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# LIGHT PENETRATION IN THE WESTERN NORTH ATLANTIC AND ITS APPLICATION TO BIOLOGICAL PROBLEMS.

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DURING the past five years measurements have been undertaken of the penetration of daylight into the sea in both coastal and oceanic areas of the Western North Atlantic. The purpose of this investigation was to obtain an accurate description of the conditions of illumination at various depths beneath the surface in representative localities. This information was sought on one hand as essential to the study of the factors controlling the diurnal vertical migration of plankton. Furthermore, a far-reaching significance must be attached to a knowledge of the amount and nature of the radiant energy beneath the sea's surface in relation to the photosynthesis of diatoms — the ultimate producers of the sea. Finally, the degree to which light penetrates is of interest as determining to what extent vision is possible for fish below the surface zone as they go about their daily business.

## Methods.

All our observations have been made at sea either from the research vessel "Atlantis" — in off-shore localities — or from the power boat "Asterias" — in the Woods Hole region. The photoelectric method of measurement developed by Poole and Atkins has been employed exclusively until recently when a pair of rectifier cells of the "Photox" type produced by the Westinghouse Electric and Manufacturing Company has been employed. The arrangement of the photoelectric cells in water-tight cases and the carefully insulated potentiometer have been completely described by Gall and Atkins (1931). The Photox cells are used with a microammeter of full-scale reading of 25 microamperes with suitable shunts for the higher intensities and a diaphragm to reduce the size of the receiving window in strong daylight. The characteristics and the standardization of the Photox photometer have been reported by Powell and Clarke (1936).

The photoelectric photometers have proved very satisfactory especially under conditions of steady illumination. Their high sensitivity makes them particularly valuable for exploring the limits of measurable light in deep water. The Photox photometers are more convenient because of their small size and the simplicity of the equipment which is used with them. These photometers are particularly useful for work in situations where the light varies rapidly and a measurement of the average illumination is desired. With the potentiometer method reliable measurements in the upper strata in rough weather are often impossible, but the needle of the microammeter employed with the Photox photometers is so highly damped that it tends to remain at a reading equal to the average value of the fluctuating illumination. Altho less sensitive than photoelectric cells without filters, the Photox photometers, which are sensitive chiefly to the green, were found to respond to practically as weak light as could be measured by the photoelectric photometer when limited by filters to the green part of the spectrum. Table I summarizes the characteristics of the various photometers employed (See also Clarke, 1933 a; Clarke and Oster, 1934; and Oster and Clarke, 1935).

## Comparative Transparency of Different Types of Atlantic Water.

The measurements of light penetration which have been undertaken in areas of the North Atlantic ranging from mid-ocean to Continental Shelf and in-shore waters reveal a profound variation in transparency. The extremes of this variation are illustrated in Fig. 1 in which the transparencies of four types of water to the blue component of daylight are compared. Taking the depth at which the light is reduced to 1 % of its surface value as a convenient method for visualizing differences in transparency, it is seen that in Woods Hole Harbor such a reduction is found at a depth of only 8 m. while in the Sargasso Sea the 1 % value is not encountered until a depth of 149 m. is reached. The water of the deep basin of the Gulf of Maine is intermediate with a depth of 32 m. for a reduction to 1 %. A transparency similar to that

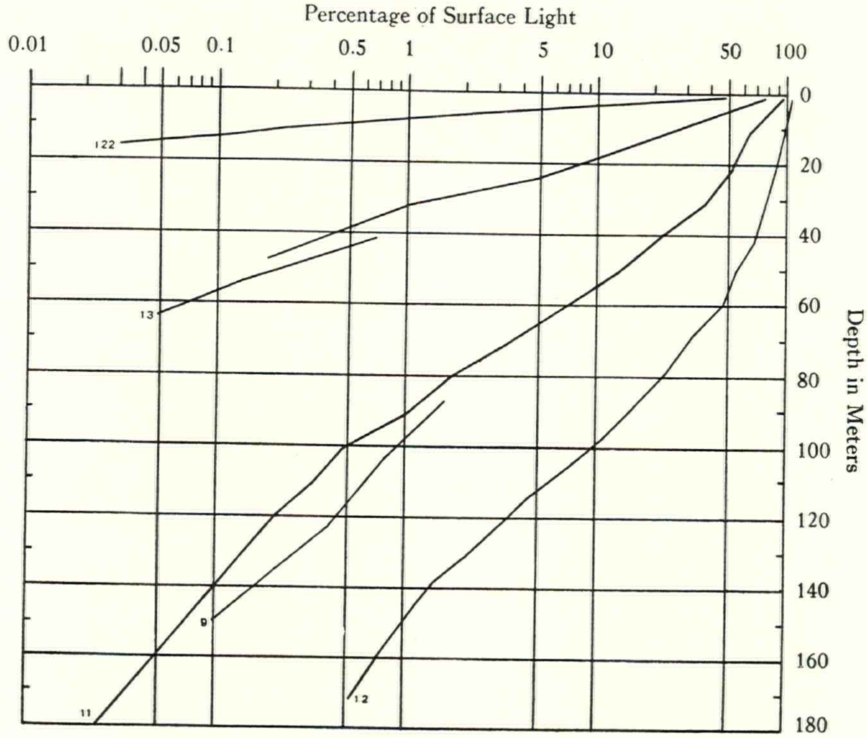


Fig. 1. Comparison of transparencies of four areas in the North Atlantic to the "blue" component of daylight.

Series 9 — near Azore Islands.
„ 11 and 12 — Sargasso Sea.
„ 13 — Gulf of Maine.
„ 122 — Woods Hole Harbor.

## Table I.

### Characteristics of Photometers Employed.

| Maximum Spectral Sensitivity. | Range of Sentitivity. | Type of Cell. | Filters Used. | Irradiation within range of sensitivity necessary to produce current of 1 μa. |
|---|---|---|---|---|
| | | Photoelectric Cells[1]) | | |
| "Blue" | 3460—5260 A° | Potassium (sensitized) | None | 135—315 μw/cm² |
| "Blue" | 3460—5260 A° | Potassium (Gas-filled and sensitized) | None | 63 |
| "Violet" | 3100—4500 | Potassium (unsensitized) | None | 181 |
| "Red" | 6000—7000 | Caesium | Schott-Jena RG—1 and $CuCl_2$ solution | 1340 |
| "Green" | 4900—6200 | Caesium | Schott-Jena BG—18 and GG—11 | 1885 |
| | | Rectifier Cells[1]) | | |
| "Green" | 4650—6250 | Copper-oxide (Photox) | None | 7 |

[1]) The minimum current which can be measured by the potentiometer used with the photo-electric cells is 0.001 to 0.005 μa depending upon the dark current. The minimum current which can be measured using the microammeter employed with the Photox cells is about 1 μa.

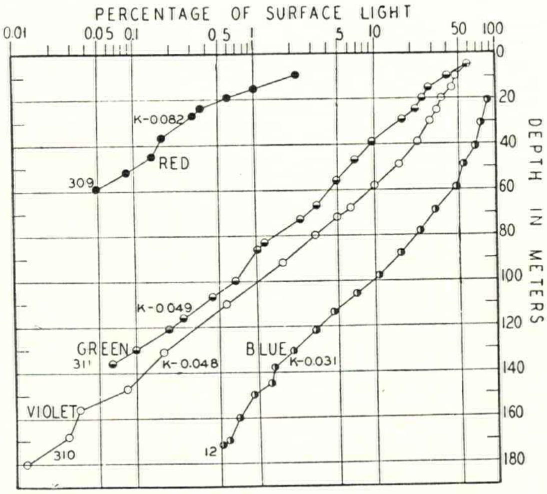


Fig. 2. Penetration of daylight in Sargasso Sea and Gulf Stream.

Series 309 — Station 2243.
„ 310 and 311 — Station 2245.
„ 12 — Station 1041.

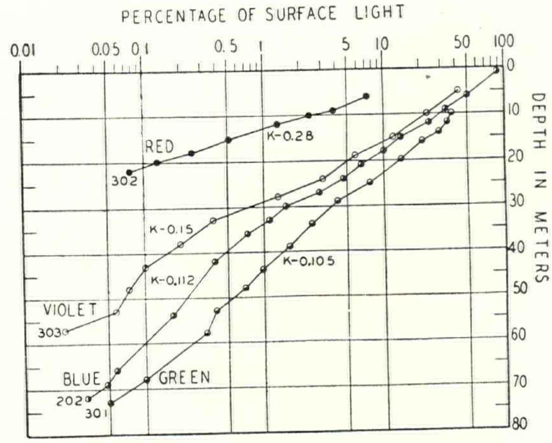


Fig. 3. Penetration of daylight in deep basin of Gulf of Maine.

Series 301, 302, and 303 — Station 2237.
„ 202 — Station 1722.

of the Gulf of Maine typifies mid-Atlantic water in latitude 52° N., but from this point south the transparency was found to increase rapidly (Clarke, 1933 a).

Not only do the coastal and oceanic areas investigated vary profoundly in general clearness but also they differ in their relative transparency to different parts of the spectrum. A comparison of the penetration of the red, green, blue, and violet components of daylight into three representative types of water, may be made from Figs. 2, 3, and 4 which show the conditions in the Sargasso Sea and Gulf Stream, in the deep basin of the Gulf of Maine, and in Vineyard Sound and Woods Hole Harbor respectively.

The water in the Sargasso Sea and Gulf Stream was found to be more transparent than any other region in the world where observations have been made (with the possible exception of the Mediterranean where Grein (1913—14) obtained certain high but doubtful values). In fact, the clearness of the water is so great in this part of the ocean that the values of the transmissive exponent, *k*, approach — and in one case surpass (cf. Clarke, 1933 a) — those for distilled water as determined by Sawyer (1934). In this type of water blue light penetrates best, green and violet are about equal, and the red component is most rapidly absorbed.

A measurement in the Gulf Stream south of the Grand Banks (Station 2484) was kindly carried out for me by Mr. Alfred Woodcock on September 15, 1935, using the Photox photometers (green sensitive). The value of the transmissive exponent was $k = 0.082$ from 2 m. to 10 m. From 10 m. to 95 m. the transparency was found to be

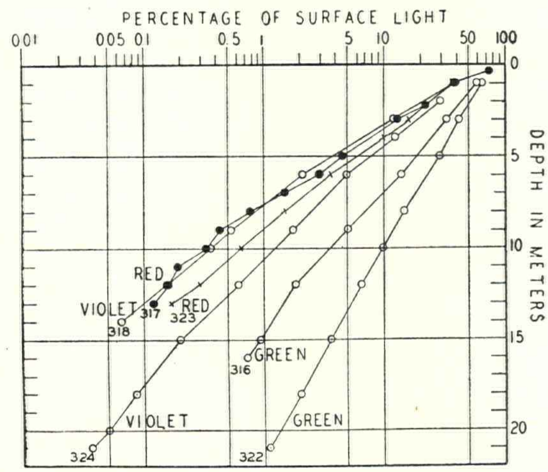


Fig. 4. Penetration af daylight.

Series 322, 323, and 324 — Vineyard Sound.
„ 316, 317, and 318 — Woods Hole Harbor.

extremely uniform with a value of $k = 0.057$. The water at this station was therefore only slightly less transparent to green light than was the case at the stations north of Bermuda (Table II) which are about 1000 miles distant.

The transparency of the deep basin of the Gulf of Maine appears to be characteristic of coastal water well out on the continental shelf. The values obtained in this area are generally similar to those reported by Atkins and Poole (1933) for the English Channel and by Utterback and Jorgensen (1934) for a point 28 miles off Vancouver Island. In the Gulf of Maine the blue and green components penetrate

## Table II.

**Comparison of Average Values of the Transmissive Exponent, k,[1]) in Oceanic and Coastal Areas of the Western North Atlantic (Arranged in order of decreasing transparency).**

| Locality | Station | Position | "Red" | "Green" | "Blue" | "Violet" |
|---|---|---|---|---|---|---|
| Sargasso Sea, E of Bermuda ... | 1041 | 36°55′ N 52°41′ W | — | — | 0.031 | — |
| Gulf Stream, N of Bermuda .... | 2245 | 37°35′ N 68°44′ W | 0.13 | 0.049 | — | 0.048 |
| Sargasso Sea, N of Bermuda .. | 2243 | 35°52′ N 65°30′ W | 0.082 | 0.050 | — | 0.053 |
| Gulf Stream, S of Grand Banks. | 2484 | 39°56′ N 48°40′ W | — | 0.059 | — | — |
| Continental Slope, S of Nantucket Shoals .................... | 2246 | 39°27′ N 69°43′ W | 0.23 | 0.074 | — | 0.098 |
| Deep basin of Gulf of Maine .. | 2237 (+ 1722) | 42°08′ N 69°04′ W | 0.28 | 0.11 | 0.112 | 0.15 |
| Continental Shelf, S of Cape Cod | 2474 | 40°48′ N 71°00′ W | — | 0.11 | — | — |
| Georges Bank ................ | 2238 (+ 1723) | 40°48′ N 68°40′ W | 0.35 | 0.13 | 0.14 | 0.17 |
| Off Gay Head ............... | — | 41°20′ N 70°57′ W | 0.37 | 0.16 | 0.27 | 0.25 |
| Vineyard Sound .............. | — | 41°30′ N 70°36′ W | 0.46 | 0.20 | 0.36 | 0.36 |
| Provincetown Harbor ......... | — | 42°03′ N 70°11′ W | — | 0.23 | — | — |
| Buzzards Bay ................ | — | 41°33′ N 70°42′25″ W | 0.50 | 0.25 | 0.51 | 0.40 |
| Woods Hole Harbor .......... | — | 41°31′ N 70°40′ W | 0.56 | 0.30 | 0.49 | 0.55 |

[1]) In the equation $I/I_0 = e^{-kL}$ where L is the thickness of the water layer (in meters) in which the intensity is reduced from $I_0$ to I.

about equally well. For violet light the transmission is slightly lower but for red it is only half as great as for the blue and green.

The low transparency found in Wood Hole Harbor and Vineyard Sound is characteristic of inshore waters generally, the conditions here being similar to the San Juan Archipelago (Utterback and Boyle, 1933) and Baltic Sea waters (Pettersson and Landberg, 1934). In these localities the green component of daylight penetrates the most effectively; the red, blue, and violet components are absorbed much more rapidly and do not differ greatly among themselves. Altho it has long been known that many lakes and ponds are relatively opaque, the magnitude and universality of this fact in comparison with ocean water was brought home to us only when we discovered that the transmissive exponent for green light for the clearest lake water ever tested (Crystal Lake, Wisconsin, cf. Birge and Juday, 1931—32) is almost exactly the same as our value for Vineyard Sound.

All the localities where measurements have been made in the Western North Atlantic are arranged in order of transparency in Table II and the average values of the transmissive exponents for the four components of daylight are compared. To generalize from this table we see that the Sargasso Sea is 2 to 4 times more transparent than the Gulf of Maine and the latter is 3 to 4 times more transparent than Woods Hole Harbor. The exact amount of the difference depends upon which part of the spectrum is compared; for example, the transparency of the Sargasso Sea is greater than that of Woods Hole Harbour by the following factors for different parts of the spectrum: 6X for green, 7X for red, 11X for violet, and 16X for blue. In other words the great increase in transparency experienced in going from inshore waters to oceanic regions consists chiefly in a very extensive improvement in the penetration of the shorter wave-lengths.

### Reflection and Absorption at the Surface.

In the foregoing measurements and in those of other investigators a "loss" of considerable magnitude has often been encountered at the surface. Attempts to measure the light present just beneath the surface of the water for comparison with that just above the surface have usually been unsuccessful because the action of the waves and the motion of the ship have made it impossible to keep the submarine photometer in the desired position long enough to make a measurement. Furthermore, the light for several meters below the surface fluctuates so rapidly that it is very difficult to obtain a reliable reading at these levels particularly when using the potentiometer method. The result is that the depth of the first point of observation has often not been less than 5 meters in off-shore localities and occasionally no satisfactory measurement could be obtained short of 10 m. When the curves representing the penetration of light from the first point downwards are extended upwards to zero depth, it is commonly found that they strike the abscissa at points indicating a reduction in the light at the very surface of from a few per cent. to 50 or 60 $^0/_0$. This discrepancy has been termed the "surface loss".

During the past summer measurements were carried out (Powell and Clarke, 1936) to determine whether large surface losses actually do exist or whether they could be accounted for by some instrumental or observational error. In addition it was hoped that it would be possible to distinguish between the loss due to reflection at the surface from the apparent loss which would be produced by a stratum of less transparent water which might have existed undetected just beneath the surface.

The incident light $I$ at the surface of the sea may be divided into three components: $A$, that which penetrates the surface and is entirely absorbed in the sea; $R$, that which is reflected either at the smooth surface of the water or by white foam and bubbles on the surface; and $U$, that which penetrates the surface but is scattered back by particles and bubbles in the water below and finally returns to the air. Therefore,

$$I = A + R + U.$$

The magnitudes of the three components $A$, $R$, and $U$ may be determined by placing a photometer in various positions relative to the sea surface and comparing the values obtained with $I$, the intensity found with the receiving surface of the photometer placed upwards and horizontal. If the instrument is suspended over the sea in an inverted position, it measures the quantity $R + U$ which is the total light coming upward from the sea's surface. If the photometer is lowered in an inverted position to a point just beneath the surface, $U$ can be measured alone.

The total light passing downwards through the surface is $A + U$, but this quantity cannot be measured directly with precision as already explained. However, since $I$, $U$, and $R + U$ can all be accurately measured, the values of $A$ and $R$ alone can be calculated. The quantity $R + U$ is of particular interest as being that fraction of the light falling on the ocean which does not contribute to its supply of energy. The remaining light, which is the quantity $A$, is absorbed by molecules of water, by bubbles, by suspended particles, and by organisms. This component is the entire source of heat for the ocean (if infrared radiation is included) and is responsible for all the photochemical reactions of marine organisms.

The light passing upward from the surface of the sea was measured by suspending the "deck" photometers in an inverted position at the top of a floating tower constructed of pipe and mounted on barrels. The heavy "sea" photometers were mounted on gimbals and used to measure the illumination on deck. Since the light from the surface of the water fluctuates rapidly the potentiometer method which gives an instantaneous measurement could not be used satisfactorily. In its stead a circuit involving a thyratron tube and relay was employed. The relay was so arranged that each time it became excited it moved the escapement of a watch thus registering the number of discharges and allowing the intensity of the light to be integrated over any desired period of time.

When the Photox rectifier cells had been procured further reflection measurements were made by mounting one of them in a light case and attaching it to the end of a long bamboo pole. In this way the photometer was held about 4½ m. out over the side of the boat and measurements were made with the receiving window turned alternately upward and then downward.

The obervations on the total upward light, or $R + U$, made with the red, green, and violet sensitive photometers showed that only a slight difference exists in the values for these components of daylight. $R + U$ for red light was almost always somewhat lower than for violet and green was intermediate as would be expected from their relative indices of refraction.

$R + U$ reaches a minimum (about 4 $^0/_0$ for violet and 3 $^0/_0$ for red) on clear days when the sun is nearest the zenith; on cloudy days the value may reach 6 or 7 $^0/_0$. After the sun has fallen below about 44° from the horizon the value of $R + U$ begins to rise. Below 30° on a clear day $R + U$ becomes steadily higher, and is higher then than under any other conditions. From 12° on the inaccuracy introduced by the unavoidable tilting of the photometers invalidates the measurements but there is every indication that $R + U$ becomes very high as predicted by theory. For solar altitudes of 12° to 30° $R + U$ ranged between 6 and 20 $^0/_0$ in clear weather. White caps were found to increase $R + U$ only slightly, apparently because the foam produced covers a relatively small proportion of the total surface. This is in agreement with a value of 12 $^0/_0$ obtained over the foamy part of the boat's wake. Altho the magnitude of the upward light has been found to remain an inconsiderable fraction of the incident light under all conditions, it must be remembered that its percentage may be two or more times greater on one occasion than on another and its absolute value varies with the strength of daylight.

Since these results point to a much lower value for the loss of light at the surface than was indicated by previous measurements of submarine illumination, an attempt was next made to measure with more care and precision than before the intensity of the light just below the surface.

Under conditions of absolute calm, clear sky, and glassy smooth water in Buzzards Bay it was possible to make measurements up to within 10 cm. of the surface where 97.5 $^0/_0$ of the light was transmitted (Series 401, Fig. 5). The trend of the

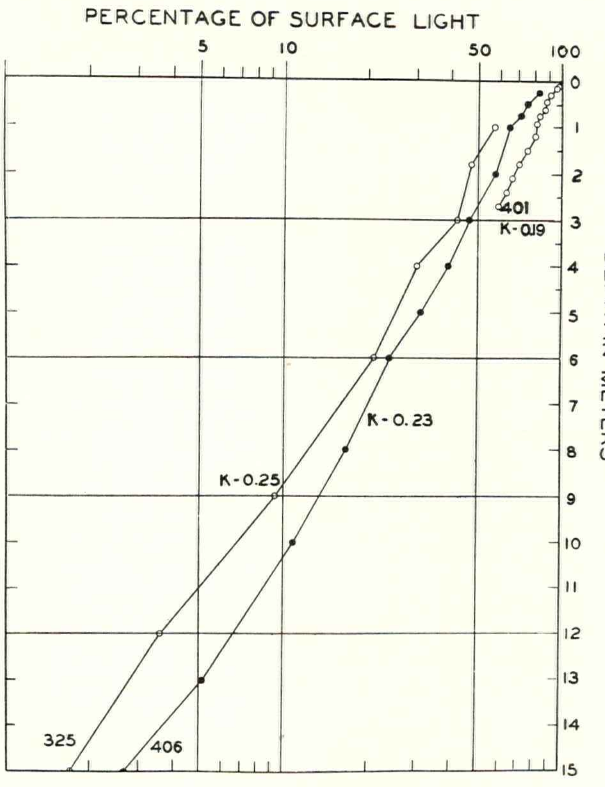


Fig. 5. Penetration of daylight showing "surface loss" under different conditions.

Buzzards Bay: Series 325. Slight sea.
„ 401. Glassy smooth sea.
Provincetown Harbor: Series 406. Slight sea.

curve is straight from this point to a depth of 2.7 meters. When the curve is extrapolated to zero depth a value of about 100 % is reached. A short time later when the sun was about 35° from the horizon $R + U$ was found to be 8.4 %. Since the theoretical reflecting power, $R$, for light incident at this angle as calculated from Fresnel's law of reflection for a smooth water surface is 5 %, the value of $U$ alone must have amounted to about 3.4 % or almost half of the total upward light.

The situation is entirely different when the surface of the sea is disturbed as is revealed by a comparison with Series 325 made at the same place the year before on a day when small waves existed. If the curve is extrapolated beyond the 1 meter level, a "surface loss" of about 30 % is indicated. Since the value of the transmissive exponent for the upper 6 meters ($k = 0.19$) is identical with that for Series 401, the difference in the position of the two curves cannot be due to a difference in the transparency of the water on the two occasions. Furthermore, we know from our present investigation that $R + U$ could not have been as great as 30 %. It was therefore suspected that the stratum of water less than 1 meter thick just beneath the surface became relatively opaque when the surface of the sea was rough and that this condition disappeared in calm weather.

Such a situation was actually detected in measurements made in Provincetown Harbor (Series 406) on a clear day with wind force 4 (Beaufort Scale), small waves, and occasional flecks of foam. If the curve is extrapolated to zero depth using only points below 1 meter it indicates a surface loss of 15 % or more. But when one extrapolates from points above 0.5 meter a loss of only 6 % is found. In this case $R + U$ was 4.6 % and $U$, measured directly by inverting the sea photometer and lowering it a few centimeters beneath the surface, was 3 %. The abrupt change of slope in the curve reveals the increased rate of absorption and scattering within the first meter of water.

In the open sea with waves a meter or more high and white caps, values for $R + U$ of 5.5 and 4.6 % were obtained at stations on Georges Bank and south of Cape Cod respectively. At the latter station it was possible in addition to make submarine measurements from a depth of 50 meters up to 0.5 meters (Series 412, Fig. 6). Without this last point on the curve the surface loss appears to be 14 % while with it the loss is reduced to almost nothing.

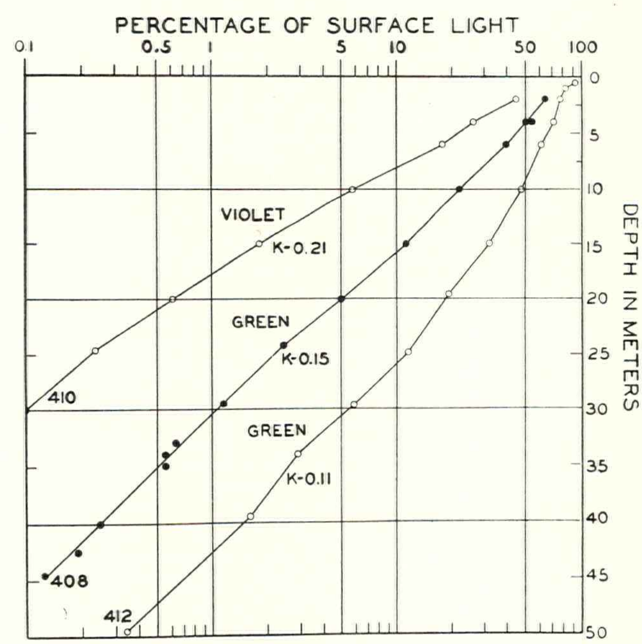


Fig. 6. Penetration of daylight showing presence of "opaque layer" just beneath surface.

Georges Bank: Series 408. Moderate sea.
„ 410. Moderate sea.
South of Cape Cod: Series 412. Moderate sea.

From the foregoing observations we may conclude that the discrepancies which have been termed "surface losses" are not due chiefly to a "loss" at the very surface. They are due, however, to a stratum of relatively opaque water which exists just beneath the surface and which has generally escaped notice.

The average value of all our measurements of $R + U$ for solar altitudes greater than 30° is about $6^1/_2$ % for cloudy days and about 4 % for clear days. Differences in the condition of the sea surface ranging from flat calm to waves with white caps has very little effect on these figures. The value of $R + U$ was not more than a few units higher in the more opaque inshore waters than in the clearer water of the Gulf of Maine. $R + U$ is never more than 9 % except for solar altitudes greater than 30° in clear weather. These conditions would exist during only a small portion of the day for most of the ocean, but the greater reflection losses at lower solar altitudes is undoubtedly of considerable importance in polar seas. For values of $R + U$ of 9 % or less, $R$ and $U$ were found to be about equal in magnitude. Therefore, the portion of daylight which never enters the water at all, namely $R$, is never more than a few per cent. of the incident light and consequently of negligible importance. These results agree very closely with measurements of the reflection from the surface of certain rivers and of Chesapeake Bay made by Kimball and Hand (1930) from an aeroplane of altitudes varying from 10 to 3000 ft.

Under conditions of absolute calm the transparency of the water remains unchanged up to within at least 10 cm. of the surface. The "surface loss" deduced from extrapolation is very small and in agreement with the low magnitude of the reflection. But as the sea's surface becomes more and more disturbed, the "surface loss" discrepancy becomes larger and larger. Its magnitude is usually about 15 % but has often been reported as much greater. Since we have found that the value of $R + U$ does not become significantly larger under rough conditions than in calm weather, it follows that the amount of light absorbed in the upper meter or so has greatly increased. Careful investigation of this stratum has proved that this is indeed the case.

The cause of this diminished transparency of the surface layer is undoubtedly the presence of bubbles produced by a disturbance of the water. Chemical substances, particles of sediment, and planktonic organisms are uniformly distributed over a much greater depth than the thickness of this anomalous stratum by the vertical mixing produced by turbulence. In every case where a large "surface loss" has been recorded either white caps or a tide rip has existed. In calm weather the phenomenon disappears.

## Rate at which Submarine Light becomes Diffuse.

The upward component of light beneath the surface was measured with an inverted photometer at each meter to a depth of 14 m. in Provincetown Harbor where the depth is about 16 m. At 0.5 m. the upward component was found to be 4 % of the downward component and this ratio increased gradually to a value of 6 % at 14 meters. In Buzzards Bay (depth 15 m.) the ratio was found to be 4.8 % at 1 m., 5.8 % at 5 m., and 8.9 % at 10 m. In the deep basin of the Gulf of Maine a ratio of 2.5 % was obtained at 0.5 m. and this value remained unchanged to a depth of 20 m.

A few approximate measurements of the horizontal component of the submarine illumination were made by suspending the sea photometer by one end so that the receiving surface was vertical. The photometer was caused to rotate slowly around a vertical axis in order that the window might face successively in all directions relative to the direction of the sun which was unobscured. A maximum and minimum intensity was thus recorded for each depth. In Provincetown Harbor the ratio of the maximum value for horizontal illumination at 1.5 m. to the vertical downward illumination at the same depth was 16 % and the ratio of the minimum horizontal illumination to the vertical illumination was 3.4 %. At 10 m. these ratios had increased to 17 % and 7 %, respectively. In the deep basin of the Gulf of Maine the ratios were 6 % and 3 % at 2 m., and 20 and 3 % at 15 m. Poole and Atkins (1929) reported an average value of 50 % for the horizontal light down to 25 m. in the English Channel. It is seen, therefore, that the illumination becomes more and more diffuse with increasing depth, but the directional character of the light is lost only slowly. One recalls that Helland-Hansen (1931) found that the vertical light was measurably greater than the horizontal at 500 m. in the Sargasso Sea.

## Diurnal Vertical Migration of Zooplankton.

Many of our measurements of light penetration have been made in connection with the study of the diurnal migration of copepods (Clarke, 1933b, 1934a and b). From careful records of illumination on deck throughout the day and several measurements of the transparency at the station where plankton hauls were being made, it was possible to construct diagrams which showed the changes both in the vertical distribution of the animals and in the intensity of light at the different depths. From an analysis of these it was hoped that the factors controlling the migration might be unraveled.

If there is one generality which can safely be made about the migration of plankton, it is that the phenomenon is an extremely variable one. Not only do different species behave differently, but the reaction of the same species may be quite contrary in one locality to what it is in another, or in the same locality at different times, as Russell (1934) has shown so clearly. If this were not enough, we find that the sexes and the various age groups of the same species in the same body of water often exhibit the most diverse behavior ranging from no migration at all to very extensive and rapid vertical movements (cf. Nicholls, 1933).

For those cases in which a clear cut diurnal migration is found the change in intensity of daylight during each 24 hour period is undoubtedly the most important single cause. In our investigations in the Gulf of Maine the migration of copepods was found to be much more closely correlated with the changes in submarine irradiation than with the changes in the hydrographic conditions or in the phytoplankton. In addition, light is of further significance because it is one of the two physical factors of the environment to which a copepod can respond *directionally*, as I have pointed out elsewhere (Clarke, 1934c). Light, gravity, and possibly stimuli from other organisms appear to be the only forces which can bring about orientation and thus make a consistent movement possible. At depths where the illumination has become so diffuse that the direction of propagation is no longer perceptible to the copepod, phototropic responses cannot take place. The intensity of the light present may, however, affect the sign of geotropism.

Altho light is generally conceded to play a major role in diurnal migration, the manner in which it exerts its effect is by no means clear. It may be that plankton animals are positively phototropic to weak light and negative to strong light. On the other hand it has been suggested that such influences as feeding or change of temperature may control the sign of the phototropic movement rather than the intensity of the illumination. But if phototropism alone is acting it is difficult to understand why the animals continue to move toward the surface after dark, as is often observed to be the case, or why they sometimes leave the surface before dawn. In these cases it seems to me more reasonable to suppose that light acts thru a modification of, or interference with, a persistent geotropism. According to this idea the negative reaction to light is thought to overpower the negative geotropism during the morning and noon hours but is less effective in the afternoon when light-adaptation has taken place. In cases where withdrawal from the surface occurs before dawn we would have to assume that some other factor acting in the upper strata reversed the geotropism after a certain number of hours.

For animals which remain continually in the deeper strata we may postulate a positive geotropism, and for those that swarm near the surface even during the middle of bright days, we may assume a negative geotropism which is stronger than any tendency to move away from the light. But the validity of these assumptions must be tested by suitable experiments in the laboratory and more precise observations at sea before any of these explanations can be excepted. The picture which seems to emerge from all this, however, is one of a plankton whose physiological adjustments are in a very delicate balance. Evidently very slight changes in the environment or undetectable differences in the internal physiological states of different ages or sexes or broods are sufficient to completely reverse the sign of the reactions.

## The Metabolism of Diatoms.

Since the photosynthesis of diatoms is of such fundamental importance in the sea, it is unfortunate that we do not have more information on the needs and limitations of this process in relation to the distribution of submarine illumination. On the western side of the Atlantic three experiments have been carried out in which the metabolism of diatoms was measured in bottles suspended at different depths in the sea, some of which were covered with black cloth and others of which were left exposed to the radiant energy existing in the surrounding water.

For the experiments in Woods Hole Harbor and in the Gulf of Maine (Clarke and Oster, 1934) phytoplankton from hauls made near by was suitably diluted and placed in the glass-stoppered oxygen bottles. In the Woods Hole Harbor experiment, which was undertaken in collaboration with Professor H. H. Gran, the plankton was exposed for four hours during the middle of the day. At the end of that time it was found that the oxygen consumed in respiration was just balanced by the oxygen evolved in photosynthesis at a depth of about 7 meters — the "compensation point". The fact that at 18 meters the loss in oxygen in the exposed bottles was not as great as in the covered bottles shows that a measurable amount of photosynthesis took place in the extremely weak light which penetrates to that depth, altho the photosynthesis was obviously much less than the respiration.

In the Gulf of Maine experiment, which was carried out by Professor A. C. Redfield, the exposure period extended from five o'clock in the morning to 2 o'clock in the afternoon. During this time the "compensation point" occurred at 24 to 30 meters, but some photosynthesis was detected down to 40 meters. The water in the Gulf of Maine is roughly three times as transparent as in Woods Hole Harbor and the "compensation point" lies about three times as deep.

It is of interest to compare with these results an experiment carried out for me by Mr. S. S. Gellis in the Sargasso Sea where the radiant energy is so much more intense. Since the diatoms growing naturally in this area could not readily be procured in sufficient concentration to produce measurable changes in the oxygen bottles, a persistent culture of *Nitzschia closterium* was used for this experiment. However, the photosynthesis of this northern diatom under the unnatural conditions of high temperature and intense illumination may have been very different from that which would have resulted had it been possible to use a native species. This possibility must be borne in mind when interpreting the results (Table III). But since this is the only experiment of its kind in tropical oceanic water to my knowledge, the data seem valuable as a first approximation.

## Table III.

**Metabolism of Diatoms in Sargasso Sea.**

Persistent culture of *Nitzschia closterium* used.
Exposure Period: 1050—1650, Aug. 24, 1934.
Sky: clear. Sea: smooth.
Oxygen present before exposure: 7.62
7.57
7.51
av. 7.57 cc./liter.

| Depth meters. | Temp. ° C. | Condition of bottles. | Oxygen after exposure cc./l. | Change in oxygen cc./l. | Difference in exposed and covered bottles cc./l. |
|---|---|---|---|---|---|
| 40 | 24.0 | Covered | 7.78 | + 0.21 | |
| | | Exposed | 11.22 | + 3.65 | + 3.44 |
| | | Exposed | 11.15 | + 3.58 | + 3.37 |
| 60 | 21.5 | Covered | 7.51 | -- 0.06 | |
| | | Exposed | 13.45 | + 5.88 | + 5.94 |
| | | Exposed | 13.48 | + 5.91 | + 5.97 |
| 80 | 20.2 | Covered | 7.70 | + 0.13 | |
| | | Exposed | 14. 11 | + 6.54 | + 6.41 |
| | | Exposed | 14.90 | + 7.33 | + 7.20 |
| 100 | 19.5 | Covered | 7.68 | + 0.11 | |
| | | Exposed | 11.71 | + 4.14 | + 4.03 |
| | | Exposed | 11.41 | + 3.84 | + 3.73 |
| 120 | 19.1 | Covered | 7.60 | + 0.03 | |
| | | Exposed | 9.87 | + 2.30 | + 2.27 |
| | | Exposed | 9.75 | + 2.18 | + 2.15 |
| 140 | 18.9 | Covered | 8.01 | + 0.44 | |
| | | Exposed | 8.51 | + 0.94 | + 0.50 |
| | | Exposed | 8.25 | + 0.68 | + 0.24 |

The results in this experiment are unfortunately not as regular as was the case in the Gulf of Maine work and considerable difference is found between bottles in the same categories. Furthermore, all the covered bottles except one showed a slight increase in oxygen instead of a decrease as they should if they are to be used as a measure of respiration alone. Possibly the light which reached them during manipulation at the beginning and end of the experiment was sufficient to account for this. However, if one assumes that this error was the same for all the bottles at each level, we may find the amount of photosynthesis which occurred at the designated depths by subtracting the oxygen produced in the covered bottle from that produced in the exposed bottles, altho the location of the "compensation point" is unfortunately impossible.

The differences in the amount of oxygen produced in the exposed bottles at the different levels is so very great that in spite of these irregularities we may draw two rather significant conclusions. In the first place it is seen that the greatest amount of photosynthesis is found at the 80 meter level. Evidently the more intense illumination (or possibly the higher temperature) of the upper strata exerted an inhibitory effect. This is in sharp contrast to the other experiments in which the largest production of oxygen took place just under the surface. The other conclusion of interest is that a considerable amount of photosynthesis went on even at a depth of 140 meters — 100 meters deeper than the lowest level of detectable oxygen production in the Gulf of Maine series.

These three experiments give an impression of the depth to which photosynthesis may extend in three different areas of the sea. They do not, however, show the thickness of the stratum in which constructive production goes on during the whole 24 hours of the day or longer periods (cf. Marshall and Orr, 1928; and Pettersson, Höglund, and Landberg, 1934). This is obviously the significant information from the point of view of the fertility of the sea and it is to be hoped that more extensive experiments will be undertaken in the near future on this problem — particularly in the great oceans.

## The Depth at which Fish can see.

At what maximum depth fish can see in the ocean and in lakes has remained a matter for speculation up to the present time, first because little was known regarding the strength of the illumination at various depths and second because no adequate tests of the sensitivity of the fish eye had been made. However, the recent work by Grundfest (1932) on the sensibility of the sun-fish, *Lepomis*, has provided us with reliable values for one species of fish. With this information and our present knowledge of the penetration of light it is possible to make an approximate calculation of the greatest depth in several different types of water at which the sun-fish could just discern an object of a certain size at a given distance. Whether the photosensitivity of other fish is similar to that of *Lepomis* can be decided, of course, only by the performance of suitable experiments. The vision of fish with "telescopic" eyes and of other highly specialized species is undoubtedly on an entirely different scale[1]).

Grundfest tested the response of the sun-fish to the movement of a screen illuminated by bands of light in different parts of the spectrum and found that radiation between wave-lengths 530 and 550 mμ was much the most effective. It is this general part of the spectrum of daylight which penetrates most effectively into most lakes and into coastal ocean water — the part of the sea in which fish occur in the greatest abundance. The minimum illumination, in the most effective region of the spectrum, under which the fish would respond was $1 \times 10^{-6}$ millilamberts. Since the bars of the screen used in the experiment were 2 mm. broad and at a distance of 1 cm. from the fish's eye (thus subtending an angle of about 11°), we may assume that the fish could just see under this minimum illumination an object 2 mm. in diameter at a distance of 1 cm., or a 2 cm. object at 10 cm., or a 20 cm. object at 1 meter, and so on.

The irradiation from 490 to 620 mμ at the surface of the sea off the coast of Massachusetts during the middle of a bright day in summer reaches an intensity of about 20,000 microwatts/cm². Now the minimum brightness for the vision of the sun-fish of $1 \times 10^{-6}$ millilamberts is equivalent to an irradiation of $1.5 \times 10^{-6}$ μw/cm². Since an intensity of 20,000 μw/cm² is approximately $10^{10}$ times this, it is apparent that the fish can see under an illumination of $10^{-10}$ times the maximum value of daylight — or a reduction of ten logarithmic units. This is approximately the same as for man. The instruments which have been found practicable for light penetration investigations have not been sufficiently sensitive to follow the reduction of light in the water for more than three, or at most four, logarithmic units. However, if we assume that the transparency of the water below the maximum depth reached by the photometer is the same as that in the surface strata, the data may be extrapolated. This assumption is justified, to some extent at least, by the fact that in many cases (and in all the cases considered here) there is no radical change in transparency within the depths actually measured. Accordingly, the approximate depth at which the minimum intensity for vision exists (during the hours of bright daylight at the surface) for each type of water investigated has been calculated by finding the average number of meters of water causing a reduction in intensity of one logarithmic unit and multiplying this value by ten.

## Table IV.

**Maximum depth for vision of fish similar to *Lepomis* in various types of water.**

| Types of water. | Thickness of stratum causing reduction of 1 log unit. | Depth of minimum illumination for vision of fish similar to *Lepomis* (10 × column 1) | Depth of water to the bottom. |
|---|---|---|---|
| | m. | m. | m. |
| Deep Basin of Gulf of Maine | 23 | 230 | 165 |
| Georges Bank . . . . . . . . . . . . . | 18 | 180 | 60 |
| Woods Hole Harbor . . . . . . . | 7.5 | 75 | 20 |
| Off Gay Head . . . . . . . . . . . . | 13 | 130 | 30 |
| Sargasso Sea . . . . . . . . . . . . . . | 43 | 430 | 4500 |
| Crystal Lake, Wisconsin . . . . | 11 | 110 | 21 |
| Adelaide Lake, Wisconsin . . | 2.8 | 28 | 22 |
| Trout Lake, Wisconsin . . . . . | 6 | 60 | 35 |
| Gunflint Lake, Minnesota . . | 7 | 70 | 50 |

In so far as it is reasonable to assume that the vision of our common marine fishes is similar to that of *Lepomis*, which inhabits fresh-water ponds and lakes, the figures in the upper part of Table IV give the extreme depths at which vision would be possible in different types of water. According to these approximations fish would be able to see objects on the bottom in coastal waters. In the case of localities where the "depth of minimum illumination" is much greater than the depth to the bottom, such as Georges Bank, it appears that vision would be possible for fish during most of the day because the intensity of daylight is within one logarithmic unit of its maximum for several hours before and after noon. Altho taste, smell, and touch are undoubtedly used in certain cases for the location of food, most fishes apparently depend chiefly upon sight. The general conclusion that vision is possible for fish on the bottom in coastal waters is supported by the following observation made by Mr. R. A. Nesbit of the United States Bureau of Fisheries. Mr. Nesbit found that white hake which he took in a bottom trawl at a depth of 132—154 m. off Bodie Island, North Carolina, were gorged with butterfish and other small active fish which presumably the hake could not have caught unless they had been able to see at that depth.

In order to compare these data on fishes with the ability of divers to see under water, I made inquiries of Mr. H. V. Greenough who had been working with conventional diving equipment on a wreck in 29 m. of water in Vineyard Sound about five miles distance from the point off Gay

[1]) A correlation undoubtedly exists between the degree of enlargement or of degeneration of the eyes of deep-sea fish and the depth (and consequently the illumination) at which they live. The issue is confused, however, by important differences which apparently depend upon whether the fish is bottom-living or pelagic and whether or not it possesses light organs. This problem has not yet been satisfactorily elucidated. *Cf.* Murray and Hjort (1912, p. 680).

Head where our light penetration measurements had been made. Mr. Greenough told me that at that depth tools could be clearly seen at arm's length during several hours in the middle of bright days in July. On one occasion sufficient light existed to permit work on the wreck to continue until 7 o'clock in the evening.

The value arrived at for the Sargasso Sea of 430 meters is of interest in comparison with Beebe's observation from the Bathysphere that complete darkness for the human eye was reached at a depth of between 520 and 580 m. Dr. Beebe has informed me (private communication) that without artificial illumination he was able to see a non-luminous fish four inches long *(Cubiceps)* at a depth of 210 m., a shark at 240 m., and a jelly-fish *(Aurelia)* at 350 m. altho entangled luminescent organisms may have aided vision in the last case. If we assume that a deep sea fish can see as well in blue light as *Lepomis* can in green light, then the maximum depth for vision in the Sargasso Sea would be about 750 meters since an average of 75 m. of this type of water are required for a reduction of one logarithmic unit in the blue region of the spectrum.

The depths for the limit of vision for the sunfish have been similarly calculated for three of the large number of lakes in northern Wisconsin whose transparencies have been carefully studied by Birge and Juday (1931, 1932) and for one lake in Minnesota investigated by Erikson (1935), altho the different methods used in the measurement of light penetration make comparisons difficult. The values arrived at for these four lakes are set forth in the lower part of Table IV. Crystal Lake is the clearest of all those investigated and Adelaide Lake is one of the most turbid with the exception of those which are deeply stained. Trout Lake is the deepest of the Wisconsin lakes studied. In all of these and even in Gunflint Lake which is still deeper, the calculations indicate that, just as in coastal waters, vision would be possible for fish similar to *Lepomis* all the way to the bottom.

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## Summary.

1. Measurements of the penetration of four components of daylight have been carried out in both coastal and oceanic areas of the western North Atlantic using photoelectric cells with a marine potentiometer and, more recently, rectifier cells of the "Photox" type with a suitably damped microammeter.

2. The water in the Sargasso Sea and Gulf Stream was found to be more transparent than in any other region of the world. The transparency of the Gulf of Maine is 2 to 4 times lower than this and is characteristic of coastal water on the continental shelf. The water in Woods Hole Harbor is 3 to 4 times less transparent than in the Gulf of Maine and is representative of inshore waters generally and of lakes. The transparency of the Sargasso Sea is greater than that of Woods Hole Harbor by the following factors: 6 × for green light, 7 × for red, 11 × for violet, and 16 × for blue.

3. The "surface loss" was investigated by suspending a photometer in an inverted position over the surface of the water and measuring the total light passing upward $(R + U)$. In Buzzards Bay, $R + U$ reaches a minimum of 3 to 4 % on clear days when the sun is nearest the zenith. The percentage is increased by one or two units when waves exist and by a few units more when the sky is cloudy, and is decreased by a few units in clearer off-shore waters. The greater part of the "surface loss" is due to a stratum of relatively opaque water which extends in rough weather to a depth of about 1 meter.

4. Measurements of the upward and horizontal components of the light beneath the surface showed that illumination becomes more and more diffuse with increasing depth, but the directional character of the light is lost only slowly.

5. Light is the most important factor controlling the diurnal migration of plankton and it is one of the two physical factors to which a copepod can respond directionally. However, it has been found that the reactions of the plankton to light are easily altered by slight changes in the environment or in the internal physiological state.

6. Experiments on the metabolism of diatoms in relation to light penetration were carried out in Woods Hole Harbor, in the Gulf of Maine, and in the Sargasso Sea. A measurable amount of photosynthesis was found to occur down to depths of 18 m., 40 m., and 140 m. in the three localities respectively. The "compensation point" for periods of a few hours occurred at 7 m. in Woods Hole Harbor and at 24 to 30 m. in the Gulf of Maine. An inhibiting effect was observed above 80 m. in the Sargasso Sea.

7. The minimum illumination for vision for the sun-fish, *Lepomis*, is approximately $10^{-10}$ times the maximum value of daylight. The depth at which daylight would suffer a corresponding reduction in different types of water has been calculated. The results indicate that for fish of similar visual sensitivity vision would be possible at the bottom in coastal regions and in lakes and at a depth of at least 430 m. in the Sargasso Sea.

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