THE ECOLOGY OF THE TAMAR ESTUARY
II. UNDER-WATER ILLUMINATION

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(Text-figs. 1–6)

Studies on illumination in the waters of the open sea made from this and other laboratories (cf. Atkins & Poole, 1933) have stressed the profound effects of varying transparency of sea water upon plant growth. Therefore during ecological investigations in the Tamar Estuary or Hamoaze, some measure of the light available for plants growing on the banks and in midstream on mooring buoys was sought. For work in shallow turbid water, the photo-electric method has certain disadvantages due to shading by the boat and the necessity of measuring the depth of the cell on a scale of centimetres rather than of metres. Steemann Nielsen (1935) has used the Zeiss Pulfrich photometer for measuring the extinction coefficients of blue and green light in Icelandic waters. For measuring the turbidity of North Sea water Kalle (1937) also has used this photometer in combination with the red S 72 light filter. In the present investigation the photometer has been used for measuring the transmission of light throughout the visible spectrum. The results can be linked up with photo-electric measurements.

Method of Measurement

The photometer measures directly the absorption or extinction coefficient of a coloured or turbid solution compared with distilled water; 0·25 m. twin absorption tubes have been employed. As commonly used the distilled water tube serves to give a balanced optical system and to eliminate from the measurement the undesired absorption by water itself, but for our purpose this absorption must be considered. When the instrument is correctly set up, the intensities of light of given wave-length entering the twin tubes, each of length d metres, will be identical, I_0, but after passing through d metres of distilled water or of sea water, the intensities will be reduced to I_1 and I_2 respectively. The following relations then hold:

$$d\mu_{DW} = \log_e \frac{I_0}{I_1}, \qquad \ldots\ldots(1)$$

$$d\mu_{SW} = \log_e \frac{I_0}{I_2}, \qquad \ldots\ldots(2)$$

where μ_{DW} and μ_{SW} are the extinction coefficients of distilled water and sea water respectively for light of a given wave-length. The measurements compare the intensities of light which emerge from the tubes, that is

$$d\mu_M = \log_e \frac{I_1}{I_2}, \qquad \ldots\ldots(3)$$

where μ_M is the extinction coefficient as measured. A simple rearrangement shows that

$$\mu_{SW} = \mu_M + \mu_{DW}. \qquad \ldots\ldots(4)$$

The transmission curves for the eight spectral filters used are shown in Fig. 1, reproduced by permission of Messrs Carl Zeiss (Jena). In most cases the cut off is very sharp. For this investigation the S 66·6 filter was not available.

Sawyer (1931) has summarized measurements of the extinction coefficients of distilled water. His own measurements extend up to 650 mμ. and appear amongst the most suitable for our purpose. Later Dawson & Hulburt (1934) redetermined μ_{DW} in the visible spectrum between 540 and 690 mμ. (Table I). Lange & Schusterius (1932) published results for an extinction

TABLE I. EXTINCTION COEFFICIENTS OF DISTILLED WATER, μ

Spectral filter	Wave-length at centre of gravity of filter $m\mu$	μ Sawyer (1931)	Dawson & Hulburt (1934)	Accepted value
...	400	0·072	0·08	...
S 43	440	0·023	...	0·02
S 47	460	0·015	...	0·02
S 50	490	0·015	...	0·02
S 53	530	0·021	...	0·02
...	540	0·024	0·04	...
S 57	570	0·038	...	0·04
...	589	0·082	0·14	...
S 61	620	0·178	...	0·18
...	650	0·21	...	...
...	670	...	0·34	...
...	690	...	0·39	...
S 72	*ca.* 720	...	...	0·47
S 75	*ca.* 750	...	...	0·54

coefficient, ϵ_{DW}, defined by the equation: $x\epsilon_{DW} = \log_{10} \frac{I_0}{I_1}$, where x is measured in centimetres (see their correction redefining their coefficient). Using the relation $\mu_{DW} = 2{\cdot}3 \times 100\, \epsilon_{DW}$, their graph gives μ_{DW} as approximately 0·27, 0·18, 0·50 and 2·8 at 500, 560, 670 and 750 mμ. respectively. On many occasions throughout the visible spectrum, as far indeed as 800 mμ., considerably lower values of vertical extinction coefficients in the open sea have been found by Poole & Atkins, Utterback, and Clarke. Since the extinction coefficients of distilled water are unlikely to exceed these values, Lange & Schusterius' figures have had to be rejected. The accepted figures in Table I for the filters S 43–61 were based solely on Sawyer's data, since we had not then discovered Dawson & Hulburt's paper. For our purposes the differences between the two sets of measurements are too small to warrant recalculation

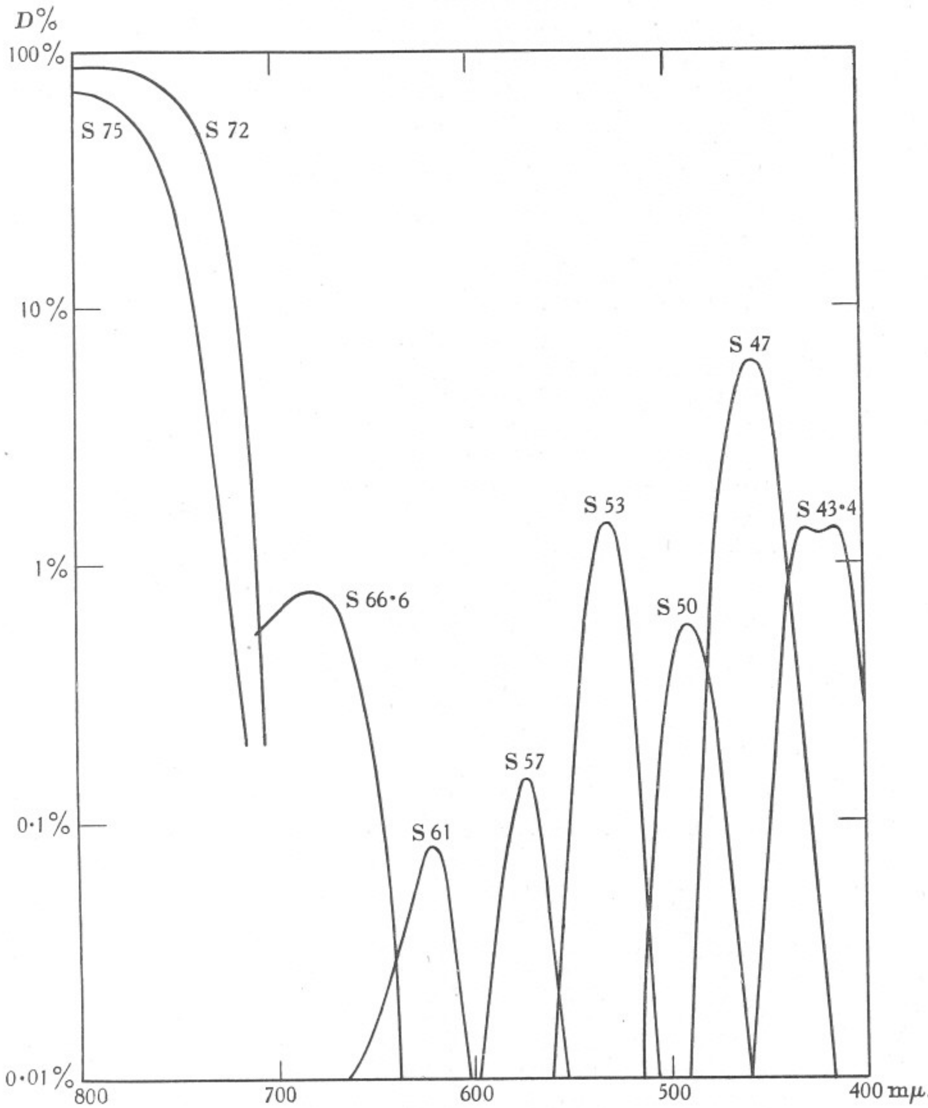

Fig. 1. Transmission curves for the spectral filters used with the Pulfrich photometer (supplied by Messrs Carl Zeiss).

of our results. The new results at 670 and 690 mμ. are of much value in arriving at the correction factors for the S 72 and S 75 filters. If, as would appear, the coefficient in this region is increasing linearly with wave-length,

μ_{DW} would be about 0·47 at 720 mμ. and about 0·54 at 750 mμ. These values have been used for the correction factors which must at present remain somewhat uncertain. Aschkinass (1895) found very high values for the extinction coefficient of pure water above 720 mμ. ($\mu_{DW} > 1$). Dr Atkins has very kindly examined for us the transmission curves of the Schott and Gen RG 7 and RG 8 filters used in his work on the transmission of red light in the sea. From his records it would seem that sea water shows nothing like such a high extinction coefficient. Thus Atkins & Poole (1933, p. 152) found vertical extinction coefficients 0·435, 0·480 and 0·567 at 660, 700 and 760 mμ. respectively. Pure water is unlikely to be more opaque than this.

Different samples of distilled water no doubt vary considerably in transparency. Our laboratory still gives water of excellent quality, so that for this investigation where the correction makes only a small change in the final value, Table I is appropriate. Should the method be used for more transparent waters, the distilled water correction would require further study.

Usually the two sides of the photometer will not be in exact optical balance. In consequence four readings with each of the eight spectral filters were made consecutively with the tube containing distilled water on the right hand. The tubes were then interchanged and a further similar series of observations made. To prevent settling of sediment, they were rotated through about 45° after every four readings. For each filter μ_M is therefore the mean of eight readings.

Comparison with the Photo-electric Method

Both methods give results in terms of an extinction coefficient μ defined by the equation

$$\mu = \log_e \frac{I_0}{I} \Big/ d.$$

Poole & Atkins use a quantity, μ_v, which they earlier (1926) described as the "vertical absorption coefficient" and now (1937) prefer, in agreement with Pettersson, to call the "vertical extinction coefficient"; μ_v is defined by the above equation in which d represents the difference in depth and not the unknown length of path travelled by the light. They concluded (1933) that for off-shore measurements below 10 m. with photometers limited to a restricted spectral range, μ_v as a measure of opacity is unlikely to be in error by more than a few per cent. It had been found by experiment to be practically independent of the angle of incidence at the surface.

Light passing through water may be transmitted, absorbed by the water, or absorbed or scattered by suspended solids. If a beam follows an oblique but straight path for n metres, the true extinction coefficient due to absorption only, $\mu_{n\,(absorption)} = \log_e \frac{I_0}{I_2} \Big/ n$, will be less than the vertical extinction coefficient due to absorption only, $\mu_{v\,(absorption)} = \log_e \frac{I_0}{I_2} \Big/ d$.

That part of the light scattered will become omni-directional but will not be lost unless it is reflected back out of the water. Nevertheless, in turbid water scattering will greatly increase the length of path of a ray passing downwards, so providing the opportunity for proportionately great absorption. The milky appearance of turbid water both in the estuary and in the photometer tubes shows this scattering to be considerable. If we consider a cylindrical sample of turbid water surrounded, as in the estuary, by similar water, as much light will be gained from the surrounding water by scattering as will be lost to it. For such a sample in a glass absorption tube in a dimly lit room, light incident on the water/glass surface at less than a certain angle will be completely lost from the water. If the water/glass and glass/air surfaces were plane and parallel, the limiting angle of incidence on the water/glass surface would be the critical angle for water/air, 48·5°. However, due to the curvature of the walls, the limiting angle of incidence for light not originating on, or from the direction of, the axis of the tube may be somewhat greater than this. As against this, the aperture of the measuring diaphragm receives only light which has traversed the central portion of the tube where conditions are more like those in nature, so that, although the measured extinction coefficient may be somewhat too great, due to loss of scattered light, the error is unlikely to be serious. Both methods are subject to inherent errors, but these are considered to be sufficiently small not to invalidate comparison between extinction coefficients determined by them.

Position of Observations

The exact positions examined will be found in Part I (Plate XVIII). The lowest is near the western end of Plymouth Breakwater and 2·0 km. to the N.N.E., still within Plymouth Sound, is Drake's Island No. 1 Buoy. Relative to the estuary this buoy is situated $-2{\cdot}5$ km. from the adopted zero line at the mouth, following the continuation of the main channel. Hamoaze No. 1 Buoy lies off Cremyll, No. 7 off Thanckes Lake, No. 15 below Saltash, and Neal Point Buoy in midstream at the junction of the Tavy, at distances of $+1{\cdot}2$, 3·4, 6·0, and 9·25 km. respectively from the estuary mouth.

Influence of Stratification

Observations in Plymouth Sound, even in the winter rainy season, have shown that the salinity varies little in the first metre or so below the surface. Salinity stratification increases in the up-river direction, and above Saltash bridge may become considerable during a winter spate (see Part III). In the Tamar Estuary, the maximum stratification may be expected at the upper limit examined, Neal Point Buoy. It will be shown in Part III that even in time of rainfall, equivalent to normal winter fall, the variations in salinity down to 1·8 m. are small and, for the top metre, negligible. Solid matter in suspension in an estuary arises from the inflowing river water and by tidal scouring of the muddy banks and bottom. The mixing processes are complex, but the amount of solid matter in any sample of water taken from the estuary is more or less directly dependent upon the degree of mixing of sea water with river water which, in times of spate, may be heavily laden with silt, and upon the time the various waters have spent in the estuary. Of this mixing the salinity is a measure, so that it is reasonable to suggest that waters of similar salinity carry, in general, much the same amount and kind of suspended solids. The considerable turbulence always present in isohaline water in a strongly tidal estuary would tend to keep conditions in the uppermost metre uniform. We therefore feel justified in considering our 0·3 m. samples representative of conditions down to rather more than 1 m. Whether there are more or less suspended solids at greater depths requires further investigation. In Gullmar Fjord Pettersson's observations showed that the underlying water may be much clearer but tidal forces are there much weaker than in the Hamoaze.

The relation between extinction coefficients and salinity is shown in Fig. 2 for green light measured with the S 50 filter. Below about 30°/₀₀ salinity a fair degree of inverse proportionality exists. With more saline water, in which sediment from the river has had a greater and more variable time in which to settle, no simple relation holds. The extinction coefficients for January 25, although of less accuracy than those determined later, are of much interest (Fig. 2). On this occasion silt determinations were also made by filtering 2–3 l. of estuarine water through a small tared No. 42 Whatman filter paper, washing with distilled water and drying at 100° C. to constant weight.

At the Breakwater (0·3 m.) salinity was very low, indicating a thin layer of river water spreading over the salter water beneath. This upper layer of water was associated with 5·3 mg./l. of silt and high extinction coefficients for light of all wave-lengths ($\mu_{500}=5{\cdot}0$; $\mu_{720}=3{\cdot}8$). Near Drake's Island the surface water was more saline and more transparent, yet carried more silt. Thence up-river to Hamoaze No. 7 Buoy, salinity, silt content and extinction coefficients varied in the way one would have forecast. Still further up-river at No. 15 Buoy, the water was still fresher but, to our surprise, contained less silt and was less opaque (Table II).

TABLE II. HAMOAZE POSITIONS, JANUARY 25 1937

	No. 1 Buoy	No. 7 Buoy	No. 15 Buoy
State of tide, hours flood	4	4·5	5
S °/₀₀	20·4	14·1	11·6
Silt, mg./l.	10·5	18·5	10·4
μ_{500}	5·1	9·0	8·4
μ_{720}	4·4	6·7	5·8

EXTINCTION COEFFICIENT

Throughout the visible spectrum the extinction coefficients in the Hamoaze (Fig. 3) are always higher, often much higher, than in the English Channel. The coefficients increase in the up-river direction and with falling tide because, first, the river is the chief contributor of suspended matter and secondly, the proportion of sea water, originally relatively clean, decreases.

In the winter of 1936–7 excessive rainfall (see Part III) saturated the watershed; most of this must have run straight off the ground into the river

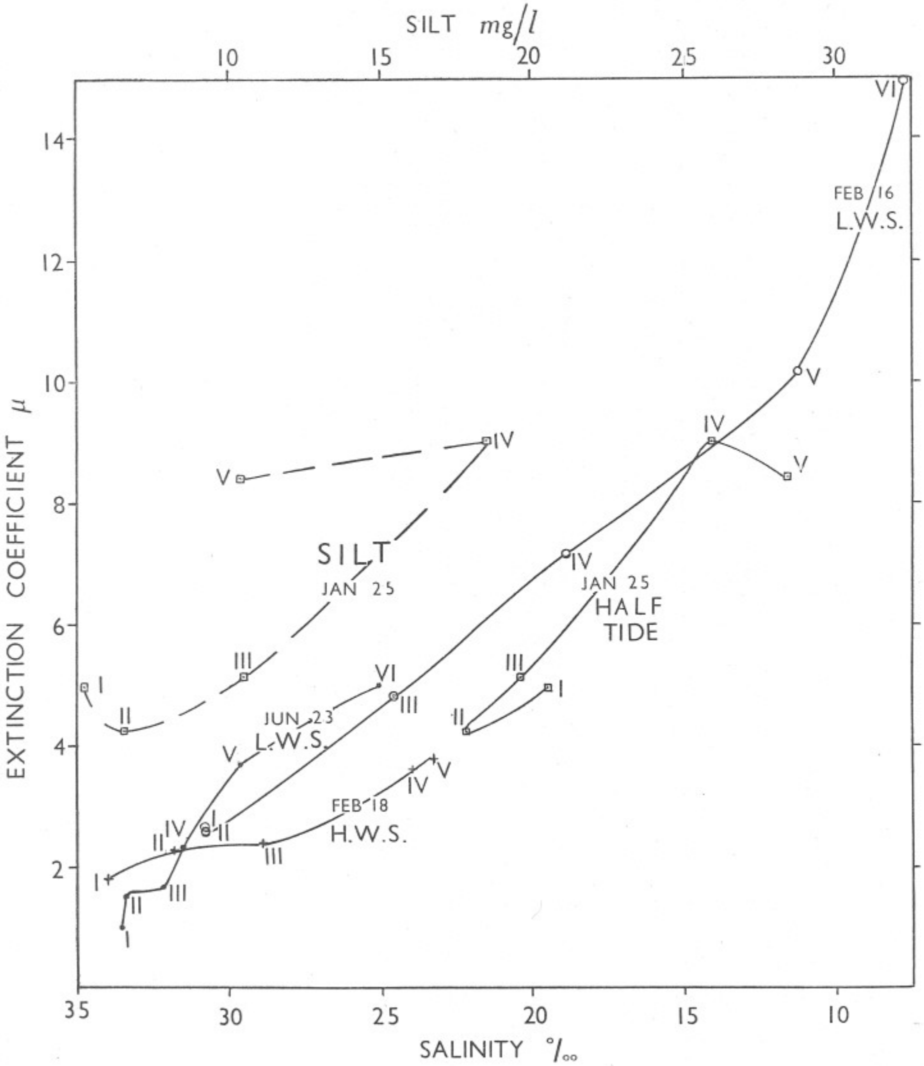

Fig. 2. Relation between extinction coefficient for green light (500 mμ.) and salinity, and also silt content on January 25 (pecked line). For key to positions of observations, see Fig. 3.

bringing with it a heavy load of silt. In February the surface waters of the estuary became so turbid that at low water at Neal Point with a salinity of 7·8 ‰ the intensity of red and blue light entering the water was cut down to one-thousandth within 0·6 and 0·4 m. respectively ($\mu = 12{\cdot}2$ and $16{\cdot}5$). Even

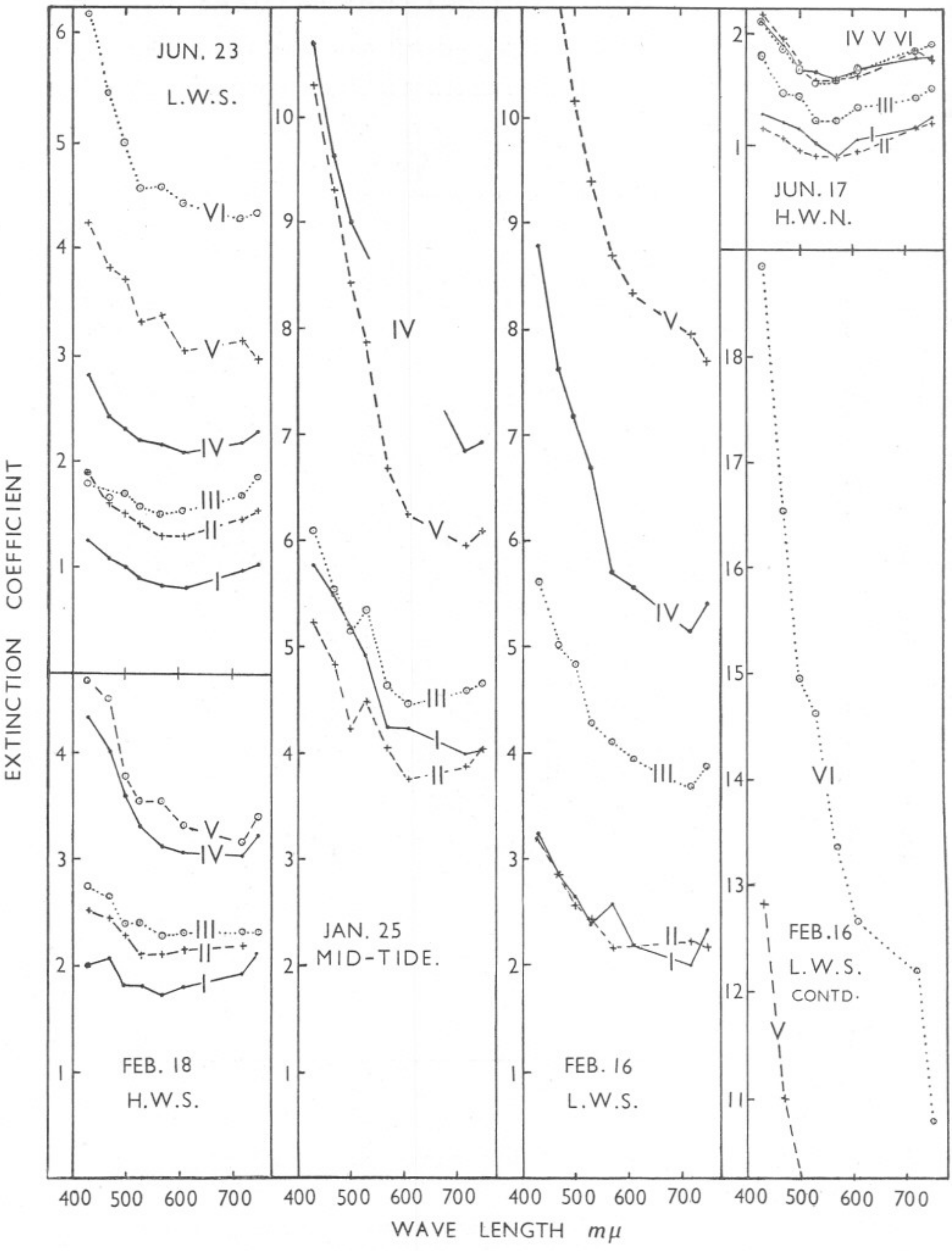

Fig. 3. Extinction coefficients in Plymouth Sound and Hamoaze.

I	——•——	Breakwater No. 1 Buoy.	IV	——•——	Hamoaze No. 7 Buoy.
II	----+----	Drake's Island No. 1 Buoy.	V	----+----	Hamoaze No. 15 Buoy.
III	····○····	Hamoaze No. 1 Buoy.	VI	····○····	Neal Point Buoy.

H.W.S. = High-water springs. L.W.S. = Low-water springs. H.W.N. = High-water neaps.

The curves for February 16 in the third panel are continued in the fourth.

at the two surface stations in Plymouth Sound, the coefficient for blue light was 2·85. This compares with the value for daylight, 2·52, found at the surface in Gullmar Fjord under somewhat similar weather conditions by Pettersson (1935).

The June measurements were made during a very dry spell (see Part III). The little rain that fell must have been absorbed by the soil, so that the fresh water draining to the river would be the minimum flow and composed of clear spring water and seepage from the moors. In consequence in June even at low water at Neal Point Buoy the surface salinity was no less than 25·1 ‰, and the extinction coefficients were similar to those at high water in February. The February and June results probably represent the extremes of conditions likely to be encountered in the estuary.

Relative Extinction of Different Wave-Lengths

Visible light of shortest wave-length is transmitted by the violet S 43 filter, but within this wave-band the sensitivity of the eye and the composition of light in air are changing rapidly. Measurements made with that filter are therefore liable to considerable error. We have accordingly preferred to arrange our February and June results in order of increasing absorption of blue light (filter S 47). These have been divided into three groups having $\mu_{470}=1\text{–}2{\cdot}1$, 2·4–2·9 and 3·8–16·5. The ratio of the extinction coefficient for each spectral filter relative to that for S 47 has been calculated for every sample. In each group the mean value for the ratio μ_λ/μ_{470} and the standard error when this is of interest have been computed (Table III). It will be seen that for light

Table III

Filter	Mean ratios of μ_λ/μ_{470} for values of μ_{470} between: 1·0 and 2·1	2·4 and 2·9	3·8 and 16·5	Entire series
S 43	1·110	1·097	1·112	1·107
S 47	1·000	1·000	1·000	1·000
S 50	0·928	0·924	0·917	0·923
S 53	0·861	0·874	0·847	0·856
S 57	0·821 ± 0·015	0·854 ± 0·025	0·805 ± 0·015	0·823
S 61	0·860 ± 0·018	0·829 ± 0·024	0·766 ± 0·010	0·812
S 72	0·962 ± 0·019	0·830 ± 0·037	0·739 ± 0·016	0·855
S 75	1·010 ± 0·020	0·881 ± 0·043	0·742 ± 0·018	0·889

having μ_{470} greater than unity, light in the spectral region 400–570 mμ. (violet to orange) is always extinguished in the same proportions, viz. 1·11, 1·00, 0·92 and 0·86 at about 430, 470, 500 and 530 mμ. respectively. This is so no matter what the absolute magnitude of the coefficient may be, provided that it exceeds unity. For red light longer than 600 mμ., the more turbid the water the less is the extinction coefficient relative to that for blue (or for that matter green). The greater the wave-length within the visible spectrum the greater this difference becomes. For the group having $\mu_{470}=1\text{–}2{\cdot}1$, the figures for the S 72 and S 75 filters may be in some error due to the uncertain distilled water correction. This source of error will be negligible in the other two groups and it does not apply to filter S 61.

Suspended particles affect the extinction of visible light in air and in water in the same way, favouring the transmission of red and yellow rather than blue and green. In marked contrast to pure clear air, pure water itself absorbs light in the extreme visible red and in the infra-red, so that such light is practically completely absorbed within 1 or 2 m., no matter what the turbidity may be (Poole & Atkins, 1937). In water, therefore, the region of optimum transmission will result from two opposing factors—absorption by suspended matter cutting out the blue and green and absorption by the molecules of water and dissolved salts cutting out the infra-red and often much of the visible red. Unlike foggy air, turbid water is unlikely ever to show an optimum transmission in the infra-red.

Depth at which Surface Light is reduced to 1 %

The depths in metres (d_1) at which the intensity of light of given wave-length was cut down to one-hundredth of that incident on the surface are set out in Table IV in which the following assumptions are implicit:

(1) That the loss of light at the surface is 15 % of that incident there. Powell & Clarke (1936) have discussed in detail the various surface losses.

(2) That the water down to the depth given was uniform with that sampled at 0·3 m. (see p. 514).

(3) That the vertical depth is a sufficient measure of the effective path of the downward penetrating light. The arguments advanced by Atkins & Poole (1933, p. 140) for open sea water below 10 m. are considered to apply at a much lesser depth when scattering, as here, is so much greater.

The equation, $\mu = 4{\cdot}44/d_1$, may be used to recalculate from Table IV the extinction coefficients which have been plotted in Fig. 3. Also the depth, d_x metres, at which the intensity of light of given wave-length is reduced to x % of that incident on the surface may be found from the relation.

$$d_x = d_1 \, (1 - 0{\cdot}518 \log_{10} x).$$

Percentage Energy Composition of Transmitted Light

Abbot (see *Seventh Internat. Congress of Photography*, 1929) has measured the relative spectral energy composition of mean noon sunlight. If we take the relative energy figures appropriate to each of our filters, we can calculate the spectral energy composition of the light transmitted to any depth. Owing to the much greater transmission of light at about 720 than at 500 mμ. in very turbid water, it is not practical to express our results as did Poole & Atkins (1937, fig. 2). In Fig. 4 we show the spectral energy composition of mean noon sunlight reaching 1 m. at the more transparent stations relative to the energy at 500 mμ. in air as 100 %. For the more turbid stations, logarithmic

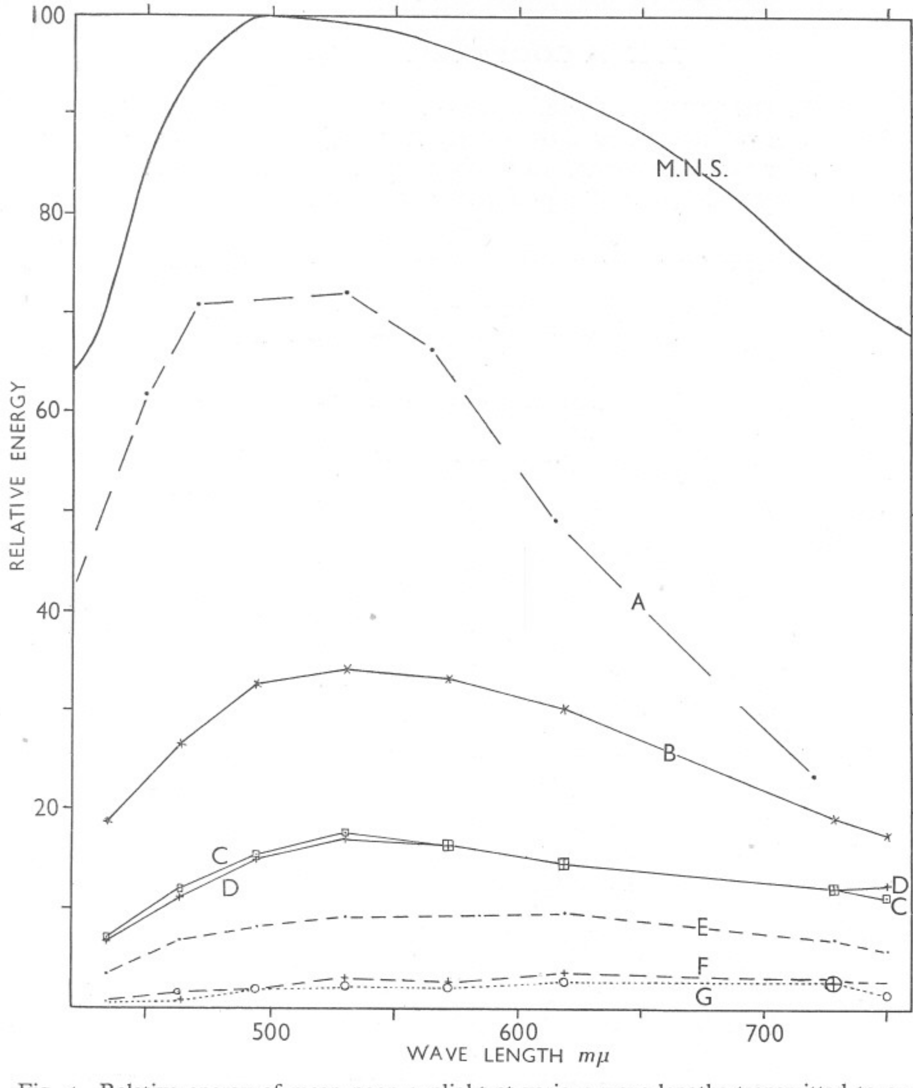

Fig. 4. Relative energy of mean noon sunlight at various wave-lengths transmitted to one metre. Allowance has been made for 15 % surface loss.

Key to Figs. 4 and 5.

June positions, high water: ———————　February positions, high water: · · · · · · · · · · · ·
June positions, low water: — — — — — —　February positions, low water: —· · ·—· · ·—

Curve *M.N.S.* Mean noon sunlight in air (Abbot).

- *A* Photo-electric measurements by Poole & Atkins (1937), half mile east of Eddystone September 21 1936.
- *B* Drake's Island, No. 1 Buoy, high water June 17 1937.
- *C* Hamoaze, No. 15 Buoy, high water June 17.
- *D* Neal Point Buoy, high water June 17.
- *E* Hamoaze, No. 7 Buoy, low water June 23.
- *F* Hamoaze, No. 15 Buoy, low water June 23.
- *G* Hamoaze, No. 15 Buoy, high water February 18.
- *H* Neal Point Buoy, low water June 23.
- *K* Hamoaze, No. 7 Buoy, low water February 16.
- *L* Hamoaze, No. 15 Buoy, low water February 16.
- *M* Neal Point Buoy, low water February 16.

plotting is necessary (Fig. 5), and some curves are included in both figures to facilitate comparison. They show clearly how little of the incident spectral energy under estuarine conditions reaches even to 1 m. and also the extent to which red light (> 600 mμ.) is preferentially transmitted.

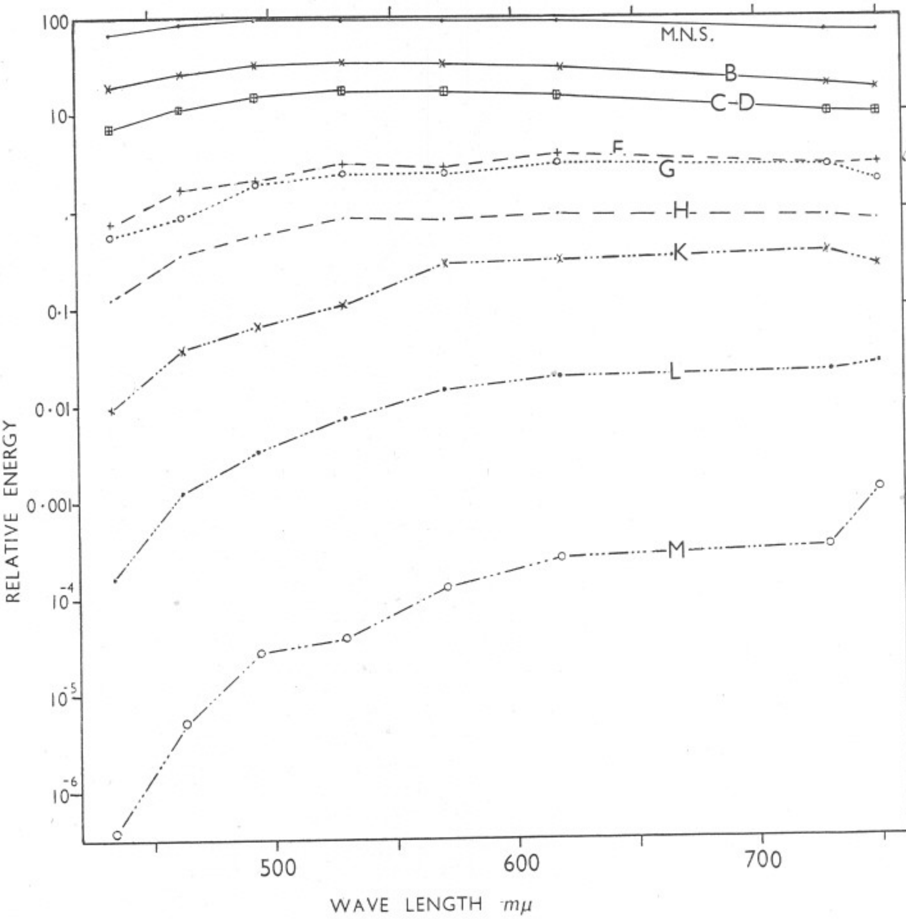

Fig. 5. Legend as for Fig. 4 except that relative energy is plotted on a logarithmic scale in order to include waters having high extinction coefficients.

If the extinction coefficients determined at Hamoaze No. 15 Mooring Buoy in February and in June are respectively plotted against salinity (as in Fig. 2), two curves are obtained which may be used to derive, from salinity records made on other occasions, extinction coefficients and the light intensities at 1 m. plotted in Fig. 6. It must be stressed very emphatically that this graph is intended to convey only a general picture of conditions in the

Hamoaze in the spring of 1937, when extensive ecological investigations were in progress, and not to represent exact results.

Preliminary experiments by H. Pettersson, Höglund & Landberg (1934) suggest that the compensation intensity at which photosynthesis just balances respiration by diatoms lies in the neighbourhood of 400 lux. The depths at which light energy incident on the surface is reduced to this value is therefore a rough measure of the compensation depth. The accurate calculation of this

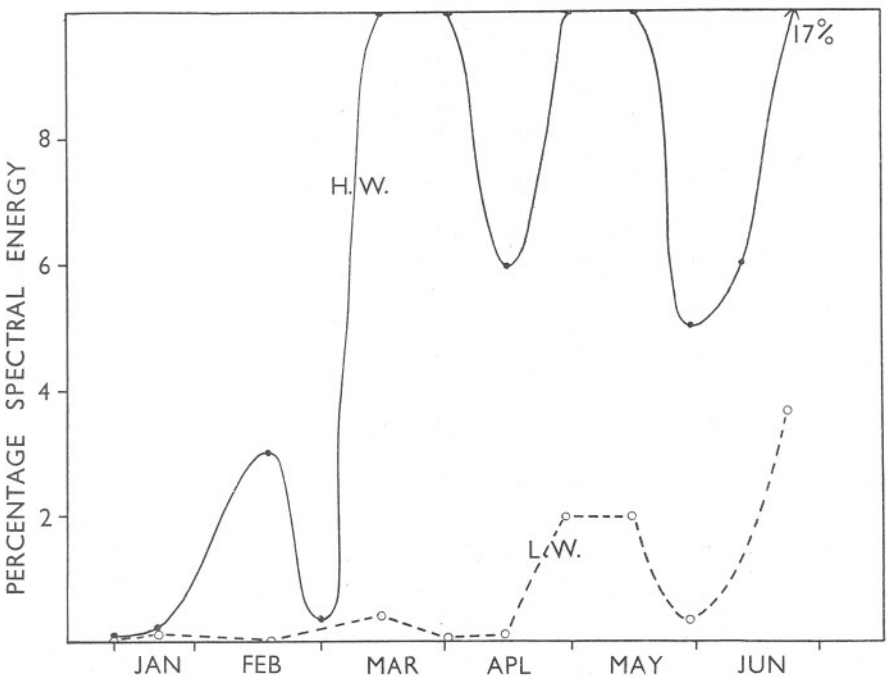

Fig. 6. Percentage spectral energy between 410 and 760 mμ. transmitted to one metre at high and at low water near Mooring Buoy No. 15 in Hamoaze, January to June 1937. Based on salinity records (see text).

depth is very tedious, but a fair approximation may be made by taking the extinction coefficient for orange-red light (S 61 filter) as representing that of all the light transmitted by the turbid water found in our estuary. The figures for this filter in Table IV will then be a very rough measure of the compensation depth when the illumination in air is 40 kilolux. Such an illumination approximates to that of a bright sunny day at the end of February or of an overcast day in summer (Atkins & Poole, 1936). On a cloudless summer day an intensity of 120 kilolux in air may be exceeded, and the compensation depth would lie about 25% deeper.

TABLE IV. DEPTH IN METRES AT WHICH INTENSITY OF LIGHT IS REDUCED TO 1 % OF THAT INCIDENT ON THE SURFACE

Assuming 15 % Surface Loss; $\mu d_1 = 4 \cdot 444$

Centre of gravity of filter mμ.	Breakwater No. 1 Buoy	Drake's Island No. 1 Buoy	Hamoaze No. 1 Buoy	Hamoaze No. 7 Buoy	Hamoaze No. 15 Buoy	Neal Point Buoy
			February 18 1937. Spring tide. High water			
434	2·20	1·76	1·62	1·02	0·95	...
463	2·06	1·81	1·67	1·09	0·98	...
494	2·45	1·95	1·85	1·23	1·17	...
530	2·45	2·12	1·85	1·34	1·25	...
572	2·58	2·12	1·95	1·42	1·25	...
619	2·48	2·06	1·93	1·45	1·34	...
729	2·31	2·02	1·92	1·46	1·41	...
750	2·11	1·79	1·91	1·38	1·31	...
			February 16 1937. Spring tide. Low water			
434	1·37	1·39	0·79	0·51	0·35	0·24
463	1·56	1·55	0·89	0·58	0·40	0·27
494	1·68	1·73	0·92	0·62	0·43	0·30
530	1·86	1·82	1·04	0·67	0·47	0·30
572	1·72	2·05	1·08	0·78	0·51	0·33
619	2·02	2·03	1·12	0·80	0·53	0·35
729	2·22	1·99	1·20	0·86	0·56	0·36
750	1·90	2·03	1·14	0·82	0·58	0·41
			June 17 1937. Neap tide. High water			
434	3·44	3·83	2·48	2·09	2·02	2·10
463	3·64	4·15	3·00	2·34	2·27	2·38
494	3·86	4·68	3·04	2·60	2·58	2·60
530	4·40	4·93	3·61	2·64	2·76	2·81
572	5·00	4·93	3·58	2·76	2·77	2·77
619	4·23	4·73	3·28	2·61	2·69	2·62
729	3·76	3·77	3·08	2·48	2·41	2·40
750	3·52	3·63	2·90	2·48	2·50	2·33
			June 23 1937. Spring tide. Low water			
434	3·52	2·36	2·50	1·57	1·05	0·72
463	4·11	2·78	2·68	1·83	1·16	0·81
494	4·40	2·94	2·63	1·92	1·20	0·89
530	5·05	3·17	2·84	2·02	1·34	0·96
572	5·42	3·47	2·97	2·06	1·32	0·96
619	5·62	3·47	2·92	2·14	1·46	1·00
729	4·67	3·08	2·66	2·04	1·42	1·03
750	4·35	2·90	2·40	1·95	1·50	1·02

ZONATION OF ALGAE ON BUOYS

The flora on the mooring buoys in Plymouth Sound and the Hamoaze may be divided into three zones with clearly marked boundaries.* The depths of these zones vary and may be correlated with differences in illumination.

The daylight factors (percentages of vertical white light having the spectral composition of mean noon sunlight) have been worked out for each of the zonal boundaries (Table V); the zones and their daylight factors vary little within Plymouth Sound, mean figures for which are given. The similarity of

* Paper in preparation by A. M.

the daylight factors in the Sound and at No. 7 Buoy in the Hamoaze on three occasions—at high and low water in June and at high water in February—shows that variations in illumination are adequate to account for the zonation found. The plants in Zone I require a surprisingly high proportion of the incident light. Even at the top of Zone III, a daylight factor as high as 67% can occur.

TABLE V. DAYLIGHT FACTORS AT BOUNDARIES OF ALGAL ZONES ON BUOYS

No correction for surface loss

	Zone I		Zone II	
	Plymouth Sound	Hamoaze No. 7 Buoy	Plymouth Sound	Hamoaze No. 7 Buoy
Depth of bottom of zone, m. ...	0·18	0·097	0·356	0·223
Daylight factor, %:				
June 17 (high water)	83·6	84·6	68·5	67·4
June 23 (low water)	80·8	80·6	65·5	60·4
February 18 (high water)	69·0	72·2	47·2	47·3
February 16 (low water)	64·6	54·6	42·3	25·3

The algae composing Zone III were found in a flourishing condition right to the bottom of all the buoys examined. The daylight factors at the bottom of the two deepest buoys are set out in Table VI. Account has been taken neither of surface losses nor of shading by the buoys themselves. Some of the adult algae no doubt float upwards into water receiving more light than shown, but in their young stages they must be able to grow in water having a daylight factor always less than 1·5% and often less than 0·5%.

TABLE VI. DAYLIGHT FACTORS AT BOTTOM OF TWO BUOYS (WITHIN ZONE III)

	Mallard Buoy (Plymouth Sound)			Hamoaze No. 7 Buoy		
Date and state of tide	Depth of bottom of buoy m.	Daylight factor %	Wave-length of maximum transmission mμ.	Depth of bottom of buoy m.	Daylight factor %	Wave-length of maximum transmission mμ.
June 17 (high water)	2·19	10·16	570	2·47	1·35	580
June 23 (low water)	2·19	7·59	580	2·47	0·42	630
February 18 (high water)	2·19	1·16	580	2·47	0·035	650
February 16 (low water)	2·19	0·59	650	2·47	0·000093	720

SUBMARINE DAYLIGHT IN THE NORTH SEA

The numerous determinations of turbidity made in the southern North Sea by Kalle (1937) in January 1935 and February 1936, using the Pulfrich photometer with the red S 72 filter, may be used to derive the extinction coefficient for red light for comparison with results elsewhere. He reported his results as "*K*-values" which are a measure of the extinction as measured in a 0·25 m. tube. When the extinction coefficient as measured is defined by equation (3), it may be shown that $\mu_M = \frac{9 \cdot 2\,K}{1000}$. From equation (4) the true extinction coefficient for the sea water

$$\mu_{SW} = \frac{9 \cdot 2\,K}{1000} + \mu_{DW},$$

and the depth in metres at which the light is reduced to 1 % of that incident on the surface (as in Table IV)

$$d = \frac{4440}{9 \cdot 2\,K + 1000\,\mu_{DW}},$$

where K is Kalle's measure of turbidity. These expressions may not be accurate for values of K less than 100, since any error in the correction factor, μ_{DW}, becomes large and a surface sample only will be inadequate to characterize all the water concerned in the absorption of light. Moreover, for such waters a 0·25 m. absorption tube may be too short.

Assuming, as in our work, that $\mu_{DW} = 0 \cdot 47$, the true extinction coefficients have been calculated for some of Kalle's more turbid stations (Table VII). These appear to be of two types, one being practically isohaline and showing greater turbidity and light extinction coefficient at the bottom than at the surface, the second having much lower salinity and higher extinction coefficient at the surface and resembling our own conditions in Hamoaze. Water of the

TABLE VII. A COMPARISON BETWEEN EXTINCTION COEFFICIENTS FOR RED LIGHT (S 72 SPECTRAL FILTER) IN THE NORTH SEA (DERIVED FROM KALLE 1937) AND IN THE HAMOAZE

Station	Date	Position		Depth m.	Salinity ‰	Extinction coefficient μ_{SW}
		Group 1				
12d	i. 35	52° 53′ N	2° 27′ E	0	34·71	3·5
				34	34·71	5·0
13	i. 35	52° 41·5′ N	2° 17·5′ E	0	34·66	3·6
				48	34·60	12·9
16	i. 35	52° 16·7′ N	1° 50′ E	0	34·45	7·8
				28	34·49	12·9
17	i. 35	52° 10·1′ N	2° 12′ E	0	35·16	2·4
				43	35·01	6·3
27	i. 35	51° 30·8′ N	1° 26·1′ E	0	35·05	3·2
				14	35·01	6·2
		Group 2				
60	i. 35	Off Rhine-Meuse Delta		0	25·63	4·3
				22	33·86	1·5
70	ii. 36	Channel N. of Sylt off		0	30·01	7·9
71	ii. 36	Schleswig		0	28·35	10·0
84	ii. 36	Off Mouth of Elbe		0	23·55	7·8
85	ii. 36	”		0	15·50	12·0
86	ii. 36	”		0	16·04	12·0
		Hamoaze, No. 15 Buoy:				
—	ii. 37	High water		0·3	23·3	3·1
—	ii. 37	Low water		0·3	11·2	8·0
—	ii. 37	Neal Point, low water		0·3	7·7	12·2

first type occurred off the East Anglian coast, and most of the suspended matter must have been stirred up from the bottom by tidal or storm action. Extinction coefficients calculated only from surface data will be too low. Part of this region of high absorption is associated with the north-west Southern Bight Eddy which Kalle discovered as a result of these cruises.

Water of the second type was found at the mouths of the Elbe and of the Rhine-Meuse delta. As in the Hamoaze, also in February, the suspended matter had no doubt been brought down by flood water from the rivers. Since these are much larger than those feeding the Hamoaze, the region of low salinity and high absorption extended farther to sea. In the North Sea off East Anglia and in the sea off these continental river mouths the light absorption may be as high as in the Hamoaze under extreme conditions (Table VII). The special distribution of plants in estuaries is usually attributed primarily to reduced salinity. Whilst this is often true, there may be cases where the distribution is the result not of reduced salinity but of increased light absorption resulting from the associated silt. A study of the flora of buoys situated off the East Anglian coast along the lines followed by one of us (A. M.) in the Hamoaze might go far towards a solution of the problem.

Some Biological Indications

From Table IV it will be seen that even under optimum conditions light is always reduced to 1 % or less within 5 m. at Drake's Island No. 1 Buoy and within 3 or 4 m. further up the Hamoaze. In Table VIII a comparison is made with conditions in other waters determined photo-electrically by various workers. Whereas the same intensity of blue light (450 or 470 mμ.) was found

Table VIII. Depth in metres at which light of various wave-lengths is reduced to 1 % (as in Table IV)

Station	Date	Wave-length mμ. 400	450	470	530	570	600+	675+	700+
Coasts of Iceland*	May 1934	...	...	2·0–12·0	2·4–19·3	...	...	...	...
Plymouth Breakwater†	Oct. 1932	...	6·3	...	10·7	...	4·6	3·0	...
Puget Sound, Pillar Point‡	June 1934	...	8·7	9·7	12·2	13·3	8·8	...	...
Puget Sound, Pillar Point	Jan. 1934	...	21·5	26	30	26	13·0	...	...
Puget Sound, Hood Canal‡	Apl. 1934	...	6·6	9·4	17·7	14·5	8·2	...	...
Puget Sound, Hood Canal	Mar. 1934	...	18·9	21	29	23	12·7	...	...
English Channel, Eddystone†	Sept. 1936	14·8	34	38	41	31	10·5	...	3·6
Pacific Ocean, 47° 26′ N., 126° 26′ W.§	...	...	63	62	59	43	14·7	9·1	...
Sargasso Sea‖	...	100	148	...	85	...	17	...	...

* Measurements with Pulfrich photometer by Steemann Nielsen (1935). Results at 490 mμ. entered as 470 mμ.

† Photo-electric measurements by Poole & Atkins (1937).

‡ Photo-electric measurements by Williams & Utterback (1935). Records at 460, 480 and 565 mμ. entered as 450, 470 and 570 mμ. respectively.

§ Photo-electric measurements by Utterback & Jorgensen (1934).

‖ Photo-electric measurements by Clarke (1936). Read from a graph of μ_v.

at 0·27 m. at Neal Point Buoy under the worst conditions and at 148 m. in the Sargasso Sea (ratio 1 : 550), the corresponding figures for red light were 0·36 and 17 m. (ratio 1 : 48).

Not only will the reduced light intensity compress the zonation of plants in estuarine waters but the season of active growth should be shorter than in the open sea. Moreover, both these effects should become more marked in an up-river direction, and species dwelling near the level of low water should be more affected than those nearer high-water mark.

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Summary

The Zeiss Pulfrich photometer, with its eight spectral filters covering narrow spectral bands within the visible spectrum, has been used to investigate the penetration of light into an estuary under winter and summer conditions.

Throughout the visible spectrum, extinction coefficients in Hamoaze are always higher, in winter often very much higher, than in the English Channel. In marked contrast to the open sea, red light penetrates as well or better than green, and blue is cut down most rapidly. Highest and lowest values of μ found at two estuarine stations were:

		Hamoaze No. 1 Buoy		Neal Point Buoy	
Colour		Lowest	Highest	Lowest	Highest
Blue	440–480 mμ.	1·48	5·01	1·87	16·5
Green	515–550 mμ.	1·23	4·28	1·58	14·6
Red	610–640 mμ.	1·35	3·94	1·69	12·7
Dark red	710–760 mμ.	1·44	3·69	1·85	12·1

The intensity of incident daylight in the Hamoaze appears always to be reduced to 1 % within 4 m., often in less than 2 m. and at low water when the rivers are in spate in less than 0·5 m.

For water having an extinction coefficient for blue light (470 mμ.) greater than unity, the light within the spectral range 400–570 mμ. is always extinguished in the same proportions (μ_λ/μ_{470} = 1·11, 1·00, 0·92 and 0·86 at about 430, 470, 500 and 530 mμ. respectively).

For red light longer than 600 mμ., the more turbid the water the less is the extinction coefficient relative to blue (or for that matter green). The greater the wave-length within the visible spectrum the greater the difference becomes.

Zonation of algae on buoys may be correlated with variations in illumination.

Measurements of turbidity in the North Sea by Kalle have been recalculated to give the extinction coefficient for red light. Off the East Anglian coast and off the mouths of the Elbe and the Rhine-Meuse delta, very turbid waters showing values of μ_{720} as high as 12·9 were encountered.

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