

POLARIZED LIGHT AND THE ORIENTATION OF TWO MARINE CRUSTACEA*

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INTRODUCTION

Naturally occurring polarized light is used for orientation by many arthropods. Various insects and chelicerates as well as crustaceans, employing either their simple or compound eyes, can detect the pattern of linearly polarized light in the blue sky and from it determine geographical direction. Among Crustacea, the semi-terrestrial beach amphipod *Talitrus* and the isopod *Tylos* show this when, on being disturbed, they are able to head directly towards the sea without using other clues (Pardi & Papi, 1953*a, b*; Pardi, 1954). Like that of the sky, underwater scattered illumination is known to be polarized in a way primarily determined by the sun's position (Waterman, 1954*a, b*, 1955; Ivanoff, 1956; Waterman & Westell, 1956).

The possibility thus exists that *aquatic* arthropods, or other underwater forms sensitive to polarization, may use this submarine light pattern as a similar sort of sun compass (Waterman, 1957). It is certain that some aquatic arthropods can in fact perceive polarized light (Verkhovskaya, 1940; Waterman 1950; Baylor & Smith, 1953; Eckert, 1953), but few quantitative data are available. No direct evidence linking this perceptive ability with their normal orientation and migration has yet been found, although an effect of sky polarization observed underwater has been suggested as a possible factor in the diurnal vertical migration of plankton (Verkhovskaya, 1940). This paper describes an experimental approach to the general problem. The major part of the work comprises a quantitative laboratory study of the responses of a marine mysid to plane polarized light, and this is supplemented by an exploratory field project in which a caridean decapod was found capable of swimming straight courses in open water where landmarks were not available.

LABORATORY EXPERIMENTS ON *MYSIDIUM*

Organisms

In seeking suitable experimental animals with which to study quantitative effects of polarized light on orientation and behaviour many species have been tested. Exploratory, and as yet equivocal, tests have been made on a number of teleosts, both marine and fresh water, but mainly marine crustaceans have been used.

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Littoral Mysidacea, Natantia and Reptantia of many varieties, Stomatopoda, pelagic and bathypelagic Copepoda, Amphipoda and Caridea have all been examined for favourable reaction patterns. So far zoeas of littoral Brachyura and the adult mysid, *Mysidium gracile* (Dana) have offered the most promise. This report is concerned mainly with the swimming behaviour of the latter form in vertical beams of linearly polarized light. Distinctive features which make this animal appropriate for such work are its sustained locomotor activity and its strongly visual reaction patterns. The latter are mediated through the large and well-developed stalked compound eyes, a median eye being absent in mysids (Mayrat, 1956) as apparently throughout the Crustacea Peracarida. Adult specimens about 5–10 mm. in length, either freshly caught or kept in sea-water aquaria, were used in the experiments. No effect of length of captivity was found in the mysid response patterns; animals were used for experiments after periods of captivity ranging from 1–2 hr. up to about 2 weeks.

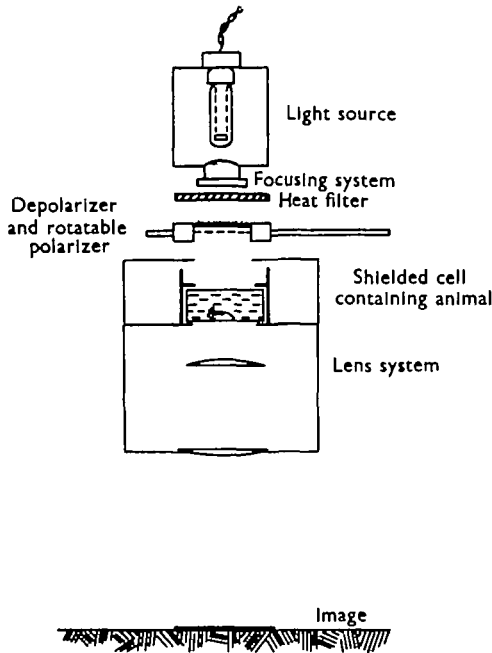


Fig. 1. Diagram of apparatus used to expose *Mysidium* to a vertical beam of nearly 100% linearly polarized light and to record the resultant swimming orientation.

Apparatus

A small experimental cell containing the animal in sea water was illuminated from above by a vertical beam of polarized light whose plane of polarization could be altered at will. This provided an illumination of 700 lux at the cell. Originating from a ribbon filament projection bulb the light passed successively through a focusing lens system, a heat filter, a depolarizer, a rotatable Polaroid linear polarizer, the experimental cell, and finally two lenses which produced an image of the latter

and its contents upon the bench beneath (Fig. 1). The apparatus was set up in a darkroom with a suitable arrangement of baffles and shields to prevent extraneous light from reaching the experimental cell. This consisted of a short length of cylindrical plastic tube 50 mm. in diameter sealed to a flat glass plate. The latter ensured a perfectly plane bottom which was important optically for good image projection and also for avoiding the possible influence of an uneven surface on the animal's behaviour. The circular shape was also critical. Preliminary tests in a square cell showed a marked and statistically significant tendency of the mysids to swim at an angle of 45° to the sides whether the light was polarized or not. The effects of the container thus masked any effect due to polarized light, and such a cell was inappropriate for experiments of this nature.

To minimize polarization artifacts several important precautions were taken. The interposition of a depolarizer, made of two sheets of waxed paper, has already been mentioned. This cut out any intensity modulation arising from the slight inherent polarization in the light source. In addition, surface reflexions from the walls of the cell were greatly reduced. These would otherwise act as an analyser of polarized light striking them obliquely. To avoid this the vertical walls of the experimental cell were given an even, non-reflecting opaque surface by coating them with a thin layer of carbon black suspended in molten wax. In addition, the possibility of reflexion was virtually eliminated by shading the walls from direct light with a circular diaphragm having an aperture 5 mm. less than the inner diameter of the cell. Control experiments described below (p. 353) tested the need for and the effectiveness of this diaphragm.

Finally, the meniscus at the margin of the water surface was eliminated in order to remove the regular pattern of light and dark spots formed by the polarized light striking this boundary and readily visible at least to the human eye. To achieve this the upper edge of the cell walls was ground smooth so that a flat glass plate acting as a cover would seal off the completely full vessel without an air-water interface. Inspection of the whole optical set-up for spurious polarization effects was made with the special interference analyser described by Waterman (1955). This is sensitive down to about 5% polarization and showed that the apparatus as used was essentially free from polarization artifacts.

Procedure

In a typical experiment the cell was filled with fresh clean sea water, a single animal was introduced and the cover put on, care being taken to exclude air bubbles. The cell was placed symmetrically in the light beam and surrounded by a cylindrical black shield. In this position it was enclosed on all sides by the black-walled observation chamber about 25 cm. square. A clear image of the animal was focused upon a sheet of squared paper placed on the bench beneath. The lens setting, depending upon the depth of the mysid in the water, could be altered as the experiment proceeded. After an interval to allow the animal to settle down, the polarizer was rotated by the operator to one of seven positions. The planes of polarization (defined by the *e* vector) customarily used were 30° apart, starting clockwise from

the horizontal direction of the recording grid as 0° . The particular plane used for a given determination was selected with the aid of a table of random numbers. It was unknown to the observer until a whole session of measurements was over.

To begin, the observer drew a line along the antero-posterior axis of the image of the mysid. Then at 5 sec. intervals this recording of its position was repeated for a total of 25 times. After that the polarizer was set at another randomly chosen angle of the seven and a further run of twenty-five positions was recorded. At the end of five such series of observations with different planes of polarization, operator and observer were interchanged and a second series of five similarly selected settings of the polarizer were tested. In the following discussion each group of twenty-five observations recorded for one plane of polarization is termed a 'run' and each group of ten runs is termed a 'set', which thus comprises 250 orientation measurements.

During such a recording period the animal would generally be swimming about in the cell fairly quickly. Some dexterity and experience were often required to fix its orientation exactly at each reading, but generally this was easy if the operator announced the time for recording and the observer had only to keep his eyes on the moving image. Every effort was made by the observer to keep his mind as blank as possible in order to avoid the chance of bias. Any possible influence of the first few lines drawn on the orientation chosen for later ones, or of guesses of the polarization plane were steadfastly resisted.

Analytical method

To detect any influence of the plane of the e vector upon the course set by the animal, the orientation of each line in a run of 25 was first measured with reference to the horizontal grid lines on the paper. The deviation of each such line (representing the animal's longitudinal axis) from the plane of polarization was then calculated. The frequency distribution of the resulting angles between 0° and 90° indicates any relationship between the animal's course and the plane of polarization. If there is no such relationship, a random distribution would be expected. But provided that orientation is generally in the plane of polarization, then a majority of readings in the neighbourhood of 0° might be expected; if at right angles to the plane of polarization, then in the neighbourhood of 90° . Most of the results are depicted in histograms representing 15° groups of angles between 0° and 90° . The data generally are insufficient to permit a more detailed analysis with smaller groups of angles. However, the large numbers of measurements in Figs. 3 and 4 are plotted for intervals of 5° .

Results

To illustrate these experiments in detail the results of two typical runs selected from a series with one animal are presented first (Fig. 2). Facsimiles of the laboratory records obtained with polarization planes 60° (A1) and 150° (B1) to the reference direction show the axial orientation of mysid at the end of twenty-five 5 sec. intervals each. The angles between these axial lines and horizontal (0°) in the reference grid are listed in Table 1, along with their differences from the plane

of polarization. For analysis these deviations have been grouped into intervals of 15° (A₂, B₂) and 30° (A₃, B₃).

A clear bias towards an orientation at right angles to the plane of the *e* vector is apparent in these histograms. If the appropriate χ^2 test is applied to the numbers

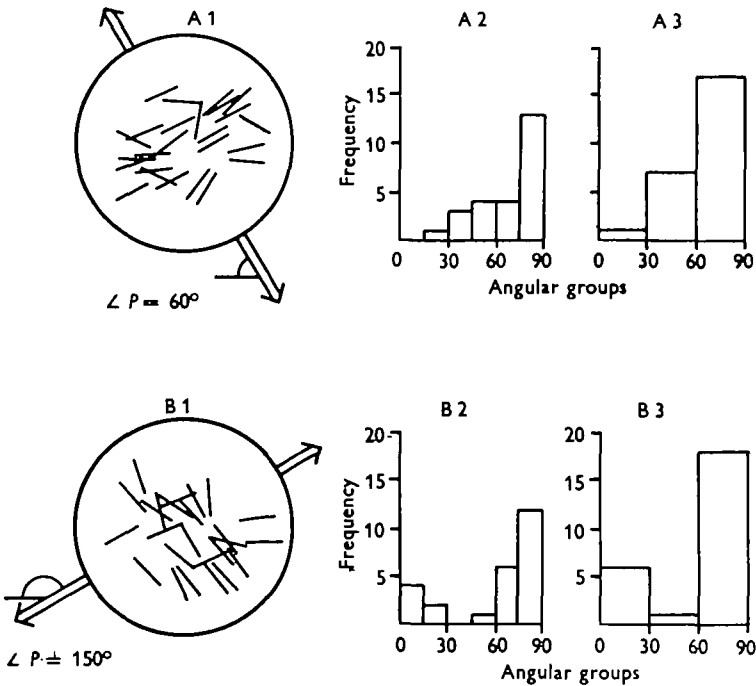


Fig. 2. Two sample runs (twenty-five observations each) of the swimming orientation of one *Myxidium* in a vertical beam of plane polarized light. In series A the *e* vector was at 60° relative to the horizontal reference direction (0°); in series B it was at 150° . A₁ and B₁ are facsimiles of the laboratory record made of the runs. Each of the twenty-five lines in the circle represents the position of the animal's longitudinal axis at intervals of 5 sec. Their deviations from the *e* vector planes are plotted in the histograms grouping angles in 150° intervals (A₂, B₂) and 30° intervals (A₃, B₃). χ^2 tests show the preponderance of orientation near 90° to be significant in both cases.

of readings falling into the various angular groups, the reliability of this inference may be tested statistically (for 30° intervals):

<i>e</i> vector	χ^2	Degrees of freedom	<i>P</i>
60° polarization plane	15.4	2	<0.01
150° polarization plane	18.2	2	<0.01

These values of *P* are within the limits normally considered significant. For the 15° intervals the values are within the significant range by an even wider margin. The data for the 150° polarization plane, in addition to the predominant 90° orientation, show some preference for swimming parallel to the *e* vector when not at right angles to it.

Table 1. Angular measurements relating to Fig. 2

Series A			Series B		
Serial no. of observation	Axial orientation of <i>Mysidium</i> relative to 0°	Angular deviations from plane of polarization	Serial no. of observation	Axial orientation of <i>Mysidium</i> relative to 0°	Angular deviations from plane of polarization
1	153	87	1	65	85
2	180	60	2	63	87
3	125	65	3	55	85
4	100	40	4	54	84
5	149	89	5	72	78
6	34	26	6	51	81
7	178	62	7	44	74
8	160	80	8	154	4
9	139	79	9	45	75
10	160	80	10	89	61
11	172	68	11	42	72
12	155	85	12	55	85
13	153	87	13	158	8
14	11	49	14	18	48
15	29	31	15	49	79
16	146	86	16	68	82
17	139	79	17	37	67
18	29	31	18	49	79
19	173	67	19	153	3
20	13	47	20	177	27
21	148	88	21	175	25
22	151	89	22	35	65
23	142	82	23	147	3
24	157	83	24	74	76
25	120	60	25	48	78

Table 2. Summary of the distribution of angular deviations of the axis of *Mysidium* from the plane of polarization

	Percentages in angular groups						No. of observations
	0-15°	16-30°	31-45°	46-60°	61-75°	76-90°	
Total results (24.5 sets)	12.6	12.6	14.7	18.2	20.3	21.6	6125
	25.2		32.9		41.9		
9 Non-significant sets	15.6	16.4	17.9	17.4	16.2	16.5	2250
	32.0		35.3		32.7		
15.5 significant sets (see Fig. 3)	11.1	10.2	12.7	18.9	22.5	24.6	3875
	21.3		31.6		47.1		
22 significant runs (29 Aug.) (see Fig. 4)	8.7	6.4	8.2	14.9	26.7	35.1	550
	15.1		23.1		61.8		

N.B. The χ^2 for the numbers in the non-significant sets is 5.4 making P circa 0.4 which is not significant. All the other χ^2 's are highly significant.

The total data presented in this report comprise 245 runs of the kind illustrated above or 6125 orientation measurements made in polarized light plus a number of controls in unpolarized light. In the sum total of all these results, as in the sample already presented, *Mysidium* shows a statistically significant preponderance of swimming perpendicular to the e vector (Table 2). Some further interesting relations become obvious if the data are considered in more detail. For instance, of the 24.5 sets which might have been expected to give 90° polarized light orientation, 15.5 did so, while the remainder showed a random orientation; thus demonstrating that under these conditions, the animal will react to the polarization pattern only about 60% of the time.

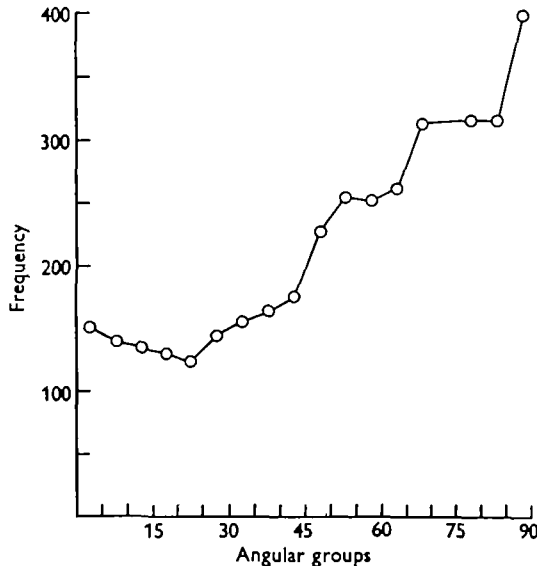


Fig. 3. Over-all swimming orientation of *Mysidium* (15.5 significant sets, 3875 measurements) relative to the e vector plane of the vertical beam of polarized light. Clear preponderance of alignment perpendicular to the e vector is shown with a minor rise parallel to the plane. The accuracy of the polarized light orientation appears to be low and the incidence of random orientation rather high.

A more precise idea of the response when it does occur can be obtained if the 15.5 significant sets are isolated and analysed alone (Table 2). There are enough measurements here (3875) to permit a grouping of the deviation angles within 5° intervals. Two major features of these selected results (Fig. 3) are the same as in many of the single runs of twenty-five measurements and in the total data. These are: (1) the marked preference for a 90° orientation relative to the polarization plane; and (2) the small upturn in the frequency at 0° as noted in the 150° run of Fig. 2.

In addition, a new feature is made obvious by Fig. 3. This is the rather gradual slope upwards of the frequency curve to a maximum in the $85-90^\circ$ group. This means that either the accuracy or the persistence of the mysid's orientation with

reference to the plane of polarization is not high. To analyse this further, one must be able to differentiate between these two contributing factors, both tending to reduce the sharpness of the average frequency distribution curve. Some experimental data obtained on the persistence factor is presented below. By inference the remainder of the broad spread of orientation angles must be primarily determined by the precision of the response.

Whatever this precision of alignment may be, we have already seen that in the data as a whole there is great variability in the occurrence (*v.* non-occurrence) of orientated response. Thus some individual mysids obviously orientate largely by this visual cue, others may not do so in the experimental situation prevailing; even in a single animal the influence of the polarization plane may vary from time to

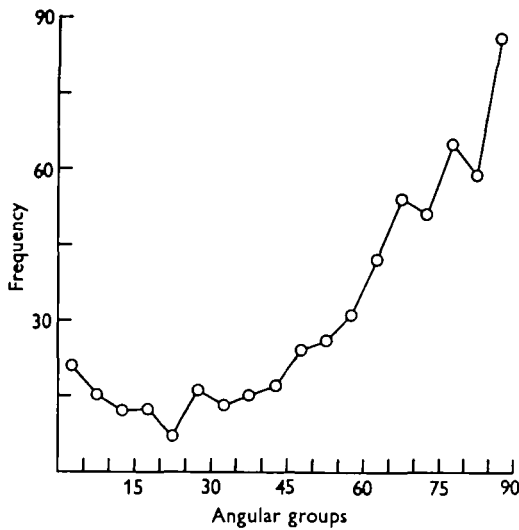


Fig. 4. Swimming orientation of *Mysidium* relative to the polarization plane in a selected series of twenty-two runs plotted with deviation angles grouped in 5° intervals. Out of thirty consecutive runs these twenty-two showed a significant preference for swimming perpendicular to the e vector, the remainder did not. Except that the random component of the over-all results is naturally reduced by this selection the relations are essentially similar to those shown by the whole data (Table 2 and Fig. 3).

time. An indication of the usual duration of a period of consistent response is obtained when the data for a single animal are analysed by runs. For example, one series of thirty runs had twenty-two which showed a significant preference for the 61–90° sector. Of the remainder five had a random distribution and three had a bias for angles between 31 and 60°.

An even more detailed idea of the accuracy of orientation is obtained if only these twenty-two runs showing the 90° bias are examined (Fig. 4). The randomness of the graph is, of course, reduced by this selection and the preponderance of polarization responses sharpened (Table 2). But the lesser peak around 0° is still present, indicating that even when the average orientation is most favourable for swimming

across the plane of the e vector, this individual tended to orientate parallel to it some of the time. Otherwise this more selected frequency curve is essentially similar to the summed distributions.

In the sole exception to the general rule for set averages, swimming parallel to the plane was obtained in five sets measured in one animal in a single experimental session (Fig. 5). The χ^2 test applied to this data gave the following results:

Groupings of deviation angles	χ^2	Degrees of freedom	P
For 15° intervals	8.5	4	c. 0.70
For 30° intervals	8.0	2	0.02

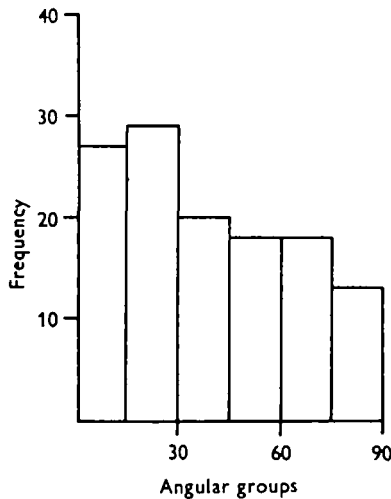


Fig. 5. Exceptional e vector orientation observed in a single *Mysidium* during five sets measured in one session. The 15° group differences are not significant on the basis of the χ^2 test, but the preference for near-parallel orientation is significant if 30° intervals are considered instead. This same animal gave the more usual perpendicular orientation for a long period on the previous day (Fig. 6).

Thus the tendency for swimming in the plane may be taken as significant for the 30° groupings of angles, but in the more rigorous 15° analysis this was not statistically sustained.

On the previous day this same individual *Mysidium* had shown the longest period of consistent polarized light behaviour noted in all these experiments. At that earlier time it behaved like the majority of other specimens and swam mainly perpendicular to the plane of polarization for 3 hr. Sample control runs separated by 75 min. of swimming under various other conditions confirmed the essential stability of its orientation pattern during this period (Fig. 6).

From these measurements it may also be concluded that fatigue does not have any significant effect in a 3 hr. period of response, although fluctuations in the

random component of orientation are clearly shown by the three sets of histograms. Comparison of the results on the 2 days quantitatively demonstrates the sort of changes in reaction pattern which may occur in a single *Mysidium* and must usually be present to some degree in a population of individuals orientating to polarized light.

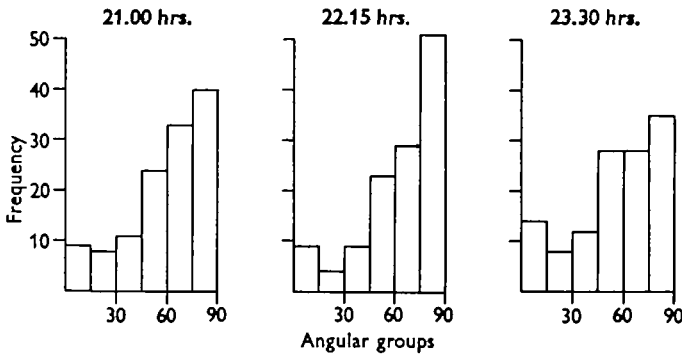


Fig. 6. Orientation to plane polarized light by the individual which, on the following day, gave the results of Fig. 5. The three sets of data were taken under identical conditions at intervals of 75 min. Between these times other tests were run. The results demonstrate the basic stability of the mysid's reaction pattern over a 3 hr. experimental period.

To check whether significant response changes of this kind were occurring within the much shorter time intervals occupied by runs of measurements with one individual, each orientation was numbered serially for the run throughout seven sets of data. Grouping these into 25 sec. intervals gives the following totals:

Time interval during 2 min. run	1-25 sec.	26-50 sec.	51-75 sec.	76-100 sec.	101-125 sec.
No. of deviation angles within the 61-90° interval	159	157	145	152	154

No indication is given here that either the animal's preference or accuracy of orientation was changing systematically or significantly within the 2 min. period of the separate runs of twenty-five observations. Under certain conditions, however, a change in some stimulus parameter after one run does influence the outcome of the next run. This occurred, for example, when balanced series of measurements were made at different intensities and wavelengths. (The data here comprise the same sequence of fifty-five runs also mentioned on p. 353.)

If the frequency distributions for ten runs made just *before* changes in *I* or λ are compared with runs immediately *after* such changes, an interesting difference is found. Before the light is altered the orientation pattern is characteristic of that found over long periods when only the polarization plane is changed; afterwards, the random element is much greater. This suggests that polarized light orientation requires at some level within the mysid a process akin to light- or dark-adaptation before a steady state is reached.

The summarizing description of our experimental results so far presented proves clearly that *Mysidium* can orientate its swimming in relation to a vertical beam of linearly polarized light and does so mainly at right angles to the e vector plane. However, the detailed data illuminate a number of further points. Of prime importance were the tests made to increase the certainty with which the general

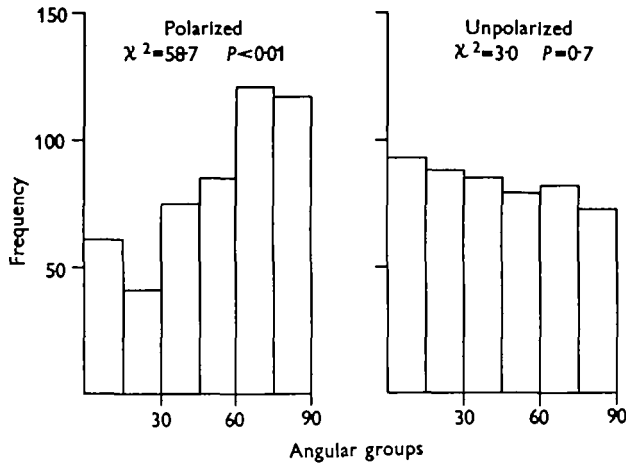


Fig. 7. Comparison of the swimming orientation of *Mysidium* in balanced runs with polarized and unpolarized light beams. Highly significant bias for orientation at right angles to the e vector plane is demonstrated in polarized light and no significant preference in unpolarized light.

conclusions may be accepted. In some of the control experiments paired runs were made with and without the light being polarized. In others an extra diaphragm, already described on p. 344, was used to exclude more thoroughly the possibility of spurious effects introduced by the experimental cell into the polarized light beam.

Two double sets with two individuals were run to compare swimming behaviour in polarized and unpolarized light under otherwise identical conditions. This was accomplished by placing a second depolarizing filter made of waxed paper in the beam either above or below the Polaroid. The first position provided completely linearly polarized light, the second completely unpolarized light of the same intensity and pattern of illumination. By alternately making the polarized run the first or second member of a pair of runs for each polarization plane any persistent effect of the previous exposure on the mysid's behaviour was minimized. In this manner 500 orientation measurements were obtained with polarized and 500 with unpolarized light.

As before, the polarized sets showed a highly significant bias for swimming at right angles to the plane (Fig. 7). The χ^2 results are shown in the figure. The unpolarized sets showed a slight trend towards a maximum at 0° , but this was not statistically significant and must be considered chance variation. Therefore these control data strongly support the general conclusion that the polarization pattern really is the significant parameter here. An interesting secondary point appears in

the data for the first mysid in these pairs of sets, namely that the animal ranged less about the cell in the unpolarized light than when it was orientating to the polarization. If this is a real difference, it may be compared descriptively to the apparent photokinetic effect of polarized light reported by Verkhovskaya (1940).

To re-check the possible disturbing effects of reflexion from the walls of the experimental cell, three pairs of sets were measured each with a different animal. This was done with balanced runs with and without the diaphragm (already described) completely shading the vessel's walls. The combined results for 750 readings with the diaphragm and 750 without show that this extra shielding did not significantly alter the outcome of the experiment. In both cases swimming was predominantly in the 61–90° sector, even though the random element, indicating lack of polarized light response, was rather high in these data (Fig. 8). This control result should allay any residual qualms about the presence of significant optical artifacts in the system.

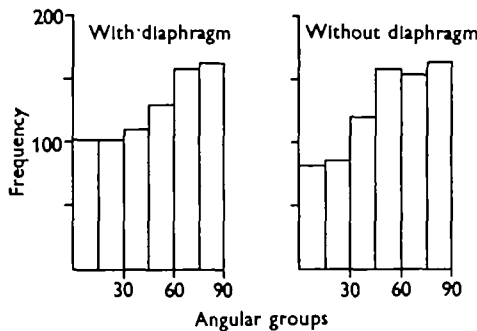


Fig. 8. Comparison of the swimming orientation of *Mysidium* to polarized light in balanced runs with and without an extra diaphragm shielding the experimental cell walls from the light beam. The extra shielding is seen not to alter the outcome, proving that even without this diaphragm, the animal is probably not reacting to artifacts reflected from the cell walls.

Finally, some of the experiments explored the effects of parameters which could provide further clues as to the sensory mechanism involved in the results described above. By means of Wratten 'neutral' filters transmitting 10 and 1%, as well as two interference filters with transmission maxima at 440 and 660 mμ, both intensity and λ of the polarized light were varied in a sequence of fifty-five runs. In one set carried out with each of these plus an initial and terminal control with full unaltered intensity, significant predominance of 90° orientation to the polarization plane occurred in every case (Fig. 9). Decreasing the intensity of the light, and perhaps also restricting the wavelength particularly to the red, caused an increase in the random element in the responses. The changes in intensity did not change the dominance of the perpendicular as compared with the parallel orientation to the plane as they have been reported to do in *Drosophila* (Stephens, Fingerman & Brown, 1953). Further experiments of the sort here described need to be done using equal spectral energies and filters actually known to be neutral for *Mysidium* whose wavelength sensitivity has not yet been determined.

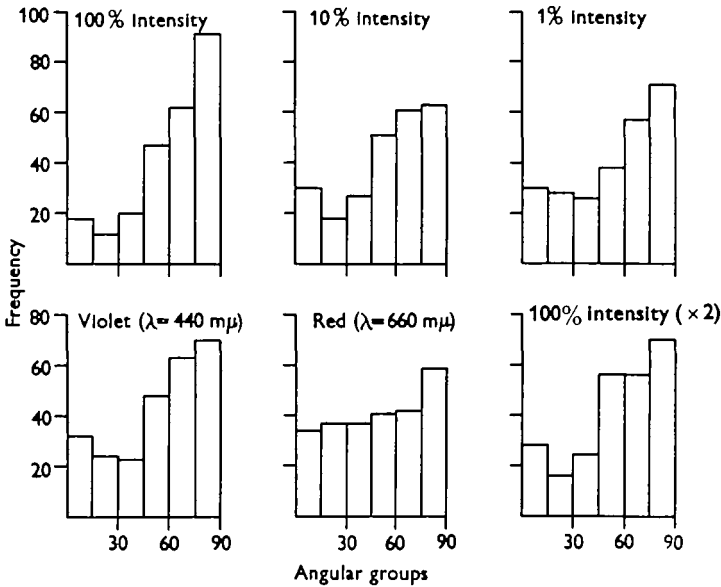


Fig. 9. Orientation of *Mysidium* in a series of sets with light passed through Wratten 'neutral' filters and narrow band interference filters. In all cases the predominance of the 90° orientation plane is clear. Decreasing the light intensity and perhaps also restricting its wavelength, particularly in the red, merely increases the random element in the swimming orientation. The final 100% intensity test was a half set and the numbers are shown here doubled.

Discussion

The responses of *Mysidium* to a vertical beam of linearly polarized light raise some interesting questions. Most of these cannot be answered definitely in the light of the present research; some, however, can be illuminated by correlation with other facts already known.

Perhaps the point of primary interest to the physiologist is whether the data provide clues to the sensory mechanism of polarized light perception. The type of reaction pattern shown by *Mysidium*, while differing in detail, is qualitatively rather similar to those found in other arthropods. Thus in a vertical beam of linearly polarized light *Daphnia*, many other species of Cladocera, and a water mite move at right angles to the plane (Baylor & Smith, 1953; Eckert, 1953). The isopods *Porcellio* and *Oniscus* orientate either parallel or perpendicular to the e vector (Birukow, 1956, personal communication). Among insects *Drosophila* aligns its longitudinal axis parallel to the e vector at high light intensities, but either perpendicular or parallel at low intensities (Stephens, Fingerman & Brown, 1953). Multiple choice is apparently available for the beetle, *Geotrupes* (Birukow, 1954). Here orientations parallel, perpendicular *and* oblique (45° and 135°) were preferred in this order. The orientation of arthropods to polarized light in the sky is a menotaxis and hence more complicated than these responses to Polaroid sheets.

On the basis of the laboratory studies cited, *Daphnia* and *Drosophila* have been claimed to use a refraction-reflexion means of polarized light analysis. According

to this hypothesis many ommatidia would be involved in the sensory part of the mechanism. This is consistent with the electrophysiological effects of obliquely incident light on single facets of *Limulus* compound eyes (Waterman, 1954*b*). The present data might be consistent with this if one assumes that the organism chooses axial orientations where the refraction-reflexion patterns possibly illuminating its retinas are symmetrical. Birukow's interpretation of his *Geotrupes* results, including alignment at 45° angles to the *e* vector, does not, however, agree with this. Instead, his explanation is derived from the pattern of eight retinula cells in a single ommatidium and follows the hypothesis of Autrum & Stumpf (1950). The latter assume that each single retinula cell is a polarized light analyser, and hence one ommatidium could measure the plane in contrast to the many required by the refraction-reflexion theory. Autrum's hypothesis has been given considerable support from the electron microscopy and polarization optics of insect eyes (Fernandez-Moran, 1956; Stockhammer, 1956). But direct evidence is lacking.

In relation to animal navigation, probably the most interesting question arising from the present work relates to the observed variability of the polarized light response. This was expressed in the different effects of polarized light on various individuals and also on the same individual at different times, a variability reminiscent of much work on taxes and simple behaviour patterns generally. Extensive evidence proves that various sensory inputs, as well as certain metabolic factors, can interact strongly before a motor act occurs (Birukow, 1954; Halldal, 1957). Thus the afferent data from a single receptor system, such as the visual, can be thought of as encountering a 'central mood' which may modify, suppress or even reverse the output that might otherwise occur under the simplest conditions. Important quantitative study of such phenomena has been made in teleosts by von Holst (1950). Nevertheless, little is known of the mechanisms involved. From a general ethological point of view *Mysidium* is obviously a visually alert animal. For this reason analytical study of the problem of its attentiveness to polarized light patterns would be both interesting and worth while.

A further important component of the behavioural variability in question arises from the inaccuracy of the polarized light orientation. Even when the effect of randomly swimming specimens is minimized (Fig. 4) there is still a broad spread of observations through all possible angles. Less than 40% of the measurements showed orientation within 15° of the perpendicular to the *e* vector. Several explanations are possible for such lack of precision. In the first place one might conclude that sensory discrimination for polarized light is actually as inaccurate as this. No electro-physiological or behavioural data are yet available on the minimal discriminable change in *e* vector position in any animal. The only relevant electrical measurements (on *Limulus*) would suggest that angular sensitivity to the plane was not great in the single optic units to which tests were limited (Waterman, 1950, 1954*b*). Behaviourally other arthropods, like *Mysidium*, show rather inaccurate alignment to the polarization pattern, and the data are subject to the same limitation of interpretation as the present work. On the other hand we know that sensitivity to angular displacement may be incredibly good in some compound eyes at least

(Hassenstein and Reichardt, 1956; Lindauer, 1957), and much could hinge on the mechanism of polarized light perception.

On the other hand, apparent, rather than real, lack of visual precision would result from the occurrence of more than one stable orientation relative to a given polarization plane. Obviously the minor peak in our data at 0° is such a secondary stable axial plane. Any additional such tendencies, even if not statistically significant as peaks, could increase the apparent randomness of the results as in Birukow's experiments on *Geotrupes* (1954).

Also in our work the small size of the experimental cell forced the actively swimming mysid to turn round frequently. This may have interfered with the setting of an accurate course relative to the plane. On the other hand, the frequent turning forced the animal continually to reset the direction of its swimming so the data perhaps comprise a large number of orientation judgements rather than just one or a few initial ones. In this connexion the field experiments are of interest because such narrow and artificial confines are not involved.

FIELD EXPERIMENTS ON *PALAEEMON*

Organism

The problem at hand clearly requires field studies of orientated behaviour in addition to laboratory experiments of the sort described above. One might hope to find, in aquatic forms, responses to underwater polarization patterns comparable with the orientation to sky polarization observed in terrestrial forms, e.g. by von Frisch & Lindauer (1954), Wellington (1955), and Pardi (1956). To this end a search was made for polarization influences on marine plankton organisms observed underwater as in previous work elsewhere (Bainbridge, 1952). But the populations of appropriate animals proved to be so sparse in Bermuda that profitable observations were rare. Consequently, the behaviour of a number of crustaceans was studied when they were released far enough from the shore and the bottom for these not to serve as landmarks.

Unfortunately the mysid used in the laboratory experiments proved to be unsuitable for the field work because it merely swam downward when released. However, some caridean decapods were found to swim away from such release points in an apparently directed manner. Relatively straight-line courses were not infrequent and sometimes were maintained for appreciable distances. As a result, this behaviour seemed promising for our purpose, and a series of releases were studied quantitatively in search of the directional clues involved. In this work adult *Palaemon northropi* (Rankin), a common littoral prawn, was utilized. The length of these animals was 25–50 mm. It was equally unfortunate that *Palaemon* proved unsuitable for laboratory experiments like those carried out on *Mysidium*. In a confined space the decapods' swimming was largely directed by contact with the walls of the experimental cell and not at all obviously by the light pattern.

Procedure

The site chosen for this field work was off the eastern shore of Hall's Island in Harrington Sound, Bermuda. A flat straight shore here falls steeply into deep water. Hence observations could be made reasonably close to the shore but quite out of sight of the bottom. At this point the Sound, an almost completely enclosed body of sea water about 3 km. across, is sheltered from large waves and appreciable tidal currents.

Three observers were required to record the prawn's path after release. One of these acted as a diver, wearing an Aqualung compressed-air breathing apparatus. He would swim out 30-40 m. with a closed jar containing a few healthy specimens of *Palaemon*. At a pre-arranged signal he dived into a depth of 3-5 m. and released one prawn while holding the jar above his head. Under these circumstances the animal would often circle and swim up to within 0.5 m. or less of the surface and set off on a horizontal course. The diver then followed the prawn at a discreet distance (1.5-3 m.) and for as long as possible.

The objection that in this situation the animal was in reality swimming to escape the diver is quite unfounded. On the contrary, the greatest skill had to be exercised to prevent the prawns from doing precisely the reverse. If when first released, the animal noticed the diver, it would swim to him and settle tenaciously on his person. Similarly, while following, if the diver strayed too far from the line directly behind the *Palaemon*, it would at once turn and swim to him. Most of the unsatisfactory runs resulted from this effect. The end of a run occurred generally because the animal was lost to sight as a result of the diver keeping too far behind to avoid detection by the crustacean. Meanwhile, the two other observers were stationed on the shore at water-level a measured distance apart. With sextants and using some prominent object on the distant shore as a reference point, they took sights at half-minute intervals on either the diver's hand which was held out of the water if he was near the surface, or on the patch of bubbles from his breathing. When these pairs of bearings are plotted on a large sheet of graph paper on which the base-line and reference point are recorded, then successive positions of the diver may be accurately plotted. The line connecting these points closely approximates to the animal's course.

If the courses were straight, a single compass reading could be readily given for each run. But the animal's paths were generally somewhat irregular. In analysing the records the choice therefore of only the straightest piece of the run would necessitate arbitrary selection. Similarly, the alternative of summing the deviations of each successive half-minute of course would have its drawbacks. It would, for example, be less accurate than the method used and would also unduly weight the apparently random circling at the beginning of each release. Consequently, it was decided to connect the first observation with the last by a straight line and call this the 'resultant course'. This was rarely the exact line followed by the animal but it appears to be the most impartial solution to this problem.

As the most plausible clue for the animal's sense of direction, the bearing of the

sun was recorded during these observations. Measurements were generally made only when the sun was shining or else under carefully noted meteorological conditions. Previous quantitative determination of the close correlation between the sun's position and the underwater polarization pattern made it unnecessary to redetermine this potential aid to orientation (Waterman & Westell, 1956).

Results

The main body of these experiments comprises sixty-one releases of *Palaemon* made on four different days during 2 weeks of August 1956. Of these, forty-one were successfully followed and gave enough points to plot a course. To provide some basic familiarity with these results, four of the courses will be presented in detail (Fig. 10).

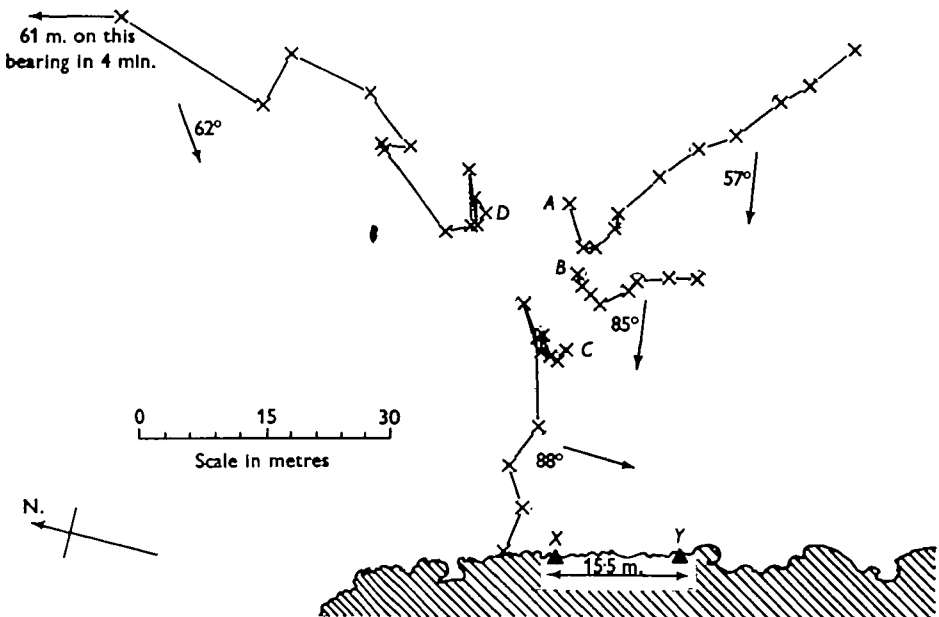


Fig. 10. Four representative courses swum by *Palaemon* released in quiet water too far from the shore or bottom for visual contact. A diver and two shore observers at X and Y worked together to fix the animal's position every 30 sec. during the run. The arrows beside the course lines indicate the bearing of the sun for each. Like all successful field data (41 cases), these runs show a predominance of courses swum at right angles to the sun's bearing, indicating that either a direct or indirect sun compass is involved.

The run represented by line A started in the direction of the sun, but the animal quickly veered through a half circle about 3 m. in radius and then set off on a fairly straight course for about 4 min. during which time it covered 37 m. The angle between the resultant course and the sun's azimuth was 57° . During this period of swimming the sun was clearly visible. The animal represented by line B started similarly by circling from the direction of the sun. It eventually set a course whose

resultant made an angle of 85° with the sun's azimuth. It also swam for 4 min. before being lost but covered a distance of only 17 m. from the starting-point. The sky was again clear at this time.

Table 3. *Summary of Palaemon navigation observations*

Release no.	Distance swum in metres	Course in degrees E. of N.	Sun's azimuth in degrees E. of N.	Deviation of course from sun in degrees
16 Aug.				
1	34.8	127	240	67
2	7.0	119	245	54
3	19.5	179	250	71
4	16.8	202	255	53
5	27.2	204	260	56
6	4.3	324	264	60
22 Aug.				
1	7.6	117	173	56
2	4.0	22	180	22
3	6.1	80	190	70
4	3.4	16	193	3
28 Aug.				
1	63.5	161	247	86
2	29.6	153	252	81
3	49.3	121	254	47
4	25.3	156	259	77
5	14.0	146	260	66
6	41.5	138	261	57
7	22.9	157	262	75
8	6.4	156	262	74
9	15.2	168	263	85
10	29.0	160	264	76
11	6.1	141	265	56
12	6.1	121	267	34
13	2.4	103	267	16
14	11.0	169	268	81
29 Aug.				
1	25.9	242	150	88
2	51.8	81	166	85
3	23.5	67	176	71
4	25.9	271	183	88
5	6.1	315	193	58
6	13.7	28	195	13
7	7.0	258	207	29
8	44.2	345	207	42
9	13.1	230	212	18
10	8.5	340	215	55
11	23.5	13	217	24
12	5.5	293	221	72
13	8.5	324	233	89
14	13.7	3	234	51
15	110.0	353	235	62
16	41.2	41	243	22
17	119.0	342	244	82

The animal of line C was a female; it moved backwards and forwards and around somewhat erratically for about 2.5 min. before setting off on a relatively straight run which carried it 33 m., in 2.5 min., to the shore. The resultant course was at 88° to the sun's azimuth. The sky was partly cloudy during this period. Finally D represents an animal which again moved erratically for the first 2 min. but then

set off on a course which, with a few deviations, took it 110 m. in 8 min. The angle between this resultant course and the azimuth of the sun was 62° . At this time the sky was partly covered by cloud, and there was a thin high haze.

Turning now to the results of all forty-one successful runs, these generally followed a common pattern. Usually after some circling and random movement but occasionally at once, the animal would set off on a fixed bearing. It then continued on this course with some deviation to left and right, but rarely turning completely, until lost by the diver. The mean length of the forty-one courses followed is 24.5 m., the maximum 119 m. and the minimum 2.4 m. The pertinent numerical data are summarized in Table 3. The last column shows that a preponderance of the resultant courses make angles close to 90° with the sun's bearing.

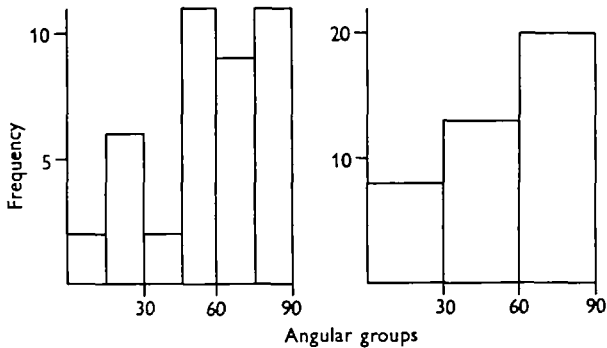


Fig. 11. Deviation angles between the sun's bearing and the resultant courses followed in forty-one releases of *Palaemon* in quiet open water. Preference shown for swimming at right angles to the sun's direction is statistically significant for both the 30° and 15° interval groupings analysed. These graphs of *Palaemon*'s field behaviour are strikingly similar to those showing the polarized light orientation of *Mysidium* in the laboratory (e.g. Fig. 2A).

These deviation angles have been analysed, as in the mysid laboratory experiments, by grouping them in 15° and 30° intervals (Fig. 11). Although the numbers are hardly sufficient for the 15° grouping to be strictly regular, both of these distributions may be counted as significant on the basis of χ^2 tests:

Groupings of deviation angles	χ^2	Degrees of freedom	<i>P</i>
For 15° intervals	12.4	5	c. 0.04
For 30° intervals	6.1	2	< 0.05

From this one can conclude that the courses followed by these prawns were significantly correlated with the sun's bearing and ran generally perpendicular to it. But the possibility of other environmental influences remains. Some water movements must have been taking place, perhaps partly from tidal action but mostly wind driven. Conceivably these or the resultant pattern of waves on the surface could have been orientating clues. The wind, however, varied from day to day; on 28 August it was fresh and from the south, blowing in a direction opposite to

most of the migrations on that day; on 29 August there was little wind. Similarly, the shore line and the bottom might possibly afford visual clues to the crustacean not apparent to the diver who was quite disorientated in the experimental region except for the sun and mnemonic assistance. But if there were such a pattern, it would be fixed, and yet the runs show significant correlation with the sun which ranged through more than 90° of arc during the time of various observations. It would thus appear just to conclude that *Palaemon* can use the sun either directly or indirectly as a celestial compass.

In addition to the main results the data provide information on one or two points of further interest. For example, they permit the speed of swimming of these crustaceans in nature to be calculated. A common rate measured along the resultant course is that for release 11 on 28 August which is 9 m./min. The maximum swimming velocity was measured in release 6 of 28 August. Here the *Palaemon* swam 34.5 m. in 2 min., which is a rate of about 0.3 m./sec. or nearly 1 km./hr. Considering that the specimen's length approximated to 0.038 m. this seems a formidable accomplishment.

A common aspect of the prawn's swimming pattern is of interest in relation to the behaviour of plankton. This is the fact that although the animal's course was straight in a horizontal plane, it often was sinusoidal in a vertical plane. The wavelength of this motion was 2-3 times its amplitude of 20-30 cm. It appears quite likely that this is a form of the 'hop and sink' behaviour by which vertically swimming plankton animals keep an optimal position in the water mass (Hardy & Bainbridge, 1954). Like them the *Palaemon* could have been sampling deeper and shallower layers and by reacting to alternating changes in factors such as light or pressure maintaining its level in the water. The distinction is that the prawn has a strong horizontal component superimposed upon its vertical one.

Discussion

The ecological consequences of such orientated horizontal swimming in nature could of course be considerable. Adaptive evolution of the mechanism might be expected if, for example, it assisted herbivorous animals in finding fresh areas of the phytoplankton, which is so patchy in distribution (Bainbridge, 1957). The whole mechanism could in fact fulfil the need postulated by Bainbridge (1953) for a system imposing directionality on the general horizontal movements of such Crustacea in the sea. Breeding and other migrations (Sutcliffe, 1953) might also be assisted by directed movements of this sort.

The resemblance between the caridean's orientation relative to the sun's bearing in the field studies (Fig. 11) and the mysid's swimming relative to the polarization plane in the laboratory (Fig. 2A) is extraordinary. It may be merely coincidental, but yet again may derive from a comparable sensory and response mechanism in the two cases. If the *Palaemon* was reacting to the underwater polarization pattern rather than directly to the apparent position of the sun itself, the question of which part of the whole pattern is involved raises an interesting point. Since under-

water polarization is generally in planes at right angles to the submarine direction of the sun's rays, the animals would have been orientating and swimming parallel to the *e* vector observed both directly beneath them and overhead. If so, this is different from the usual polarized light response of *Mysidium* observed in the laboratory, where perpendicular alignment predominated.

The task of differentiating between a sun compass and a polarized light compass underwater is a challenging one. It would require essentially the discovery of an orientated behaviour pattern which will continue to appear even when the animal is shaded from the direct, but not the scattered, rays of the sun. This, of course, has been the basis for proving the use of sky polarization by terrestrial arthropods. An additional demonstration that a polarizing film interposed in the animal's line of sight will change its orientation as the *e* vector is rotated, would support and complement the evidence of the first criterion. Further field work is planned to extend the results herein described and to test these crucial points. At the same time the further development of the quantitative data from the laboratory experiments will be pursued in an effort to analyse the effective parameters of the polarized light stimulus. So far these are practically unknown.

SUMMARY

1. Quantitative experiments are described, designed to test the hypothesis that underwater polarized light is used for orientation by aquatic animals as that of the blue sky is by terrestrial arthropods.
2. Studied in the laboratory the littoral mysid, *Mysidium gracile*, was found capable of orientation relative to the *e* vector in a vertical beam of linearly polarized light.
3. Statistically significant preference was shown by this animal for aligning its longitudinal axis at right angles to the plane of polarization.
4. A secondary slight preference was shown for swimming parallel with the plane and the degree of random orientation was often high (40% mean).
5. The littoral prawn, *Palaemon northropi*, when released in quiet water far enough from the bottom and the shore to prevent visual contact, was found to swim on relatively straight horizontal courses for appreciable distances in forty-one out of sixty-one tests.
6. The mean length of these runs was 24.5 m., the maximum 119 m.; swimming velocities up to about 1 km./hr. were measured.
7. The sun's position seems to be the only directional clue not controlled in these tests, and the general direction of the runs is significantly correlated with the direction of the sun, being at right angles to it.
8. It is thus concluded that this animal can use the sun, either directly or through the polarization pattern, as a celestial compass.

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