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EYE/PHOTOPHORE COORDINATION AND LIGHT-FOLLOWING IN KRILL, *EUPHAUSIA SUPERBA*

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SUMMARY

Eight of the 10 photophores of the Antarctic krill, *Euphausia superba*, are located at the ends of muscular stalks and exhibit coordinated orientation responses to incident white light; light emitted from the photophores is directed away from the incident light. Moreover, eye rotation occurs synchronously with photophore movement. Immobilization of one or both eyes eliminated the photophore light-following response in 40% of the trials, but in the remaining 60%, photophores continued to exhibit oriented, but less stable responses. In the presence of a stationary light source the eyes could be passively rotated without affecting photophore position. Furthermore, eye removal or covering the head with an opaque hood eliminated coordinated photophore movement. We conclude that vision is necessary for light-following responses by the photophores. In addition, the control signal for that movement is CNS-derived, may occur spontaneously or may be light-induced, and appears to be accompanied by a parallel signal governing eye rotation. Subtle differences in photophore response when krill were oriented other than horizontally imply that krill may have a gravity sense that could help them orient in darkness.

INTRODUCTION

The Antarctic krill, (*Euphausia superba*), is a euphausiid crustacean that exists in large numbers in the Southern Ocean, and is important not merely as a major food source for whales, seals, penguins and a number of other antarctic animals, but also as a potential source of animal protein for human consumption. Krill often occur in large and highly organized schools (Hamner, Hamner, Strand & Gilmer, 1983), and undergo vertical migrations from depths of 100–150 m to near the surface and back during much of the year (Mauchline & Fisher, 1969; Baker, 1970). They lack the statocysts that provide other crustaceans with necessary equilibrium and gravity information (Mauchline & Fisher, 1969), but have prominent mobile eyes and are

Key words: krill, photophore, Antarctica, *Euphausia*, light-following.

strongly visual in their orientation. In the presence of a single light source they orient their bodies with respect to the light, and several authors have shown in other euphausiids that the eyes rotate to follow a source of light (Hardy, 1962; see Land, 1980). There is even the suggestion, for *Nematoscelis atlantica*, that light directly affects swimming direction by determining the position of the animal's abdomen and tail (Land, 1980).

Other evidence for the importance of light in the lives of these euphausiids is that almost all representatives of the family have prominent luminescent organs, called photophores. In *E. superba*, as in most species, there are 10 photophores – one in the ventral side of each eye, two pairs placed laterally on the ventral side of the thorax, and four arranged in a rostral–caudal line along the ventral mid-line of the abdomen. At light and electron microscopic levels, the photophores of *E. superba* closely resemble those of other euphausiids, which are highly organized, bell-shaped structures (Petersson, 1968; Herring & Locket, 1978) producing light *via* a luciferin–luciferase-type of biochemical reaction that is apparently regulated by hormonal and neural control of the circulation of the light-generating cells (Herring & Locket, 1978). Light emission is directional, with a dark pigment masking emission in most directions, and a highly reflective lining behind the photocytes (Fig. 1).

Little is known about the function of the krill bioluminescent organs under natural conditions. Research, primarily in the euphausiid *Meganyctiphanes norvegica*, has shown that the emission can be induced by handling, by a light flash (Mauchline, 1960; Kay, 1965) or by treatment with $10\,\mu g\,ml^{-1}$ of 5-hydroxytryptamine (Kay, 1962, 1965). Individuals in a jar occasionally emit spontaneous flashes (Petersson, 1968). Perhaps the most interesting proposed role for the photophores is in ventral counter-illumination, i.e. production of light to compensate for the luminescent organism's own absorption of downwelling light, thereby making an individual in a school less easily detectable by predators below (Dahlgren, 1916; Clarke, 1963; Young & Roper, 1976; Morin, 1983). Several observations support this hypothesis: (1) emitted light is maximal at approximately the same wavelength (463–476 nm) as sunlight filtered through several metres of sea water (Clarke, 1963; Latz & Case, 1982; Herring, 1983; Widder, Latz & Case, 1983); (2) the angle of light emission from photophores approximates that of the downwelling light from the surface (Denton, Gilpin-Brown & Wright, 1972; Herring & Locket, 1978); (3) the eyes rotate over approximately 180° following a point light source (Hardy, 1962; Land, 1980), in such a way that the photophores associated with the eyestalk complex point away from the light source, hence any light they produce will be directed in the same direction as the light striking the animal. In addition, the other eight photophores are also reported to rotate approximately in phase with the eyes (Hardy, 1962; Land, 1980). Finally, (4) there are suggestions that euphausiids vary the level of luminescence to match that of incident illumination (J. Morin, personal communication). [Small numbers (10–20) of *Euphausia superba* were placed in six containers, each illuminated with a different level of white light for 10 or more min.

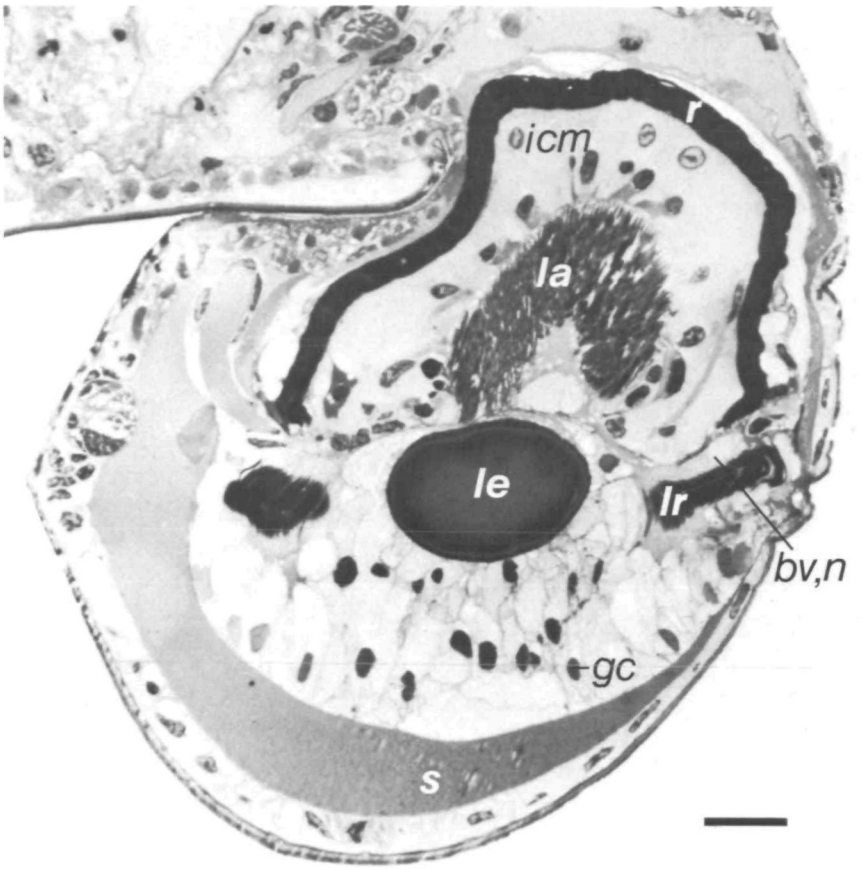

Fig. 1. Photograph of a toluidine-stained cross-section of a *Euphausia superba* thoracic photophore, with principal features indicated. The structure appears virtually indistinguishable from that described for other euphausiids (Bassot, 1966; Petersson, 1968; Herring & Locket, 1978). The photophore is surrounded by a blood sinus (*s*). The luminescence is produced by a chemical reaction in the lantern (*la*), which consists of specialized microvillar projections of one of four types of cells in the inner cell mass (*icm*). These are enclosed in a multilamellar reflector (*r*) and a red pigment layer. Light is collimated by a refractive lens (*le*) and a surrounding lamellar ring of reflective fibrils (*lr*). Distal to the lens is a layer of glandular cells (*gc*). Blood vessels (*bv*) enter the photophore between the reflector and the lamellar ring, where blood flow can be regulated by sphincters receiving two types of innervation (*n*). Scale bar, 0·1 mm.

The illumination was suddenly and simultaneously removed from each container and the photophore brightness was noted (by a fully dark-adapted observer) to be proportional to the previous incident illumination.]

During January 1985, we had the opportunity to study *E. superba* in Antarctica, at the Palmer Research Station and aboard the research vessel *Polar Duke*. We investigated several aspects of photophore movement in this species: its extent or

range, its accuracy in following a light source, and the mechanisms underlying its visual control. Unfortunately, most of this work was done before we learned of the excellent study by Land (1980) on *Nematoscelis atlantica*. Our findings confirm relevant portions of his work, and extend it with an analysis of the neural control of photophore movement. Our data are consistent with the ventral counter-illumination hypothesis, but do not rule out other roles for photophores.

MATERIALS AND METHODS

This study was done during January 1985, partially at Palmer Station, Anvers Island, Antarctica (64°46′ S, 64°5′ W) and partially on the research vessel *Polar Duke*. Fresh specimens of Antarctic krill *Euphausia superba*, a relatively large (4–5 cm) euphausiid, were netted and placed in seawater holding tanks either at the station or on board the ship. To observe an individual, we used the technique of Hamner *et al.* (1983) in which one end of a 2-mm diameter glass rod was glued to the dorsal carapace of the animal, and the other end inserted into the centre of a rubber stopper (5 cm diameter). The stopper was placed in the top of a Lucite observation chamber (9×10×8·5 cm) supplied with a constant flow of oxygenated sea water at approximately 1–2°C. The tethered animals swam normally, and we were able to monitor eye and photophore movements from both sides of the animal simultaneously by using two horizontally-mounted dissecting microscopes, placed on a heavy metal table top and shock-mounted with foam tubing to reduce ambient substrate vibrations. Videotapes that were subsequently time-striped and analysed frame-by-frame (resolution: 0·033 s) were used to determine the time course of rapid eye movements.

The visual stimuli were produced with either a Durabeam portable flashlight (illuminance 400 lm m^{-2}) or a fibre optic light source with a flexible lamp guide (AO Scientific 1177; used at an illuminance level of approximately 200 lm m^{-2}). For dim-light observations of spontaneous eye and photophore movements, a broad-spectrum far-red transmitting filter (Wratten no. 29 spectral transmittance peak: 720 nm) was inserted in the flashlight beam, reducing the illuminance to 35 lm m^{-2}. Illuminance was measured with an illumination meter (Weston model 756).

Photophore orientation refers to the direction opposite to that of light emission, i.e. the direction in which the rounded top of the 'bell' was facing. Photophore angles were measured to the nearest 7·5° using a clock coordinate system in which the animal's body axis with the head facing towards 9 o'clock is defined as 0° (Fig. 2). For comparative purposes, all absolute angles cited in this paper use this reference system, regardless of the animal's orientation in space. Since the eye of *E. superba* is spherical (1·8 mm in diameter) and uniformly black, its motion in response to light is not easily discerned. Blowing air into the chamber until a bubble adhered to the eye provided us (and the krill) with an unambiguous reference that facilitated visual and photographic observation of eye movement.

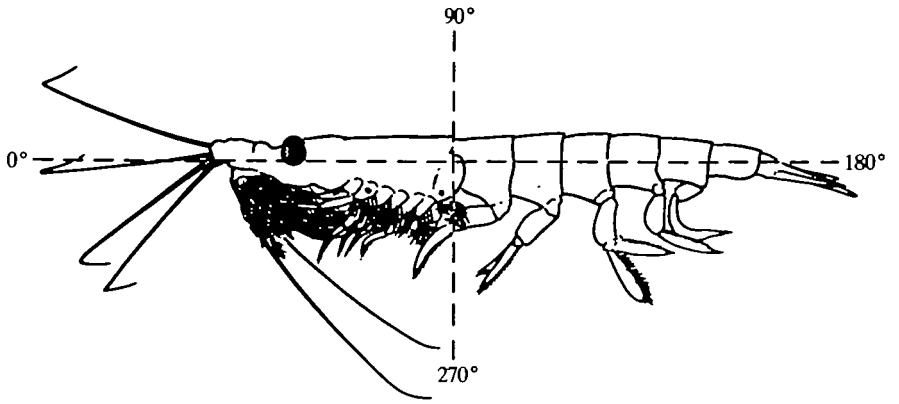

Fig. 2. Diagrammatic representation of a krill showing the axes used in measuring eye- and photophore-orienting responses. All angles are expressed relative to the direction the animal is facing.

Typically, one observer would monitor eye movement, a second observer would record the movement of the contralateral photophore on the seventh thoracic segment, and a third person would position the stimulus and record the responses on a cassette recorder for subsequent transcription and analysis. Data were collected from 39 animals.

For testing the role of gravity on the ability of photophores to follow a light source, the animal's body orientation was altered. The krill was positioned in either the head-up or the head-down orientation by bending the glass tethering rod through an angle of 90° prior to mounting the animal. In experiments requiring eye immobilization, one or both eyes were affixed to the carapace ringing the eye with a thin strand of 'superglue'.

RESULTS

Accuracy of following of a light source by the eye and photophores

The photophores were highly mobile and all moved approximately in phase. Careful examination of thoracic photophores on both sides of an animal showed that their movement was almost exactly correlated. Often the abdominal photophores would be pointing in a different direction if the abdomen was flexed, but they too rotated whenever the thoracic photophores rotated, apparently by the same amount. The photophores moved whenever the animal's eyes moved. Fig. 3 shows data from two experiments in which the degree of rotation of the eyes and photophores were correlated as the eyes moved to follow a shifting light source. Movement of the eyes and photophores was not always equal. While the eyes occasionally moved through a greater angle than the photophores (open symbols), more often the reverse was the case, especially in responding to movement of a light to positions towards the rear of the animal (filled symbols). Moreover, whereas the eyes were restricted to movement

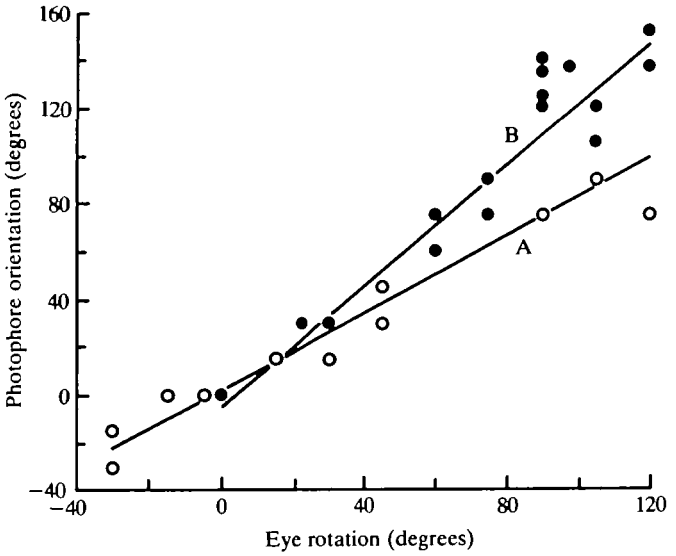

Fig. 3. Relationship between eye position and photophore orientation during rotations in response to changes in angle of incidence of a light source, for two representative animals. Best-fit linear regression lines are shown. Experiment B is more characteristic, with the photophores showing a somewhat greater degree of rotation than the eyes. (Note the difference in scale for the axes.)

in the sagittal plane, the photophores also showed the ability to rotate significantly from side to side (see also Land, 1980). All our measurements, however, were of eye and photophore rotations in the sagittal plane.

Light elicited orientation (rotation) of both eyes and photophores only from certain angles, as found for eye rotation in *Nematoscelis atlantica* (Land, 1980). Fig. 4 shows a sample record correlating the positions of a light, the eyes, and the thoracic photophores. In this animal, the eyes followed the light whenever it was moved between the angles 0° to 180°. However, the eyes moved only through approximately 105°. The photophores rotated through approximately 165° in following the light through 180°. At the extremes of their extent of rotation, both eyes and photophores often acted as if they had reached a mechanical limit to further rotation, maintaining that angle as the light moved further around the animal and then, at some point, reaching an unstable state in which they would rotate quickly to the other extreme position, often wobbling back and forth between the two extremes.

In different animals (Fig. 5) the angles reached by the photophores at the extremes of their following did not match exactly those of the light position at the same time (below the axis in Fig. 5), probably because of mechanical restraints to extreme rotations. Thus the mean light angle at the forward extreme of following was 333° (±14°S.D.), i.e. in front of and about 30° below the horizontal axis of the animal. The extreme forward angle of the photophores was a mean of 7·5° (±S.D.), a lag of about 35°. At the posterior extreme of following, the photophores were more

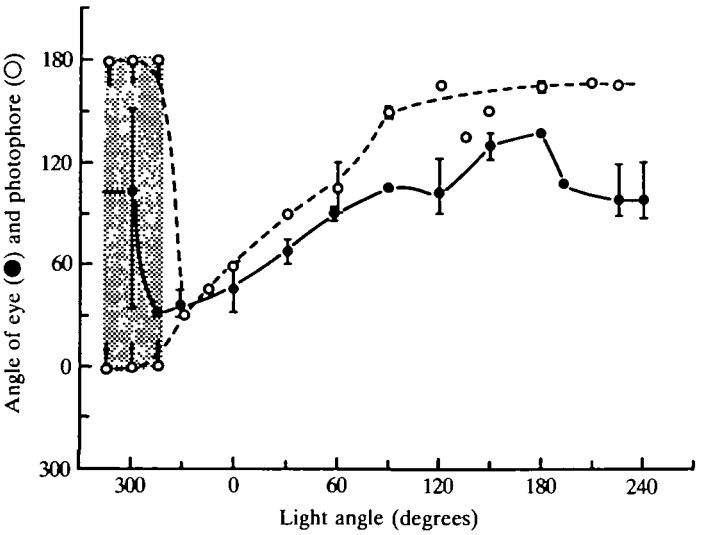

Fig. 4. Following-responses of eye (●) and photophores (○) as a function of light angle. Note the characteristic region of accurate following, between about 330° and 90–120° with respect to the body axis, and the greater range of movement seen in the photophores than in the eyes. Points with bars represent the mean and range of multiple determinations. The shaded area joins points between which the photophores wobbled back and forth in position.

accurately aligned with the light (both at a mean of 157°, but with greater variability in the light angles at which 'following' ceased than in the angle the photophore had reached when it stopped following). Thus, over the range of light angles effective in eliciting changes in photophore position, the photophores underwent approximately 0·8 times as much rotation as the light ($N = 24$). Eye movement, for which fewer measurements were made ($N = 11$), followed over a similar range of light angles, with greater variability in the extent of rotation and, in general, less total rotation. However, in certain animals, perhaps those that were healthier, younger or had recently moulted, both eyes and photophores followed light accurately over a full 180°. As in *N. atlantica* (Land, 1980), the direction of light movement *en route* to a given position does not affect the steady-state angle ultimately adopted by the photophores. Our impression, however, was that following of a moving light source was more accurate than was the eventual match between stable photophore and light position, in part because of the mechanical limits referred to above, and in part because of the tendency of the eyes and photophores to 'wander' occasionally in the presence of a stationary visual stimulus (see below).

A complete study of the dynamics of movement of the photophores in response to light movement was impracticable, but we made some video records of eye rotation in response to an abrupt 60° shift in light direction. For the example analysed in Fig. 6 there was a response latency of 80–120 ms and a maximum angular velocity of approximately $210° s^{-1}$. These compare with values in *N. atlantica* (Land, 1980) of

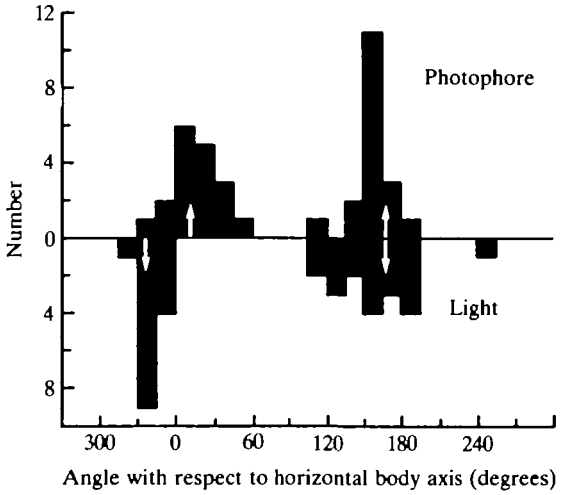

Fig. 5. Bar graphs showing angles in front of and to the rear of animals at which photophores reached their limit in their following response to light (upward bars), and the light angles at which these extreme following angles were elicited (downward bars). Following towards the front of the animal consistently reached a limit when the light reached 330–0° (mean light angle, 333°), even though the photophores usually did not manage accurate orientation at these extreme angles (mean value 15°, arrow). Conversely, photophore following consistently reached an extreme of approximately 160° (mean 157°), even though the light angles at which this limit was reached varied between 100° and 180° (mean 157°).

approximately 80–100 ms latency, and about $200°s^{-1}$ maximum angular velocity. Note the apparent 'correction' in eye position after the initial response in Fig. 6.

Control of photophore movement

A series of experimental manipulations indicated that vision was needed for the light-following response by the photophores. Removing the eyes or covering the head with an opaque (aluminium foil) hood stopped movement of the photophores in coordination with light. (More precisely, the combination of eyes and eye stalks was necessary. The photophores associated with the eyestalk complex were also removed or masked during such tests, and could in theory be the receptors driving the other photophores. This seems highly unlikely to us, however). When one eye was removed, all photophores continued to rotate in coordination with the light and the remaining eye.

Four categories of possible mechanisms of control of photophore movement occurred to us: (a) the photophores might be mechanically linked to the eyes (e.g. by ligaments, which are known to link the abdominal photophores, Hardy, 1962), so that eye movement is automatically translated into approximately equal photophore movement; (b) the photophores might be controlled by feedback from receptors sensing the eye position so that as the eyes follow a moving light, the photophores would be instructed to do likewise; (c) the photophores themselves might be

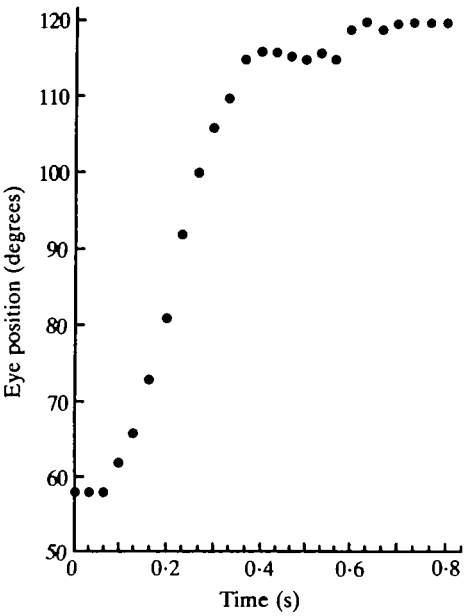

Fig. 6. Eye position measured from successive single frames of a video tape as the eye responded to an abrupt change in light angle from 60° to 120°.

directionally light-sensitive (this possibility was ruled out by the results of our 'hood' experiments); and (d) light falling on the eyes from any given angle within the range of following might elicit a parallel signal from the CNS to both the eye and the muscles that move the photophores, telling each how far they must rotate to achieve a desired position. In this case, the position of the eye must be independently calibrated by some sort of receptor, but feedback from eye position detectors would not be an adequate photophore-coordinating signal by itself.

The first of these possibilities – the obligatory mechanical coupling between eyes and photophores – is not entirely implausible, since under normal conditions the photophores rotate whenever the eyes do, independently of light position (see next section). However, as Land (1980) noted for *N. atlantica*, passive rotation of their eyes does not cause photophore movement. We repeated this experiment, showing that gentle rotation of both eyes through about 180° does not cause any detectable photophore movement. This was the case even in the presence of a stationary light, whose position would presumably appear to the animal to be changing as the eyes moved. Moreover, removal of the eyes did not prevent photophore movement, only movement correlated to light position.

The second possibility – the role of feedback from receptors sensitive to eye movement or position – was tested by immobilizing one or both eyes. In practice, immobilizing one eye is almost the same as immobilizing both, since the eyes are connected near their base to a semi-rigid cuticular plate and rotate together. (If one is immobilized, the other is capable of no more than 15–30° rotation from that

position.) In some cases (40%), when one or both eyes were immobilized, the photophores showed poor following of light (Fig. 7A). More often (60%), however, photophore following was quite good after eye immobilization (Fig. 7B). Thus neither eye movement nor feedback information about eye movement are *necessary* for coordinated photophore rotation, and we favour the hypothesis that parallel CNS instructions control photophores (see Discussion). Nevertheless, we cannot exclude the possibility that feedback resulting from eye movement is useful, when available, and that following is often degraded in its absence.

Spontaneous photophore movement

As noted above, when the eyes were free to move, they always moved together with the photophores. In the absence of a directional source of illumination, and with no apparent light movement, both eyes and photophores showed spontaneous movement (Fig. 8A). Note that both eyes and photophores rotated through 60–90°. In many of these records they also moved extensively in the 5-s intervals between position readings. With a point source of light, fluctuation about the light source direction tended to be lower. The eyes mostly fixated on the source, and the photophores followed suit. This was true even in dim red light barely adequate for us to see the photophores (Fig. 8B). Immobilizing the eyes made no apparent difference to the amount of spontaneous photophore movement. Truly spontaneous photophore movement (in the absence of visual following) was measured best when the eyes were removed (Fig. 8C). Here again, over short periods the changes in position were small, no more than 15–30°. However, there was sometimes a gradual shift from one general direction towards the other extreme, uncoordinated with any light movement.

Role of gravity in light following

Krill are capable of migrating vertically in a diurnal rhythm. This may be governed by light levels, and light appears to be pre-eminently important in other forms of orientation; e.g. the body position assumed in the water (back to the light), and the position of the tail and swimmerets during swimming (Land, 1980, confirmed by us in *E. superba* at low light intensities, but not at high intensities). However, during much of the year there is little or no light in the krill's environment, so it would be useful to have other means of determining up and down.

We have used the photophore light-tracking response to determine whether an animal's body position with respect to gravity influences photophore movement. Krill were fixed in the experimental chamber in the normal horizontal position, head-up or head-down, at 45° to the vertical, or upside down. To a first approximation, the photophores tracked a light over the same approximate angles with respect to their bodies, independent of body position with respect to gravity (Fig. 9). Following in all cases was between about 330° and 150–180°. However, the patterns were not identical. In particular, in the head-down position, photophores responded consistently to light movement in the region 180–270° where normally, in the horizontal position, there was little or no following response. Often, in animals in the

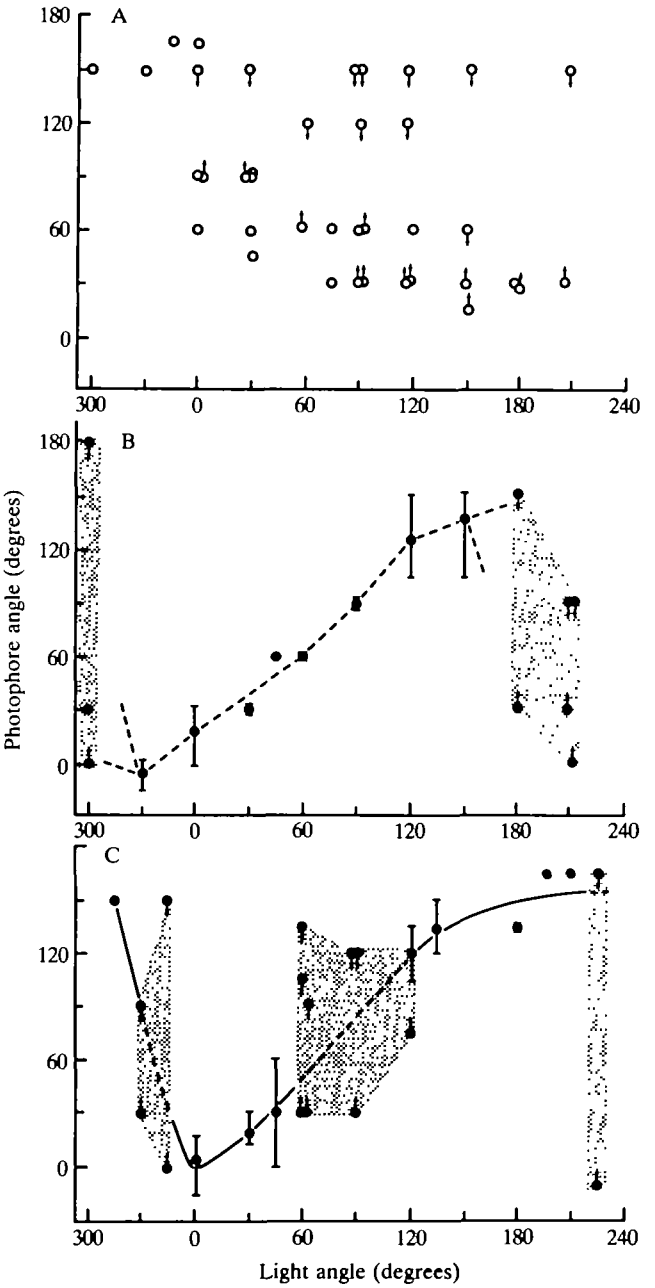

Fig. 7. (A) Photophore orientation as a function of light angle when the eyes were immobilized. Bars represent ranges of multiple measurements, and arrows and shaded areas indicate light angles at which the photophore position was unstable, rapidly wobbling or flipping back and forth between the extreme positions indicated. In this case, photophore orienting responses were essentially eliminated by eye mobilization, but returned to approximately normal after the immobilizing strand of glue had been removed, freeing the eyes (B). (C) Another experiment of the same type, in which photophore orienting responses were quite accurate even when the eyes were immobilized.

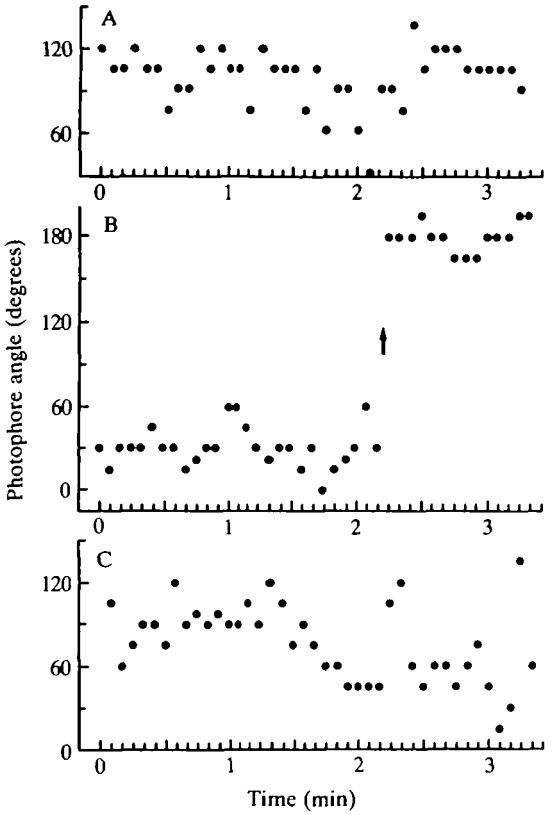

Fig. 8. 'Spontaneous' photophore movement under three different experimental conditions. In each case, photophore angle was measured every 5 s for 3 min or more. Position changes between readings, though common, are not indicated. (A) A typical record of the position of each of 50 successive readings, 5 s apart, during which the whole chamber was covered with white paper, except for a small hole for the microscope objective so we could watch the animal. The light was reasonably bright, but almost equivalent in intensity from all directions. (B) Photophore movement with a directional source of dim red light ($<35\,\mathrm{lm\,m^{-2}}$), barely adequate to permit observation of photophore position. That the animal was sensitive to this light source is seen by the abrupt shift in photophore orientation that coincided with moving the light source from 30° to 180° (arrow). (C) Photophore movement after removal of the eyes.

head-down position, following occurred in two regions, one in the normal 0–120° region, the other between 210° and 270°. The photophores were not aligned with light when it was at 210–270°, this apparently being outside the range of movement possible. However, the photophores would rotate to the extremes of the position possible, e.g. to about 210° in the instance of Fig. 9. In six experiments investigating the effects of gravity, there was a mean shift in photophore position of 51° of arc with movement of the light between 210° and 270° in animals mounted head-down, compared with 14° in those mounted head-up, and 40° in horizontally mounted animals. Moreover, the shift in the head-down position (Table 1) was typically to

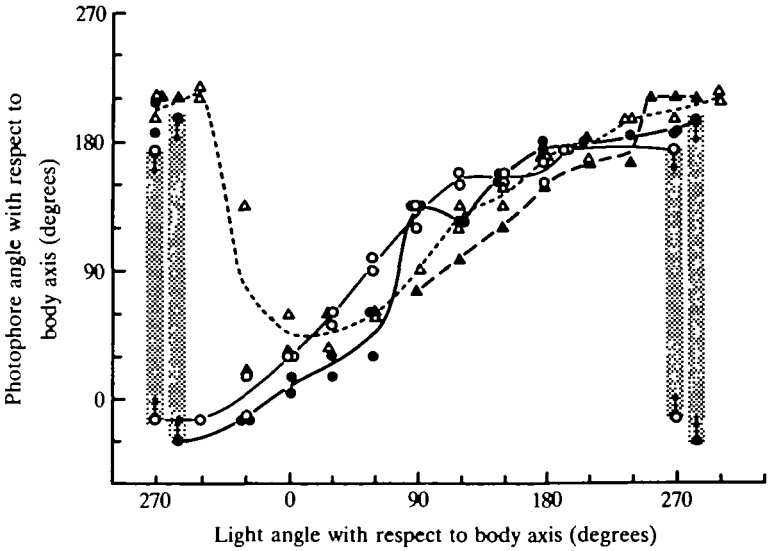

Fig. 9. Effects of gravity on photophore orientation with respect to light angle. Curves showing photophore angle *vs* light angle when the same krill was mounted horizontally with its dorsal (○) or ventral (●) side up, or vertically with its head up (△) or down (▲). Although the patterns are generally similar, there were consistent differences in following when the light was near the normal limits of following with respect to the body axis (see text). Shaded area represents points between which the photophores wobbled back and forth in position.

Table 1. *Amount of additional posterior rotation of photophores in response to a 60° shift in light position (from 210° to 270° absolute animal angle), with the animal held horizontal, facing up or facing down*

Animal no.	Horizontal	Facing up	Facing down
21	0°	30°	67°
22	15°	0°	45°
23	0°	0°	60°
24	15°	0°	60°
27A	0°	30°	75°
27B	0°	22°	52°
31	0°	30°	45°
Mean	4·3°	16·0°*	57·7°†

* Not significantly different from the horizontal position ($P > 0{\cdot}05$).
† Significantly different from either the horizontal or facing-up positions ($P < 0{\cdot}001$).

extreme posterior angles (to 210° or beyond), while in the head-up position there was a strong tendency instead to 'wobble' between about 0° and 150°. These figures reflect only the additional rotation in the same direction as the light over this

restricted range of angles. They do not include the larger shifts in position in the other direction (see below).

The light position at which the eyes and photophores shifted abruptly from one extreme of rotation to the opposite extreme (or wobbled between them) also tended to differ with body position with respect to gravity. In the horizontal position, this normally occurred somewhere between 240° and 330°. In 50% of the cases (11/22) this occurred with light between 210° and 270°. With the animal in the head-up position, abrupt shifts or wobble occurred when the light was between 210° and 270° in five of eight experiments. In the head-down position, it was seen in only one of seven experiments. The differences were independent of the sequence in which different light angles were tested. While our measurements of stimulus angle and animal orientation were only accurate within ±7·5°, we feel that the consistency of these findings suggests that the subtle differences we observe in photophore light-tracking as a function of body orientation are non-artefactual. Krill may have receptors of some kind other than statocysts that are sensitive to gravity and that interact with visual input to modify photophore movement.

DISCUSSION

The thoracic and abdominal photophores appear always to move in phase with movement of the eyes and the single photophores that are associated with the eyestalk complex. It is generally thought that visual tracking of a light source and the corresponding rotation of photophores so that they always point away from the light are a mechanism for protective 'counter-illumination', i.e. emission of light of similar wavelength and in the same direction as downwelling light to compensate for light absorption by the semi-translucent animals (Clarke, 1963; Herring, 1978; Land, 1980). Especially for krill in large schools, this is an attractive hypothesis, and our findings are consistent with it. However, little is known about the natural conditions under which euphausiids luminesce. Divers in the water report that luminescence is seldom observed in the light, even among disturbed krill, but it is sometimes seen in the dark (W. M. Hamner & P. P. Hamner, personal observations). Tomo (1983) noted spontaneous luminescence at night in a school of *E. superba*, which he said resembled 'the milky way'. Under the conditions of our experiments, we virtually never saw luminescence. Hence photophore rotation is apparently coupled in an obligatory way to active eye rotation, with a luminescence function that is independently triggered. However, the photophores are not physically linked to the eyes. In *E. superba*, as in *N. atlantica* (Land, 1980), the eyes can be rotated passively without influencing photophore position. Hence the coordinated movement is accomplished by the nervous system. Much of the work we report was directed at understanding the nature of this nervous control.

Although photophore movement is clearly a function of light input to the eyes, several lines of evidence indicate that the neural instructions to the photophores are not a direct reflex response either to eye movement or to shifting a visual image on the surface of the eye. The simultaneous in-phase rotation of eye and photophores, even

in the presence of a stationary dim red light, shows that a moving visual stimulus is not necessary for the coordinated movement. However, the absence of photophore movement when the eyes were passively rotated shows that the receptors sensing eye position are not, in themselves, able to drive photophore movement. Indeed, the lack of photophore movement when the eyes were rotated in the presence of a stationary light source, the image of which would be moving across the eye, shows that a moving visual stimulus, by itself, is also not an adequate driving stimulus. Thus the photophores respond to a CNS signal thay may occur spontaneously or may be triggered by a light stimulus, and that seems always to be accompanied by a parallel signal governing eye rotation.

Presumably a shift in position of a light produces a motor command that moves the eyes until a desired portion of the dorsal surface of the eye is pointed towards the light. The photophores might be controlled either by the same command [as suggested by Land (1980)] or by a command determined by receptors sensing the position of the eyes. Immobilization of the eyes would eliminate sensory feedback information from the mechanoreceptors monitoring eye position. Hence it is not surprising that photophore following was severely degraded in a large fraction (40%) of eye immobilization experiments. However, the fact that in some cases photophores followed light accurately with the eyes immobilized indicates that neither the feedback monitoring of eye position nor the effects of the eye movement on visual input during the following response are necessary for accurate photophore following. Instead, a light signal falling on the eye at an angle that triggers eye movement also carries the information necessary for accurate rotation of photophores, without any corrections based on sensing eye position or monitoring of degree of approximation of the visual image to the desired spot on the eye. Presumably the same information is adequate for an accurate visual following response, without corrections based on sensory feedback. Having such a sensorimotor map of the retina would greatly increase the speed of reflex light-following. The map would be interpreted correctly only if the eye were in a known position, however, which does require proprioceptive sensory feedback or a knowledge of the output to the eye muscles (efference copy). In many cases when the eyes were immobilized, accurate monitoring of eye position was probably disrupted. Only if the eyes were fixed in such a way that the information provided by eye position detectors was correct would instructions to motor centres be correctly interpreted. A comparable disruption of forelimb 'striking' accuracy is seen in mantids in which the head has been fixed at an angle with respect to the axis of the thorax, but not when the head is fixed on the axis of the thorax (Mittelstaedt, 1957).

In addition to their possible role in protective counter-illumination, eye/photophore coordination and the visual light-following response may have other uses. Land (1980), working with *N. atlantica*, found that light angle could influence tail position and postulated that this constituted a mechanism of vertical steering. We observed a similar influence of light angle on tail position at very low light levels. Since light penetrating the sea surface is almost directly downwelling, irrespective of sun azimuth, presumably the eye/photophore following, and any influence on

swimming direction, will be relevant mainly when the krill are not oriented horizontally, but rather are changing depth in the water column. This happens when a school is migrating towards or away from the surface, or when an individual backflips off the underside of an ice block after filling the feeding basket with algae. Typically they orient almost vertically (head up) when scraping off ice algae, then dive steeply (but never straight) down on termination of feeding (W. M. Hamner, personal observation). The restricted range of eye movements (less than 180°) probably limits the change in swimming direction to a similar range.

E. superba, like other krill (Fraenkel & Gunn, 1961; W. M. Hamner, personal observation), will orient on their sides or even upside down in response to a point source of light located to the side or below them. Hence light is a powerful orienting influence, but not all orientation is necessarily visual. Not only did we find evidence for various differences in eye/photophore following as a function of animal orientation with respect to gravity, but other aspects of the behaviour suggest that light angle is only one determinant of body orientation and swimming behaviour. *E. superba* have been observed to swim for several days in one direction (Kanda, Takagi & Seki, 1982), during which time the angle of the sun changed repeatedly with respect to their swimming direction. Moreover, our data suggest the possibility of some kind of gravity (or perhaps hydrostatic pressure) receptors that might contribute to oriented swimming and vertical migration.

Another possible role for luminescence and eye/photophore movement is in schooling, especially in the dark. Within a school, *E. superba* occur at concentrations of 20 000–30 000 m^{-3}, and swim at rates of up to 20 cm s^{-1} (Hamner, 1984). A given euphausiid must either watch (or respond rheotactically to) animals in front and above. Although rheotactic cues appear most important in schooling, if eye-following coupled with photophore movement and flashing alerts follower krill to an abrupt change in body position, it could help in coordinating rapid school movement.

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