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Behavioural studies on the lesser sandeel *Ammodytes marinus* (Raitt) II. The effect of light intensity on activity

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The behaviour of the lesser sandeel, *Ammodytes marinus* (Raitt), has been investigated at light intensities of 1, 10, 100 and 1000 lux, using a photographic method of recording activity. The level of swimming activity was high at 1000 and 100 lux, declining to a very low level at 1 lux. It was concluded that this was due to the limiting effect of light on feeding. The threshold light intensity for swimming activity in the tank was estimated as being approximately 20 lux but it was considered that in the area of the sandeel fishing grounds the threshold might be higher than this, in the region of 100 lux. The number of hours light per day above 20 and 100 lux at a depth of 15 m in the area of the Outer Dowsing sandbank (53°30′N, 01°00′E) was estimated for the various months of the year. It was shown that during the winter the light intensity does not normally reach 100 lux and only exceeds 20 lux for a few hours each day. It is suggested that this could limit swimming activity and accessibility at this time of year. Measurements were made of the penetration of light into sand and it was concluded that fish which are buried might be able to detect light, possibly via the pineal gland.

I. INTRODUCTION

The importance of light in the phasing of diurnal rhythms of activity has been discussed by Harker (1964), and in fishes many of the diurnal changes of behaviour observed at sea and in the laboratory appear to be controlled or co-ordinated by the daily light/dark cycle (Woodhead, 1966). In feeding rhythms, light is a limiting factor for species which are visual feeders and the main decline in feeding activity appears to be in the region of 1–0·01 lux (Blaxter, 1970). Winslade (1974*a*) showed a diurnal pattern of activity for *A. marinus*, in which swimming activity was confined to the hours of light and dependent on the availability of food. The present experiment was therefore designed to investigate the swimming activity of *A. marinus* at different light intensities in order to establish whether or not light is a limiting factor. The role of light in the control of the annual cycle of activity has also been investigated.

II. MATERIALS AND METHODS

Activity was recorded by a photographic method, and the experimental apparatus and basic technique are described by Winslade (1973*a*). The experiments were carried out in the months of October and November 1969 using nine fish which had been caught on the Haddock Bank (53°20′N, 01°30′E) in December 1968. The fish were allowed ten days to acclimate to the conditions in the experimental tank. During the acclimation period and during the experiment itself, the photoperiod was 11½ h, from 06.00–17.30 h; the temperature was controlled at 10° C and 1 million *Artemia* nauplii were pumped into the tank per day. The light intensity, which was set at 100 lux for the acclimation period, was varied during the course of the experiment. Four different light intensities were used: 1, 10, 100 and 1000 lux. 100 lux was regarded as the standard intensity and the procedure was to change the intensity to one of the other values for one day and then to bring it back to 100 lux for at least another day before changing it again, e.g. 100 lux to 1 lux to 100 lux to 10 lux, etc. Activity was recorded only from 05.00–18.30 h, covering the light period and the hours immediately before and after it. The dark period was not fully covered because Winslade (1973*a*) showed that little swimming activity took place then. Light intensity was measured in photometric units, using an E.E.L. Selenium Cell fitted with a Vλ filter and calibrated from 1–10 000 lux. The instrument had the same response as the photopically-adapted human eye, which has its maximum sensitivity (λ_{max}) at 555 nm. When using photometric units to measure light in relation to fish behaviour the accuracy of the results will depend on the degree of variation of the spectral response of the fish's eye from the photopic Vλ response. No data exist for the spectral response of the eye of *A. marinus* or indeed any *Ammodytes* species, but data on the relative spectral sensitivity of fish, based on absorption characteristics of the visual pigments, electrophysiology, optomotor responses and other behavioural techniques, have been recently reviewed by Nicol (1963), Protasov (1968) and Blaxter (1970). General values for λ_{max} for marine fish species appear to be around 500 nm for scotopic and 550 nm for photopic vision, which is about the same as for human vision. It was assumed that the sensitivity of the eye of *A. marinus* would be similar to that of other marine species, and so it was considered that photometric units would be sufficiently accurate for a preliminary investigation of the effect of light intensity on the activity of the fish and for an estimation of the amount of light available to the fish in their natural environment.

TABLE I. Average levels of swimming and partial emergence activity of *A. marinus* during the light period, at four light intensities

Light intensity (lux)	Number of days	Average level of swimming activity (%) ±S.E.	*P* values*	Average level of partial emergence activity (%) ±S.E.	*P* values*
1	3	2·8±0·5	0·02 +	11·0±2·0	0·001+
10	4	20·0±3·7	0·001+	3·7±1·2	0·001+
100	10	64·0±3·8	>0·10 –	0·74±0·23	>0·10 –
1000	4	63·2±7·0		0·12±0·12	

* These refer to *t* tests made against the values for the next highest light intensity.
\+ = Significant difference.
— = No significant difference.

III. RESULTS

Table I shows the average levels of activity during the light period at the four different light intensities, and Fig. 1 shows the patterns of activity at these light intensities. In Fig. 1 the recording period 05.00–18.30 has been divided into hourly periods apart from 17.00–18.30, which was divided into half hours because the lights were switched off daily at 17.30. The average number of fish swimming and partially emerged was then calculated for each of these time periods and the data for all the days of each particular light intensity were used to calculate a second average and its standard error for the same time periods. These are shown in Fig. 1. There was little difference in the pattern of activity between 1000 and 100 lux, but when the light intensity was reduced to 10 and 1 lux the pattern was radically changed. At 100 and 1000 lux the level of swimming activity during the light period was high, being approximately 65%. The number of fish swimming increased rapidly in the first 2 h of light and then levelled off and tended to decline slightly towards the end of the light period. Very few fish were recorded as partially emerged from the sand when the lights are on. At 1 lux there was little swimming activity. The level of partial emergence activity, 11%, was significantly greater than at the higher light intensities. The number of fish partially emerged was constantly changing during the light period, as shown by the relatively large standard erros in Fig. 1. More than one or two fish were involved, up to five having been recorded in this state on one frame, and so it appears that, throughout the light period, fish which were completely buried in the sand were moving up and partially emerging from it. A few fish might emerge fully and start swimming but only for a relatively short period of 10–90 min. There was a general decline in both forms of activity during the light period. If the fish were dark-adapted at the low light intensity, the flash of white light every 10 min might destroy or interfere with the dark adaptation and consequently affect the behaviour of the fish. In order to test this criticism of the recording method the fish were observed by the experimenter one morning from 06.00–10.00 with the light intensity at 1 lux and with the normal feeding arrangement but without the flash. In this period only two fish emerged, no more than on the days when the camera was recording. The fish spent most of the time swimming along the sides of the tank,

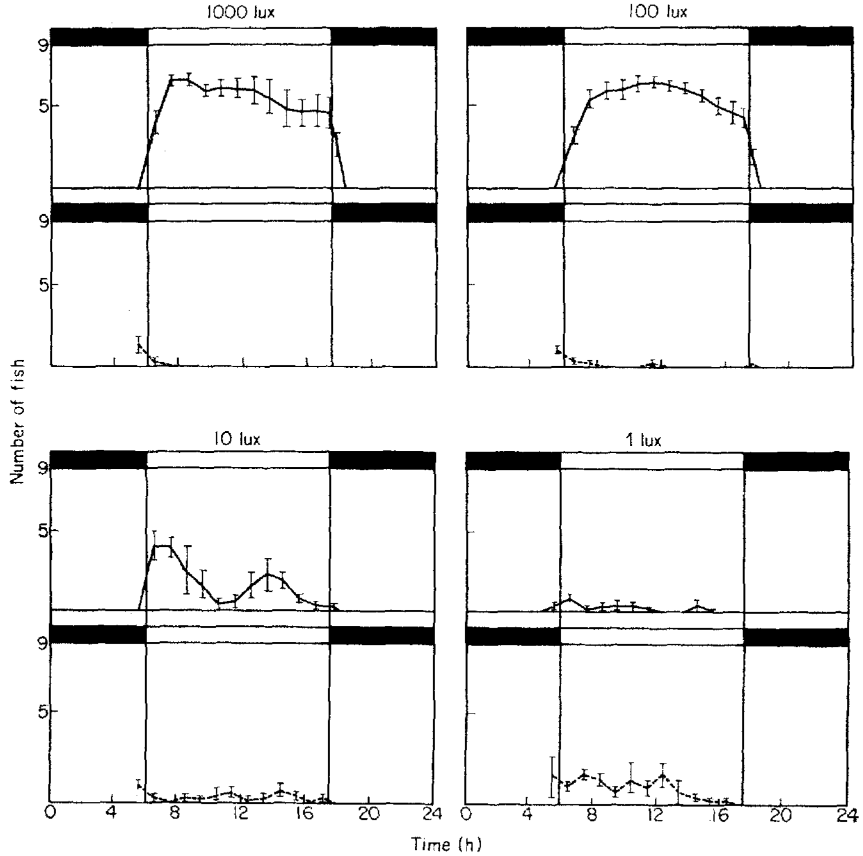

FIG. 1. Activity patterns of *Ammodytes marinus* at four light intensities: 1000, 100, 10 and 1 lux (activity plotted hourly). ——, number of fish swimming; – – –, number of fish partially emerged. Dark bands represent hours of darkness. Vertical lines represent the standard error of the mean.

with their snouts pressed against the glass, at the surface of the water and in the corners of the tank. At 100 lux the fish could be seen feeding and they swam around in the tank and rarely came into contact with its sides or corners or the surface of the water. At 1 lux, although a few fish might emerge to swim, they appeared to be swimming abnormally and were not feeding. The effect of the flash might be to shorten slightly the length of time that the fish remained swimming, but in these observations without the flash no more fish emerged to swim than when it was operating. The light intensity at which swimming activity would fall to 50% of the level at 100 and 1000 lux has been calculated as being approximately 20 lux (Fig. 2) and this will be referred to as the threshold light intensity for swimming activity. Although a small number of fish were recorded swimming when the lights were not on, most of these were recorded in the first half hour after the lights had been switched off and it appears that it took up to half an hour for the fish which had been swimming at this time to bury themselves. This may have been because, in the dark, they had difficulty in burying. Under natural conditions the light intensity would decrease gradually before the onset of night, but this effect was not simulated in the laboratory experiments.

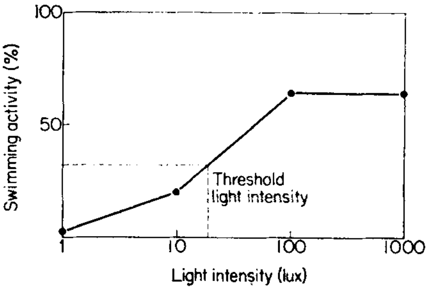

FIG. 2. The relation of the level of swimming activity of *Ammodytes marinus*, during the light period, to light intensity.

IV. THE PENETRATION OF LIGHT INTO SAND

To assess the possible effect of light on fish which are buried, measurements were made of light penetration into sand. The sand used had a granule composition similar to both the type used in the experimental tanks and that found on the sandeel fishing grounds, i.e. it was predominantly fine sand (0·125–0·25 mm). Light intensity was measured in lux, using a Gamma 2020 photometer fitted with a V_λ filter. It was used with a long fibreoptic probe fitted with a cosine receptor head. The light source was the same as used in the other experiments, a daylight fluorescent tube of colour temperature 4300 K. All the light measurements were made in a small Perspex tank with 5 cm of water above the sand. The results are shown in Fig. 3. After the measurements were taken the photometer was calibrated on an optical bench against an NPL standard tungsten filament vacuum lamp. The attenuation of light in sand is very rapid, there being a decrease in intensity of about 3 log units in the first 0·5 cm and about 1 log unit for every subsequent 0·25 cm. There was probably considerable reflection of light at the sand surface and so it is reasonable to assume that there is a decrease in light intensity of about 4 log units per cm, in addition to an initial decrease of about 1 log unit due to reflection of light from the sand surface.

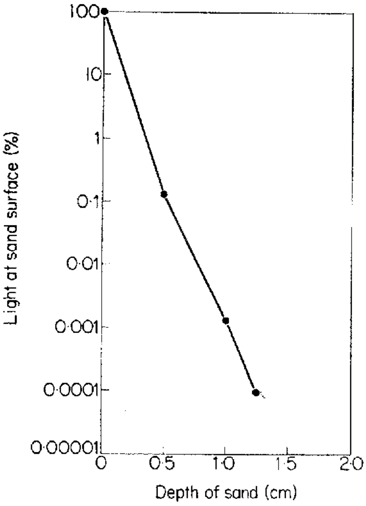

FIG. 3. The attenuation of light in sand.

V. ESTIMATION OF UNDERWATER LIGHT INTENSITY AT THE OUTER DOWSING SANDBANK

Measurements of downward irradiance were made at the southern end of the Outer Dowsing sandbank (53°30'N, 01°00'E) in June 1970, using the Clairex Cell Photometer described by Winslade (1971). There is a regular fishery for sandeels in June on this sandbank. The photometer had the V_λ response function and the irradiance measurements have been used to calculate a diffuse attenuation (=extinction) coefficient, k, using the formula given by Clarke (1954): $I/I_0=e^{-kL}$, where I_0 is the initial light intensity and I is the intensity at depth, L, in metres and e is the base of natural logs. The photometer was not fitted with a cosine receptor and so the measurements were almost certainly lower than the true downward irradiance, but the diffuse attenuation coefficient is a ratio of irradiance values and is only affected by systematic errors that change with depth. The coefficient was calculated for the water mass between 2 and 10 m depth and was found to be 0·212±0·008 (S.E.). It is not known whether the instrument had any systematic error which changed with depth.

Craig & Craig (1965) have produced diagrams which can be used to calculate the light intensity, in lux, just below the surface at any particular time on a ' normal ' day, taking into account latitude and season. They define a normal day as being one with light overcast sky, bright but shadowless, and estimate that a brilliant sun will give values about 50% higher, whilst a heavy overcast sky may reduce the light intensity to a half or quarter of that on a normal day. Their diagrams were used to calculate the light intensity, just below the surface, at the Outer Dowsing sandbank for each hour of a day in the middle of each month of the year. In order to make some allowance for the change in weather conditions with season the values obtained for each month have been adjusted by a weighting factor. This factor has been calculated by reference to the average hours of bright sunshine at Spurn Head (53°35'N, 00°07'E) for the years 1931-60 (Meteorological Office, 1963), this station being only 35 miles from the Outer Dowsing sandbank. The daily mean for the whole year is given, together with daily means for each month. Similarly, the daily mean duration of possible sunshine is given for the year and each month. The mean daily percentage of bright sunshine can then be calculated for the year and each month. The daily percentage for the year has been taken as the standard and regarded as being equivalent to the normal day of Craig & Craig (1965). The ratio of the daily percentage for the month to that of the year has then been called the ' weather weighting factor ' for that month (Table II). The attenuation of light in sea water is due to absorption and scattering, both of which will depend on the amount of inorganic and organic material in the water, i.e. turbidity. No data of changes in turbidity during the year appear to be available for the Outer Dowsing or similar areas, but Lee & Folkard (1969) showed that the overall level of turbidity at any one time is influenced by the amount of wave action, and wave data are available for the Smith's Knoll lightvessel (Draper, 1968), which are thought to be representative of the Outer Dowsing, Norfolk Banks area (Draper, 1967). These data are for winter (January–March), spring (April–June), summer (July–September) and autumn (October–December) and show the percentage exceedance, in time, of waves from 1–15 ft in significant height. The influence that a wave of any particular height will have on the bottom will depend on the maximum orbital velocity of the wave particles at the sea bed, V_{max}, where

TABLE II. Weather and turbidity weighting factors used in estimation of underwater light intensity

	Weather weighting factor	Turbidity weighting factor
January	0·60	0·53
February	0·76	0·34
March	0·93	0·51
April	1·15	0·69
May	1·18	0·87
June	1·18	1·00
July	1·10	1·13
August	1·13	1·28
September	1·12	1·16
October	0·95	1·04
November	0·66	0·92
December	0·57	0·72

$$V_{max} = \frac{\pi H}{T \sin h\, 2\pi D/L},$$

and H=waveheight, T=period, D=water depth and L=wavelength (Inman, 1963). Draper's data can be used to calculate the mean period for the different waveheights from which the wavelength can be derived (see Inman, 1963) and hence V_{max}. On the Outer Dowsing sandbank the main fishery for sandeels takes place at a depth of between 10 and 20 m and so V_{max} has been calculated for the intermediate depth of 50 ft (approximately 15 m). It would be 0·31 ft/sec for a 1 ft high wave and 0·69 ft/sec for a 2 ft high wave. The former would probably not cause any significant motion of material at the sea bed, whereas the latter would cause coarse sand to move (Inman, 1963) and so might be expected to influence the overall level of turbidity. The percentage of time for which 2 ft high waves are not exceeded, a measure of calmness, has therefore been obtained from Draper's data. Plotting these for the mid-point of each season and joining the points gives a percentage value for the middle of each month of the year and these values have been expressed as a percentage of the June value to give a ' turbidity weighting factor ' for each month (Table II). It is difficult to predict what the precise relation of turbidity is to wave action, since the former will depend on other factors such as speed of tidal stream and the amount of organic material present. The levels of light intensity at 15 m depth on the Outer Dowsing sandbank have been calculated by applying the diffuse attenuation coefficient $k=0{\cdot}212$, obtained in June 1970, to the predicted levels of light intensity just below the surface. They have then been multiplied by the ' turbidity weighting factor ' in order to make some allowance for the probable changes in turbidity and, therefore, light attenuation during the year. Fig. 4 shows the estimated values of light intensity at 15 m depth for an average day in December, March and June. It can be seen that in December the laboratory threshold of 20 lux is only just exceeded for a very short period around midday, whereas in June light intensity is well above the 100 lux level for about 16 h. Fig. 5 shows the number of hours at which the light intensity would be above 20 and 100 lux on an average day for each month of the year.

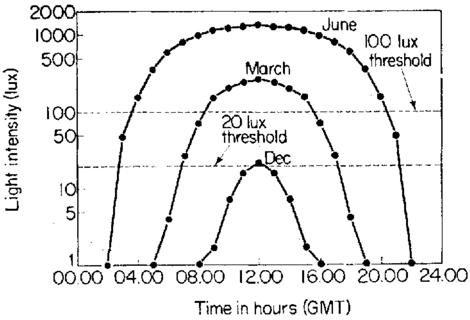

FIG. 4. Estimated daily light intensities at a depth of 15 m on the Outer Dowsing sandbank for the months of December, March and June.

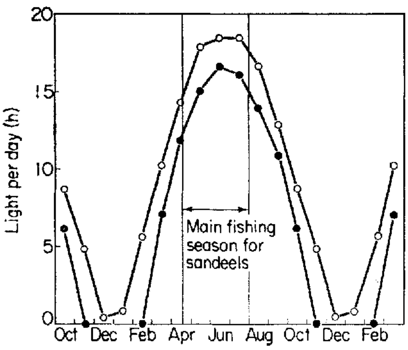

FIG. 5. Estimated daily number of hours of light above 20 lux (○—○) and 100 lux (●—●) at a depth of 15 m on the Outer Dowsing sandbank, for the different months of the year.

VI. DISCUSSION

The results show that light intensity has a controlling effect on the level of swimming activity and this activity was shown by Winslade (1974*a*) to be associated with feeding and the availability of food. The detection of an object in water relies on contrast perception. The contrast may be one of colour or radiance but the latter is probably of more importance to *A. marinus*, which feeds on planktonic organisms, copepods in particular. It can be seen from the theory of underwater visibility proposed by Duntley (1962) that radiance contrast is independent of light intensity. The ability of a fish to perceive contrast in radiance generally declines with decreasing light intensity (Hecht, 1937; Hester, 1968; Protasov, 1968), as do both acuity and movement discrimination (Nakamura, 1968; Protasov, 1968) and so, for visual feeders, light will be a limiting factor. Observations of *A. marinus* which were swimming at 1 lux showed that they were not feeding, probably because they were unable to detect and capture the nauplii at this low light level. The fish were feeding actively at 100 lux, though, and so feeding may be said to decline between 100 and 1 lux. The definition of a visual threshold for feeding varies in the literature and so it is best to take the range over which feeding declines, when making comparisons between species. The herring, *Clupea harengus* (L.), which is also a plankton feeder, shows a decline within the same range as for *A. marinus*, 100–1 lux (Blaxter & Holliday, 1958). Blaxter (1970), in a review of the subject of light in relation to fishes, considered that the main decline for visual feeders takes place at a lower level, 1–0·01 lux. Part of the recorded variation between species is due to the photometric measurement of light, which cannot take account of the variation in the spectral sensitivity of fishes' eyes or the variation in light sources used in different experiments. The gear used in the commercial fishery for sandeels in the North Sea is a bottom trawl which lightly skims the sand bed and has a high headline. The fishery takes place only during the hours of daylight, catches at night being very small (Roessingh, 1957; Bertelsen & Popp Madsen, 1958; Macer, 1966). This diurnal variation in catch can be explained in terms of the visual feeding habits of the fish as shown by the experiments described in this paper. Feeding and swimming activity is limited by light and when the fish cannot feed they remain in the sand, either completely buried or partially emerged, and so they would be inaccessible to the standard sandeel trawl. In June, which is usually the month when landings of sandeels reach their peak, the light is generally above a level of 20 lux for about 18½ h on a normal day and above 100 lux for about 16½ h. The latter time corresponds approximately with the duration of the daily fishery, which extends from about 04.00–20.00 (GMT), and 100 lux is thought to be a more realistic estimate of the threshold for swimming activity at sea. This is because the conditions in the experimental tank were probably more favourable for food detection than at sea, due to the clear water used, the high density of nauplii present and the good contrast provided by the black background of the tank. In addition to marked diurnal variations, the fishery is also very seasonal in nature. It generally begins sometime in April and extends to July or occasionally August, with peak catches in June (Reay, 1970). Outside the normal fishing season large quantities of *A. marinus* are rarely caught. To be accessible to the type of trawl used in the sandeel fishery the fish must be completely emerged from the sand and swimming. The results of the prediction of light at sea in the area of the sandeel fishing grounds show that for three months in winter the light intensity does not reach the 100 lux level at any time on a normal day and only exceeds 20 lux for a few hours, and so could limit swimming activity and, therefore, accessibility during the winter months.

The spawning period of *A. marinus* is December and January (Kändler, 1941; Macer, 1966) and fish kept in laboratory holding tanks spawned each year in the latter half of January (Winslade, 1971). Many species of fish show an annual periodicity in their reproductive timing which may be very precise, as shown by Cushing (1969), and in mid- and high-latitude species has often been shown to be under photoperiodic control (Schwassman, 1971), probably the most stable of all environmental factors. Since it is thought that *A. marinus* remains buried in the sand from the end of one summer until the next spring, apart from emergence for spawning (Winslade, 1974*b*), the question arises as to whether the fish will be responsive to light when they are buried. Examination of the head of *A. marinus* shows that the dorsal side of the skull is very transparent and the pineal gland may be seen lying on top of the brain, which suggests that it may be involved in light perception. Hamasaki & Streck (1971) estimated the pineal sensitivity of the dogfish, *Scyliorhinus caniculus* (L.), to be in the order of 4×10^{-6} lux, and values for the sensitivity of the gland of other species range from 2×10^{-2}–$2{\cdot}5 \times 10^{-6}$ lux (Morita, 1966; Hanyu & Niwa, 1970). Values of the absolute visual thresholds for fish appear to be within a similar order of magnitude, 10^{-5}–10^{-6} lux (Grundfest, 1932; Blaxter, 1968, 1969). Assuming that the pineal gland of *A. marinus* may be sensitive to light intensities as low as 10^{-6} lux, and taking a mean summer value of light intensity at the sand surface on the sandeel fishing grounds of 1000 lux, then the fish may be able to detect light to a depth of 2 cm in sand. In winter the depth of detection might be reduced to about 1·5 cm. It is possible that the attenuation of light in sand *in situ* is not as rapid as measured in the laboratory, because the water content is probably greater due to irrigation of the sand bed by wave action (Webb & Theodor, 1968). Observations of fish in the laboratory suggest that they rarely bury to a depth greater than 5 cm and some lie much shallower than this. It is possible that they may normally be within the range of light detection of the pineal. A more detailed knowledge of the depth of burial and orientation of the fish in the sand would be required before it could be confirmed that photoperiod played a part in the control of spawning or annual cycle of activity of the fish whilst they remain buried.

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