

OBSERVATIONS OF THE  
EFFECTS OF CHANGES IN HYDROSTATIC PRESSURE  
AND ILLUMINATION ON THE BEHAVIOUR OF  
SOME PLANKTONIC CRUSTACEANS

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INTRODUCTION

Since the first evidence of barosensitivity in planktonic crustaceans was provided by the field experiments of Hardy & Paton (1947), a number of workers have investigated the effects that small changes in hydrostatic pressure have on the behaviour of marine invertebrates. The results of these experiments were recently reviewed by Knight-Jones & Morgan (1966), with a discussion of the possible adaptive significance of the pressure responses. In many cases the behaviour which results from a pressure fluctuation appears to be depth-regulatory: an increase in pressure causes an increase in swimming activity and an upward swimming excursion, whilst a fall in pressure leads either to passive sinking or to an active downward movement. The factors which exert control on the vertical migrations of planktonic animals, particularly light and temperature, have been the subject of lengthy discussions in the past. It is now generally accepted that light plays a major role with other factors, physiological and environmental, having a modifying effect on the underlying pattern. More recently it has been suggested that sensitivity to hydrostatic pressure may be an important factor in limiting the overall range of these migrations. In the simplest terms this would involve accommodation to the slow build-up of pressure during the downward migration, until the level of pressure was sufficient to evoke a prolonged compensatory swimming excursion.

The importance of the direction of illumination on the orientation of the response has been studied at length by Rice (1964) in a variety of planktonic animals, both larval and adult. Rice (1966) reports that in a number of his experiments the magnitude of the pressure response seemed to change with different conditions of illumination. The dominant role of light in the behaviour of the freshwater cladoceran *Daphnia magna* was demonstrated in a series of experiments reported recently by Lincoln (1970). It was shown that a population of *D. magna*, exhibiting a laboratory-scale vertical migration under the influence of a changing light regime, is affected only briefly by a large pressure increase. A marked increase in activity was noted on compression, but this was of quite brief duration and the migration pattern returned rapidly at the high ambient pressure. Under the conditions of this experiment the

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response of the animal to light appears to depress any prolonged response to pressure.

It is interesting to note that apart from the migration experiments mentioned above there is no direct evidence for pressure affecting the behaviour of freshwater planktonic crustaceans. A field investigation of the behaviour of freshwater animals in Lake Windermere was undertaken by Paton. Although this work was not completed the results were analysed and reported briefly by Hardy (Hardy & Paton, 1947). *Cyclops strenuus*, but not *Diatomus gracilis*, gave results which indicated barosensitivity. Some of the results did, however, show a correlation with light intensity and not with depth, and as a result of this any conclusions had to remain tentative. Baylor & Smith (1957) imply that *Daphnia* are pressure sensitive, but do not give any details. Digby (1967) says that they are not normally responsive to changes of one atmosphere (1 bar), but can be made so either by pretreatment with a solution of sodium bicarbonate or by lowering the pH of the water. Various freshwater cladocerans and copepods were studied by Knight-Jones & Qasim (1966) but no pressure responses were revealed.

In the present investigation the combined effects of light and pressure have been examined in two common planktonic crustaceans, the freshwater cladoceran *D. magna*, and the marine copepod *Calanus helgolandicus*. In addition, experiments were carried out to establish the sensitivity of *Calanus* to small pressure changes at a high ambient pressure. *Calanus* is known to undergo considerable diurnal vertical migrations in its natural environment, and any barosensitive mechanism would have to operate at high ambient pressures. To date, all studies of behavioural pressure effects have been carried out at, or near, atmospheric pressure.

#### MATERIALS AND METHODS

*Daphnia magna* were collected from a shallow freshwater pond close to the laboratory. The animals were transported in large vacuum flasks and transferred to an aquarium in a 15 °C constant room temperature. The *Calanus* material was supplied by the Lowestoft Fisheries Laboratory. The plankton sample was usually collected by a short haul with a Henson net, and the animals were placed in large plastic bins on the deck of the research vessel. At the end of the cruise the copepods were placed in vacuum flasks of clean sea water for the trip to the laboratory, and kept finally in small aquaria maintained at 5 °C. The *Calanus* were fed with small amounts of a culture of diatoms (*Nitzschia*) and dinoflagellates (*Dunaliella*).

The pressure vessel used in these experiments has been described in an earlier paper (Lincoln & Gilchrist, 1970). The rectangular steel vessel has large plate-glass windows incorporated along two sides, with smaller windows at each end. The experimental chamber is provided by a rectangular Perspex chamber, measuring 44 × 51 × 368 mm, which fits loosely inside the pressure vessel (Lincoln, 1970). The experimental chamber is filled with clean, well aerated, sea water or pond water, and the animals are introduced by pipette. The pressure vessel is then flooded with a liquid-paraffin hydraulic fluid and sealed off. Hydrostatic pressure is applied to the system by an air-hydropump, details of which are also available in the above reference (Lincoln & Gilchrist, 1970). The air-hydropump is suitable for applying pressures of

3 bar (50 p.s.i.) or greater, but in a number of the experiments with *Calanus* much smaller pressures were required. These were achieved by closing off the hydraulic pump circuit and attaching the low-pressure air supply directly into the hydraulic system. Small increments of pressure could then be applied by operating the demand valve on the air cylinder, and measured on a gauge on the outlet side. This arrangement was suitable for pressures ranging from about 7 bar (100 p.s.i.) down to 0.07 bar (1 p.s.i.).

The necessarily accurate temperature control was achieved by enclosing the entire pressure vessel in a large Perspex water jacket, with a rapid water circulation from a constant-temperature bath. The experiments with *Daphnia* and *Calanus* were carried out at 15 and 7 °C respectively. It was anticipated that prolonged use of a high-intensity overhead light might warm up the top of the pressure vessel and establish a temperature gradient. Since the experiments involved the vertical movement of animals up and down the chamber any thermal gradient had to be avoided as far as possible. It was found, however, that even after several hours of high-intensity illumination the temperature difference between top and bottom did not exceed 0.1 °C.

A high-intensity microscope lamp was fitted above the pressure vessel as the light source. The intensity was controlled by a hand-operated rheostat, and measured with a photocell calibrated from a standard light source. To produce red or blue monochromatic light the appropriate Cinemoid filter was introduced into the light path.

Much of the work was carried out in total darkness, or under conditions of very low illumination where there was insufficient light for direct observation of the animals. For this reason the animals were studied under infra-red light using a Leitz infra-red converter mounted in front of the pressure vessel, with infra-red light source placed against the opposite window. The converter was fixed to a Palmer adjustable stand so that it could be moved vertically up and down, scanning the entire window area. It was necessary to adjust the focal length of the acceptance lens (Leitz Elmar f. 2.8, 50 mm) to bring the converter close enough to the vessel to resolve small planktonic animals. The addition of supplementary lenses totalling 4.50 diopters was found to be sufficient for this. Two tungsten lights mounted in a wooden box were used for an infra-red radiation source, the visible spectrum having been removed completely by a series of Cinemoid filters. A spectroradiometer plot showed total absorption of light up to 775 nm. The filters used were 1 No. 1 (deep rose), 1 No. 5 A (deep orange), 3 No. 24 (dark green), 3 No. 20 (deep blue). Observations were made of the *Daphnia* to see whether they were sensitive to this infra-red radiation. It was, in fact, found to produce a slight response when first switched on, but the effect did not last for more than a few seconds. The light was therefore turned on well in advance of each experiment and left on throughout. The entire pressure apparatus was housed in a darkened constant-temperature room with a light trap across the door.

For the purpose of tabulating the results the experimental chamber was divided into six equal sectors by means of opaque tape. The tape appeared as black cross-lines when viewed through the converter. The distribution of animals in the water column could be quickly determined by racking the converter rapidly from the top of the vessel to the bottom, while the number of animals in each sector was counted.

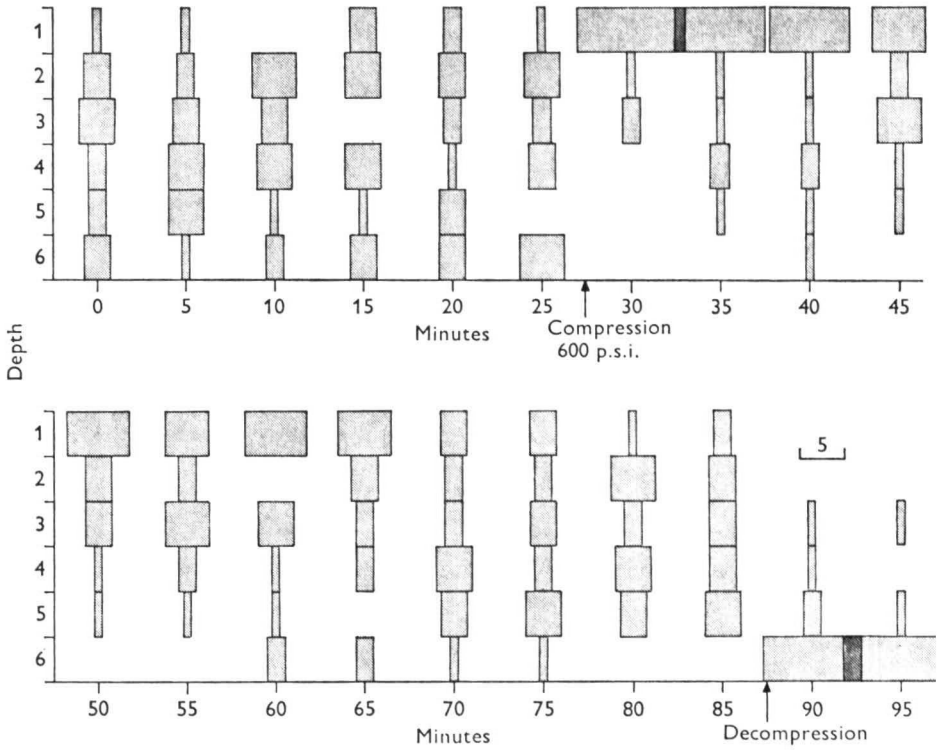


Fig. 1 A. Effect of 40 bar (600 p.s.i.)/20 s on the distribution of *Daphnia* in total darkness.

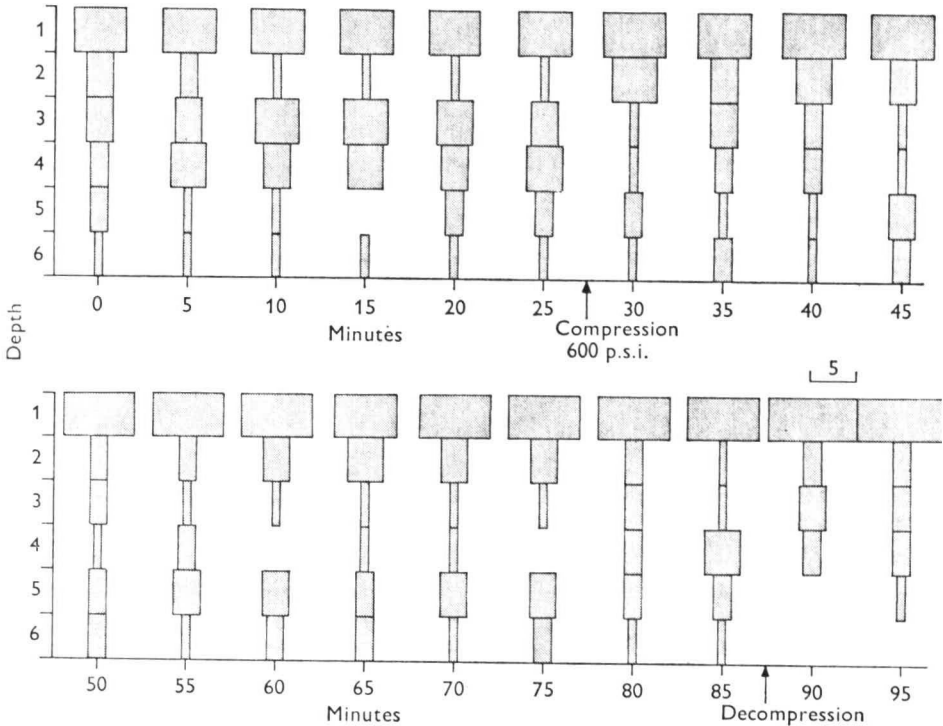


Fig. 1 B. Effect of 40 bar (600 p.s.i.)/20 s on the distribution of *Daphnia* with overhead illumination. Intensity  $3650 \mu\text{W cm}^{-2}$ .

## RESULTS

For the experimental work with *D. magna* the distribution of the animals within the vessel was recorded at 5 min intervals. The initial 30 min, before pressure was applied, serves as a control for that population. The results are given as distribution histograms, the area of the histogram at each ordinate level being a measure of the number of animals present in that division of the water column. The application and removal of pressure was made midway between two consecutive readings and is indicated on the time base of the results. The time taken to apply a particular pressure is of special significance and is given in abbreviated form where appropriate in the text (e.g. 40 bar (600 p.s.i.)/20 s). For convenience of presentation the results will be considered under a number of subheadings.

(1) *Daphnia magna*

(a) Total darkness: effect of 40 bar (600 p.s.i.)/20 s. The results are given in Fig. 1 A. At the opening of the experiment the animals are well spread along the water column, and this is maintained during the 30 min control period with slight fluctuations as individuals move about the chamber. Following compression there is a sudden change in the distribution indicated by a rapid shift in the population to the top of the experimental chamber. The animals were observed closely at this time and found to be swimming very actively in the uppermost parts of the chamber. Maximum numbers had reached the top sector before the first post-compression reading was taken. The response to compression was immediate, expressed by a marked increase in swimming activity and a rapid ascent through the water column. The high pressure was maintained for 60 min during which time the animals gradually redistributed themselves in the body of the chamber, and the excited swimming behaviour returned towards the level exhibited before compression.

Decompression was marked by an equally sudden response. In this case there was a rapid shift in the distribution towards the bottom of the chamber, resulting from an almost total loss of antennal activity, the animals sinking passively downwards with antennae outstretched. Within 30 s the swimming rhythm had returned to all animals, although at much reduced level, and they remained close to the bottom. Over the following 60 min they gradually recovered their normal activity and an even distribution along the chamber was established.

(b) White overhead illumination: effect of 40 bar (600 p.s.i.)/20 s. The overhead light was switched on 2 h in advance of the experiment. A light intensity equivalent to  $3650 \mu\text{W cm}^{-2}$  was used. The results are given in Fig. 1 B. At the beginning of the experiment the animals are well distributed along the column, with smaller numbers towards the bottom. On compression the population shows a slight upward shift but this is very much less pronounced than the rapid migration recorded in the previous experiment. The animals were observed for several minutes after compression, and an increase in the rate of swimming activity was evident, although the distribution of the population did not change very much. In comparison with the results obtained in total darkness the response was of very short duration, and it was only a few minutes before the swimming rate had returned to a near-normal level. Also, in marked contrast to the previous experiment, the removal of pressure did not

lead to any large shift in the distribution. The animals did exhibit a temporary reduction of swimming rhythm, but had recovered their position by the time the first post-decompression reading was taken. Following the experiment the overhead light was extinguished and the animals were left for about 4 h. At the end of this period the pressure response was recorded in total darkness. It was again evident that in the absence of overhead illumination there was a very strong response to both compression and decompression.

Having established that the overt effect of pressure is greatly reduced by a high-intensity light, a number of additional experiments were undertaken with a light of much lower intensity. In all cases there was only a slight movement of the animals, and a correspondingly brief change in swimming activity. The vertical movement of the population at very low levels of illumination ( $30 \mu\text{W cm}^{-2}$ ) did appear a little more marked than that observed at higher intensities. A control in total darkness was carried out with all the experiments, and under these conditions the energetic 'dark' responses were apparent.

(c) Effect of 40 bar (600 p.s.i.)/20 s with monochromatic overhead light. A detailed study of the effect of different wavelengths of light on the behaviour of Cladocera has been made by Smith & Baylor (1953). Two discrete 'colour dances' are described in *D. magna*, which the animals exhibit when exposed to different wavelengths of monochromatic light. Under red light (over 600 nm) the animals swim with the characteristic 'hop and sink' pattern parallel to the light beam. However, when they are exposed to blue light (under 500 nm) the activity is quite different. The body is inclined forward and the direction of swimming has a marked horizontal component at right angles to the light beam. This reaction provides an opportunity to investigate the effects of pressure on the orientation of *Daphnia*, and to discover whether the pressure response includes a specific orientation of movement or is simply kinetic.

Monochromatic light was obtained in these experiments by placing the appropriate Cinemoid filter in the light path. Results were obtained using red, blue and white light. In each case the initial 30 min offered a steady distribution, although the population under blue light was grouped closer to the bottom of the chamber. Following compression the animals were observed for a short period and it was found that a small increase in swimming activity took place in each of the three experiments. A contrast was evident, however, in the extent to which the separate populations moved up the water column as a result of the change in activity. The greatest shift occurred with red illumination, the least with blue, and with white light somewhat intermediate. The influences of the 'colour dances' are thus apparent. With red light the animals are swimming parallel to the light beam so that an increase in the rate of activity results in a relatively large vertical displacement of the animals. Under blue light the orientation is at right angles to the light beam, and although there is a definite increase in activity upon compression this is expressed mostly by horizontal excursions and a minimum of vertical shift. White light offers an intermediate situation as the animals may at any one time be exhibiting either red or blue dances. The white light used for these experiments had a large red component in its transmission spectrum, and in addition the red component increased as the lamp was dimmed. This may explain the greater shift in population which occurred with the very low-level white light. It must be made clear at this point that in none of the experiments involving illumination does

the pressure response in any way approach the excited behaviour which prevails in total darkness.

Following decompression a somewhat similar downward shift occurred in all cases, although it was not readily apparent from the results for the blue light as the animals were already close to the bottom. This situation might be anticipated as the orientation of the animal does not markedly effect the rate at which it sinks during periods of reduced activity.

The main conclusion which is drawn from this series of experiments with *D. magna* is that the pressure response appears to be largely kinetic and does not involve a specific orientation of the activity. In total darkness the orientation of the swimming movement is largely vertical and thus any increase in activity which follows compression causes the animals to move directly upwards.

(d) Effect of smaller increments of hydrostatic pressure: 7 bar (100 p.s.i.)/5 s and 3.5 bar (50 p.s.i.)/5 s. These experiments were carried out in total darkness as the overt threshold for a pressure response would be most clearly defined under these conditions. With a pressure of 7 bar there was a distinct increase in activity immediately after compression, although the upward shift of the population was quite small and the duration of the response relatively short. A similarly transient response was observed following the removal of pressure. The reaction to a pressure change of 3.5 bar was also studied, and although an observable change in activity did accompany both compression and decompression it lasted for less than 1 min, and as little as a few seconds in some individuals. The overall distribution of the population in the vessel was not affected by such a brief response. With pressure increments appreciably below 3.5 bar there was no visible evidence of any change in activity of the animals. The threshold for an overt response under these experimental conditions seems to be in the region of 3.5 bar (50 p.s.i.).

(e) Effect of repetitive compression and decompression on the barosensitivity. Digby (1967) has reported that the barosensitivity of small marine crustaceans is often reduced or totally lost if they are roughly handled, or damaged during collection. Digby also noted a loss of pressure response when the animals were subjected to repeated compression and decompression at 45 p.s.i. (3 bar) or above. This latter situation was investigated with *Daphnia* as preliminary observations had not shown any apparent loss of sensitivity after a series of rapid high-pressure fluctuations. The animals were subjected to repeated compression to 27 bar (400 p.s.i.), applied rapidly in 2-3 s and held constant for 1 min before being quickly released. This procedure was repeated ten times at 1 min intervals, and the behaviour of the animals was observed throughout the experiment. With each increase in pressure there was a pronounced rise in swimming activity and upward migration, and the reverse reaction accompanied decompression. When the final pressure change had been completed the animals were still responsive in a typical manner to pressures of 40 bar (600 p.s.i.) and 27 bar (400 p.s.i.), and also gave a brief positive reaction to 3.5 bar (50 p.s.i.). There was no suggestion that repetitive stimulation had abolished the barosensitivity.

## (2) *Calanus helgolandicus*

Because *Calanus* was not readily visible with the infra-red converter, by reason of its small size and relatively transparency, the experiments had to be carried out in the

presence of an overhead illumination which was just adequate for direct observations to be made. The results are given as distribution histograms, taken at 2 min intervals with the points of compression and decompression indicated on the time base.

(a) Effect of pressures ranging from 0.7 bar (10 p.s.i.) to 14 bar (200 p.s.i.), with constant overhead light. The experiment at 14 bar will be considered first as the reaction was the most marked (Fig. 2), although similar in effect to the responses exhibited at smaller pressures. During the initial part of the experiment the distribution within the vessel remained steady. The *Calanus* were swimming with a slow 'rise and fall' motion over

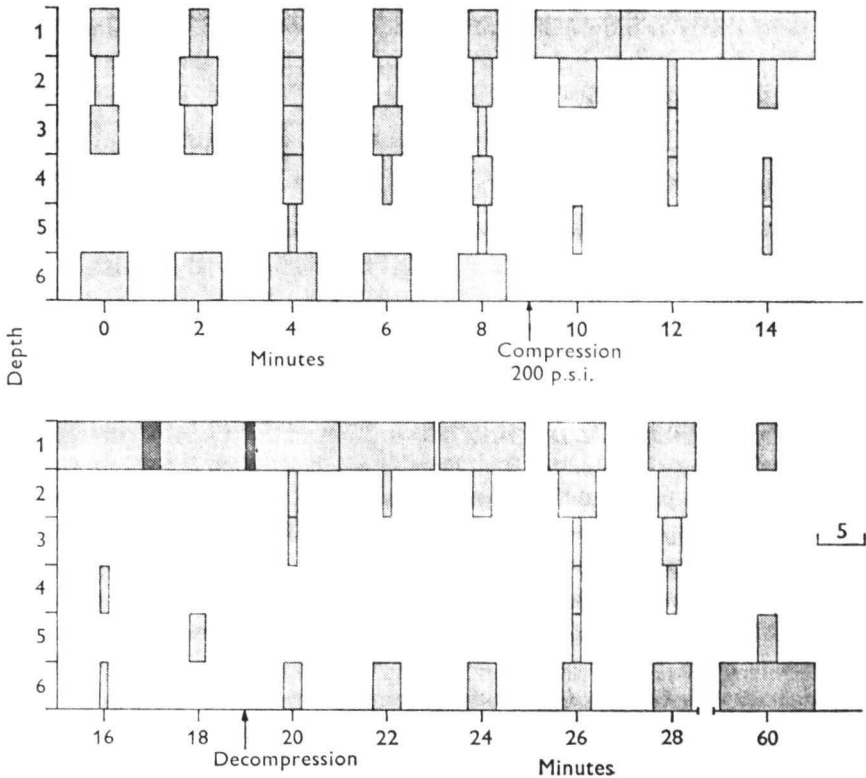


Fig. 2. Effect of change in hydrostatic pressure of 18 bar (200 p.s.i.)/10 s on the distribution of *Calanus*.

a distance of some 1-5 cm; the antennae held outstretched and motionless. The application of 14 bar/10 s brought about a sudden burst of activity, and within 10 s the majority of the animals had reached the top of the chamber. This sudden darting movement was achieved by vigorous use of the antennae. After a minute or so the excited behaviour was lost, the slow 'rise and fall' pattern returned, and once again the antennae appeared motionless. Throughout the 10 min at high pressure the distribution changed little, the animals remaining in the uppermost part of the chamber. Decompression produced no visible effect on behaviour. However, over the following 10 min there was a gradual fall in the level of the population, caused presumably by a slight drop in the swimming rate. A further 30 min and most of the animals were in the bottom part of the chamber.



The application of 7 bar/10 s produced a response pattern similar to the above except that the effect was less dramatic. The upward migration was much more gradual and there was no burst of antennal activity. Instead, the animals swam smoothly up the chamber. Decompression resulted once more in a very slow sinking towards the bottom, but without any apparent change in behaviour.

With the smaller increments of 1.7 and 0.7 bar a brief response was quite evident and the animals moved a short distance before resuming their characteristic swimming behaviour. The reaction was seen in almost all individuals, but at 0.7 bar the distance moved was so small that the overall distribution was little affected.

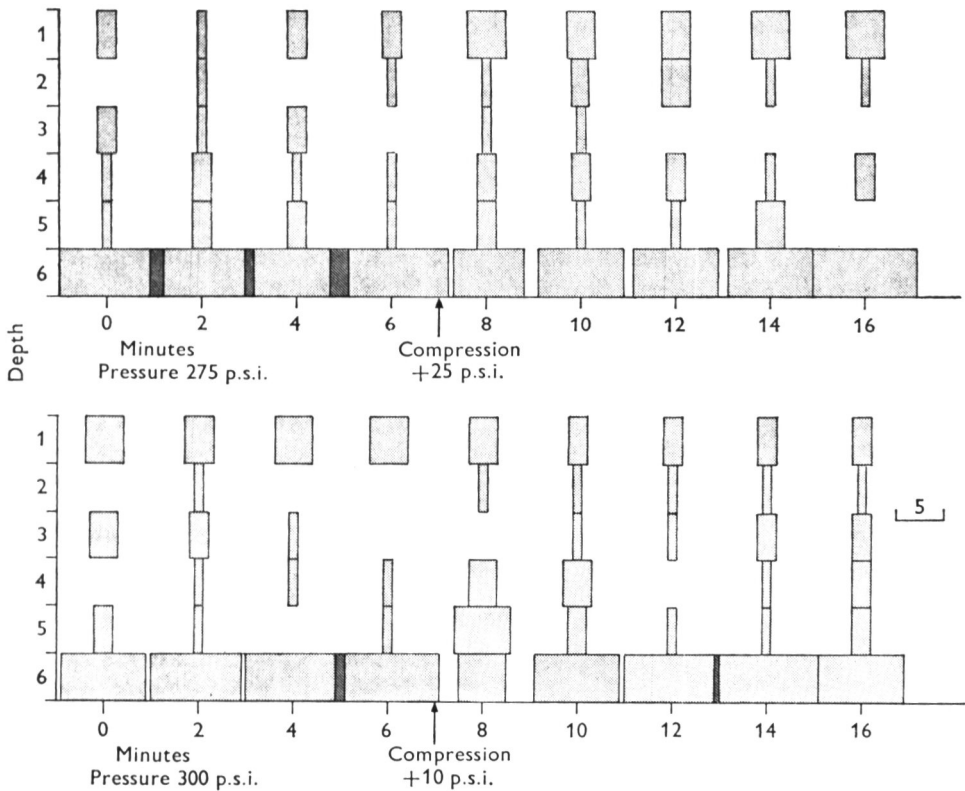


Fig. 3. Effect of small pressure changes on the distribution of *Calanus* at high ambient pressure (20 bar (300 p.s.i.)).

It was noted during the *Calanus* work that the animals remained sensitive to a pressure of 1.7 bar even after this pressure had been applied a number of times over a short period. As with *Daphnia* there was no evidence of the pressure sensitivity being lost as a result of repetitive stimulation.

(b) Effect of small increments of pressure at high ambient pressure. These experiments were undertaken to determine whether the pressure-sensitive mechanism would operate at high background pressures. Two levels of pressure were used, 8.5 bar (125 p.s.i.) and 20 bar (300 p.s.i.), and the results for 20 bar are given in Fig. 3. The animals were exposed to the high ambient pressure for an overnight period of 12 h, and at the end of this time their response to 1.7 and 0.7 bar was observed and recorded. It is clear

from the results that the animals remain responsive to small increments of hydrostatic pressure when maintained at high ambient levels. Qualitatively and quantitatively the responses appeared similar to those expressed at atmospheric background pressure.

#### DISCUSSION

It is clear that the pressure responses of *Daphnia* are much influenced by light. The rapid movement following pressure increase in darkness contrasts strongly with the limited response in the presence of light. This suggests that the depth-regulatory pressure responses, in some crustaceans at least, may be confined to the hours of darkness or perhaps times of very low light intensity. The results with *Daphnia* show also that this overriding effect of light is exerted over a wide range of intensity. In the case of *D. magna* the large threshold values obtained for overt pressure responses make it highly improbable that pressure can have any real part to play in the natural behaviour of this animal. The figure of 3.5 bar (50 p.s.i.)/5 s represents a very rapid change of depth of some 35 m.

The orientation of *Daphnia* is known to be affected by the wavelength of light incident upon the compound eye (Smith & Baylor, 1953). In the natural environment the swimming patterns probably involve both horizontal and vertical excursions, depending upon the particular light spectrum present at the time. This light response can under certain circumstances be overruled by physiological or environmental conditions. Hunger gives rise to the 'blue dance', whilst excess of food or low temperature result in the 'red dance', regardless of the wavelength of light or previous orientation of the animal. For pressure sensitivity to have a depth-regulatory function in cladocerans it would have to impose a vertically orientated swimming response. The current laboratory experiments have shown that the response to a change in hydrostatic pressure is in fact largely kinetic: the rate of swimming activity is subject to change, but there is no alteration of the existing orientation. To what extent 'colour dances' occur in other Crustacea is not well known, although they have been recorded in a number of freshwater Cladocera, two marine pontellid copepods and a harpacticoid copepod (Baylor & Smith, 1957).

It seems probable that the combined effects of pressure and light on the behaviour of *Calanus* differ from those found in *Daphnia*. Observations made with the marine copepod have indicated that the pressure response is not inhibited by light. This together with a much lower overt pressure threshold may point to a significant role for the pressure sense in *Calanus*. It must be pointed out, however, that in the laboratory experiments the short duration of the response of both animals, even when close to their thresholds, was far from sufficient to compensate for the imposed change of depth. The rapid accommodation to an increase in hydrostatic pressure is a very prominent feature of all the results, and at all levels of pressure.

The mechanism of pressure sensitivity is still obscure, although laboratory experiments have revealed a number of important factors. The existence of some form of gas vesicle was postulated by Hardy & Bainbridge (1951) to provide a system sensitive to small changes in pressure. The swim bladder of teleost fish (Qutob, 1960, 1962) and the gas organs of some aquatic insects (Thorpe & Crisp, 1947) have been shown to have a pressure-sensitive function based on the high compressibility of gas. However,

it has not been possible to demonstrate the existence of any such gas vesicle in a wide variety of aquatic animals which are known to be barosensitive. For example, the larval stages of the teleosts *Pleuronectes platessa* and *Centronotus gunnellus*, which lack any trace of a swim bladder, have been shown to respond to changes of pressure (Qasim, Rice & Knight-Jones, 1963). Microscopic examination of a number of invertebrates including medusae and ctenophores (Knight-Jones & Qasim, 1955), the amphipods *Synchelidium* (Enright, 1962) and *Corophium* (Morgan, 1964), and the annelid *Nephtys* (Morgan, 1964), has not revealed any form of gas filled body.

A more recent theory for a pressure sensitive mechanism has been put forward by Digby (1961). The author was able to show that a pressure of about 40 p.s.i. caused a 5–10 % change in the electrical potential across the cuticle of the prawn *Palaemonetes*. To explain this phenomenon Digby proposed that a thin layer of gaseous hydrogen, produced electrolytically, exists on the outer surface of the cuticle. Such a gas layer would be compressible and thus sensitive to hydrostatic pressure. A change in thickness of this layer is thought to bring about a change in the electrical properties of the cuticle and thus modify the electrical potential. This hypothesis is an attractive one but it does not seem to account for the strong tendency that such a thin gas film would have to pass into solution at high ambient pressures. With the pressure vessel used in the present study it has been possible to impose small increments of pressure on animals which have been kept at high pressure for several hours. From both a qualitative and quantitative viewpoint the responses at 300 p.s.i. seem to be similar to those exhibited at normal atmospheric pressure. If the Digby hypothesis is to operate under these conditions it is necessary to make the additional proviso that either the gas is somehow prevented from passing rapidly into solution or that it is produced at a rate proportional to the ambient pressure. Enright (1963) considers the 'gas layer theory' unsatisfactory in explaining the barosensitivity of the amphipod *Synchelidium*. This animal has an extremely low pressure threshold, and the calculated compression of the gas layer would be only  $2 \times 10^{-10}$  m or so.

Measurements of the compressibility of a number of marine crustaceans have been made by Enright (1963). Isopods and euphausiids are respectively 35 and 10% less compressible than sea water. The different body tissues probably offer a range of compressibilities, and these together with a semi-rigid exoskeleton could lead to some degree of distortion of the cuticle when the pressure is altered. The cuticle is well supplied with receptor organs sensitive to local stress patterns, and these could be responding indirectly to changes in hydrostatic pressure.

A final possibility to be mentioned involves the direct effect of pressure on the activity of the nervous system. Pressure has been shown to modify the hydration of ions, and cause changes in the ion flux through biological membranes (Podolsky, 1956). Spyropoulos (1957) reports that an increase of 100 p.s.i. has a marked effect on the membrane threshold of a giant axon fibre of *Loligo*. Although this is much in excess of the small threshold pressures for behavioural responses it does point to a possible mechanism for barosensitivity.

#### SUMMARY

1. *Daphnia magna* responds vigorously to a large increase in hydrostatic pressure when in total darkness, but this response is very much depressed in the presence of light.

2. The weak response of *Daphnia* in light is apparent over a wide range of intensity.
3. The effect of pressure on *Daphnia* appears to be largely kinetic and does not involve a specific orientation of the swimming activity.
4. The overt threshold for *Daphnia* and *Calanus* under laboratory conditions are in the region of 3.5 bar (50 p.s.i.) and 0.7 bar (10 p.s.i.) respectively.
5. The barosensitivity is not abolished by repetitive compression and decompression.
6. Observations made of the behaviour of *Calanus* indicate that the pressure response is not inhibited by light as it is in *Daphnia*.
7. *Calanus* which have been maintained at high ambient pressure for several hours remain sensitive to small increments of pressure. The response appears similar to that obtained at the level of atmospheric pressure.

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