

RESPONSES OF ZOOPLANKTON TO CHANGES IN HYDROSTATIC PRESSURE

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ABSTRACT

Pressure responses of a depth-regulatory nature have been demonstrated in all planktonic animals investigated. These animals responded to a rapid increase in pressure by active, continuous or intermittent, upward swimming, while a slow decrease in pressure was followed by less active downward swimming or passive sinking. The transient responses with respect to directional light varied among different species. With illumination directly from above, almost all swam upwards and towards the light in response to an increase in pressure, followed generally by a passive downward sinking or swimming away from the light when the pressure was decreased. With the illumination directly from below, movement of *Calanus* and *Clupea* larvae was still directed upwards (and away from the light) after an increase in pressure, while the nauplii of *Balanus*, *Eurydice* and zoea larvae of *Porcellana* remained mostly near or on the bottom, the last two showing evidence of dorsal reflex reactions. In horizontal experiments, with illumination from one side, the responses of most animals to an increase in pressure were first upward and then generally light-ward. With a decrease in pressure, they tended to sink or swim away from the light. Thus the depth-compensatory mechanism relies primarily on orientation to gravity and secondarily, in certain species more than others, on reactions to light. In darkness, however, the responses were clearly oriented to gravity. Sustained pressure increases stimulated the animals to swim upwards, but this was soon followed by a brief temporary depression of activities in megalopa larvae of both *Porcellana* and *Carcinus* for no apparent reason.

INTRODUCTION

FIELD experiments of Hardy and Paton (1941) suggested that behaviour associated with pressure changes might be concerned with depth-regulation. Pressure sensitivity has now been shown to be wide spread among plankton animals (Hardy and Bainbridge, 1951; Knight-Jones and Qasim, 1955; Baylor and Smith, 1957; Rice, 1964; Singarajah, 1966; Knight-Jones and Morgan, 1966). The most usual response seen, in captivity, is an active upward movement with increase in pressure and a

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passive downward sinking with decrease in pressure; the latter is seen particularly in non-buoyant animals. Moore and Corwin (1956) found evidence in the field that some depth-related factor, presumably pressure, together with temperature and illumination, contributed to controlling the vertical distribution of a number of plankton animals. Enright (1961, 1963) demonstrated increased activities, in response to rapid changes in pressure, in inter-tidal amphipods. Sensitivity of *Nymphon gracile* to pressure changes of tidal amplitude and frequency has been shown by Morgan *et al.* (1964). Bayne (1963) observed a pressure response in the early larvae of

Mytilus edulis and suggested that the mechanism might aid in dispersal of species. Straight-hinged and pediveliger larvae of oysters have also been shown to respond readily to changes of pressure equivalent to 190 mm Hg (Singarajah, 1979).

While evidence of pressure sensitivity continues to accumulate, the mechanism of pressure perception remains rather obscure. There is no theoretical difficulty with mechanisms involving compression of gas-filled vesicles, like teleostean swim-bladders (Harden-Jones and Marshall, 1953) and the tracheal systems of certain insects (Thorpe and Crisp, 1947), but no such compressible vesicles have been reported in marine invertebrates (apart from siphonophores). Extensive searches have shown none in such transparent animals as *Pleurobrachia*. A possible pressure perception mechanism, postulated by Digby (1961 a, b), was based on membrane tension increases, which cause changes in potentials across the surfaces of the prawn *Palaemonetes varians* and the shrimp *Crangon vulgaris*. These potentials were shown to vary with imposed pressure changes and Digby suggested that the pressure sensitivity of these crustaceans was a consequence of 'changes in area' of a hydrogen layer, a few molecules thick, which he visualized as being produced in association with these potential differences. On the other hand, subsequent observations (Enright, 1963), on the compressibility of some marine invertebrates, provide no support for the hypothesis that sensory system by which these animals perceive small pressure changes is based on ultrathin layers of gas.

The present paper deals with the results of experimental studies on various plankters, all of which showed depth-regulatory responses to pressure changes.

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MATERIALS AND METHODS

The pressure apparatus consisted of a pair of thick walled glass jars, 40 cm tall and 12 cm internal diameters, one or both of which could be used at a time (Fig. 1). Each tank was sealed with a rubber diaphragm and closed by an aluminium lid which was connected to a compressed air (or vacuum) system and mercury manometer through a series of glass T-pieces and lengths of rubber tubing. An increase or decrease of pressure was given by closing or opening one of the lengths of rubber tubing, through which air could be compressed or evacuated.

All experiments were conducted in a controlled temperature room at 12-14°C. Initial observations on behaviour were made in general room lighting, which was obliquely from above. In subsequent experiments, using directional illumination, observations were made in a 'Perspex' tank, 30 × 4 cm *i.d.*, with all sides sealed except for an aperture near one end; this aperture could also be sealed and closed tightly. The tank could be placed vertically, horizontally or in any other desired position and illuminated by a 100 W lamp shining through a slit to produce rays parallel to the axis of the tank.

In a few experiments involving changes of pressure of the kind associated with waves, the apparatus was similar to that used by Morgan *et al.* (1964) to simulate tides.

Pressure was measured in meters of sea water. Atmospheric pressure was not added as the pressure in water is directly a depth-related function and, therefore, the normal pressure at sea level was assumed to be zero (Sverdrup *et al.*, 1961).

Freshly collected plankton animals, not exceeding 15, were introduced into each tank.

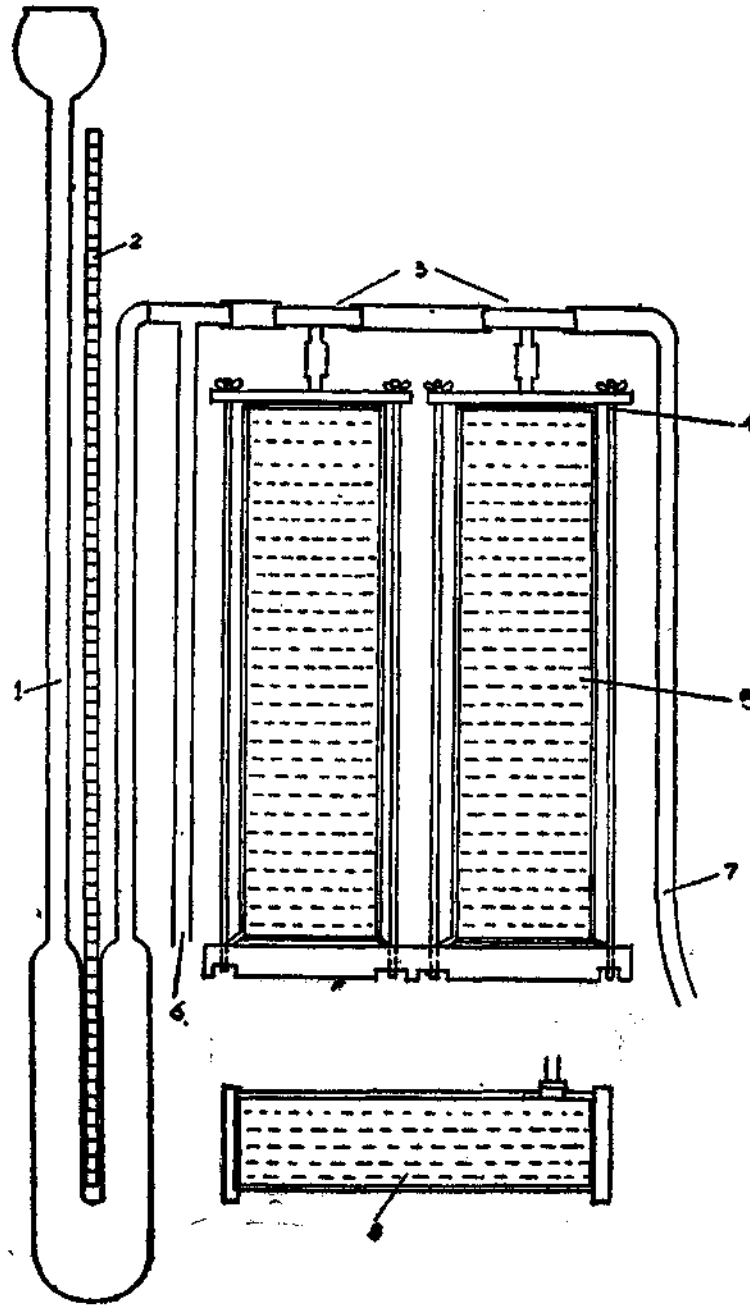


Fig. 1. Apparatus used in the experiments to measure responses to changes in hydrostatic pressure. 1. Mercury manometer, 2. Scale, 3. T-piece connections, 4. Wing-screw support system for pressure tanks, 5. Pressure tank, 6. Regulating end of the pressure tubing, 7. Connection to compressed air and 8. Pressure tank for horizontal experiments.

Each tank contained filtered sea water collected freshly from the same area where plankton hauls were made. The tank lids were secured with wing-nuts and changes of pressure were given at one minute intervals in gradually increasing magnitudes. Unless stated otherwise, the numbers of animals swimming is given for 15 sec. intervals in the upper half of tank in vertical experiments and in the half nearest to the light in horizontal experiments. Recordings in the dark was done with a red lamp switched on momentarily.

RESULTS

Essentially a depth regulatory behaviour was observed in all animals investigated, though considerable variation occurred among individuals with respect to the nature and intensity of responses, particularly under directional illumination'.

Calanus helgolandicus : These were caught in day time surface hauls during summer and subjected to changes in pressure within an hour. Initially, at normal pressure, more *Calanus helgolandicus* were seen to swim up and down near the bottom of the pressure tank, while only a few swam near the surface. With the increase in pressure, the majority swam upwards, some rapidly, but others intermittently. On decrease of pressure nearly all sank down with occasional intermittent surges upward. Clear evidence was obtained of response to changes of pressure (Fig. 2) equivalent to 2.5, 5.0, 7.5 and 10 metres of sea water. But some individual variations occurred. When pressure was increased to 10 m, all responded readily by upward movements. There was a tendency for the response to decline when the batch of animals was subjected to repeated pressure changes. Those individuals showing a tendency to remain or swim near the surface for longer periods always responded more readily (to pressure changes as low as 60.8 mm Hg) and their ability to respond was longer lasting.

With directional illumination from above and the pressure ambient, the majority remained at the bottom while some swam near the surface. On increasing the pressure to 5 m, 80% of the individuals from the bottom swam rapidly upwards, while the few that remained in the bottom half of the tank still made some attempt to swim upwards, but soon sank. On decrease of pressure, approximately the same numbers that had previously moved up from the bottom half began to sink with their usual intermittent up and down surges.

With illumination directly from below, the responses were clearly reversed. At normal pressure, of those that remained initially near the bottom only 40% swam rapidly upward in response to increase of pressure, 60% remained at the bottom. Some of the latter turning toward the light (head downwards) and others surged slowly up and down within a few cm from the bottom. On decrease of pressure, the small numbers that remained at the surface soon began to sink downwards. Amongst those that had remained near the bottom, some swam a few cm upwards, away from the light, before sinking back to the bottom.

In some experiments the tank was positioned horizontally and the light directed from one side. With normal pressure, about 40% of the copepods collected towards either end while 20% swam more centrally. On increasing the pressure all swam instantaneously upwards, evidently in a depth-regulatory manner. Of those that remained at the end far from the light, only 20% tended to move towards the light and often with intermittent surges up and down at the surface. The rest continued to surge near the surface without marked horizontal displacement, displaying the usual 'hop-and-sink' movements. However, when the pressure was decreased, all sank and those that had moved towards the light now moved away from it, re-establishing the original pattern of distribution. In almost all experiments, during upward surges or 'hops'

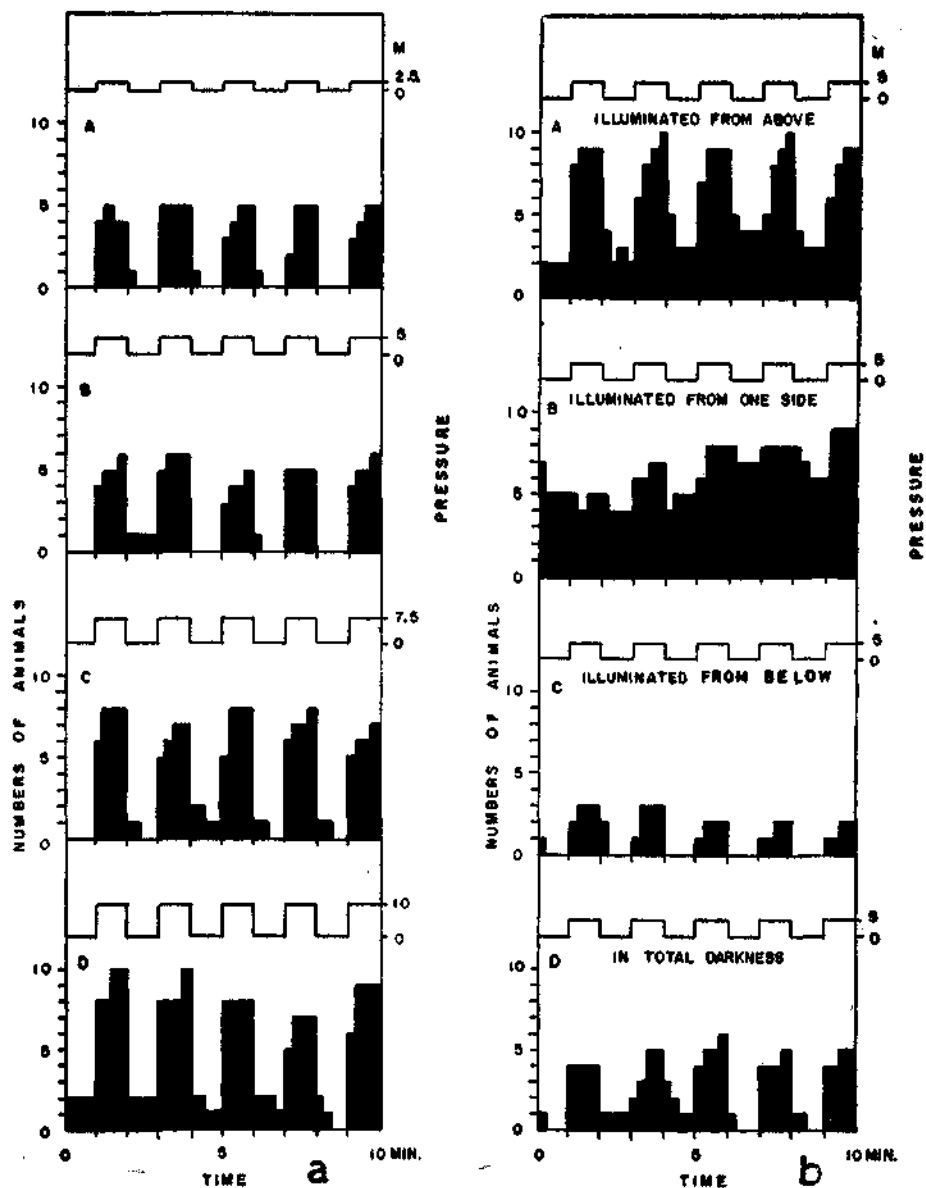
CALANUS HELGOLANDICUS

Fig. 2 a. Number of animals swimming above half-depth out of ten *Calanus helgolandicus* (Claus), recorded every 15 seconds in an experimental tank 40 cm deep, when given pressure changes equivalent to 2.5, 5.0, 7.5 and 10 m respectively, each alternating with atmospheric pressure at 1 minute intervals, under general illumination mostly from above and b. Number of animals swimming above half-depth (or in the half nearest to the light) in an experimental tank 30 cm long, when given pressure changes equivalent to 5 m, under different conditions of illumination.

in response to pressure, the antennules were often seen to beat at high frequency.

Balanus balanoides: Freshly liberated nauplii were strongly photopositive and remained near the surface, where light was apparently maximal. However, in about half an hour some of these nauplii became photonegative and were located at the bottom of the tank. Before any negative photic signs occurred, if the larvae were subjected to changes of pressure equivalent to 2.5 m at 1 minute intervals, all responded readily by swimming up more strongly. In response to decrease of pressure, some swam down for the first time, but a proportion of these soon returned to surface. Clear responses were also seen to changes of pressure as low as 55.5 mm Hg.

After half an hour at normal pressure, some of the larvae became distinctly photonegative and remained at the bottom. With increasing pressure, all larvae swam upwards more actively; with subsequent decrease of pressure, a number similar to the originally photonegative animals swam to the bottom, whilst the rest swam down as far as mid-depth only to swim back to the surface.

Essentially, similar behaviour was observed in response to changes in pressures of all magnitude, but with actively also correspondingly enhanced at higher pressure (Fig. 3 a). The same batch of nauplii also responded to brief pressure pulses of similar magnitudes, lasting $\frac{1}{2}$ a second, but the actual response was discernible only after the pulse, *i.e.* when the pressure had returned to normal.

Larvae hatched out from the same batch, which comprised photopositive and photonegative ones, were subjected to changes of pressure with the tank illuminated from above. All swam upward to the surface (Fig. 3 b), but a few of the more photonegative larvae soon tended to adapt a location a few cm below the surface. On release of pressure, however, more

photonegative larvae began to swim rapidly to the bottom, restoring the original behavioural pattern.

When the tank was illuminated from below and at normal pressure, the originally photonegative nauplii left the bottom and swam away from the light to the surface while the photopositive ones swam down to the bottom, thus the reversal of their positions clearly indicated their photic behaviour. When pressure was imposed, all larvae that had remained near the surface now swam actively downward towards the light (Fig. 3). Although one or two soon swam back to the surface, the majority remained at the bottom. On decreasing the pressure, some still remained at the bottom while the remainder swam upwards.

In horizontal experiments at normal pressure with illumination from one side, some of the larvae remained towards either end of the tank and a few swam randomly towards the centre. On increasing the pressure, they all first swam upwards and then light-ward. With a subsequent decrease of pressure, their earlier positions were reestablished. If, however, the tank was now illuminated with equal intensity from both sides and the pressure increased, some of the larvae that had remained near either end tended to swim towards the middle of the tank, as if to adjust to an optimal light condition.

Responses to changes in pressure in the dark were similar to those observed under general illumination and clearly the animals orientated to gravity (Fig. 3).

On subjecting the nauplii to negative pressure pulses, within a -5 m range and lasting $\frac{1}{2}$ sec, under general illumination, all the larvae near the surface swam actively downwards and those that were near the bottom made further attempts to swim downward. If light was directed from above, none swam upwards in response to such negative pulses of pressure. But when the light was directed from below,

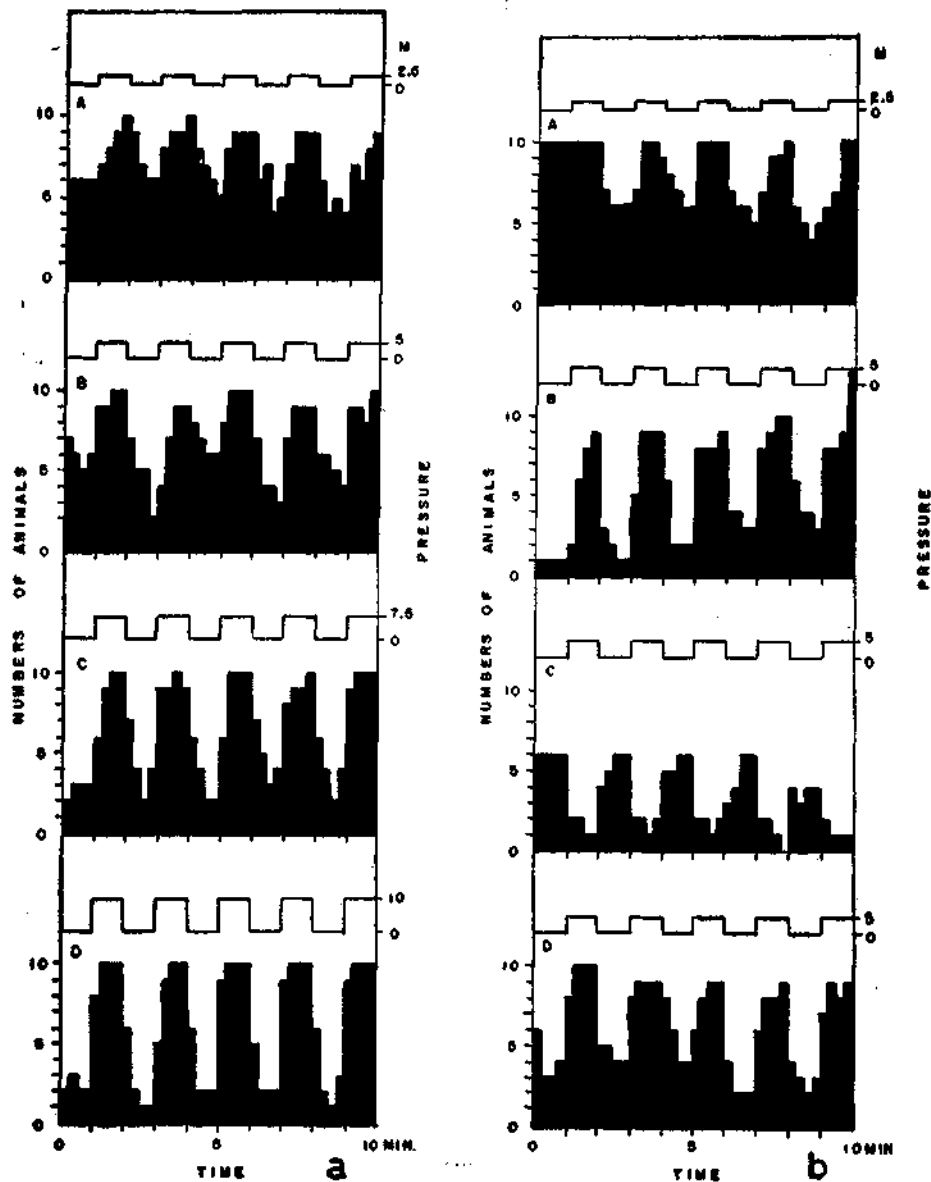
BALANUS BALANOIDES

Fig. 3 a. Numbers out of ten nauplii of *Balanus balanoides* (liberated more than half an hour previously) swimming above half-depth, recorded every 15 seconds in an experimental tank 18 cm deep, in response to pressure changes equivalent to 2.5, 5.0, 7.5 and 10 m respectively, each alternating with atmospheric pressure at 1 minute intervals, under general illumination, mostly from above and b. Response of freshly liberated (within first half an hour) nauplii to changes of pressure equivalent to 2.5 m under general illumination, mostly from above. (b : c. As in B, but with illumination from below and D. As in B, but in total darkness.)

some of the originally photonegative animals responded by swimming away from the light to the surface first, after which they swam downward more rapidly toward the end of the negative pressure pulses.

Elminius modestus: Responses to changes in pressure were generally similar to those observed in *Balanus nauplii*. In general illumination, the net response to an increase of pressure was an active upward swimming and to a decrease in pressure, swimming that was directed downwards. The overt responses to short pulses of positive pressure lasting $\frac{1}{2}$ a sec, were discernible only after the pressure had returned to normal.

Eurydice pulchra: The behaviour of this species, in response to changes of pressure under a variety of conditions, resembles, in many respects, that of zoea larvae of decapods. The responses clearly indicate (Fig. 4) high sensitivity to changes in pressure. With normal pressure, these animals swam rapidly at all depths. With increase in pressure, they swam rapidly upwards, whilst a subsequent decrease in pressure was followed by resumption of their usual random swimming behaviour, but mostly in the lower half of the tank. Although similar types of response were obtained with different magnitudes of pressure, their overall activity and the numbers swimming upward increased correspondingly at higher pressures. They remained sensitive to pressure changes as low as 57 mm Hg over several days. If however, clean sand collected from the sea was placed in the bottom of the vessel, they abandoned free-swimming in about six hours and remained buried in the sand, a behaviour trait presumably coinciding with the inactive phase of a tidal rhythm. Whilst in their buried state, if changes of pressure equivalent to 2.5, 5.0, 7.5, 10.0 and 12.5 m were imposed, none of the animals left the bottom. Thus pressure had no obvious effect if animals were in close contact with the sand particles. But, if the

sand was swirled up and a pressure increase imposed, all *Eurydice* swam rapidly upward. With a subsequent decrease in pressure, they resumed random swimming and made no attempt to bury themselves in the sand.

With illumination from above, after an increase in pressure, all animals readily swam to the surface. After reaching the surface, about 30% of these animals folded their limbs and allowed themselves to sink passively; however they soon swam back to the surface again. On lowering the pressure, they swam rapidly downward and away from the light.

When illuminated from below, the responses to changes of pressure closely resembled those of zoea larvae of *Porcellana*. The majority of the animals usually stopped swimming with the dorsal surface downwards, in an inclined position, with the head touching the bottom. Increase or decrease of pressure caused no significant change in this behaviour. Occasionally two animals swam upwards after a reduction of pressure, only to swim downward again with pressure increase imposed. This behaviour also shows evidence of a reflex dorsal light reaction, like those described in mysids (Foxon, 1940; Rice, 1961).

In experiments where horizontal tank was illuminated from one side, many animals first swam upwards in a depth regulatory manner and then towards the light during increased pressure. With decreased pressure, they swam initially away, but soon many more resumed random swimming toward the light.

The behaviour in total darkness was similar to that observed under general illumination, but the movements apparently were orientated to gravity; in addition, greater numbers swam in the lower half of the vessel during periods of low pressure.

Zoea larvae of *Porcellana longicornis*: Under normal pressure, these larvae often

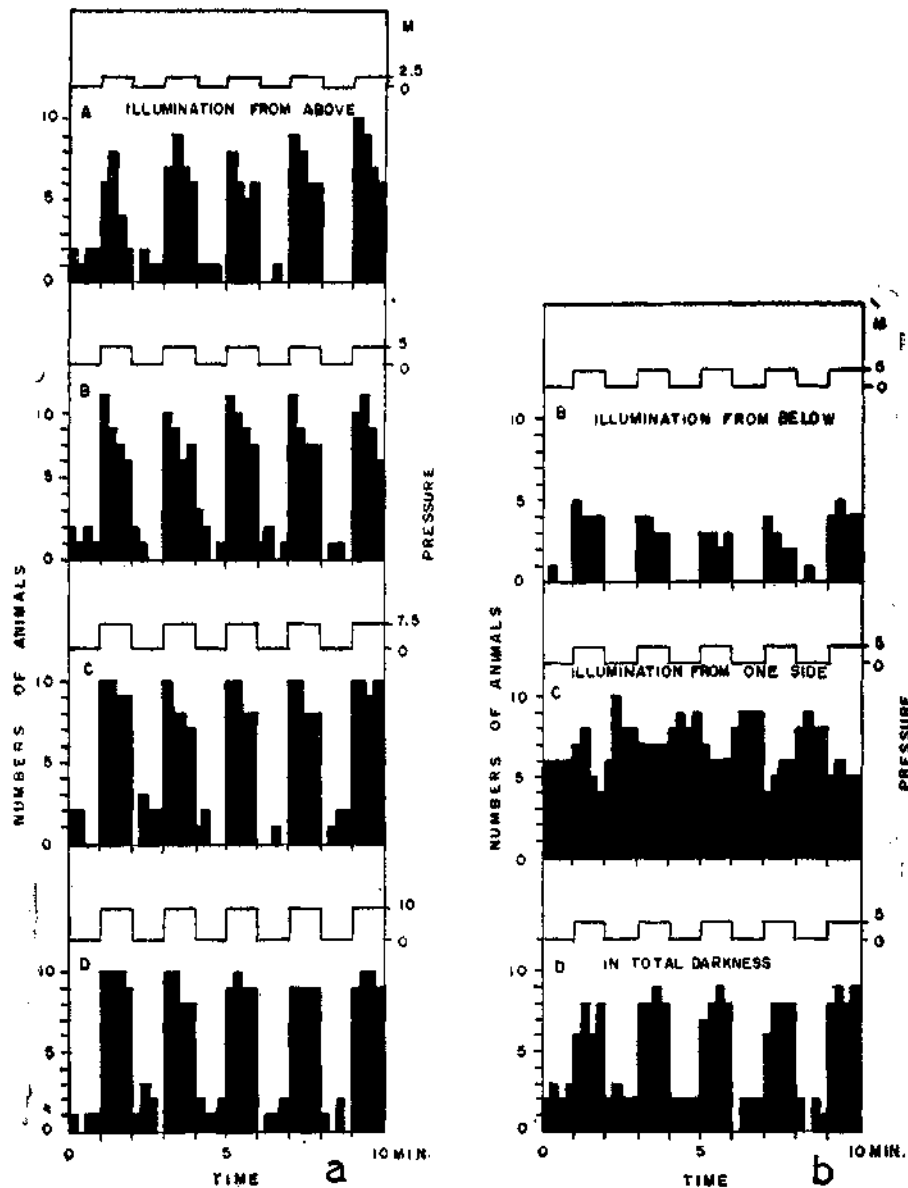
EURYDICE PULCHRA

Fig. 4 a. Number of animals swimming above half-depth out of ten *Eurydice pulchra*, recorded every 15 seconds in an experimental tank 40 cm deep, when given pressure changes equivalent to 2.5, 5.0, 7.5 and 10 m respectively, each alternating with atmospheric pressure at 1 minute intervals (A. Illuminated directly from above; and B, C and D in general illumination, mostly from above) and b. Number of animals swimming above half-depth (or in the half nearest to the light) in an experimental tank 30 cm long, when given pressure changes equivalent to 5 m, under different conditions of illumination (B, from below; C, from one end of the experimental tank; D, in total darkness).

floated motionless at the surface film with the rostral and paired posterior spines being evidently unwetted, or they swam at all depths, or sank rapidly. With increased pressure, all swam rapidly upwards, usually with the rostral spine foremost and with frequent backward strokes of the telson, thus reaching the surface in a few seconds (Fig. 5). Alternatively, they responded by swimming vertically upwards with the posterior pair of spines in advance, depending on the position they had previously adopted when resting on the bottom. Such swimming in the reverse position was equally effective. With decrease of pressure, most larvae sank rapidly and motionless whilst others continued to swim, but less energetically; eventually they too sank downwards, but at a lesser rate. They all showed sensitivity to changes of pressure corresponding to little low as 47.1 mm Hg.

With illumination from below and pressure normal, the larvae swam at all depths, with no strong tendency to collect near the surface. With increase of pressure, all swam rapidly to the surface and with decreased pressure they swam less actively or stopped swimming, allowing themselves to sink. Similar behaviour has been noted in megalopa larvae of *Carcinus* (Rice, 1964).

With illumination from below and pressure normal, the zoea larvae generally swam downward and remained laying with dorsal side facing the light. When pressure was increased, almost all moved actively forward, sliding on their ventral side on the bottom. Occasionally, however, a few showed outbursts of upward swimming for a few cm and then returned to their reflex dorsal light reaction. With experiments with the tank horizontal and illumination from one side, the immediate response to increased pressure was invariably quick upward movement, followed by swimming directed towards the light, with rostral spine foremost; those that already had reached the lighted end surged up and down near the surface. When

the pressure was then reduced to normal, most sank and swam slowly away from the light, with the rostral spine pointing lightwards.

In total darkness, the responses were distinctly orientated to gravity and the larvae moved up and down, with changes of pressure, while maintaining their vertical posture. It appeared that this posture might have resulted automatically from the disposition of the rostral and paired posterior spines, which must influence the sinking rate. However, the orientation to light was not determined by sinking posture, for if the light was switched on momentarily from below, while the pressure was increased, the up-swimming larvae tended to dart downward without changing the posture.

Clupea harengus: A sample of benthic eggs (1.30 mm diam.) were selected from a fresh collection and subjected to changes of pressure equivalent to 10 m of sea water at one minute intervals for a period of 30 minutes. This had no obvious effect on hatching. Hatching occurred both in the experimental and control batches almost simultaneously, within two days.

The results of subjecting early yolk-sac larvae to alternate minutes of high and low pressures, equivalent to 0.8-10 m and atmosphere (zero), in a series of eight experiments are shown in Fig. 6.

At ordinary pressure, the larvae with their heavy yolk sacs are non-buoyant, but tended to swim head upwards at all depths in the pressure tank. However, recently hatched larvae were observed to be sensitive to changes of pressure as low as 60.8 mm Hg.

Under general illumination, with increase in pressure, they swam rapidly upwards; with decrease in pressure, they swam less actively downwards.

With the container lighted vertically from above and with pressure increase, almost all

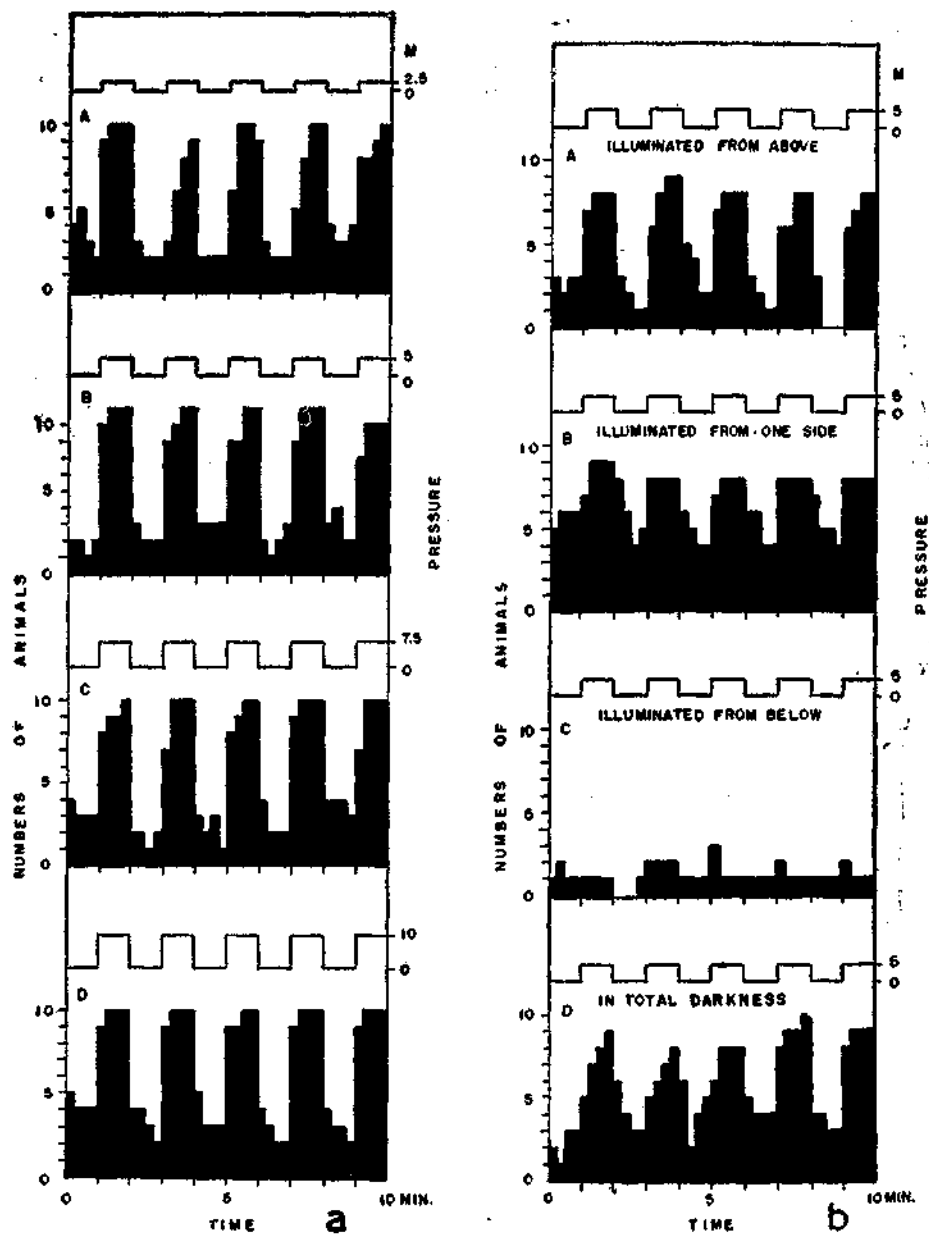
ZOEAE OF *PORCELLANA LONGICORNIS*

Fig. 5 a. Numbers swimming above half-depth out of ten zoea larvae of *Porcellana longicornis*, recorded every 15 seconds in an experimental tank 40 cm deep, when given pressure changes equivalent to 2.5, 5.0, 7.5 and 10 m respectively, each alternating with atmospheric pressure at 1 minute intervals, under general illumination mostly from above and b. Numbers swimming above half-depth (or in the half nearest to the light) in an experimental tank 30 cm long, under different conditions of illumination as shown in A, B, C & D.

of the larvae swam rapidly toward the surface ; with decreased pressure they tended to swim or sink downwards.

When the pressure tank was illuminated from below at normal pressure, most larvae swam downwards and remained at the bottom until pressure was increased, following which there was an active upward swimming away from the light. This behaviour was in direct contrast that of decapod larvae.

With the tank horizontal and illumination from one end, the larvae showed a general tendency to swim and collect at the end near the light during intervals of reduced pressure. When the pressure was increased, all swam instantaneously upwards and those that had remained initially away from the light moved towards the light ; those that had already reached the lighted end made attempts to move still further upwards. It seemed that their depth compensatory mechanism relied primarily on orientation to gravity and secondarily to reaction to light.

Responses to sustained pressure increases : Freshly collected plankton animals were kept in experimental tank. During a 30 min. period at normal pressure, before any changes of pressure were imposed, the various plankton animals usually remained less actively near the bottom, with occasional, apparently spontaneous upward movements. Following a pressure increase, the responses shown were clearly depth-regulatory in nature, but the level of activities fluctuated among the different individuals and stages of the same species. The swimming levels adopted by *Calanus*, and by zoea and megalopa larvae of *Porcellana* and *Carcinus* in responses to sustained pressure increases equivalent to 5.0 m of sea water and lasting for 40 min, are shown in Fig. 7. Initially, all were stimulated to swim upward, but this was soon followed by a depression of activities in megalopa larvae of both *Porcellana* and *Carcinus* during which they sank slowly and

remained near the bottom with only occasional outbursts of increased activity. However, after this temporarily reduced activity, which lasted about 10 minutes, the megalopa larvae resumed upward swimming more persistently during the last 20-30 min. until the pressure was reduced to normal. In *Calanus* and zoea larvae the increased activity persisted, with only a slight variations in swimming levels, throughout the period of sustained pressure.

DISCUSSION

Depth-regulatory responses : It is interesting to note that the behaviour of all planktonic animals examined in these experiments was depth-regulatory in nature. Behavioural responses in the different animals appear to be closely related and comparable even though there had been some subtle degrees of variability of form and intensity of response within the different stages of the same species. The most obvious mechanical responses observed in the various animals were their abilities to detect changes in ambient pressure, with resultant movements in preferentially oriented directions — an active upward swimming response to increased pressure and passive downward swimming or sinking under the influence of gravity in response to decreased pressure.

Hardy and Paton (1947) first suggested that *Calanus finmarchicus* (Gunnars) might have a 'sense of depth' and that many decapod larvae might be sensitive to even smaller changes in hydrostatic pressure and their vertical movements might be influenced by pressure difference at different depths. Early laboratory experiments (Hardy and Bainbridge, 1951 ; Knight-Jones and Qasim, 1955) showed no clear evidence of pressure sensitivity in *Calanus finmarchicus*. Rice (1962), however, eventually succeeded in demonstrating such sensitivity in this species. In contrast, the present study has shown convincing evidence for the pressure evoked responses in the relatively important and very closely related neritic species *Calanus*

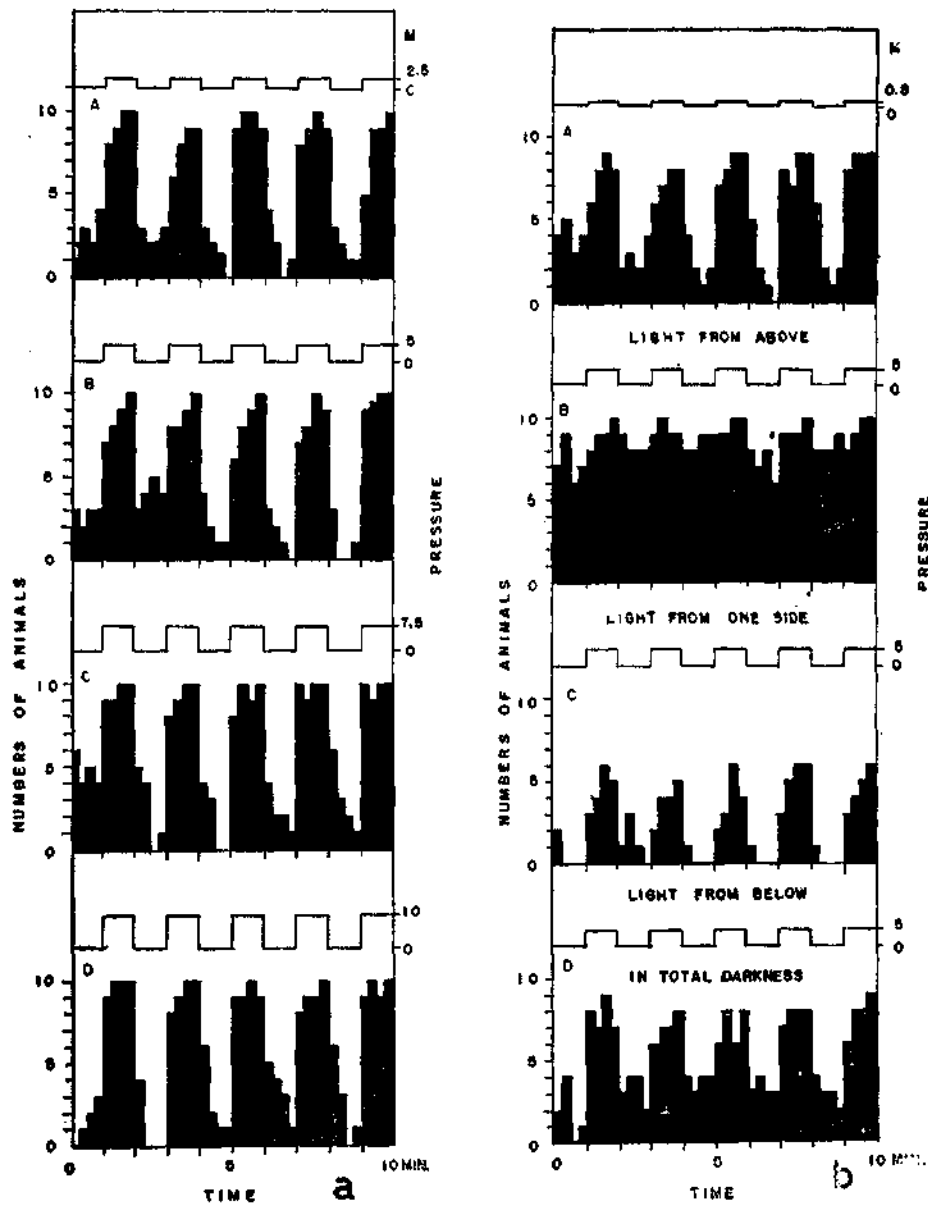
CLUPEA HARENGUS

Fig. 6 a. Numbers swimming above half-depth out of ten yolk-sac larvae of *Clupea harengus*, recorded every 15 seconds in an experimental tank 40 cm deep, when given pressure changes equivalent to 2.5, 5.0, 7.5 and 10 m respectively, each alternating with atmospheric pressure at 1 minute intervals, under general illumination, mostly from above and b. Numbers swimming above half-depth (or nearest to the light) in an experimental tank 30 cm long, when given pressure changes equivalent to 5 m, under different conditions of illumination as shown in A, B, C and D.

helgolandicus. Their ability to respond readily was long lasting, a characteristic also seen in *Sagitta setosa* (Singarajah, 1966). Although it is now known that this behaviour is fairly widespread, we do not know the exact mechanisms whereby the pressure stimulus is detected. Nevertheless, the behaviour seems to be correlated with adaptive values (Hardy, 1959; knight-Jones and Morgan, 1966; George and Marum, 1974), and probably used to adjust

something to do with mechano-reception, though copepod antennules are known to contain both chemo- and mechano-receptors (Gill, 1986).

Behavioural response to changes in hydrostatic pressure in nauplii of *Balanus* and *Elminius* appeared strongly influenced by light where even the initially photonegative nauplii left the bottom and responded readily and strongly to pressure. In the absence of any evidence

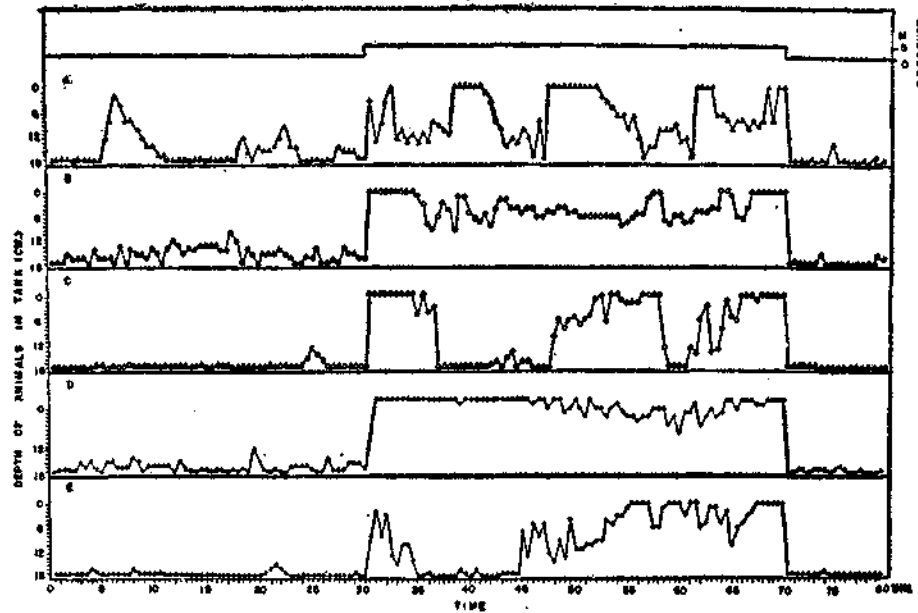


Fig. 7. Comparison of responses of different planktonic animals to sustained pressure increases under identical experimental conditions. See the swimming levels adapted to sustained pressure increase equivalent to 5.0 m by: A. *Calanus*; B. Zoea and C. Megalopa larvae of *Porcellana*; D. Zoea and E. Megalopa larvae of *Carcinus* respectively.

and maintain their optimal depth in the sea during vertical migration. Adaptive behaviour of zooplankton in response to selective forces of environment relating to vertical migration has been considered to be important (Heinle, 1981).

Calanus helgolandicus regularly flicked its antennules at a higher frequency from the onset of upward surge in response to increased pressure. It is not clear whether this has

of statocysts in Cirripede nauplii, the orientation of upward movement toward the light in horizontal experiments during responses to pressure changes seems more correlated to light than to gravity. Strong photopositive responses under different conditions with fed and unfed nauplii larvae had been reported previously (Singarajah *et al.*, 1967).

The apparent lack of response of *Eurydice pulchra* when in close contact with the sand

particles in their burried state cannot be easily explained. If formation of the gas vesicles on the cuticle of Crustacea during pressure increase as suggested by Digby (1961 a) were to be effective as a pressure sensory mechanism then there ought to have some reactions, but none were seen. On the other hand, studies (Campe-not, 1975) on shallow water lobster *Homarus americanus* and the deep-living crab *Geryon quinquedens* indicate that effects of hydrostatic pressure depress the neuromuscular excitatory potential as a result of reduction in the amount of neurotransmitters released at the nerve endings.

Because of the economic importance, behaviour of early herring larvae was largely confined to growth and survival mechanisms of larvae in the sea (Rosenthal and Hempel, 1970). The pressure sensitivity of larvae of *Clupea harengus*, which lacked a swim bladder, has not been previously reported. Sensitivity to changes in hydrostatic pressure has been considered as one of the functions of swim-bladders (Qutob, 1962; George, 1981), but teleosts lacking swim bladders also have been shown to be clearly sensitive to changes in hydrostatic pressure (Qasim *et al.*, 1963). Hardy (1959) described their remaining in the bottom of an aquarium tank after hatching, but Nikol'skii (1962) found them swimming to middle layers. Lebour (1921, 1924), on the basis of remnants of phytoplankton found in the guts of yolk-sack larvae, concluded that they swam to the surface soon after hatching. Ford (1928) also noted their abundance in the surface layers. On the other hand, Nelson-Smith (1964) reported that more larvae were caught in deep waters than in surface nets. However, recently hatched fed and unfed larvae were clearly sensitive to changes of pressure less than 60.8 mm Hg. The most obvious response in herring larvae during increase in pressure was strongly photopositive. Generally, Spooner (1933) found herring larvae to be photopositive and it seems that their depth-compensatory mechanism relies primarily

on orientation to gravity and only secondarily on reaction to light. Detailed studies on sensory awareness of herring larvae in relation to light has been reported (Blaxter and Jones, 1967; Blaxter, 1968; Blaxter and Batty, 1987).

Tests for threshold pressure stimuli (Table 1) in different plankton animals suggest that sensitivity to pressure changes differs not only among different groups, but also within the developmental stages of the same species. Generally, the larvae seem to be more sensitive to pressure changes than the adults, a phenomenon also seen in different stages of oyster larvae and *Artemia* larvae (Singarajah, 1979, 1981). Similar observations have been noted in larvae of *Ostrea edulis* (Bayne, 1963).

Eurydice and zoea larvae of *Porcellana* distinctly displayed reflex dorsal light reactions which resembled closely those of mysids (Foxon, 1940; Rice, 1961). It is still not known whether these reactions were mediated by the optomotor system, although many organisms are sensitive to light which may strike the body and not the eyes (Steven, 1963). The strongest turning movement in the dorsal light reflex seems to be induced by laterally incident light and is comparable to gravity reflex (Waterman, 1961). However, in *Porcellana* larvae, the responses were distinctly oriented to gravity as shown by the results of experiments in total darkness. The disposition of the rostral and the posterior paired spines probably assist in maintaining posture during orientation to gravity, although statocysts may not be fully developed in the early decapod larva (Prentiss, 1901; Gurney, 1939).

Except for a brief temporary depression of activities, after an initial burst, the zoea and megalopa larvae of both *Porcellana* and *Carcinus* in common with other planktonic animals tested, showed no activity decline and remained consistent over the subsequent prolonged periods. The brief depression of these larvae, though, appeared adaptive.

It is now fairly well established that pressure is one of the more important parameters of marine environment which determines, together with light and gravity, the distribution of the planktonic species within their pelagic habitats. (Knight-Jones and Morgan, 1966). but contains no clear baro-sensory mechanism. Neuro-transducer mechanisms are most likely to be involved in almost all pressure sensitive behaviour, like the stretch receptors in skeletal

TABLE 1. *Threshold pressure stimuli required to elicit overt responses in different species of zooplankton*

Group/Species	Stage : Larvae/Adult	Observed minimum pressure (mm Hg) required to evoke a response	General direction of swimming
Decapoda			
<i>Porcellana longicornis</i>	.. zoea	47.1	↑
	.. megalopa	47.9	↑
<i>Carcinus maenas</i>	.. megalopa	49.4	↑
Copepoda			
<i>Calanus helgolandicus</i>	.. adult	60.8	↑
Cirripede			
<i>Balanus balanoides</i>	.. nauplii	55.5	↑
<i>Elminius modestus</i>	.. nauplii	53.2	↑
Isopoda			
<i>Eurydice pulchra</i>	.. adult	57.0	↑
Teleost			
<i>Clupea harangus</i>	.. larvae	60.8	↑

The responses to changes in pressure were observed mainly under three conditions : (1) general illumination ; (2) directional illumination and (3) total darkness. Occasionally negative pressure pulses were given (see Text). The threshold responses of the same species, under different conditions, were not significantly different and therefore, the results were averaged. For clarity measurements of pressure in sea water are converted to mm Hg.

Relatively little is understood about the actual pressure selective mechanism. Swim-bladders in teleosts seem to control depth-regulatory function (McCutchen, 1958 ; Qutob, 1962 ; Laverack, 1968 ; George, 1981) and a number of other possible mechanisms are discussed

muscles (Katz, 1950) ; the deflection of ciliary receptors in *Pleurobrachia* (Horridge, 1965) ; and the deformation of Pacinian corpuscles due to pressure leading to generator potentials (Loewenstein, 1972).

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