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Sensitivity to light and circadian activity of Pontoporeia affinis (Crustacea, Amphipoda)[1]

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Pontoporeia affinis Lindström is a benthic species which, however, rises from the bottom during the night and swims around freely. This behaviour was studied under laboratory conditions in aquaria where swimming activity was recorded by counting interruptions in beams of infra-red light. The results show that the main factor regulating swimming activity is visible light, but that the animals also possess an innate circadian rhythm which influences their behaviour in this respect. The threshold for light as a Zeitgeber is extremely low (0.36×10^6 photons/cm^2/sec at 564 nm), corresponding to an incidence of approximately 2.5 photons/sec per ommatidium of the eye.

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1. Introduction

The amphipod *Pontoporeia affinis* Lindström, generally classified as a benthic species of soft mud bottoms (see Segerstråle 1959), rises from the bottom mainly at night and swims around in the overlying body of water (Hessle & Wallin 1934, Segerstråle 1937a, b, Larkin 1948, Wells 1960, 1968, Marzolf 1965a, b). Vertical migration of this kind is particularly evident in the sexually mature males.

This species thus displays behaviour similar to that described for other amphipods in response to various environmental stimuli: *Synchelidium* (Enright 1963), *Corophium volutator* (Morgan 1965), *Gammarus* species (Jansson & Källander 1968, see also Segerstråle 1944, Rygg 1972), *Bathyporeia pelagica* (Fincham 1970), *Orchestia* species (Wildish 1970), *Bathyporeia pilosa* (Preece 1971), *Marinogammarus marinus* (Fincham 1972), *Cheirimedon femoratus* and *Tryphosella kergueleni* (Bregazzi 1973).

Many of these investigations have demonstrated the presence of an endogenous timing mechanism, in which both light and tidal (mechanical, hydrostatic) stimuli can act as Zeitgebers. It can therefore be assumed that similar mechanisms regulate the onset of swimming activity in *Pontoporeia*. In the Baltic sea tidal stimuli are excluded as possible Zeitgebers. Here *Pontoporeia* is found at depths from 2—3 m down to almost 300 m. Daily changes in temperature do not occur in the coastal waters at depths below 10 m. Thus, the only major circadian variable in the aquatic environment of these animals is light intensity. Changes in illumination can therefore be assumed to act as Zeitgebers for the swimming activity, which is observed almost exclusively at night (Segerstråle 1937a, Marzolf 1965a, b). In laboratory tanks these amphipods readily show this behaviour: they emerge from the bottom and swim freely about when in darkness, but burrow into the bottom substrate when exposed to light.

Furthermore, changes in illumination and daylength apparently affect and control the reproduction of *Pontoporeia* (Segerstråle 1967, 1970, 1971). Examination of samples taken from various depths shows that in the Baltic Sea sexually mature specimens are generally found during November — December. At depths of over 60 m, however, reproduction is observed during the summer season also (Segerstråle 1967). These observations suggest that maturation of the

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gonads is dependent on the decrease in light in autumn, and that light has less influence at greater depths. This conclusion receives support from laboratory investigations on the development of the gonads of *Pontoporeia* in aquaria, some exposed to daylight, and others in complete darkness. In the latter gonadal development was found to reach a much more advanced stage during the same period of time (Segerstråle 1970).

The attenuation of light in the waters of the Baltic Sea is strong as compared to the situation in oceanic waters. Jerlov (1970) reports a reduction in overall light intensity to about 1 % for a 10 m increase in depth. From this value and from the threshold for vision, which can be deduced from ERG measurements on *Pontoporeia*, a rough estimate shows that at depths below 80—90 m light is below the perception threshold of these animals even with full daylight at the surface. Thus at such depths they can be assumed to have no perception of light at any time of day. The simple compound eye, containing 30—40 ommatidia in mature specimens, appears particularly well adapted for vision at low light intensities. The spectral sensitivity of the eye peaks at 550 nm, which is the wavelength of maximal transmission of light in the Baltic Sea (Donner 1971).

The present paper reports the results of a laboratory investigation into the swimming activity of *Pontoporeia*. The aim was to study the basic characteristics of this activity, the possible presence of an endogenous circadian rhythm, and the effect of different light intensities as Zeitgebers, and thus to obtain a threshold value for a reaction to light under these conditions. The activity was measured by recording impulses caused when swimming animals interrupted beams of infra-red light passing through the aquaria; a counter summed these impulses for predetermined periods of time, usually 1 h. Thus the activity could be recorded in full darkness, as well as under various conditions of illumination. A similar recording technique has been described by Cripe et al. (1973).

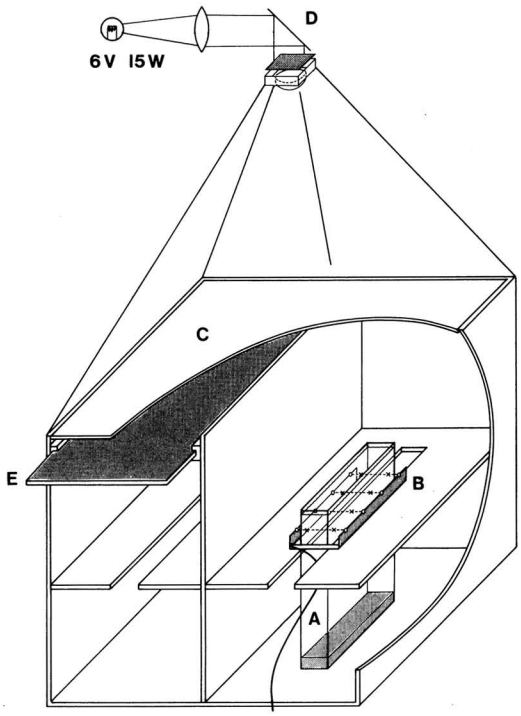

Fig. 1. Drawing of the essential features of the box containing the test aquaria and the system giving the illumination inside the box. — A: test aquarium. — B: recording frame with light-emitting diodes and phototransistors, the broken lines showing the beams of infra-red light. — C: opalescent screen of acrylic plastic. — D: illumination system with 6 V, 15 W lamp, convex lens, mirror and condenser lens together with holder for interference and neutral filters. — E: board shutter to cut off the light completely from the second aquarium (not shown). The front of the box was provided with a light-tight door.

2. Methods

The work was carried out at Tvärminne Zoological Station in 1972—78. The equipment shown in Fig. 1, built into a temperature-controlled room maintained at +3 — +4°C, was used to record swimming activity under controlled conditions.

The light-tight box containing the test aquaria was of the shape shown in Fig. 1. Two test aquaria (Fig. 1: A, only one shown) were used, each with dimensions 35 × 33 × 6 cm, in a separate compartment of the lower part of the box. They had metal frames, and were made of 2-mm glass. For the experiments they were filled with brackish sea water, with a 2-cm layer (about 400 ml) of mud as bottom substrate taken from the bottoms from which the animals were caught. No aeration was used; measurements showed that under these conditions there was a steady oxygen content of about 8 mg O_2/l. Under these conditions experiments could be run for 4—5 months without great changes in average activity. In experiments lasting 165 days the mortality was 15—27 %. Occasionally a film of bacteria formed on the surface and had to be removed. This was done in darkness and was found not to disturb the prevailing activity.

The recording apparatus consisted of a frame (Fig. 1: B) provided with four infra-red light-emitting diodes (ME 7024, dominant wavelength 900 nm, width of light beam about 5°) on one side and four corresponding phototransistors on the opposite side of the aquarium. A signal was generated when any one of the beams was intercepted by a swimming *Pontoporeia*. The resulting electric

pulses were led to a counter provided with a printer that printed the number of pulses recorded during a predetermined interval, usually 1 h. The timing was given by a separate timing device, operated by a synchronous motor switch.

In this way a continuous record was obtained giving the number of pulses/h. This value was used as a measure of activity. Obviously, such recording does not allow discrimination between the effect of a few, very active animals and a larger number of slowly swimming ones. The recording apparatus was developed and constructed by Mr. V. Matila (Sondi Oy).

The lower part of the box, housing the aquaria, was painted black inside (Fig. 1). At C a sheet of opalescent acrylic plastic separated this part from the upper, pyramid-shaped part, which was painted white inside to ensure homogeneous distribution of the light admitted through the top at D. Light from a microscope lamp (6 V, 15 W) was projected through a convex lens and reflected by a mirror down through a condenser lens fitting the hole in the top of the pyramid. In front of the condenser lens filters could be placed. Interference filters (Balzers, half-bandwidth 11—13 nm) and neutral filters (Balzers) were used to obtain near-monochromatic light of different intensities inside the box. The light was automatically switched on and off at predetermined times of day. In most experiments the light:dark (L:D) ratio was 7 : 17.

The illumination inside the box at the level of the recording frame (Fig. 1: B) was measured with the aid of an Airam UVM-8LX luxmeter, calibrated in absolute units by Airam Laboratories for the wavelength 564 nm, which was the one mainly used in the experiments. The relative intensities of the other wavelengths used, in relation to 564 nm, were calibrated separately with the aid of a thermocouple placed at the light focus (cf. Donner & Reuter 1968). The optical density of the combinations of neutral filters used to attenuate the light was measured in a photometer used for the study of rhodopsin photoproducts (see Donner & Hemilä 1975).

Since very weak light intensities were used in most of the experiments, great care was taken to eliminate any stray light and to make the box completely light-tight. Thus when the light from the top was switched off, the only light inside the box was the infra-red light emitted by the diodes of the recording apparatus. A basic assumption is that this light is invisible to the animals. As stated above, the light emitted has its peak wavelength at 900 nm, with a range of 800 — 1 000 nm. The eye of *Pontoporeia* has its sensitivity maximum at 550 nm (Donner 1971).

A rough extrapolation of the spectral sensitivity curve shows that at 900 nm the threshold intensity should be at least 7 — 8 decades higher than at 550 nm. The threshold value obtained in the present experiments is of the magnitude 10^{-7} $\mu W/cm^2$ at 564 nm, which would thus correspond to 10 — 100 $\mu W/cm^2$ at 900 nm. The average unattenuated output of each light-emitting diode is 500 μW, although this is partly reflected and absorbed during passage through the aquarium. Thus, a faint effect of the measuring light on the animals when passing the beam cannot be completely excluded, as the extrapolation of the sensitivity curve to 900 nm is wholly conjectural.

The experimental animals were fairly large ones (length 6 — 8 mm), freshly collected with a van Veen sampler from Tvärminne Storfjärden at a depth of 31 m. Occasionally they had been stored for some time under natural lighting conditions in large tanks in the laboratory. In experiments 40 — 50 animals were used in each aquarium.

The present results are based on recordings carried out during a total of 1442 days.

3. Results

3.1. General properties of the circadian activity

The typical situation when an experiment was started on an L:D 7:17 regime is shown in Fig. 2. During the first 3 days of recording the illumination had only a very slight effect on swimming activity. Gradually, however, the activity was reduced during the L period so that finally very little swimming occurred while the light was on, signifying that the animals remained on the bottom.

Light of wavelength 564 nm was used here, which closely corresponds to the spectral sensitivity maximum of the eyes of these animals and to the wavelength of maximum transmission in the Baltic Sea (Donner 1971). After 12 days under the L:D regime, the experiment was continued in full darkness for 5 days (Fig. 2). Some of the rhythm induced by the light is seen to have persisted, though it was less regular.

From experiments of the kind shown in Fig. 2 some general features emerge concerning the reaction of *Pontoporeia* to light:

1. Animals taken from nature and placed directly in the experimental aquaria seem to have no rhythmicity and react only weakly to light. Possibly the handling of the animals has made them asynchronous with regard to any circadian rhythm they may possess, so that the summed activity of the 40 — 50 animals in the aquarium shows no trace of any rhythmicity.

2. The reaction to light, i.e. the reduction or complete absence of swimming activity, is entrained after 3 — 4 days of an L:D regime. This activity, high in darkness and low or absent during the L phase, is consistent with the behaviour of *Pontoporeia* in nature.

3. After the entrainment of rhythmic behaviour to light the animals, when placed in full darkness, display a rhythmic circadian activity. This is irregular, however, and less pronounced than under L:D conditions.

The observation, mentioned under 1 above, that animals collected from nature, though placed directly in the experimental conditions,

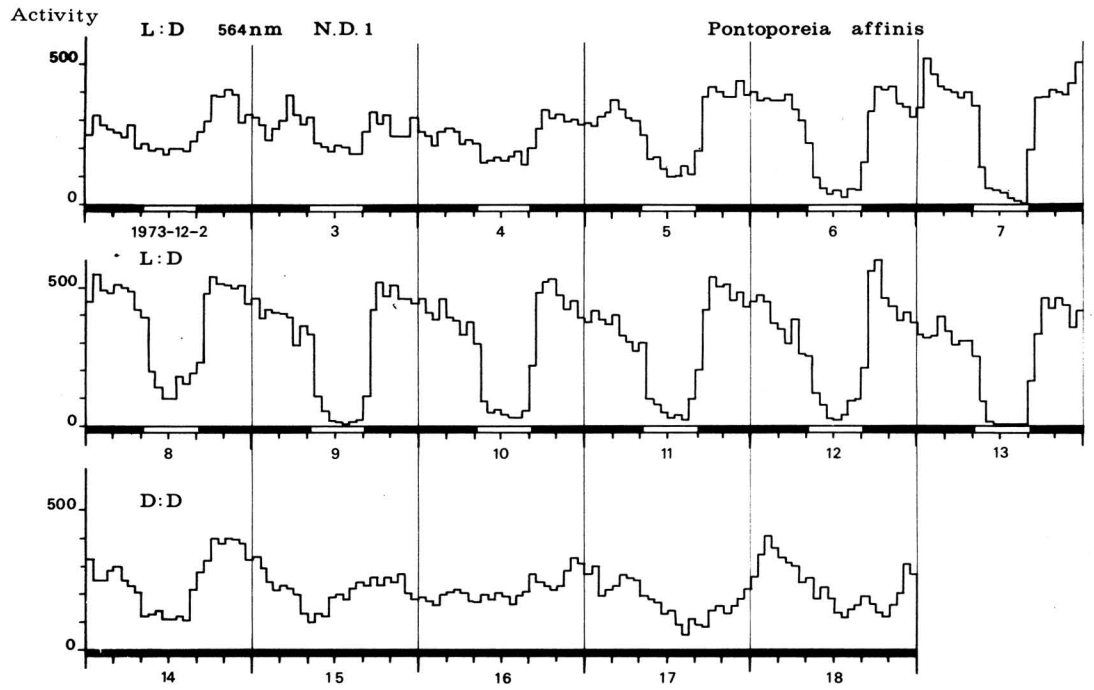

Fig. 2. Activity recording for 17 days, beginning 2.XII.1973. The first day corresponds to the start of the experiment with L:D 7:17. Light 564 nm, intensity corresponding to log —1 in Fig. 6. Ordinates pulses/h. Light period shown along the abscissa for each day. After the establishment of a reaction to the light period, seen as a strong decrease in activity during the time the light was on, the experiment was continued in constant darkness for 5 days (lowermost row).

appear arrhythmic or are totally asynchronous is consistent with what Morgan (1965) observed in *Corophium volutator*. He found that animals collected from non-tidal brackish pools were arrhythmic. To see whether prolonged recording of the swimming activity of *Pontoporeia* under conditions of constant darkness would show the development of some kind of rhythm, the experiment shown in Fig. 3 was performed. It lasted for 36 days and was carried out in a cellar in Bromarv, not far from Tvärminne, where the ambient temperature remained fairly constant, showing no diurnal variations, but rising during the test period from +4° to +10°C. The experiment also served as a check on whether external Zeitgebers of some other kind could induce a circadian rhythm. No such rhythm appeared during the 36 days of recording, although irregular fluctuations in activity were seen. Two conclusions are possible: either the animals do not possess an endogenous circadian rhythm in nature and hence swimming activity is regulated by the prevailing conditions of illumination, or alternatively the rhythmicity is disturbed or destroyed by handling when the animals are collected (see Enright 1976). During this procedure they are also exposed to full daylight, which is a very strong light stimulus compared with the intensities they encounter in their natural environment.

To examine further the existence of an endogenous rhythmicity after the establishment of a light-induced rhythm, prolonged recordings of activity were carried out under constant conditions. An example is given in Fig. 4. The first day shown (upper left) is the activity on day 55 of the experiment with a L:D regime of 9:15. The light stimulus used was very weak (564 nm, intensity corresponding to log —4, Fig. 6). The experiment was then continued under constant conditions in darkness for a further 15 days. The rhythmic activity was seen to persist after removal of the external Zeitgeber, but the periodicity was no longer exactly 24 h. During the last few days (lowermost row, Fig. 4) activity was minimal soon after midnight. According to these particular data, the period of the endogenous circadian clock is 23.4 h. In other experiments similar values

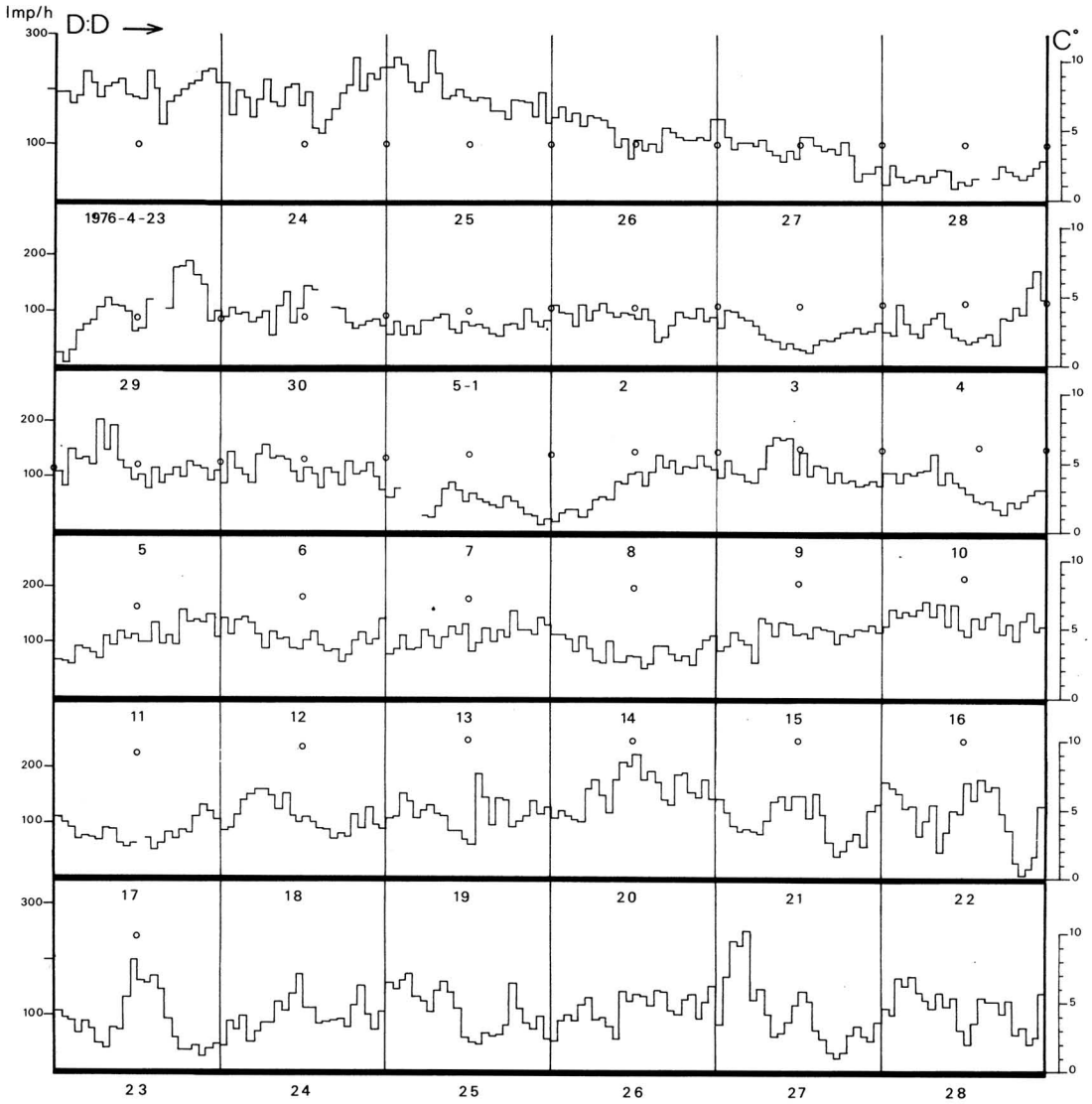

Fig. 3. Experiment in constant darkness with animals freshly caught from the sea, without preceding L:D regime. Symbols as in Fig. 2. Temperature for each day given as a dot, temperature scale on the right. Recording for 36 days starting 23.IV.1976.

were found, but there is so far no consistent picture of the way in which the length of the period may vary in relation to the length of the photoperiod used to establish the rhythm or the intensity of illumination used, or when a constant light is used instead of full darkness. However, in experiments of the type shown here the period of the endogenous rhythm in full darkness is slightly shorter than 24 h (23.2 — 23.8).

A result of the kind shown in Fig. 4 will be obtained only if the 40 — 50 animals used are well synchronized with each other and possess biological clocks with the same period. A variation of 0.5 h in the period among the individual animals used for the experiment in Fig. 4 would in 15 days cause phase differences of 7.5 h, i.e. the record would become progressively less rhythmic on successive days. However, as

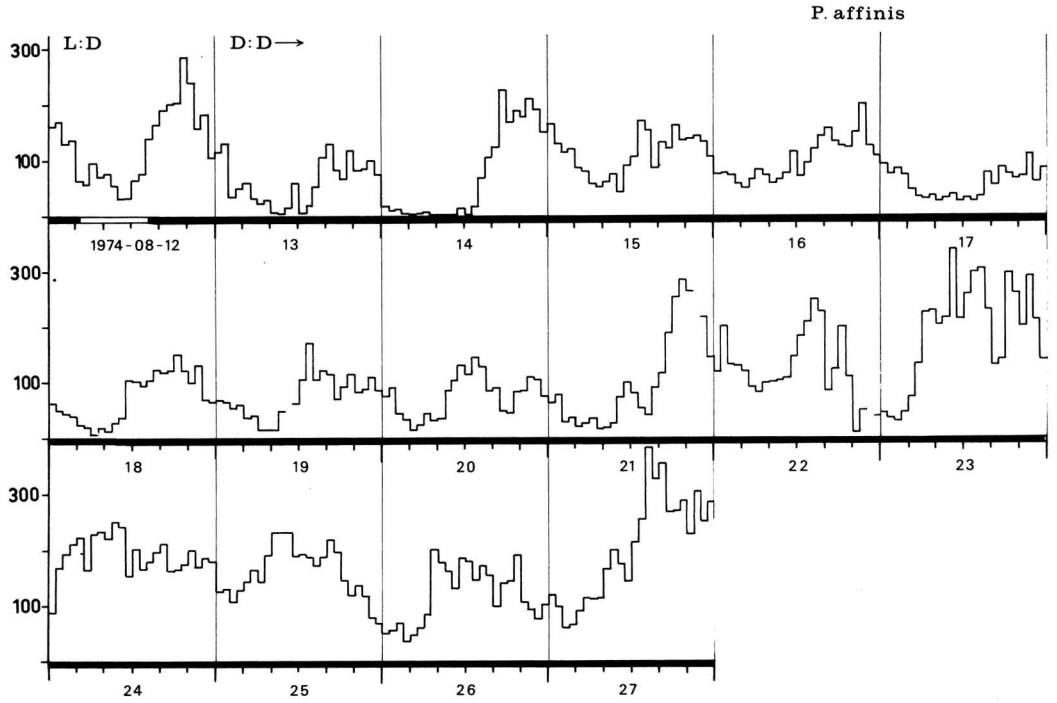

Fig. 4. Activity in constant darkness after 55 preceding days on an L:D 9:15 regime. The last day in L:D conditions shown (upper left, 12.VIII.1974). Note persistent rhythmicity during the following 15 days, with a period of about 23.4. h.

found by Bregazzi & Naylor (1972) when studying the rhythm of locomotor activity in the littoral amphipod *Talitrus saltator*, amphipods appear able to synchronize mutually when the phase difference between individuals is small. Presumably, such a mutual synchronization explains the present results. The particular experiment shown in Fig. 4 gave the clearest evidence of the persistence of rhythmicity. In the others the rhythmicity frequently disappeared after 6 — 7 days in constant conditions.

3.2. The threshold value for light as a Zeitgeber

The effect of varying the intensity of the light used during the L period is illustrated in Fig. 5. Here examples are given for 5 consecutive days of recording in two cases where the higher light intensity used (upper row) was 1 000 times (3 log units) stronger than the lower intensity (lower row). Activities are given as 3-h running averages for each hour. At the higher intensity the effect of light was very clear, swimming activity diminishing rapidly when the light was switched on and increasing again steeply when it was switched off.

At the lower intensity, however, there was much more variation and light had a less clear-cut effect. Indeed the record could be interpreted as endogenous circadian activity of the kind shown in Fig. 5 under constant conditions, with an internal rhythm of around 24 h. However, the experiments carried out on endogenous activity in constant darkness showed a rhythm with a period of less than 24 h and thus also after several days of recording a phase-shift in relation to the 24-h day. This did not occur under the conditions of the experiment shown in Fig. 5. A number of experiments lasting 10 — 15 days all showed a significantly lower average activity during the L phase than during the corresponding D period.

To investigate quantitatively the effect of light intensity, average hourly activities during the L and D periods were calculated from experiments lasting 12 — 15 days. The results are shown in Fig. 6 as a rhythmicity index I_r = Act L/Act D.

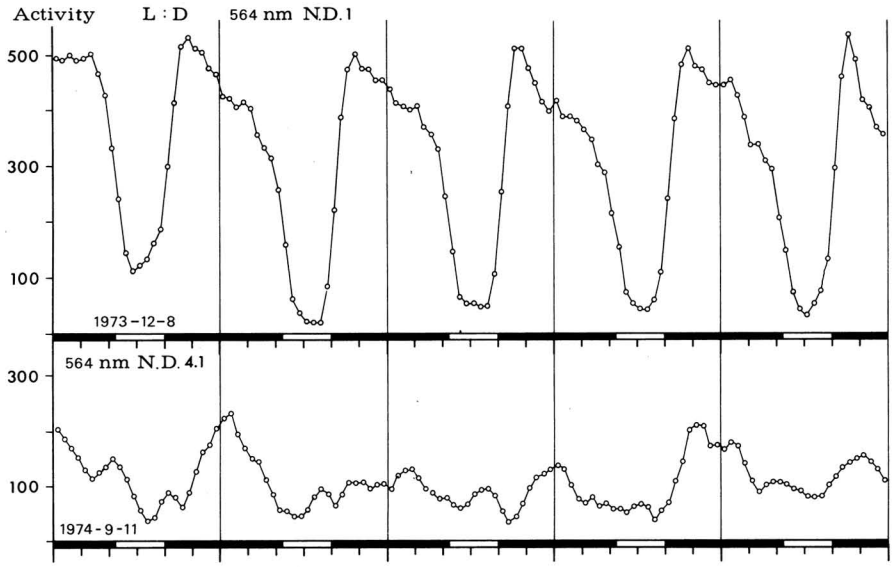

Fig. 5. Activities under L:D 7:17 after several days of preceding conditioning to the light rhythm with two different light intensities. Upper record, first day 8.XII.1973, 564 nm, log $I = -1$ (scale in Fig. 6). Lower record, first day 11.IX.1974, 564 nm, log $I = -4$. Activities given as 3-h running averages.

Obviously, in the ideal case with a strong light this index can be expected to give values near zero, with little or no activity during the light period (all animals in the bottom layer) and considerable activity during the dark period. On the other hand, index values close to 1 would be expected when the light used is too weak to be perceived by the animals. This is true even in the presence of some endogenous rhythmic activity of the kind shown in Fig. 4, where during the last few days of the experiment the peak of activity occurs during what was originally the L period. Fig. 6 gives values for this index in relation to the intensity and wavelength of the light. The dots are data from three experiments carried out in constant darkness after previous entrainment to an L:D regime. The values are seen to be close to unity. Moreover, in full agreement with prediction, strong white light (squares) gives an index close to zero.

Considering then first the values obtained for light of wavelength 564 nm (circles), it can be seen that with reduced intensities the index gradually increases and approaches a value of 1, the value obtained in full darkness. The light threshold is then given by the value on the log I scale at which the curve (drawn free-hand) reaches an index value of 1. This point lies at log $I = -4.5$. According to the intensity

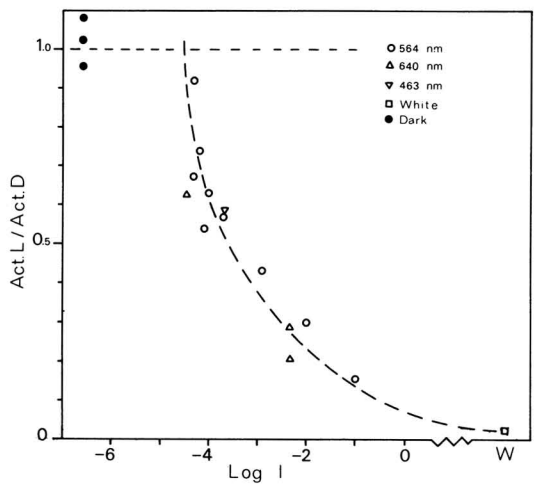

Fig. 6. Values for the activity index I_r = average activity/h in L: average/h in D for light of various intensities and wavelengths during the L period. Index for experiments in continuous darkness given on the left-hand side of the diagram (dots), 564 nm (circles): intensities given by log I scale, where log $I = 0$ corresponds to 1.09×10^{10} photons/cm^2/sec. The intensities for 640 nm (open triangles) and 463 nm (filled triangles) have been corrected to give a probability of quantum absorption equal to that at 564 nm, using the relative calibration of the lights and the spectral sensitivity of the *Pontoporeia* eye (Donner 1971) as a basis for the calculation.

calibration, log $I = 0$, and, when reduced by the neutral density 4.5, this corresponds to an intensity of $0{,}36 \times 10^6$ photons/cm^2/sec. The receiving area of an ommatidium of the *Pontoporeia* eye is about 700 μm^2 (Donner 1971). Hence the average photon flux incident on a single ommatidium at the threshold equals approximately 2.5 photons/sec. The calculation assumes that the luminous flux coming from all parts of the opalescent screen above the aquaria (see Fig. 1) is equally effective and also that the angle of acceptance of an individual ommatidium is very wide, an assumption that seems consistent with their shape and structure (see Donner 1971). However, the calibration of the light was carried out at the level of the recording frame, i.e. fairly high up in the aquaria, only 2.5 cm below the surface of the water. Thus the threshold value obtained probably represents a maximum value.

In addition to the wavelength of 564 nm, wavelengths of 640 and 463 nm were tested (open and filled triangles in Fig. 6). The results, given in terms of the index obtained, have been corrected as regards intensity to correspond to an equal probability of quanta being absorbed as compared to the data for 564 nm. The calculation is based on the relative sensitivities of the eye at the wavelengths used, obtained from the spectral sensitivity curve (Donner 1971), and a calibration of the relative intensities of the light of different wavelengths. The index values obtained for red (640 nm) and blue (463 nm) light fall reasonably well along the same curve as those obtained for yellow (564 nm) light, which confirms that the action of light is actually mediated through the eyes, or through a photosensitive system with the same spectral sensitivity as that of the eyes. The latter alternative is excluded, however, since no other photosensitive organs have been found in amphipods except the eyes (Elofsson 1965).

4. Discussion

The results of the present investigation show that in *Pontoporeia* vertical migration is governed by two factors: the prevailing illumination and an endogenous clock with a period of slightly less than 24 h in full darkness. At least at relatively high light intensities, however, light appears to be the sole factor determining the activity pattern recorded.

So far experiments have been carried out mainly with a 7-h light period and with the preferred bottom substrate of these animals in the aquaria. Variations in these parameters may well be of ecological importance. Marzolf (1965 a) has shown that the distribution of *Pontoporeia* in Lake Michigan correlates only with the presence of bacteria and organic matter in the bottom sediments. Such a distribution is hard to understand unless the quality of the bottom substrate has an effect on the tendency to rise from the bottom, a preferred substrate reducing this activity and an unsuitable substrate having the opposite effect. Indeed Fincham (1970) demonstrated an increase in the activity of the sand-burrowing, intertidal amphipod *Bathyporeia pelagica* after removal of sand from the aquarium. Experiments described by Lindström & Lindström (1980a) show that effects of this kind are present in *Pontoporeia* too, and that the time of year is another factor influencing the general level of activity.

Pontoporeia, being very abundant in the northern parts of the Baltic Sea (up to 20 000 ind/m^2), is an important component of the food web. The fish species known to feed on *Pontoporeia* include the Baltic herring (*Clupea harengus* var. *membras*), the smelt (*Osmerus eperlanus*) and the fourhorn sculpin (*Myoxocephalus quadricornis*) (Segerstråle 1937b, Aneer 1975). A point of particular interest is that, according to Aneer (1975), the Baltic herring, which presumably catches its food in open water, preys on *Pontoporeia* mainly during the period October — December, whereas the fourhorn sculpin, being a bottom-feeder, feeds on this amphipod all the year round, although taking a heavier toll during the summer months. This difference probably reflects seasonal differences in the swimming activity of *Pontoporeia*. If so, any change in this activity induced by environmental changes or pollutants will affect the availability of the animals as a source of food for the Baltic herring (Lindström & Lindström 1980b).

The present experiments illustrate the extremely high visual sensitivity of these animals, in which light can act as a Zeitgeber for rhythmic activity at intensities well below the absolute threshold of the human eye. This is mainly because a single ommatidium has a wide angle of acceptance and thus collects light from a large area of the visual field, whereas the summation area for the human eye is around 1°. At threshold, the number of quanta received per ommatidium per second is about 2 — 3, of which hardly more than 1 is absorbed by the visual pigment. In view of the fact that single quantum

events (quantum bumps) have been recorded in a number of rhabdomeric photoreceptors in compound eyes (see e.g. Lillywhite 1977, 1978) it is not surprising that very low light intensities can act as Zeitgeber stimuli. Indeed, effects at very low levels of illumination on the entrainment of a rhythm have been described for the median eyes of a scorpion, *Androctonus australis*, by Fleissner (1977a—c). The light threshold found in the present experiments is consistent with the value that can be deduced from ERG recordings from the eye of Pontoporeia (Donner 1971).

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