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SUBMARINE ILLUMINATION IN RELATION TO ANIMAL LIFE.

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SUBMARINE illumination is one of the conditions of the environment which shows the greatest fluctuations. While such conditions as salinity and temperature may remain relatively constant for long periods of time, the illumination of the upper layers and shallow waters may vary from that of full sunlight to complete darkness during 24 hours. Under such widely varying illumination it is natural to find that many species of animals are able to withstand a considerable range of intensities of light. Nevertheless, probably all animals react in some way towards changes in light conditions and each species tends to seek an optimum of intensity and composition, having an upper maximum condition which it avoids and a lower threshold of illumination below which it ceases to react. The values of these points on the light scale of an animal's requirements vary for each species, and within any one species during its life history and at different seasons of the year.

Now that accurate methods for the measurement of the strength and composition of light beneath the sea surface have been evolved, it is necessary that all ecological observations should include the study of light as one of the factors of the environment.

I propose to summarize briefly such observations as have already been made and draw attention to certain aspects in the study of animal life in the sea in which light conditions play an important controlling influence. In doing this I shall lay most stress on the work on plankton animals; but I shall also consider the relation of illumination with other marine animal communities as this will assist in emphasizing, if that be necessary, the need for a more complete knowledge of the variations in submarine illumination from place to place and time to time.

Our present knowledge of the relations of submarine illumination with animal life may be summarized under the following headings.

1. Zooplankton.
   a. Light and vertical distribution.
   b. Physiological effects of light on plankton animals.
   c. Light in relation to zooplankton production and distribution.
2. Bottom Fauna.
   a. Light and the zonation of sedentary and bottom animals.
   b. Physiological effects of light on bottom animals.
3. Fishes.
   a. Light discrimination.
   b. Physiological effects of light and colour change.

Zooplankton.

a. Light and vertical distribution.

It has been known for many decades from observations on the habits of plankton animals that light is of importance in its effects on behaviour. Most plankton animals show in the laboratory very distinct tropistic responses by moving to or from the source of the stimulating factor. This is especially obvious in their responses to light, the organisms being either positively or negatively phototrophic. An immense amount of study has been given to this problem (see, e. g. Spooner, 1933) and it has often been stressed that the intensity and composition of light were important controlling factors.

In 1926 I indicated the apparent importance of light intensity in the sea by bringing to notice certain similarities in the vertical distribution of plankton animals with the theoretical behaviour that might be deduced from a knowledge of the light conditions. This had been stimulated by the pioneer observations being made then by Poole and Atkins, and was based on a comparison between their results and the behaviour that I had found by field observations. Although it had been realized by many that the strength of light was evidently a factor of great importance, this was the first attempt to correlate behaviour with the actual results of the measurement of submarine illumination. This was followed in the next year by a review (Russell, 1927) summarizing our knowledge of the vertical distribution of plankton animals and the theories in which light had been considered as a factor by past workers. Since that date much attention has been given to this aspect of the problem and the literature on the subject has increased considerably. The evidence for the importance of light in affecting the behaviour of plankton animals is now overwhelming and it is manifested by the following facts.

i. The periodic migrations of many animals towards the surface in the dark, and downwards away from the highly illuminated layers in the daytime.

ii. The changes in the daylight vertical distribution of the same species of animal from day to day and place to place according to the illumination as affected by weather conditions and the opacity of the water.

iii. The fact that animals will migrate vertically according to light intensity changes during the 24 hours in spite of large vertical variations in the isotherms occurring at the same time.

This was suggested by Russell (1927, p. 241) as a crucial test to establish the major influence of light over temperature, and has been confirmed by Clarke (1934, a, p. 445; 1934, b, p. 537). For instance at St. 1722 on July 16th, 42° 50′ N. 67° 05′ W., in the morning all the isotherms were rising rapidly between 3 and 6 o'clock, that of 10° C. being displaced vertically during that time by some 12 metres, from about 26 m. to 14 m.; yet during the same time Calanus made an extensive downward migration with the increasing illumination.

The first simultaneous measurements of submarine illumination and the vertical distribution of the plankton were made by Atkins (Atkins and Poole, 1933) and Russell (1934) in the English Channel, and by Clarke (1933 and 1934, a) in the Gulf of Maine. These observations showed a certain amount of agreement between vertical movements of the zooplankton and changes in light intensity, but more work of this nature is desirable.

b. Physiological effects of light on plankton animals.

(i) Effects of intensity.

Welsh (1932) showed a correlation between the intensity of the light and the rate of swimming of the larvae of the mussel crab, *Pinnotheres maculatus*. (e. g. page 319).

Larvae 20 hours old. Temperature 24.5° C. ± 0.1.

Light intensity[1]) in metre candles.	Seconds taken to swim 29 cm. towards the light.
0.47	33.9
0.93	31.8
2.3	27.2
4.7	23.5
9.3	21.5
23.3	17.5
46.5	16.7
93.0	16.6

Similarly with the copepod *Centropages typicus* Welsh (1933) showed that increase of intensity led to an increased speed of locomotion. Centropages in intensities of 1394 metre candles swam 10 cm. on an average in 4.4 seconds, but at 0.7 metre candles they took 8.5 seconds to travel the same distance. He found, however, that this relation apparently did not hold true for animals moving by means of cilia.

Marshall, Nicholls and Orr (1935) exposed specimens of the copepod *Calanus finmarchicus* to daylight in ordinary clear glass bottles. They found that, while there was no apparent increase in activity, their oxygen uptake increased considerably. "In bright diffuse light, or in sunshine, the respiration may be even double what it is in the dark".

Experiments with Calanus in vessels submerged to different depths, however, showed that the light had an effect on respiration at the surface and 0.5 m., but hardly any at 5 m. and 10 m. This does not necessarily imply that light intensity beneath the sea surface is not an important factor in this respect. Calanus is a copepod which, compared with many other species, lives relatively high in the water. Deeper living species may consequently be strongly affected on entering the well illuminated layers above their normal habitat. At certain times of the year Calanus also is found swarming at the surface.

These authors also found that if Calanus are returned to the dark after exposure to light their respiration shows after a period of time a value much below that of the controls which had not been exposed. This suggested that the Calanus had been injured by the light.

[1])The light source was a 6-volt, 18-ampere, ribbon filament lamp. Intensity was controlled by means of Wratten neutral tint filters, and was measured with a Macbeth Illuminometer.

(ii) Effects of different wave lengths.

A number of workers have shown the greater power of one portion or another of the spectrum to evoke a response to light stimulus in different animals. Some examples of the wave lengths to which certain animals are most sensitive are given below.

Larvae of the hydroid, Eudendrium, to blue (460—480 mμ)
Larvae of the worm, Arenicola, to green (*ca.* 495 mμ)
Larvae of the Squid, Loligo, to blue green (470—510 mμ)
Cyprid larvae of barnacles, to green (530—545 mμ)
(cited from Visscher and Luce, 1928, p. 348).

Harvey (1929) showed that the rate of heart beat of Calanus decreases as injury is inflicted by direct sunlight. He found that the blue end of the spectrum was more effective in causing injury than the green or red. Klugh (1929) in demonstrating the lethal effects of the ultraviolet component of sunlight found that with filters transmitting the ultraviolet the copepods *Calanus finmarchicus*, *Tortanus discaudatus*, and *Eurytemora herdmani*, were killed on the average in 36, 16.5 and 16 hours respectively. By contrast (Klugh, 1930) certain shallow water animals and a ctenophore which lives very near the surface were found to be more resistant.

Lepeschkin (1931) found that if certain species of copepods were exposed to direct sunlight their resistance to poisons, such as mercuric chloride, was decreased. Using *Paracalanus parvus*, *Oncaea venusta* and *Euterpe acutifrons* he gives the following survival times for different concentrations of poison at 22° C.

% $HgCl_2$	Survival time in minutes. Kept in dark	Exposed to direct sunlight.
0.025	1.7	
0.0125	2.3	
0.006	3.8	
0.003	6.4	4.5
0.0013	10.8	7.5
0.00026	41.0	30.0

If however a filter (586-A by the Corning Glass Company) was used cutting out the visible rays and allowing only the ultraviolet to pass, it was found that the resistance of the animals was increased by 15 % if the exposure lasted not longer than 10 minutes. It was concluded "that ultra violet rays protect the animals from the injurious effects of visible light". But prolonged exposure to ultra violet was naturally harmful. It may be therefore that occasional short excursions to the sunlit layers may thus have a beneficial effect on the organism in increasing its resistance to light.

The penetration of ultraviolet rays into the sea must have some significance in the production of vitamin D in the liver oils of fish. The ultraviolet rays are quickly absorbed, wave lengths of 303 mμ being reduced to 1 % at 2.1 m. and of 313 mμ to 1 % at 2.2 m. (Atkins and Poole, 1933, p. 161). Yet at times plankton animals are abundant actually in the surface waters and it is possible that on these occasions irradiation takes place (Russell, 1930). A slight antirachitic value has been shown by Drummond and Gunther (1934) for zooplankton oil.

c. Light in relation to zooplankton production and distribution.

The seasonal change in submarine illumination and its variations from year to year caused by weather conditions may have important effects upon the production of zooplankton. In northern temperate waters there is, for instance, a regular seasonal cycle of plant production characterized in many localities by a heavy vernal production of diatoms and a second smaller production in the autumn. But the amount of production and times of onset of these outbursts vary greatly from year to year, being dependent upon the illumination. There are also typical life cycles and brood productions among the different species of plankton animals. It can be realized that the extent to which brood production falls out of tune with the sequence of production of the plant food supply will decide the success or failure of a brood to survive. This is possibly a factor of great importance in the autumn months. Many species of animals produce, in August or September, their last brood of the year. The extent to which this brood will survive to form the stock for the breeding population in the following year must depend upon the supply of plant food. The autumn outburst of diatoms shows a considerable degree of variation, and is especially likely to be curtailed by inclement weather conditions since at that time of year the strength of the light is waning daily.

Recent work by Hardy and Gunther (1935) has brought into prominence the relationship between zooplankton and phytoplankton. Their results supply very strong evidence that in certain areas the animals may be positively excluded by excessive growth of diatoms. Since light intensity plays such an important part in the vertical migrations of plankton animals and since it controls plant production the bearing of illumination on the problems of horizontal distribution is obvious. The very fact also that production of the planktonic plant life is limited to the upper illuminated areas must have a considerable bearing on the distribution and production of the fauna living in the dark depths of the ocean.

2. Bottom Fauna.

a. Light and the zonation of sedentary and bottom animals.

The intensity and spectral composition of the light are possibly important factors in determining the settling positions of a number of sedentary animals. This is especially the case among those animals which cause so much damage by fouling the bottoms of ships and other submarine structures. Many of the smaller bottom-living invertebrates also are probably limited in their distribution by that of the algae among which they dwell. In this respect the first actual measurements of submarine illumination in the sub-littoral zone have been made by Kitching, Macan and Gilson (1934). These authors made observations in connexion with a study of the sub-littoral fauna on a rock surface in a gully in Wembury Bay on the coast near Plymouth. An illumination 1 $^0/_0$ of that in air was found in the Laminaria forest at midday in August in water 3.7 metres deep.

The depth to which algae can grow on the bottom is also of importance in the distribution of the animals, and the measurement of bottom intensities in different localities and latitudes would be of value. It is of interest that Steuer (1935, pp. 11—13) has recently shown the presence of extensive fields of green algae in the Mediterranean off Alexandria, where Caulerpa may be found on the bottom in water up to 50 fathoms (91.5 m.) in depth, while red and green algae still occurred at 55 fathoms (100.6 m.).

Many animals carry within their tissues symbiotic algae whose growth and reproduction must depend upon the presence of sufficient light. Perhaps in no group of animals are these more prevalent than in the reef-building corals of the tropics. Although the exact relationship of these symbiotic algae to the animals within whose tissues they live is still under discussion it is evident that from their prevalence they must bear some vital relationship one to another. The work of Verwey (1930) and Yonge (e. g. Yonge, Yonge and Nicholls, 1932) on the physiology of corals has shown the necessity for having measurements of the submarine illumination at different depths in the various types of locality in which these corals live.

b. Physiological effects of light on bottom animals.

Bottom animals which live habitually in a world of low illumination are probably very sensitive to variations in intensity. It is possible that many species are purely nocturnal, retreating into burrows in the daytime. It has been shown by Welsh (1934, p. 343) that the worm, *Terebella*, if kept in the dark for ½ hour or longer will lie with its tentacles relaxed and fully extended. In this condition they are very sensitive to light and extremely low illumination results in rapid contraction and writhing movement.

Klugh and Newcombe (1935) have found indications that light intensity may be a factor in the growth of marine animals. A study of the barnacles, *Balanus balanoides*, growing on a wharf at St. Andrews, New Brunswick, showed that there was an increased rate of growth with a decrease in the amount of illumination. In three positions chosen with decreasing amounts of illumination the sizes of the barnacles 2 years of age were approximately 5 mm. in height by 6 mm. in width, 7 mm. by 7 mm., and 15 mm. by 9 mm., respectively. This possibility needs following up more closely and experiments should be made under controlled conditions, since so many factors such as food supply and wave exposure enter into the problem (cf. Moore, 1935 and 1936).

The possible relationship between illumination and the onset of maturity, that is now receiving attention in the study of birds and land mammals, should also be considered for marine animals.

3. Fishes.

a. Light discrimination.

Fishes possess the highest type of organ evolved for the detection of light, the eye, and it is natural that much research has been done to discover their powers of observation and colour discrimination. Recently Bull (1935), in his most careful studies on the perceptive faculties of fish by the conditioned reflex method, has shown that the blenny, *Blennius pholis*, possesses a wide range of colour vision. This is a fish that does not discriminate wide differences in intensity and it is therefore unlikely that the colour discrimination could have been an intensity effect. Such work indicates the need for a detailed knowledge of the spectral composition of light beneath the surface and its effects on the visual interpretation of colours as seen at different depths.

It is also possible that detection of differences in light intensity may play a part in the control of the migrations of some fishes. It is for instance notable that the tunny, *Thunnus thynnus*, migrating into the North Sea do not pass through the English Channel neither do they occur in numbers in the southern North Sea far south of about 54° N. latitude. It seems possible that the opacity of the silt laden waters of the eastern end of the Channel and the southern North Sea may be an effective barrier. The possibilities of the effects of artificial light in attracting or diverting fish should be considered. Tauti and Hayasi (1926) found that if a light be projected at night vertically downwards into the water, fish swimming in numbers deeper in the water are only attracted individually to the light when by random movements they swim upwards into a certain threshold intensity.

The vertical migrations of such fish as the herring and the hake must also to some extent be a function of the light intensity.

b. Physiological effects of light and colour change.

It has been suggested by Dannevig (1932, a) that the number of vertebrae in the cod may be influenced in the early stages of development by light. Fish reared in a shallow water pond had a lower number of vertebrae than those of the open sea. He also drew attention (Dannevig, 1932, b) to the susceptibility of cod fry to light in the sea-fish hatchery.

Another manner in which illumination affects fishes and other marine invertebrates is shown by their responses of colour change. The subject of colour change has given rise to a big literature and two recent summaries by Parker (1930) and Sand (1935) may be mentioned. Light influences the colour change both through the eye and directly on the skin surface. A knowledge of the intensities at which the different species normally live is necessary; the adaptive function of colour change in an environment in which illumination is very low, and at which many colours are eliminated has to be taken into consideration. Work by Brown (1936) on the colour change of the minnow, *Ericymba buccata*, indicates an adaptation to very low intensities. For instance the average diameters of the melanin masses in fish kept on a black background varied as follows:—

Light intensity metre candles.[1]	Diameter in μ.
0.00000046	43.1
0.0000049	43.4
0.000058	53.4
0.00116	59.2
0.023	67.9
0.163	78.3
2.21	78.0

In these experiments the sources of illumination were a 200 watt tungsten lamp, a 75 watt daylight Mazda lamp, and a 25 watt tungsten lamp with a daylight filter. The lowest intensities were obtained by means of an iris diaphragm and neutral light filters. Light intensity was measured with a potassium photo-electric cell with maximum sensitivity in the blue end of the visible spectrum, constructed by Professor J. Kunz.

[1]) converted from foot candles.

In the above pages I have attempted to collect together a number of observations dealing with various aspects of submarine illumination in relation to animal life. While not intended in any way as a comprehensive review of the subject sufficient indications should have been given to show how necessary it is to have a thorough knowledge of light conditions beneath the sea surface. This knowledge is essential before the biologist can attempt to relate behaviour observed under experimental conditions in the laboratory with the habits of the animals in the field. To this end there is great need for carefully controlled experiments in the laboratory in which conditions of illumination such as are likely to be found in the animals' normal habitat are used. The elaboration of technique and the advance of our knowledge of conditions in the sea make these aims much more obtainable than they were a few years ago, and the future should show an attempt to regard light as a factor in experimental work every bit as needful of control as temperature.

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