l. or for the whole jar somewhat more than 30 cc. in 8 hours. We do not know if the organic matter consisted of algae, other plankton or detritus, but we may safely assume that the production of oxygen by the coral was about 5—6 times larger than the consumption.

On February 23rd I repeated the experiments with filtered sea water, the oxygen content of which amounted to 2.55 p. l. (2.45, 2.51, 2.61, 2.62) at 8 a.m. when the jars were filled. The pieces of coral were cleaned with filtered sea water before being put into the jars. They had again been freshly collected and weighed wet.

<div align="center">TABLE VIII.</div>

Number of jar	Weight of *Acropora hebes* in gr	Kept	Duration of experiment	cc. O_2 per litre		increase in O_2 (cc. p.l.)	temp. at end of experiment
				at beginning	at end		
1	60.85	in the sun	8.a.m.—1.30 p.m.	2.55	3.51(3.50, 3.52)	0.96	29.°8
3	73.85	in the sun	8.a.m.—2.30 p.m.	2.55	4.88(4.87, 4.89)	2.34	30.°9
4	no coral	in the sun	8 a.m. 3.— p.m.	2.55	2 51(2.50, 2.51)	0.04	31.°1
2	60.5	in the dark	8.a.m.—3.20 p.m.	2.55	1.38(1 29, 1.46)	1.17	29.°4

The polyps of the corals were retracted during the experiment. Jars 3 and 4 contained under the cover a small number of air bubbles at the end of the experiment (due to the high temperature?).

These experiments show that the filtered water of jar 4 is practically devoid of organic matter (filtration found place with a piece of fine meshed plankton gauze) and that 60.5 gr *Acropora hebes* consume in 7½ hours 1.17 cc. O_2 p. l., i.e. 0.16 cc. p. l. per hour. Further the total production of oxygen (measured production + consumption) may have been for jar 1 about 8 cc. p. l. in 5½ hours, for jar 3 about 3.4 cc. p. l. in 6½ hours. For the whole jar these values may have been about 16.7 and 31.6 cc. respectively.

If now we reduce all four values for the experiments of 22 and 23 February to p r o d u c t i o n p e r j a r p e r h o u r we get that 83.5 gr *Acropora hebes* produce 5.1 cc. of O_2, 73.1 gr produce 4.1 cc., 73.9 gr produce 4.9 cc., 60.9 gr

produce 3 cc. We can also express that in another way: 100 gr of *Acropora hebes* produce in full sunlight and shallow water 6.1, 5.7, 6.6, 4.9 cc. of oxygen per hour.

C o n s u m p t i o n: The experiments cited above teach us at the same time something about the *consumption* of oxygen by *Acropora hebes* [1]). On February, 22, 1928, 71.3 gr consumed per hour about 0.74 cc.; on February, 23, 60.5 gr consumed in the same time about 1.5 cc. I do not know whether the consumption in the sun may be much more than in the dark, but we can safely assume that in shallow water the production of oxygen by coral zoöxanthellae during the day is about 2.5—5 times as great as the consumption of oxygen through corals and zoöxanthellae together.

If now we return again to the reef itself, we find that these figures are of much interest in connection with the low oxygen pressures found in early morning. 60 gr of *Acropora hebes* consume in one hour about 1.4 cc. of oxygen. So this coral consumes more than 20 cc. of oxygen per kilo and per hour. An ordinary colony of a large *Acropora* weighs from one to several kilos and thus consumes during one tropical night of 12 hours as many times 250 cc. of oxygen as it weighs kilos. According to such a calculation a reef of some thousands of kilos consumes several hundreds of litres oxygen during one night. And as we may say that the water around these reefs contains about 5 litres of oxygen per cubic metre we understand that such a reef is able to deprive about 120 cubic metres of wholly saturated water of all its oxygen. And we should not forget that this reef abounds with thousands of fishes, small and large, and numerous other animals, as well as algae. A kilogram of a small species of fish, McClendon studied, "would use up all of the O_2 in 3600 litres of the sea water of the Gulf stream in 24 hours". "With 1 kg of fish in 300000 litres of warm sea water we should be able to detect a distinct fall in O_2 concentration during the night. In order to attain this effect there need be organisms, the equivalent of 1 kg. of fish, to 10 square meters of bottom in water 30 meters deep". One is indeed inclined to ask whether these reef animals do not suffer from a severe short of oxygen now and then [2]).

The same rise and fall in the oxygen content of the water of tropical reef flats was observed by McClendon (1918), who made his measurements on the Florida Keys. His figures range from 3 to 4.5 cc. per litre about dawn to 4.5 to 7 cc. at 3 p.m.

McClendon (1918, p. 277) remarks that this rise in oxygen content in Tortugas waters is due to "attached seaweed and symbiotic algae and diatoms at the bottom".

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[1]) Fuller details on the oxygen consumption of species of the genus *Acropora* are given in another paper of this series.
[2]) The toxic effect of CO_2 may, however, be independent of asphyxation, and this supposition is strengthened by the fact that with the exception of *Acropora muricata*, all of these corals (i.e. *Orbicella annularis, Porites astraeoides, P. clavaria, P. furcata, Maeandra areolata, Favia fragum, Siderastrea radians*) can survive in the dark for more than 11 hours in sea-water deprived of oxygen under an airpump; and even *Acropora muricata* can withstand 6 hours of this treatment (Mayer, 1918b, p. 175). — From this and other observations [Henze, 1910 (anemones), Krogh, 1916, McClendon, 1917 (*Cassiopea*)] we know that the rate of respiration in such animals is greatly affected by the oxygen content of the water and that therefore the reef will be able to stand low oxygen pressures a long time.

— "On coral reefs the symbiotic algae of corals and actinians are very effective, and in lagoons or other water which is not too agitated the symbiotic algae of the bottom medusa *Cassiopea* are a significant factor. One *Cassiopea xamachana* (11 cm. in diameter, weighing about 117 grams) in the sunlight gave out 1.9 c.c. O_2 per hour, whereas in the dark it absorbed 2.8 c.c. per hour, showing that 4.7 c.c. per hour was produced by the photosynthesis, at 30°. In other words, the O_2 given out in the day is about twothirds the amount used at night". — Though McCLENDON remarks that the symbiotic algae of corals are very effective, measurements of the oxygen production of corals appear not to have been made by him. Observations on the oxygen production of coral zoöxanthellae were, however, made by the late ALFRED G. MAYER who remarks (1918 b, p. 176) : "In these experiments the corals were kept in the dark to prevent photosynthesis in their commensal plantcells, for in sunlight the surrounding water soon becomes supersaturated with oxygen from this cause". As to oxygen production by Alcyonaria CARY (1918, p. 188) remarks: "This aquarium was covered with a black box to exclude the light, as some of the species studied contained within their tissues enough symbiotic algae (zoöxanthellae) to materially influence the results when the experiments were carried on in the diffuse light of the laboratory". As to actinians "the investigations of BRANDT (1883), TRENDELENBURG (1908) (working with *Anemonia sulcata*) and PÜTTER (1911) prove that actinians with zoöxanthellae may derive a large part of their oxygen from these algae, and that actinians with zoöxanthellae can better resist unfavorable circumstances than those which do not harbor unicellular algae" (BOSCHMA, 1925, p. 431).

As to the consumption of oxygen we know, especially from measurements of KROGH and MONTUORI and calculations of McCLENDON the number of cubic centimetres of oxygen, used per hour per kilogram by various groups of animals. CARY has published observations for Alcyonaria and MAYER (1918b, p. 176) for corals. Especially the latter's figures are of much value to us. Whereas a kilogram of living tissue of *Siderastrea radians* consumes about 25 cc. of oxygen per hour, that of *Maeandra areolata* consumes 3.8, of *Favia fragum* 5.5, of *Orbicella annularis* 6.1 and that of *Acropora muricata* 18.7 times as much. Thus *Acropora muricata* consumes per kilo of its living tissue per hour about 500 cc. oxygen. Compared with the figures given for related animals — i.e. *Cassiopea* (26 cc.), Anthozoa (40), Alcyonaria (living tissue only) (14-75) — this figure and doubtless also that for *Acropora hebes* given above is very high, especially if one realizes that we are dealing with sessile animals. Higher, fast moving animals of course do show high figures: cephalopods and crustaceans 200 and more, fishes 200-500 cc. and more (compare the literature cited above). For Alcyonaria CARY has shown that those species which have the greatest surface for a unit of weight $\left\{ \dfrac{cm\ 2}{gr} \right\}$ have by far the highest metabolism; this rule, however, does not hold, when different groups of animals are compared here.

The foregoing observations all tend to show that the quantity of oxygen, present in the water, must often be the limiting factor in reef growth. Of course there are many reefs, lying in more or less strong currents which do not bother about lack of oxygen. MEINDERT's reef, at the northeast point of Java, lying in the dangerous current of Bali Strait (a current of up to 8 miles per hour) has to endure such a strong flow of water that we might call it a typical current reef, many of the corals — especially *Acropora* — not growing upward, but in the direction of the current, bowing as trees before the wind. But when we take, on the other hand, reefs in bays or in the open sea, with only a feeble current, it is quite another thing. For that reason let us consider the influence of currents first.

2. THE IMPORTANCE OF CURRENTS FOR CORAL REEFS.

VAUGHAN (1914, p. 225), to study the influence of darkness on corals, placed 18 species, representing practically all the reef corals of Florida, in a submarine dark chamber and found that after 43 days most of them were very pale, due to the death of the algal symbionts, but in only 5 species did the corals die. More recently EDMONDSON (1928, p. 57—58) made a similar experiment in placing 17 species of Hawaiian corals in a floating dark box. Only 4 species survived the experiment, which had lasted 45 days. "All were more or less injured by the loss of coenenchyma and were very much paler than at the beginning of the experiment". Finally YONGE (1929) made the experiment for the third time and found that "corals, kept for four months in a light tight box on the reef flat showed no ill effects other than those caused by the heavy deposition of sediment which smothered some; the survivors were pale, almost all the algae being dead, but otherwise healthy". From these experiments one might be inclined to believe that the corals in general (i.e. the reefs) are perhaps able to grow without light, so that the latter cannot be the limiting factor as to depth. The point of interest, however, is not only whether it is possible to grow corals in the dark when they get enough oxygen and food, but whether the coral reefs themselves would be able to stand the darkness a sufficiently long time. We must keep in mind that nowhere else than on coral reefs it is possible to find such a dense population in such a small area. The heavy outbursts of plankton in the northern Atlantic in spring are nothing compared with the thousands of cubic metres of reef life in a sea which is filled up to the limits of possibility. The enormous numbers of fishes, which in the North Sea and elsewhere gave rise to such important fisheries, are in no smaller number met with on the coral reefs, where, however, they form only a small part of the total amount of living matter. Whereas in northern seas, through lack of plant life during winter, there is a gradual increase in phosphates and nitrates in the water, until these are used up by the phytoplankton after its outburst in spring, we are dealing here with a never diminishing production of phosphates, ammonium compounds and nitrates. In shutting off the light we would create the conditions occurring at greater depths, where the phosphates and nitrates are continually showing high figures. And so we should not ask whether corals may grow in the dark under artificial conditions, but whether the water on and round the reef is able to remove the waste products of the latter. Therefore we now may see what is known about currents in the Java Sea.

In the years 1914, 1915 and 1916 Mr. K. M. VAN WEEL, then hydrographer at the Laboratorium voor het Onderzoek der Zee at Batavia, and Capt. VAN KOESVELD made a number of current measurements in the Java Sea on six trips in the months of February, May, August and November. These months, under mean conditions, may be said to represent the westmonsoon, spring transition, eastmonsoon and autumn transition respectively. Their observations on direction and velocity of the currents were published in extenso by VAN WEEL (1923). His figures, together with those on salinity, temperature, etc., which for

a good deal had also been worked out by him, formed the basis for a paper on the monsoon currents in the Java Sea by BERLAGE (1927). — BERLAGE finds a very good agreement between the old observations on the monsoon currents, mentioned in the Nautical Guide, and the exact measurements of VAN WEEL and VAN KOESVELD. He compares the Java Sea with a rectangle with two large openings: one in the northern long side between Sumatra and Borneo and one in the eastern short side east and north of Madura. During the east monsoon the water is coming in through the lastnamed opening and flowing away through the northern one, in the westmonsoon the reverse is the case. But moreover the rectangle leaks in its southwestern corner, as the water is flowing out through Sunda Strait the year round. During the westmonsoon the strong wind through Sunda Strait is driving the water of the southwestern Java Sea in an easterly direction, this is only a superficial phenomenon, however. As to the direction of the currents at different depths in one and the same place, it nearly always tends to change clockwise or counterclockwise from surface to bottom; for these and other particulars the reader is referred to the papers in question. — To us the velocities of the currents especially are of much interest. The first point, attracting attention, is that there generally is a decrease in current velocity from surface to bottom. Especially the higher velocities show this phenomenon; the lower ones do not show it, I suppose because the instrument registrates these velocities less exactly [1]). The second point of interest is that the velocities — as may be expected — differ in the different seasons. This is already obvious from a superficial glance at the figures and was known long ago. The Nautical Guide gives the maximum velocities attained during east and west monsoon as 1 and 2 miles per hour respectively.

BERLAGE finds as mean current velocity during the westmonsoon 28, during the east monsoon 17 cm p. sec. To this purpose he has reduced all currents to east and west ones. We ourselves, however, do not need the precise east and west currents, but the currents as such, the directly observed ones, consisting of a mixture of tide and monsoon currents. The first are small but cannot be wholly neglected, as is shown by rather important differences in velocity of neighbouring or even the same places on one and the same day. For that reason I have calculated the means for the totals of the different seasons.

TABLE IX.

Depth in metres	5	15	25		
7 — 26 Febr. 1914	42	34	35	Westmonsoon:	40, 32, 30.
5 — 19 „ 1916	37	29.5	25		
6 — 22 May 1914	29	25	23	Transition spring:	24, 22, 19.
7 — 31 „ 1915	19	19	15.5		
3 — 19 Aug. 1915	32.5	29	27	Eastmonsoon:	33, 29, 27.
6 — 20 Nov. 1915	33	29.5	27	Transition autumn:	33, 30, 27.

[1]) For the same reason the direction of the currents is often not wholly trustworthy.

These figures show us that the lowest mean velocity for the currents in the Java Sea may be about 20 cm per sec. Now, when a current has a velocity of 20 cm per sec., it takes 5 seconds for a cubic metre of water to flow over a m² of bottom. Let us assume that the quantity of coral growing on that m² of bottom is 500—5000 times larger than the quantity of coral used in one of my experiments mentioned above. A rough estimation shows that this often may be the case. As in one of my experiments 60 gr of *Acropora hebes* consumed about 1.4 cc. oxygen per hour, 5000 × 60 gr may consume 5000 × 1.4 cc. per hour, or $\frac{5000 \times 1.4}{720} = 10$ cc. O_2 in 5 sec. If now this cubic metre of water flows along a piece of reef of about 100 m long, the corals would consume about 1000 cc. of its oxygen and the oxygen pressure of the water would sink about 20%, if there existed no diffusion, convection or other manner of intermingling. Whereas the rate of diffusion of oxygen in water is so small that it may be neglected, we possess no means of observing the influence of convection or another type of intermingling, so that we cannot go further into the matter. When, however, a feeble current is flowing over a shallow lying reef, there is probably little reason to assume that convection plays an important rôle and in such a case we are dealing with consumption only, whereas diffusion — as already stated — may be neglected.

The rate of diffusion of oxygen in water may be derived from the following formula:

$$dS = kq \frac{dc}{dx} dt \times 10^3.$$

dS is the quantity of oxygen, moving at the point x in the time dt through the section q under the influence of the difference in concentration; this difference in oxygen in fresh water; at 16°-17°C. it is 1.62, at 22° perhaps 1.64, so I assume that concentration is the change of concentration dc along the distance dx; k is known for at 28° it is about 1.66. — Let us assume that its value for oxygen in sea water is not much different. Let us further assume that the concentration of ogygen falls from 5 cc. to 4 cc. p. l. over a distance of 1 m = 100 cm and let us express dc in cm³ O_2 per cm³ H_2O.

Then the diffusion through 1 cm² amounts to:

$1.66 \times \frac{0.002}{100} = 0.0000332$ cm³ in 24 hours, so that the diffusion per m² per 5 seconds (see above) is about 0.000002 cc.

So it is not impossible that the reef gets short of oxygen already when a current as mentioned before flows along the corals. — In reality, however, when a current of a certain velocity passes a reef, the corals themselves have to depend on water which is flowing much more slowly. Near the coralbottom, along and between the corals, the water meets so much resistance that we will find a basal layer of water there, which moves very slowly only. Where a reef has grown up to little below the surface we may see that the water is flowing scarcely over it, whereas some fifty metres farther, along the edge of the reef, it is flowing rather fast. When I measure a current

velocity of 10 cm p. sec. in the Bay of Batavia not far from Haarlem, I may be sure that the water flows along the corals with a velocity of perhaps 5 cm p. sec. or still less. In that case it takes 20 sec. for one metre of water to pass the corals and the corals on one m² may use up 40 cc. O_2 from that m³ of water. If this water flows again along a piece of reef of 100 m long, 4000 cc. oxygen are consumed. And as this cubic metre contains only about 4700 cc. the corals get short of oxygen in a very short time. It may be easily understood that in this way low oxygen pressures may arise night after night.

3.   SILT MEASUREMENTS.

The foregoing considerations lead us to the supposition that the depth from which a coral reef arises in calm water may often depend, from want for oxygen alone, on the silt quantity of the water. But for other reasons too it is quite probable that the development of coral reefs is influenced, directly or indirectly, by the silt quantity of the water, directly because the corals themselves may need light, indirectly because their zoöxanthellae need it and the corals may need these algae.

So it need not wonder us that the hypothesis has been advanced more than once that the depth of the living reefs is limited by the depth of light penetration. But as far as I know no one has tried to show if there exists a direct relation between the depth of the living reef and the average depth to which the light penetrates the water round about that reef. I already stated above: if we could prove that a high average of silt content (equivalent to reduced penetration of light) corresponds to a small maximum depth of the living reef, and vice versa, this would be a very strong argument in favour of the relation reef and light.

It is now generally recognized that the limit of most active coral growth lies at a depth of about 40 m. Sometimes much greater depths are reached by reef corals, but they probably build rarely reefs there. And where they do so, these reefs must be very uniform in composition, as only some very few species reach these greater depths. So QUELCH in his Reefcoralreport of the Challenger Expedition (p. 35) mentions only 3 species of corals from depths of up to 40 fathoms, which, according to him, are definite reef-builders: *Porites lichen, Montipora capitata, Pocillopora nobilis*; they are the only ones of nearly 300 species of reef-building corals.

CROSSLAND, in a recent publication even expressed his doubt as to the correctness of these statements, because .... on Tahiti he found no corals below 20 metres. One may ask why he did not conclude: the depth of the reef seems to be smaller in Tahiti than in other places. The reason for this is obvious. For whereas his reef reached to about 20 metres, the visibility reached about 12 m deeper; so opacity (silt quantity) of the water could in his judgment not be of influence. At first sight it might really seem, that CROSSLAND was right in his conclusions. If then, however, one reads, that the water was so clear under the best possible conditions only, one may ask: what would be the average depth

from which the bottom would be visible to our eyes? — So we have in the first place to study the variability in the quantity of silt of one and the same place, accompanying stormy and calm periods, at the same time learning the average quantity of silt for the place in question.

The measurements given below (Table X) were all made in the western half of the Bay of Batavia in the neighbourhood of the islands Onrust and Kuiper, Purmerend and Kerkhof, Schiedam, Rotterdam, Hoorn and Haarlem. They were made by using a variety of SECCHI's disc, modified after HEDLEY and UMBGROVE (UMBGROVE p. 4). As stated by HARVEY (p. 156—157) the measurements taken in this manner give a fairly exact idea of the quantity of floating matter (silt and plankton), the depth at which the disc disappears from sight not being affected by the intensity of light on the surface within fairly wide limits. In general the transparency of the water is larger when direct sunlight fails, as the floating particles disperse the light falling on them and largely throw it back; this is especially the case when the silt quantity is important. The difference in depth seeing may then amount to at its most 10%, perhaps even somewhat more. As the method itself is, however, so easy that it makes control measurements possible without much loss of time, the method is quite sufficient for our purpose. It should be remarked here that POOLE & ATKINS (1929, p. 309—310), who compared the readings of SECCHI's disc with those of their photoelectric cells, found that the percentage illumination at the limit of visibility may be said to be about 16% and "further that we may use the SECCHI disc to estimate the opacity of the water without paying attention to even comparatively large variations in the brightness of the daylight."

The figures thus obtained, though they represent the state of affairs during the westmonsoon only, distinctly show

1° that the quantity of silt — as may be expected — is immediately correlated to the depth of the water, so that round about the island Onrust the quantity of silt is always greater than round about the island Haarlem; with increasing depth of the water, however, especially on windy days, the depth increases faster than the visibility;

2° that it takes some time (at least three days) after a stormy or windy period before the large quantity of silt has settled again, so that the average quantity of silt during the monsoons is rather high.

During the transition periods the clearness of the water shows that higher figures for the visibility are to be found than during the monsoons. For that reason the average quantity of suspended matter for the whole year must be smaller than that for the monsoon periods. The mean disc visibility for Onrust may be 4, for Haarlem 8—10 metres; but these figures are still very hypothetical. In my preliminary paper I assumed a mean visibility of at its most 12 m for Haarlem; this figure will be too high, however.

In studying these figures one must well realize that the field of operation is situated close to the mangrove coast and that not only there, but farther from the coast too, the bottom — like that of a great part of the Java Sea — is

Table X.

Data	Weather	Near Onrust, Kuiper, Purmerend, depth 9—12.5 m [1]	Near Schiedam, depth 12—17.5 m	Near Rotterdam, depth 16.5—19.5 m	Near Hoorn, depth 18.5—21 m	Near Haarlem, depth 21—23 m
Jan. 21	Windy	4, 4, 4.				
23		4 5, 4.5, 4				
24		3 5, 3.5, 4	5			
25		3.5, 4.5	7, 8.5, 8	7		8
27	Very fine weather, nearly no wind, ± west.	3.5, 6 5	8, 7, 7, 7, 8	7.5, 8.5	10, 10 5	11.5, 11
Febr. 13	Strong wind, during the night much rain.	2, 1.8, 2.5		5	7, 5	7.5, 8.5
14	Nearly no wind, rain.	1.5, 3, 1.5	3, 3	4		
15	„ „ „ .	1.5, 2.6, 2, 2.2, 2.8,	5.2	6.6		
16	Rain during the night, wind W.	3.3, 2.8, 2.1, 3				
17	Rain, rather strong wind, W.	2, 2.5, 2.5				
18	Windy.	2.3, 3, 3.				
20	Sunny, strong W. wind.				6—7	
21	Sea rather calm. Little wind, W.	4, 5,		6.5	6	
22	Nearly no wind. Sea like a lake.	3.5, 5, 4.5, 4.	7, 6	7.5, 7	8	8, 10
23	Nice weather, no wind.	4.4, 4.3, 3 8, 4.3.	9.5, 9	8.8		
24	As 23	6.5, 6.3, 7 5, 5, 5.5,	11, 8	9.5		
March 9		1.6, 1.5, 1.5, 1.7,	1.8,	2.5	3	4
23		4	4.5	8.5	12.8	9
April 30		4.6		6.6	8	
May 9		8.6		7.6		
June 12					11	
13		6.6			12	
15		6.4		8.6		13.6
	median values =	3.7	6.7	7.—	8.3	9.1

[1] All depths are given as measured on the days in question, without taking into account the water level.
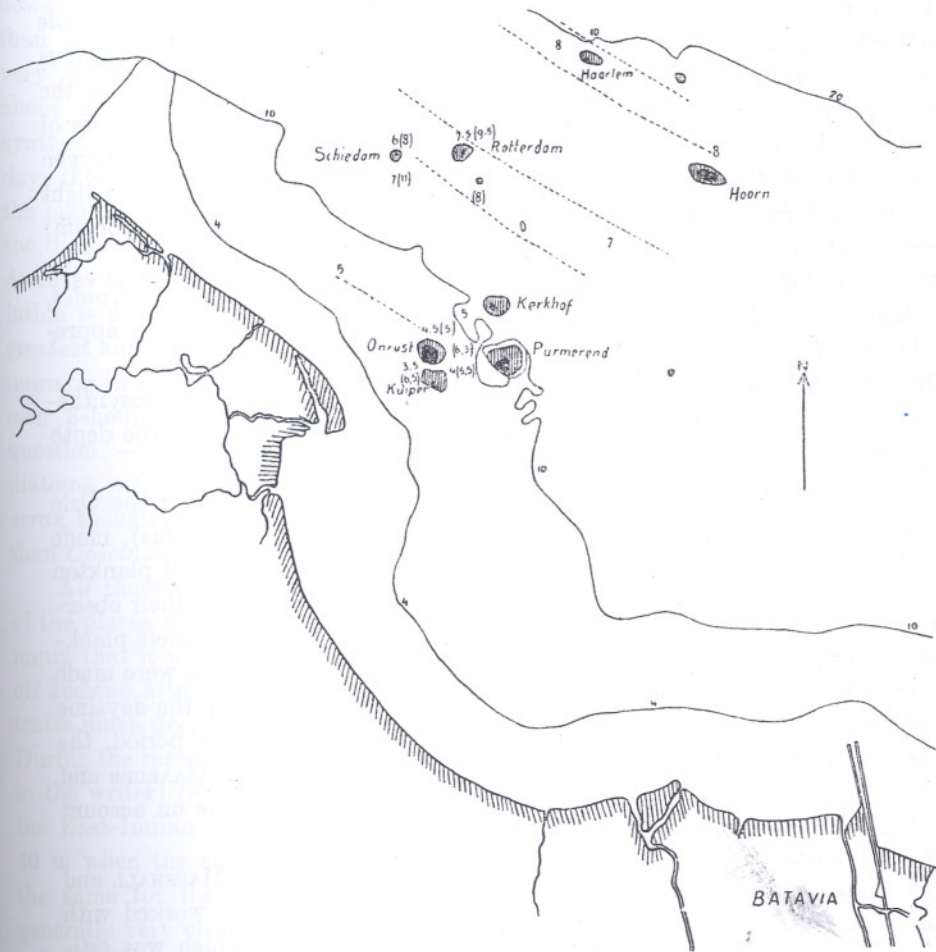
Fig. 1. Map of western half of Bay of Batavia, showing the lines of equal silt quantity running parallel with the coast. The figures represent the depths at which Secchi's disc disappeared to the eye on 22 and (between brackets) on 24 February 1929.

covered with silt. This silt is stirred up by the influence of the waves and so brought into suspension when the wind grows strong enough, sooner or later, according to the depth. A moderate storm is able to stir the water up to a depth of 50 metres and more. "In the open Atlantic ripple marks have been found at a depth of 200 meters, but in the English Channel they occur only down to a depth of 40 meters, and to depths of 50 meters in the Roman mediterranean. Off the Florida coast, too, Agassiz has noted disturbances to a depth of 200 meters" (Grabau, 1924, p. 218—219). One can understand that it is not possible for this silt to sink down again in one single day.

The accompanying map shows that the lines of equal disc visibility (i.e. silt quantity) run parallel with the coast.

4. Depth of Light influence.

The penetration of light into the water can be studied by a very simple method, viz., by hanging jars filled with water with algae in the sea at various depths. Where light penetrates photosynthesis causes production of oxygen; in the dark this production does not occur. At the same time respiration causes loss of oxygen in the light as well as in the dark. In the light the production of oxygen exceeds by far the loss, in the dark we have loss only. Between dark and light there is a point where assimilation and dissimilation are showing equilibrium: the compensation point of Gaarder, Gran, Marshall, Orr.

Jönsson (1903), in the Olso Fjord, using the moss *Climacium dendroides*, found that photosynthesis fell off rapidly from the surface, and was not appreciable below 17—27 metres [1]).

Gail, working in Puget Sound, found the lower limit at which photosynthesis takes place by red or brown algae to be about 35 metres and that the depth of maximum photosynthesis differs much in different species.

Gaarder and Gran, studying the production of phytoplankton in the Oslo Fjord (mixed animal and phyto plankton, mainly consisting of diatoms), made among others observations on the connection between the production of plankton and the variations in the oxygen content of the water. It follows from their observations that in the second half of March the compensation point of their plankton was to be found at a depth of about 10 m. As their measurements were made over a three day period, so that assimilation produced oxygen during the daytime only, whereas respiration [1]) caused oxygen loss during the whole period, the compensation point for the day may have been lying a little deeper. Gaarder and Gran state that during the experiment the water was rather opaque on account of the density of diatom plankton.

By far the most valuable work on the subject is that of miss Marshall and Orr of the Scottish Marine Biological Station at Millport. They worked with cultures of the diatom *Coscinosira polychorda*, the density of which was estimated for each experiment, so that the authors could express their results as the amount of oxygen produced by a million diatoms. As far as possible cultures of about the same age and cell contents were used in their experiments and the experiments were preferably carried out while the sea was free from diatoms. Their valuable investigations therefore represent a unique piece of standardized work. — The principal results of their studies are the following. In inshore water the compensation point for a pure culture of *Coscinosira polychorda* (when measured over 24 hours) may lie at a depth of 10—20 m in March or 20—30 m

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[1])   „Early experimental work on the effect of light at different depths was carried out at Monaco by Regnard (1891), who germinated seeds of cress and radish at different depths, and found that little chlorophyll was formed at 30 metres" (Marshall and Orr, 1928, see also Atkins, 1926, p. 103-104).

[2])   The term "respiration" is used here and furtheron to denote the consumption of oxygen. Gaarder and Gran have shown, however, "that the auto-oxydation of dissolved and suspended organic matter, and the bacterial oxydation are very important factors in relation to the respiration of the phytoplankton". See also Föyn & Gran.

in summer when the water is clear. When the sea is rich in diatoms, however, the compensation point may lie much higher, even little (less than 5 m) below the surface on a dull day in March [1]. And on a very foggy winter day the compensation point was found to lie at about 2 m, the least depth which was found. — Observations on photosynthesis during three hour periods at different depths showed that on bright days there is a fall in the oxygen production of diatoms near the surface during the middle of the day, this fall being most marked (indeed quite important) for the diatoms at the surface. Even at six metres depth the diatoms show a slight decrease in assimilation during the middle of the day. This decrease in assimilation is due to the injury caused to the diatoms by the strong light. Thus the greatest amount of photosynthesis at or near the surface takes place in the early morning in sunny water. — For further observations, giving the photosynthesis over 3-hour periods on days of different brightness, I refer to the paper in question. — Miss Marshall and Orr also compared two different species of diatoms, a *Chaetoceras* and *Coscinosira*. This comparison showed that *Chaetoceras*, though a summer form in Scotland, appeared much more sensitive to light than *Coscinosira*, a spring form.

All these observations tend to show that the compensation point at none of the places in question reaches a depth of more than 30 metres. This does not imply that it never reaches a greater depth. Already the fact, that brown algae off Iceland after Gran reach a depth of about 50 m, shows that the light penetrates much deeper there; but such a case will probably remain an exception [2]. During the recent expedition of the Willebrord Snellius (personal communication to the writer) Secchi's disc disappeared at about 30 m in several deep seas of the East-Indian Archipelago in turbid water, whereas it disappeared at about 40 m when the surface was smooth [3]. Marshall and Orr recently remarked the same for the northern coast of Australia: "Beyond the Barrier water is generally very clear and the Secchi disc reading may be as high as 40 m" (1931, p. 123). This shows that the compensation point may have reached a depth of 50—60 m at these places (see below). But such a deep lying compensation point is just found over these large depths only.

My own researches intended to make out how far the influence of light would reach under the different conditions caused by the silt contents as given above. So I made my measurements on the oxygen production of algae together with comparative readings of the white disc. I too used the method of hanging

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[1] Fuller details on the influence of dense diatom plankton on the penetration of light in the water are given by Marshall and Orr 1930, p. 865-866; Poole and Atkins (1929) found evidence of a decrease in the intensity of illumination due to the zooplankton.

[2] In the Mediterranean according to Walther the red algae reach a depth of 130-160 m, but it is practically certain "that the red algae can and do utilise light at the blue end of the spectrum, since they live at depths to which little but blue light penetrates" (Harvey, p. 17).

[3] The disc was observed from 3-3.5 m above the water surface. In my own observations when necessary a sea glass was used to take away the rippling of the water surface, so that the latter little influenced the results.

jars with sea water and algae at different depths in the water. For technical reasons I preferred to use the largest possibly jars, i.e. of about 9.3 litres. They can contain a larger quantity of algae and make control measurements possible twice, when the results seem doubtful. The oxygen quantity was measured after WINKLER, but at the advice of Ir. MARKUS I did not use the ordinary oxygen jars, but the oxygen pipet with two cocks after ROMIJN. As may be wellknown and is shown moreover by the series of measurements given in table IV this pipet gives exact duplo-figures, if one takes care that each time the same quantity of $Mn(OH)_2$ gets lost. It took a long time, however, before I sufficiently realized that rather important differences in the duplo-measurements may be caused by small differences in the amounts of lost $Mn(OH)_2$ and for that reason several of the duplo-measurements in the beginning gave bad figures.

GAARDER and GRAN worked with mixed phyto and animal plankton (principally diatoms), miss MARSHALL and ORR with diatom cultures. In connection with the problem under consideration I concluded that for my purpose it would be best to study bottom algae, as the latter, together with the zoöxanthellae of the corals, are of importance for coral reefs. I collected these algae from the wall or from the bottom of the tanks of the Onrust Aquarium and weighed them wet, i.e. after having spread them out on a piece of gauze for a short time. This weighing of wet matter had of course the disadvantage that the portions were not exactly alike and for that reason it was a fault that I did not weigh all algae dry after the experiment was over. I did so the second time and one will see that the greatest deviation from the median value amounted to 13% of the latter, whereas the greatest difference between the lowest and highest value amounted to 25% of the lowest value. These figures are high. — The algae used during the first experiment consisted probably of a species of *Bryopsis*, probably with a very rich growth of diatoms and a number of protozoans. Those used in the second experiment consisted of a species of *Cladophora*, nearly without any growth of foreign organisms.

The jars had a height of 0.75 m, hung vertically and the algae covered their bottom. Thus the light partly had to pass the thick cover, partly the jars themselves. The depths to which the jars were lowered were measured from the surface of the water to the bottom of the jar.

The jars hung down from long bamboos which had been fastened crosswise to the small rowing boat of our Laboratory. The bamboos projected about 3 m to the left and right of the boat. It was believed that through this procedure the shadow of the boat could never fall on the jars. Afterwards I have tried to prove this by a small calculation, bringing into account the declination of the sun during the days of the experiments (11°—13° S. for the first and 7°—10° N. for the second series), the declination of Batavia (6° S.) and the breaking at the water surface. In doing this I came to the conclusion that it may have been possible that the lowest jar in the second series of experiments has fallen within the shadow of the boat for a short time about noon. This cannot therefore have influenced the results to any practical degree. Moreover,

it is doubtful if the shutting off of the direct light would be of any influence at a depth of **18 m**, where all light perhaps may be said to be indirect.

I preferred to use sea water with a low initial oxygen content, as the oxygen increase could be considerable then before supersaturation occurred. I therefore always used water from one of the tanks of the Onrust Aquarium, which has a low oxygen tension in the early morning. As this measuring of the oxygen content, filling and closing the jars and their transportation took a long time (1—3 hours), the initial oxygen content as given below is always somewhat too high (the jars were kept in the dark all the while), so that the real production of oxygen has always been somewhat greater than that given by the figures. As may be seen from the figures given below the respiration amounted to about 0.06—0.07 cc. p. l. per hour in the first and about 0.05—0.06 cc. p. l. per hour in the second series of experiments. As the time in question was different in the different experiments, but the same for each jar, I add the figures for the possible amount of respiration during transport, etc. under each experiment. As I observed before GAARDER & GRAN, as well as miss MARSHALL and ORR measure the production and consumption of oxygen per 24 hours, so that the algae consume during a longer time than their production of oxygen lasts, for during the night production stops and consumption goes on. For that reason the compensation point (i.e. the point of equilibrium between consumption and production) is different from that found when one works during the day only. In connection with our problem it is of greater importance to know the compensation point during daylight, as the oxygen made during the day is of little or no use during the night. It goes without saying that, though the difference between the depths of these two compensation points is not important, the compensation point in my experiments must lie a little deeper than the one of GAARDER, GRAN, etc.

One will see that I give the hours of sunshine in percent of the maximal quantity. I owe these figures, as well as those for solar radiation, to the kindness of the staff of the Meteorological Observatory at Weltevreden. The figures for 1929 were recorded (automatically) at Batavia, those for 1930 at the island Kuiper in the Bay of Batavia itself. Whereas the latter figures give the exact data for the place of the experiments, the figures for 1929 may differ from the real values for the Bay. They agree, however, in that there was a more or less covered sky at both places during the experiments of 1929. The figures for solar radiation give the total quantity of d i f f u s e radiation expressed in calories per cm². I also add the diagram for diffuse radiation for one of the days in question.

Production of oxygen in the light at different depths.

First series. Algae: probably *Bryopsis*, with a rich growth of diatoms, and a number of protozoans, wet weight of each portion 2.9 gr.

17 February, 1929.

Between Onrust and Purmerend. Depth of water 10 m. Experiment from

10.45 a.m.—2.45 p.m. Initial oxygen content measured as about 1 cc. (0.81 and 1.20) p. l., but probably higher [1]).

Oxygen consumption before beginning of experiment 0.2 cc. p. l. Sunshine 76% of maximal value, total diffuse radiation 253 cal. per cm^2 (figures for Batavia).

Number of jar	Depth of jar (in m)	Oxygen in cc. p. l.	Increase in oxygen in cc. p. l.	Visibility of Secchi disc.
5	0.75	4.67 (4.66, 4.68)	3.7	
1	3.75	4.4? (4.24, 4.57)	3.4 ?	3 m
2	5.75	3.90 (3.89, 3.90)	2.9	
4	8.75	3.05 (2.95, 3.15)	2.1 [1])	

18 February, 1929.

Between Onrust and Purmerend. Depth of water 10 m. Experiment from 9.— a.m.—2.15 p.m. Initial oxygen content of the water about 2.97 cc. p. l. (2.87, 3.07).

Oxygen consumption before beginning of experiment 0.14 cc. p. l. Little sun, sky covered, now and then cloudless, sunshine at Batavia 76% of maximal quantity, total diffuse radiation 240 cal. per cm^2 there. Sea far from smooth.

2	3.75	4.34 (4.30, 4.37)	1.37	
1	5.75	4.60 (4.57, 4.62)	1.63	3 m
5	8.75	3.22 (3.20, 3.23)	0.25	

20 February, 1929.

East of Hoorn. Depth of water 20 m. Experiment from 8.15 a.m.—12.15 p.m. (12.15—12.45). Initial oxygen content 3.28 (3.26, 3.30). Oxygen consumption before beginning of experiment 0.16 cc. p. l. Windy, sky now and then clouded, sunshine at Batavia 86%, total diffuse radiation 168 cal. per cm^2 there [2]). Sea turbid.

1	9.75	3.84 (3.82, 3.85)	0.56	
2	12.75	3.47 (3.43, 3.51)	0.19	
4	15.75	3.14 (3.12, 3.16)	— 0.14	6 m
5	18.75	2.86 (2.82, 2.90)	— 0.42	

Consumption of oxygen of these algae in the dark.
14 February, 1929 (jar 1).

Time	Oxygen in cc. p. l.	Consumption.
8.45 a.m.	4.36 (4.31, 4.42)	Consumption in 8.25 hours 0.6 cc.
4.30 p.m.	3.76 (3.74, 3.78)	p. l.; content of jar 9.3 l.; total consumption per hour 0.68 cc.

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[1]) In my preliminary paper on this subject I neglected these results because I did not take care that the water, when I filled the jars by means of a siphon, took up no oxygen. I give these observations therefore for what they are worth, especially for completeness sake.

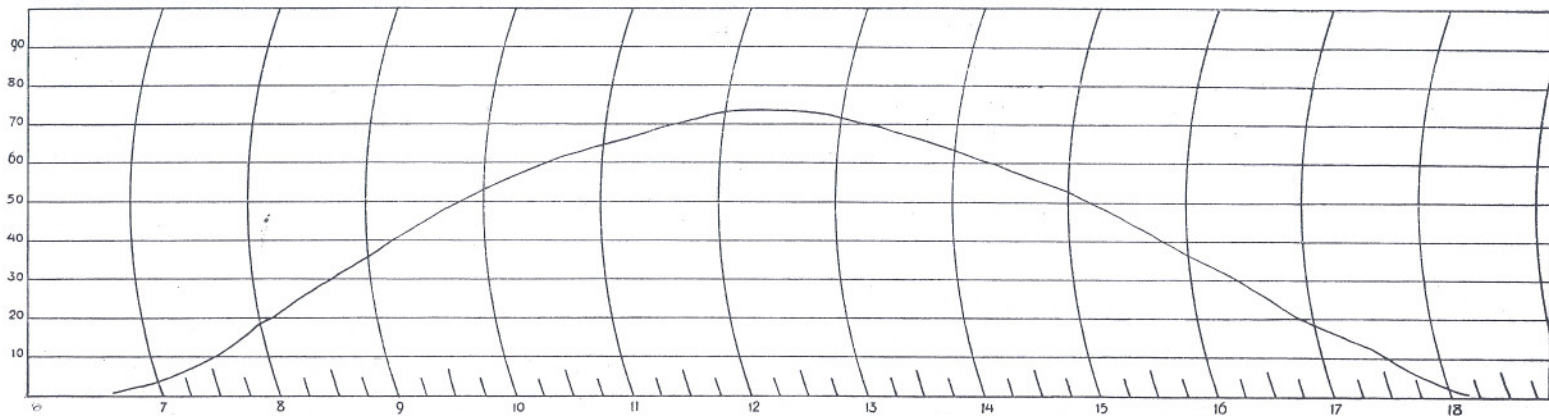[2]) The number of calories is small here because the experiment began and finished early.

Fig. 2. Quantity of sunshine as measured by solarimetre of Meteorological Observatory, Batavia, at 29 August 1930. The quantity can be expressed in calories per cm² by the use of the formula: (Sum of readings: number of readings) × time in minutes × 0,0187. The diagram represents the state of affairs for a bright tropical day with a cloudless sky.

15 February, 1929 (jar 1).

7.— a.m.	3.33 (3.32, 3.34) ⎱	Consumption in 7 hours 0.48 cc.
2.— p.m.	2.85 (2.82, 2.89) ⎰	p. l.; total consumption per hour 0.64 cc.

Production of oxygen in the light at different depths.

Second series: Algae: a species of *Cladophora*, wet weight of each portion 4 gr, dry weight after the experiments had finished: 0.570, 0.655, 0.695, 0.716 gr (jar I: 0.655, II: 0.570, III: 0.716, IV: 0.695).

29 August 1930.

Between Hoorn and Haarlem. Depth of water 21 m. Experiment from 8.30 a.m.—1.30 p.m. Initial oxygen content 2.77 (2.75, 2.79) cc. p. l. Oxygen consumption before beginning of experiment 0.15 cc. p. l. Sunshine at Kuiper 100%. Total diffuse radiation 368 cal. per cm² there.

Number of jar	Depth of jar (in m)	Oxygen in cc. p.l.	Increase in oxygen in cc. p.l.	Visibility of disc
1	3.—	6.90 (6.89, 6.90)	4.13	
2	8.—	5.80 (5.78, 5.81)	3.03 [1])	8.30: 6.60 m
3	13.—	4.20 (4.16, 4.24)	1.43	1.30: 8.— m
4	18.—	3.29 (3.27, 3.30)	0.52	

3 September 1930.

N.W. of Haarlem. Depth of water 22 m. Experiment from 8.40—12.45 (jar I from 8.20—12.45). Initial oxygen content 3.46 (3.38, 3.53) cc. p. l. Oxygen consumption before beginning of experiment 0.15 cc. p. l. Sunshine at Kuiper 100%. Total diffuse radiation 289 cal. per cm² there.

4	3.—	7.27 (7.22, 7.32)	3.81	
3	8.—	5.73 (5.71, 5.74)	2.27 [1])	8.15 a.m. and 12.45 p.m.: 11 m
2	13.—	5.03 (4.96, 5.10)	1.57	
1	18.—	4.42 (4.41, 4.42)	0.96	

4 September 1930.

Between Onrust and Purmerend. Depth of water 11.5 m. Experiment from 7.15 to 11.15. Initial oxygen content 3.34 (3.30, 3.38) cc. p. l. Oxygen consumption before beginning of experiment 0.06 cc. p. l. Sunshine at Kuiper 98%. Total diffuse radiation 178 cal. per cm² there.

3	3	6.03 (6.02, 6.04)	2.69	7.15 a.m.: 7.3 m
2	6	5.32 (5.26, 5.37)	1.98	11.15 a.m.: 4.— m
1	9	4.22 (4.21, 4.22)	0.78	

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[1]) It is a remarkable fact that on both days jar 2 produced more oxygen at a certain depth than jar 3, though it contained the smallest quantity of algae.

Oxygen consumption in the dark.

The oxygen consumption of the algae of the second series of experiments gave the following figures:

4 September 1930.

jar 3: 1.50 p.m.   5.75 (5.74, 5.76)   } Consumption in 2 hours 0.12 cc. p. l.;
       3.50 p.m.   5.63 (5.61, 5.65)   } total consumption per hour 0.56 cc.

jar 2: 1.50 p.m.   5.75 (5.74, 5.76)   } Consumption in 3.5 hours 0.19 cc. p. l.;
       5.15 p.m.   5.56 (5.54, 5.57)   } total consumption per hour 0.50 cc.

When I gave my preliminary paper on this subject after the oxygen measurements of February, 1929, had been made, I had not yet seen the fine paper of miss MARSHALL and ORR and for that reason did not sufficiently realize how gross my method of working had been. The hours of sunshine had not been recorded, the algae were very "unpure" (probably a mixture of *Bryopsis*, diatoms and a rich vegetation of protozoans) and moreover I made the mistake of rounding off my figures, without there being any obvious reason for it. Finally my end conclusion, that the compensation point would lie about 7—8 m deeper than the limit point of disc visibility, was based on two observations only. It is therefore little astonishing that the few results of the second series of experiments were different from those of the former. For in comparing the results of both series the data at hand first of all tell us:

1. that there was less sunshine in 1929 than in 1930;
2. that there was more wind, therefore more turbid water and more silt in 1929 than in 1930, so that there was more reflection of light at the surface and more dispersal of light by the matter in suspension.

The data further teach us:

1. that the algae used in 1929 contained more non-assimilating products (animal organisms, possibly detritus) than those of 1930, so that their oxygen production in relation to their consumption must have been somewhat smaller;
2. that the absolute consumption of oxygen of the 1929 algae was somewhat higher than that of the 1930 algae though the latter weighed more (the algae of 1929 were of another species, they were unpure and contained protozoans, which use more oxygen than plants).

But finally there is a very bad source of errors: the portions of algae were weighed wet and it was shown later (see above) that the weight of the different portions was not the same. Moreover miss MARSHALL and ORR have called attention to the fact that young cultures of *Coscinosira* produce more oxygen than old ones and here we do not know anything about the age of the algae in question [1]).

For all these reasons it is evident that the value of my figures becomes greatly restricted. Nevertheless the compensation point may be found to lie at the following depths.

[1]) See foot note on page 192.

	Neighbourhood of Hoorn and Haarlem (depth of sea 20—22 m)		Neighbourhood of Onrust (depth 10 — 11.5 m)	
	Limit point of disc visibility	Compensation point	Limit point of disc visibility	Compensation point
1929, February 18 th.			*3*	9.5 — 10.5
20 th.	*6*	14.5		
1930, August 29 th.	first 6, later *8*	19 — 20.5		
September 3 rd.	*11*	20 — 25.5	first 7.3, later *4*	10 — 12
4 th.				

Putting it in another way we find the following:

Disc visibility	Compensation point
3 m	9.5 — 10.5 m
4 „	10 — 12 „
6 „	14.5
8 „	19 — 20.5 „
11 „	20 — 25.5 „

It follows from these figures, when they are compared with those of table X, that in clear water the compensation point in the Bay of Batavia may lie near the bottom. It may then even lie a little *below* the bottom, i.e. there is production of oxygen at the bottom then. On the other hand it lies much higher when the water is opaque and as this is the rule during many days (even weeks) especially in the westmonsoon [1]) we may be sure that the mean value for the depth of the compensation point lies several metres above the bottom. It goes without saying that a larger number of observations is necessary if we wish to get more exact figures; these few observations, however, may suffice for the moment.

I refrain from comparing these few results with the ones already existing, especially with the valuable figures of miss Marshall and Orr. But we see that even in the tropics, so close to the equator, and even in a coral reef region, we need not always have the blue clear water one dreams of in thinking about reef formation. Marshall and Orr (1931, p. 123) already called attention to the same fact in relation to the lagoon inside the Australian Barrier reef.

I should like to emphasize once more that my supposition, the compensation point is to be found 7—8 m below the limit point for disc visibility, is wrong. The question is of great interest in connection with ecological studies and the work should be completed through exact photoelectric measurements.

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[1]) It follows from the experiment of February, 20, 1929, that at 18.75 m depth there was a consumption of oxygen of 0.42 cc. p. l. in 7 hours; that means that the total consumption per hour amounted to 0.60 cc. And as flask 1 consumed per hour 0.68 and 0.64 cc. there was at 18.75 m no oxygen production at all, i.e. no light.

5. DEPTH OF THE LIVING REEF.

The only question which remains to be studied concerns the depth of the living reef.

The method of working was very simple. Using the diving helmet I went down the slope of the reef at the northern side of the island (where the reef descends deepest) and having reached the limit of coral growth at the margin of the layer of limy mud I veered out my rope (divided into metres) and bamboo until the bamboo had reached the surface. In this way the depth between surface and lowest corals could be accurately measured. The measurements were reduced to low spring tide and rounded off to half metres. These observations, made in August, 1930, gave the following results.

Island	Depth of living reef in m	Depth of sea in m
Onrust	7 — 7.5	9 — 10
Kerkhof	8	10 — 12
Rotterdam	10	14 — 16
Hoorn	12	16 — 20
Haarlem	15	20 — 22

I must add at once that at all these reefs some few species of corals only reach these depths and that most species do not reach below 5—8 m; I hope to deal with this question in a following paper, however.

A glance at the figures shows that the living parts of the reefs descend deeper, as we go farther away from the coast, but that the depth of the sea increases faster than the reef depth, so that the difference between the depth of the living part of the reef and the depth of the surrounding sea increases away from the coast. At Kerkhof the sea is about 3, at Haarlem about 7 m deeper than the living reef. This in itself is a quite interesting problem, for one may ask how these reefs developed from the bottom. As I hope to treat this question in a following paper, however, we may for the moment pass on to our conclusions.

FINAL CONCLUSIONS.

We have seen that the oxygen consumption of a coral reef is very great, not to say enormous. Currents are therefore of vital importance to the development of reefs. Where they fail, the reef may be greatly hampered by lack of oxygen from this cause alone. For such a reef light may be assumed to be a limiting factor as to depth. But it is quite probable that for several other reasons too a coral reef needs a large amount of light. We therefore have tried to show whether there would perhaps exist a direct relation between the depth of the living reef and the average depth of light penetration round about that reef. The existence of such a correlation would be a very strong argument in favour of the relation between reef depth and light influence.

We have shown that the silt quantity greatly influences the light pene-
tration as measured by the oxygen production of algae at different depths and
that the light for that reason penetrates much deeper near Hoorn and Haarlem
than near Onrust, where the silt quantity is so very great. When dealing with
the visibility of SECCHI's disc we have seen that the depth of the sea, in going
away from the coast, increases faster than the disc visibility. In precisely the
same way we have found that the depth of the sea, in going away from the
coast, increases faster than the depth of the living reef. This shows that there
exists a neat correlation between the silt quantity and the reef depth. And as
the silt quantity is a measure for the (reduced) penetration of light, there is a
neat correlation between light penetration and reef depth.

One could object that not the light, but the silt itself, is of prime importance
here, and that the Onrust corals are killed by the large quantities of silt below
7 m, whereas those at Haarlem are killed by the silt below 15 m only [1]). This
cannot be the case, however. I have pointed out in my former paper (1930, p. 309
—310 and p. 353) that the quantity of silt on one and the same reef decreases
with increasing depth of the water, because this quantity greatly depends on
wave action. And that several clear water forms, which at Haarlem live near the
surface, at Hoorn live in deeper water only. For that reason the influence of
falling silt is more bad at smaller than at greater depth and the fact remains
that there is a neat correlation between light penetration and reef depth. As
stated before this means a very strong argument in favour of the dependence of
coral reefs on light.

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[1]) It was WOOD-JONES (1912) who assumed sedimentation of silt to be the limit-
ing factor as to reef depth. He believed that at greater depths the currents are not
capable of carrying sediment in suspension and that therefore the corals there are
subjected to a constant raising of it.