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THE ONTOGENY AND SPECTRAL SENSITIVITY OF POLAROTAXIS IN LARVAE OF THE CRAB *RHITHROPANOPEUS HARRISI* (GOULD)

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Both terrestrial and aquatic arthropods have been shown to possess polarization sensitivity (Eguchi and Waterman, 1968; Shaw, 1966, 1969b; Snyder, Menzel and Laughlin, 1973; Waterman, Fernandez and Goldsmith, 1969; Waterman and Horch, 1966) and frequently stereotyped polarotaxes are displayed (reviewed, Waterman, 1974). Among crustaceans the ontogeny of polarotaxis during larval development is unknown, since nearly all experiments on polarized light perception have concerned adults. In these experiments, we have studied polarotaxis in the planktonic larvae of an intertidal crustacean.

Because planktonic organisms are small and can travel rapidly over short distances, difficulties in monitoring their movements accurately and conveniently have limited their use, a problem which is augmented for larval forms by factors reducing success in rearing them to advanced stages in the laboratory. With a closed circuit television system combining real-time recording and slow motion playback, we have been able to accurately monitor the swimming directions in response to polarized light of larvae of the low intertidal crab *Rhithropanopeus harrisi*. These larvae are especially suited for such a study, since they are good swimmers and their phototactic responsiveness to light is well described (Forward, 1974; Forward and Costlow, 1974). In addition, Costlow, Bookhout and Monroe (1966) have characterized the developmental sequence and established extensive rearing techniques, thereby eliminating many potential difficulties in raising larvae for these experiments.

Results of our examination of the ontogeny of polarotaxis in *R. harrisi* indicate that only zoeal stages II and III respond to polarized light. Consideration of the intensity and spectral characteristics of the response reveals that maximal responsiveness occurs at an intensity of 10^{-2} W/m^2 and at 500 nm. Larvae are strongly phototactic and when intensity distributions and polarization are offered antagonistically, they respond with nearly equal phototaxis and polarotaxis. Following dark adaptation, the polarotactic response disappears.

Materials and Methods

Experimental animal

Ovigerous females of the low intertidal crab *Rhithropanopeus harrisi* were allowed to hatch under controlled conditions: salinity, 20‰; L:D cycle, 12:12; temperature cycle, 20–25° C. The experiments described in the ontogeny section

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were performed on larvae of crabs procured in Florida, while crabs collected locally were utilized in the experimental determination of the wavelength sensitivity. After hatching, larvae were changed daily to fresh filtered 20‰ seawater, fed newly hatched *Artemia* nauplii, and maintained under a 12:12 L:D cycle at a constant temperature of 25° C. These conditions were selected because previous work has indicated that they produce maximum developmental success (Costlow *et al.*, 1966).

Apparatus

The arrangement of the basic apparatus is depicted in Figure 1. A slide projector with a tungsten lamp acted as the stimulus source. Light passing through the projector optics was filtered by two hot mirrors (Baird Atomic), and two Corning No. 1–75 filters to remove heat, plus selected neutral density filters (Oriel Corporation of America). Wavelength was controlled by either an interference filter (Optics Technology, λ's 453, 470, 499, 556, 620 nm; half band pass 3–5% of wavelength), or a thin film absorption filter (Ditric Optics Inc., λ's 420 nm, half band pass 7 nm; 520 nm, half band pass 8 nm; 600 nm, half band pass 10 nm). A 300 W lamp was used for stimulus intensities below 0.1 W/m^2, while a 750 W lamp was used for a higher intensity. Intensities were measured with a radiometer (Yellow Springs Instruments, Model #65).

Light thus filtered first passed through two layers of waxed paper to depolarize any polarized light emitted from the source and then was linearly polarized by a polaroid sheet (Carolina Biological Supply.) The advantage of using this depolarizer/polarizer sandwich is that uniformly unpolarized light of approximately the same intensity as the polarized test light could be provided as the stimulus for control experiments by turning the waxed paper to the underneath side. The polaroid was mounted in the center of a rotatable circular mask. Horizontal shielding was provided directly above the experimental vessel in the form of a circular mask overhanging the sides by 1 cm. This eliminated potential interaction of the light with the sides of the vessel, a clear plastic dish (diameter 8.5 cm). To minimize other possible sources of scattering, all baffling surfaces were painted flat black, and the room was completely darkened for experimentation.

Responses were monitored by a video camera (Cohu Model 4300) positioned directly below the vessel. Circular baffles extending downward around the lens from the glass sheet on which the vessel rested insured that the only visible portion of the camera was the lens itself. The video picture was viewed on an Electrohome monitor (Model #EVM–11), and recorded on a Panasonic video tape recorder (#NU–3020 SD). Time markers were entered on the tape by voice commands.

Analysis and statistical treatment of data

In analysis, the tapes were replayed at slow speeds, and the swimming path of each animal visible within a given time period was traced onto a Plexiglas sheet fitted over the monitor face. Since the animals are small and can frequently change swimming direction, a criterion had to be devised to standardize the portion of the path chosen for measurement, and so it was decided to measure the swimming

direction of the first straight segment longer than 1.5 cm on the Plexiglas sheet within a given time interval after the onset of stimulation. This technique is similar to that previously employed by other investigators (*e.g.*, Bainbridge and Waterman, 1957; Umminger, 1968). In all experiments 150–200 individual paths were measured, and final distributions represent an average of larvae from 3–6 different hatches.

The compass direction of each path was measured with a protractor and recorded in 10° sectors centering on 0°, 10°, etc., through 350°. 0° was arbitrarily established and served as a reference direction for swimming paths and polaroid alignment.

Under polarized light, four angles of the polaroid relative to the 0° reference (0°, 50°, 90°, 140°) were tested to minimize possible effects of intensity artifacts within the experimental vessel. Then, to combine these data into one angular distribution of swimming paths relative to the angle of polarization, the distributions under each polarization condition were transposed and plotted relative to the e-vector placed at 0°. Since within the experimental situation, the 0° direction is identical to 180°, and 10° to 190°, etc., the data at these angles were combined to produce an angular distribution showing swimming directions between 0° and 170° with the e-vector at 0°.

Chi squares were computed for the resulting distributions, and a significance level of 0.05 was used as the cutoff for a non-random distribution. The significance of orientation at certain angles as compared to the distribution mean was further checked using the McNemar test for significant changes. To standardize the graphs of orientation angle versus directional frequency, the percentage of the total number of paths that occur at a particular angle are plotted rather than the actual number of paths.

Experimental procedure

The responses of both light and dark adapted animals to different stimulus intensities were first-tested. Animals were light adapted under room lights plus a 60 W incandescent lamp placed directly over the bowls. All experiments were performed on the second day of the three-day molt cycle of zoeal stages I–IV. The megalopa were not tested because preliminary experiments indicated that they rarely move upon stimulation. To avoid variations in responsiveness due to a possible biological rhythm, experiments were always performed between two and six hours after the onset of the light phase.

Approximately 50 larvae were placed in the vessel which was then positioned above the camera and filled to the brim with water to eliminate the differential reflection effects of a meniscus. The plastic experimental vessel may have differentially transmitted polarized light and thereby provided an orientation cue. To reduce the possible effects of this cue, the dish was randomly oriented relative to the e-vector direction for each trial. The larvae were maintained in darkness for 15 seconds and then stimulated for 15 seconds with various intensities of 499 nm light. This wavelength was selected because it is the primary maximum in the sensitivity spectrum for phototaxis in *R. harrisi* (Forward and Costlow, 1974).

Swimming paths were recorded from 10–15 seconds after the initiation of the stimulus, since preliminary trials demonstrated consistent responsiveness during

this time interval. Then, after the animals had rested in darkness for 15 seconds, a second stimulus was presented and responses recorded similarly. At a given intensity, four angles of the polaroid were tested, but to preclude fatigue effects, each group of larvae was used for only one angle, that is, one set of two stimuli Although repetitive runs were usually necessary, there were always at least 15 minutes between reuse of any larvae, and upon reuse, the animals were exposed to a different angle of polarization and/or stimulus intensity. Controls were performed in the same sequence by simply reversing the polaroid/depolarized sandwich so that the animals were exposed to unpolarized light of the same intensity and angular distribution.

Dark adaptation was accomplished by placing larvae in experimental vessels on a table beneath a lightproof cover for a minimum of 1½ hours prior to the beginning of testing. This preplacement eliminated the necessity for subsequent visual transfer under light. Any light then needed for examination was interference filtered to 600 nm, since larvae are largely phototactically unresponsive to this wavelength (Forward and Costlow, 1974). Since light-adapted stage II larvae proved to be the most responsive to polarized light only these were tested in the dark adaptation experiments. To avoid excessive light adaptation, responses were recorded for the interval 0–5 seconds after stimulus initiation, and the time between stimuli was lengthened from 15 to 30 seconds. Although the stimuli for these experiments were shorter than those used in light adaptation, preliminary experiments showed that this interval was satisfactory to maintain dark adaptation and to initiate directional swimming.

Since stage II larvae are most responsive to polarized light, their spectral sensitivity for polarotaxis was tested between 420 to 620-nm light. At 499 nm, an intensity of 2.5×10^{16} quanta/m^2/sec (10^{-2} W/m^2) produced the greatest response. Thus, quantal intensities for other wavelengths were adjusted to this value ($\pm 9\%$) by means of neutral density filters. The experimental sequence was basically the same as in the previous experiments. Four angles of the polaroid were tested for each wavelength, with two stimuli per preparation. Responses were again recorded during the interval 10–15 seconds after the initiation of the stimulus, and larvae of each hatch were examined at all wavelengths. The data from three hatches were grouped and the percent swimming perpendicular to the e-vector computed for each wavelength.

To determine that the observed polarotaxis does not result from phototaxis to the intensity distribution pattern created by polarized light, experiments with light-adapted stage II larvae were performed in which phototaxis was competitively tested against polarotaxis. Phototaxis was established by recording swimming paths in unpolarized light with a collar of alternating black and white sectors each subtending an angle of 90° surrounding the vessel. Phototactic sign was determined by grouping swimming paths into those toward the white (+) and those toward the dark (−). An antagonism between phototaxis and polarotaxis was then produced under polarized light by aligning the e-vector parallel to the white sectors. Thus, animals responding to the e-vector should swim perpendicularly into the black sectors, while at the same time animals should also be drawn phototactically to the white sectors. For both experiments, the stimulation and recording procedure was the same as described previously for light-adapted larvae.

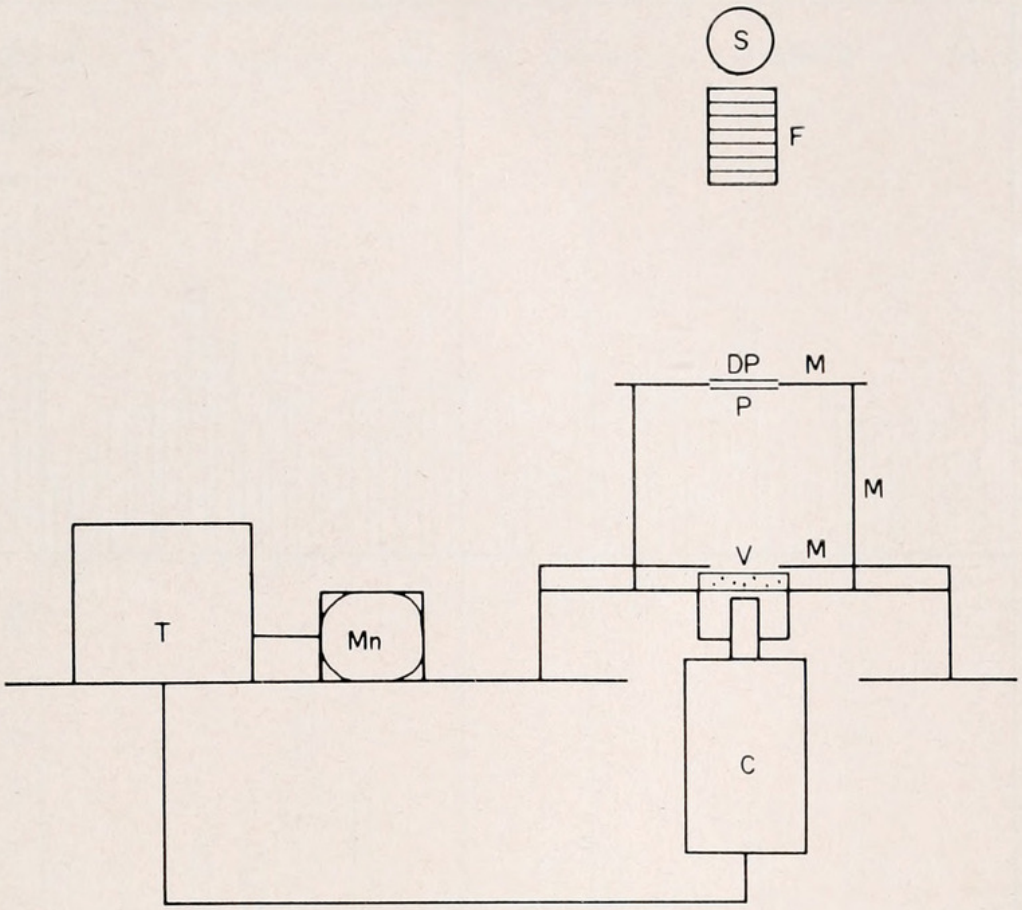

FIGURE 1. Experimental apparatus. The various components are tungsten light source (S), filter holder (F), depolaroid/polaroid (DP/P), masks painted flat black (M), experimental vessel (V), television camera (C), video monitor (MN), video tape recorder (T).

RESULTS

Ontogeny of polarotaxis

Light-adapted larvae of *R. harrisi* can show a definite response to polarized light which is not only non-random, but is stereotyped within a given stage as to the preferential swimming direction in relation to the polarization plane. In our experiments, however, not all stages were responsive, and even among those which showed significant non-random swimming, the strength and angular maximum of the response varied.

For stage I (Fig. 2) none of the angular distributions for any of the test intensities differ significantly from a random distribution nor do any of the angles have a number of swimming paths that differ significantly from the mean. In contrast, stage II (Fig. 3) shows strong swimming orientation perpendicular to the e-vector with the strongest response (19.5%) occurring at a stimulus intensity of 10^{-2} W/m^2 (Fig. 3c). Stage III (Fig. 4) exhibited a weaker response, as well as a change in the preferred swimming direction. At intensities of 10^{-1} and 10^{-2} W/m^2 significant swimming occurred parallel to the e-vector. Stage IV (Fig. 5) shows no orientation to polarized light, as none of the angular distributions at different stimulus intensities differs from a random distribution. Swimming under unpolarized light in the control experiment was random in all stages and at all intensities (Table I).

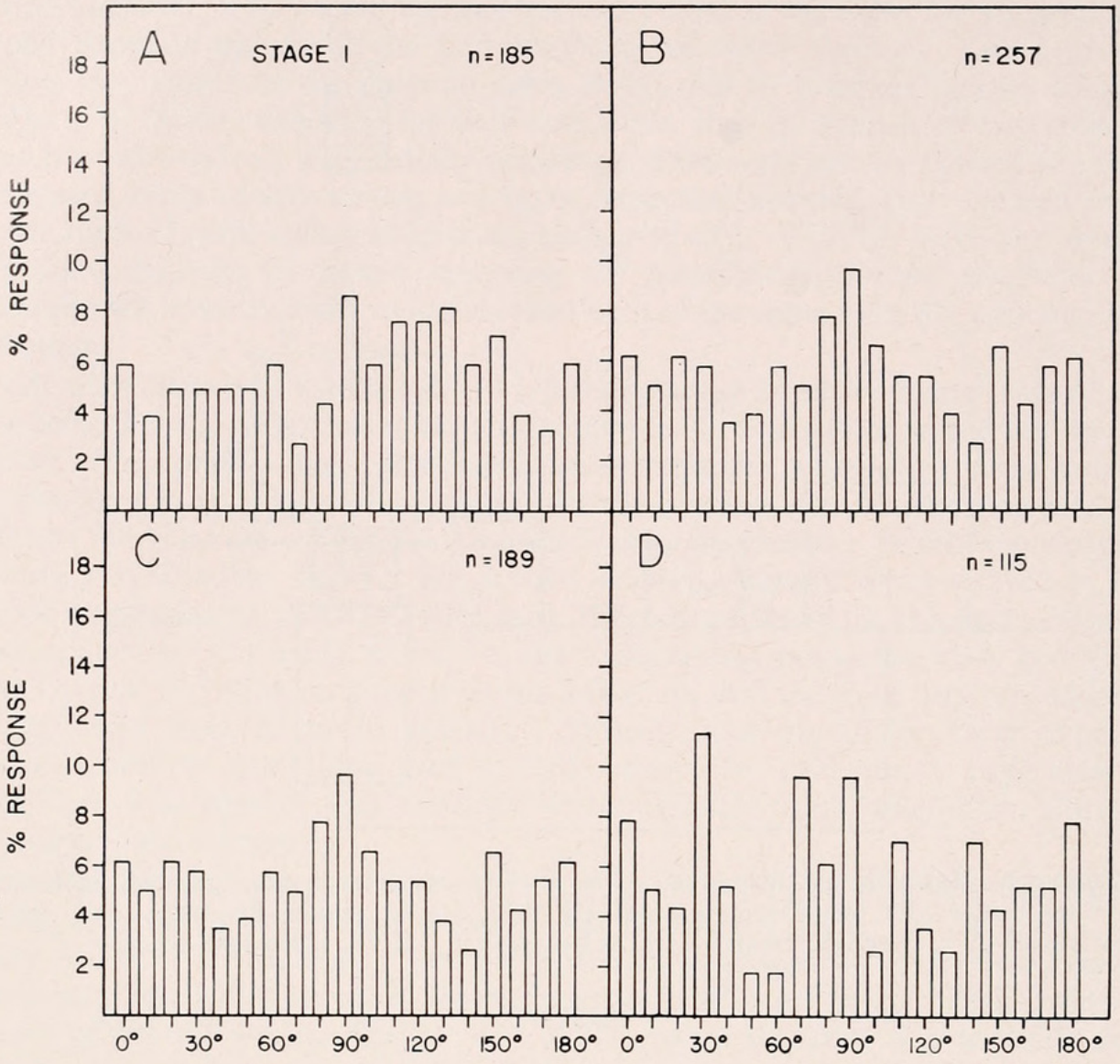

FIGURE 2. Angular distributions of swimming directions in stage I zoeae under linearly polarized light at 499 nm at intensities of 2×10^{-1} W/m^2 (A), 10^{-1} W/m^2 (B), 10^{-2} W/m^2 (C), and 10^{-3} W/m^2 (D). For symmetry, the percent response at 0° has been replotted at 180°. The χ^2 for the overall distribution at each intensity (A. 16.697, B. 10.760, C. 14.450, and D. 26.651) indicates none of the distributions differ significantly from random. In all figures, if the number of swimming paths at a particular angle is significantly different from the mean, one asterisk indicates $P \leq 0.05$ and two asterisks indicate $P \leq 0.005$.

Stimulus intensity had a pronounced effect on the response. The highest intensity tested, 2×10^{-1} W/m^2, was apparently above the upper intensity threshold for polarotaxis, as it evoked random swimming in all stages. In both stages II and III, responsiveness increased at lower intensities to a maximum at 10^{-2} W/m^2, and then disappeared entirely at the very dim 2×10^{-4} W/m^2. From Figures 3 and 4, the upper intensity threshold for polarotaxis by stages II and III can be placed between 1×10^{-1} and 2×10^{-1} W/m^2, and the lower threshold between 2×10^{-4} and 1×10^{-3} W/m^2.

The typical perpendicular orientation seen in light-adapted stage II larvae was absent subsequent to dark adaptation (Fig. 6). Although a non-random angular distribution did occur at 10^{-2} W/m^2 (Fig. 6c), there are no significant maxima.

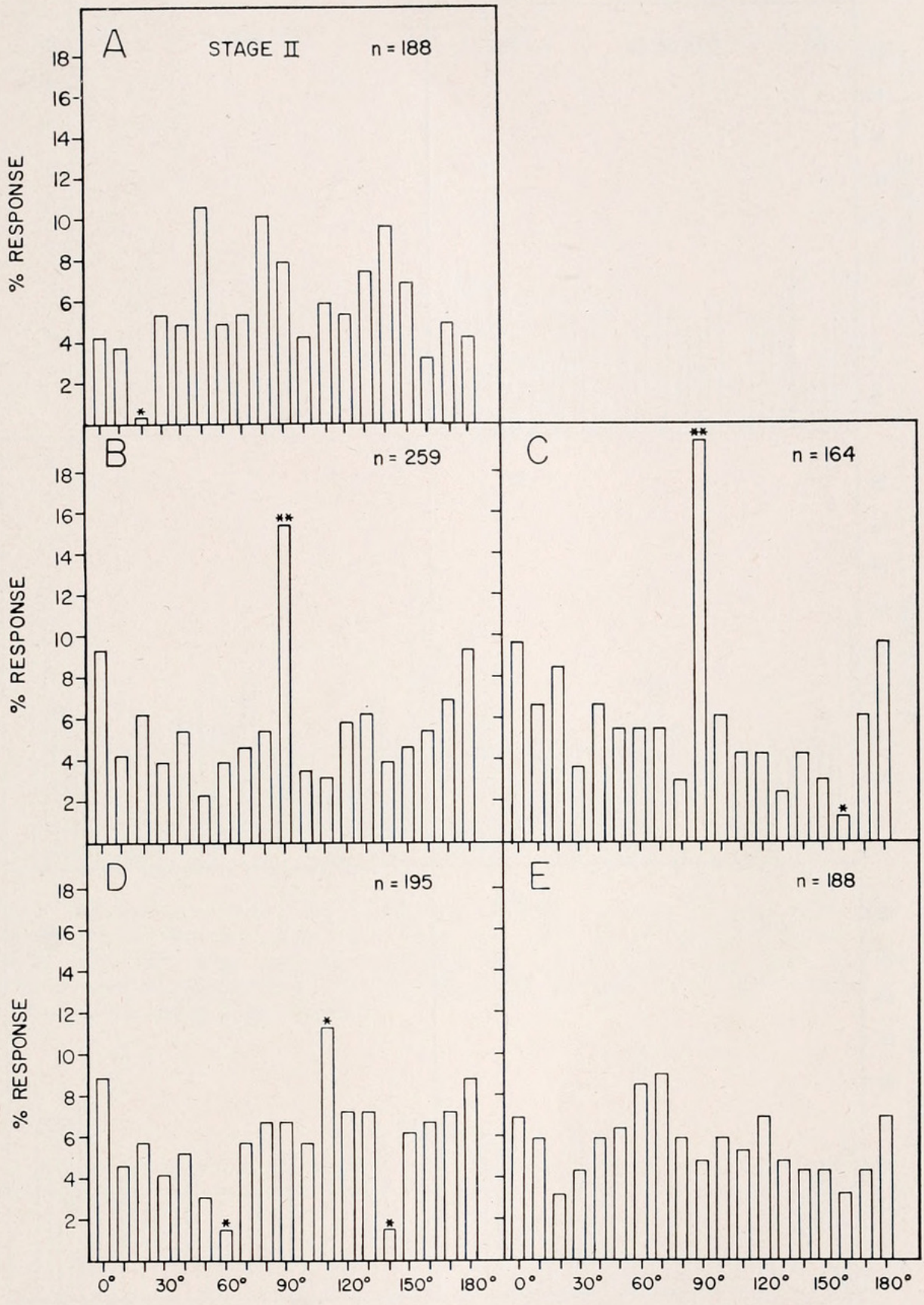

FIGURE 3. Angular distributions of swimming directions in stage II zoeae under polarized light at 499 nm at intensities of 2×10^{-1} W/m^2 (A), 1×10^{-1} W/m^2 (B), 10^{-2} W/m^2 (C), 10^{-3} W/m^2 (D) and 2×10^{-4} W/m^2 (E). Treatment and presentation of data are the same as in Figure 2. The χ^2 values (A. 36.349, B. 68.682, C. 80.949, D. 31.75, E. 11.752) indicate that all distributions except E differ significantly from random.

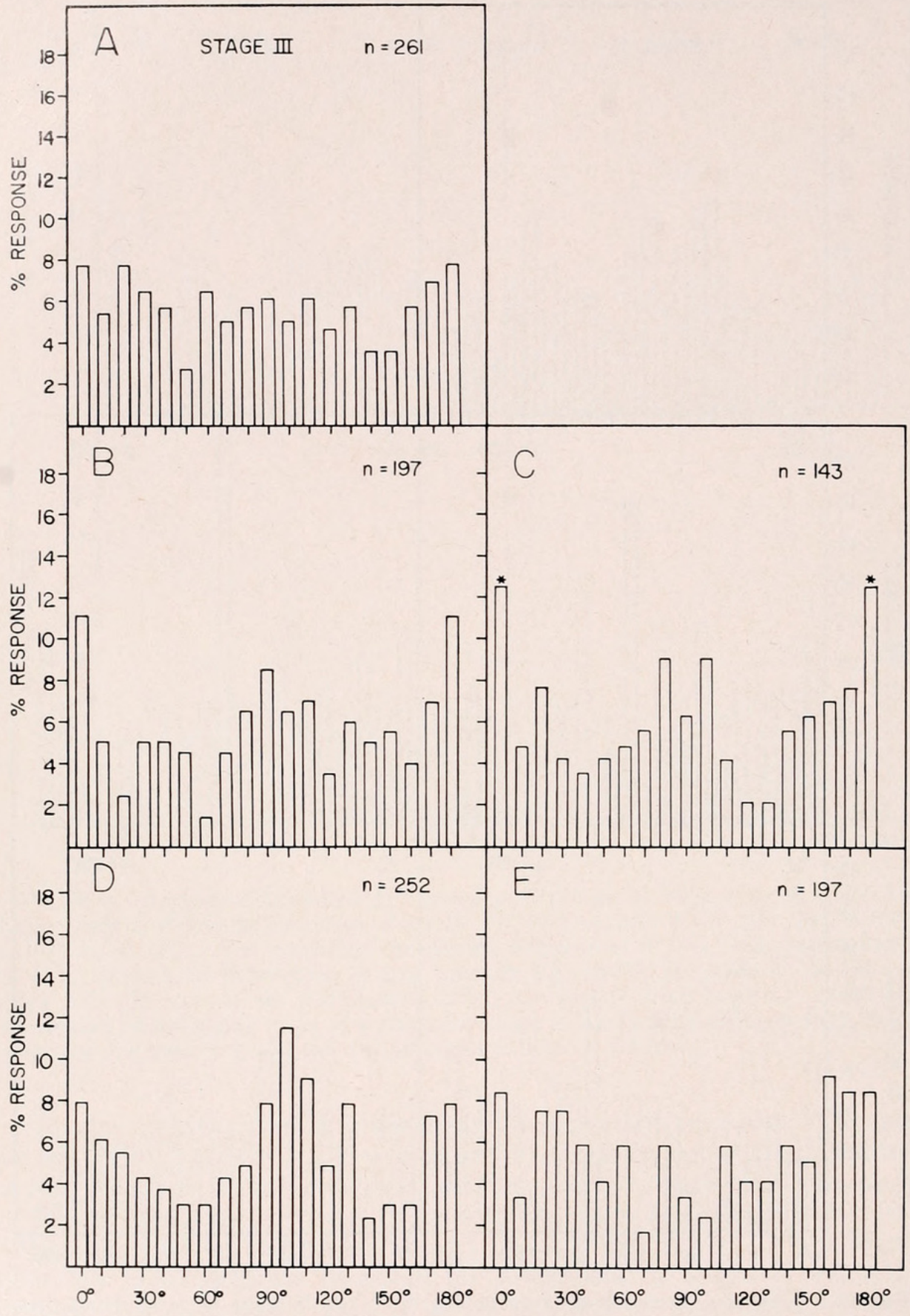

FIGURE 4. Angular distributions of swimming directions in stage III zoeae under polarized light at 499 nm at intensities of 2×10^{-1} W/m^2 (A), 10^{-1} W/m^2 (B), 10^{-2} W/m^2 (C), 10^{-3} W/m^2 (D) and 2×10^{-4} W/m^2 (E). Treatment and presentation of data are the same as in Figure 2. The χ^2 for the overall distributions (A. 15.067, B. 29.174, C. 28.004, D. 32.985, and E. 15.037) indicate only those in B, C and D differ significantly from random.

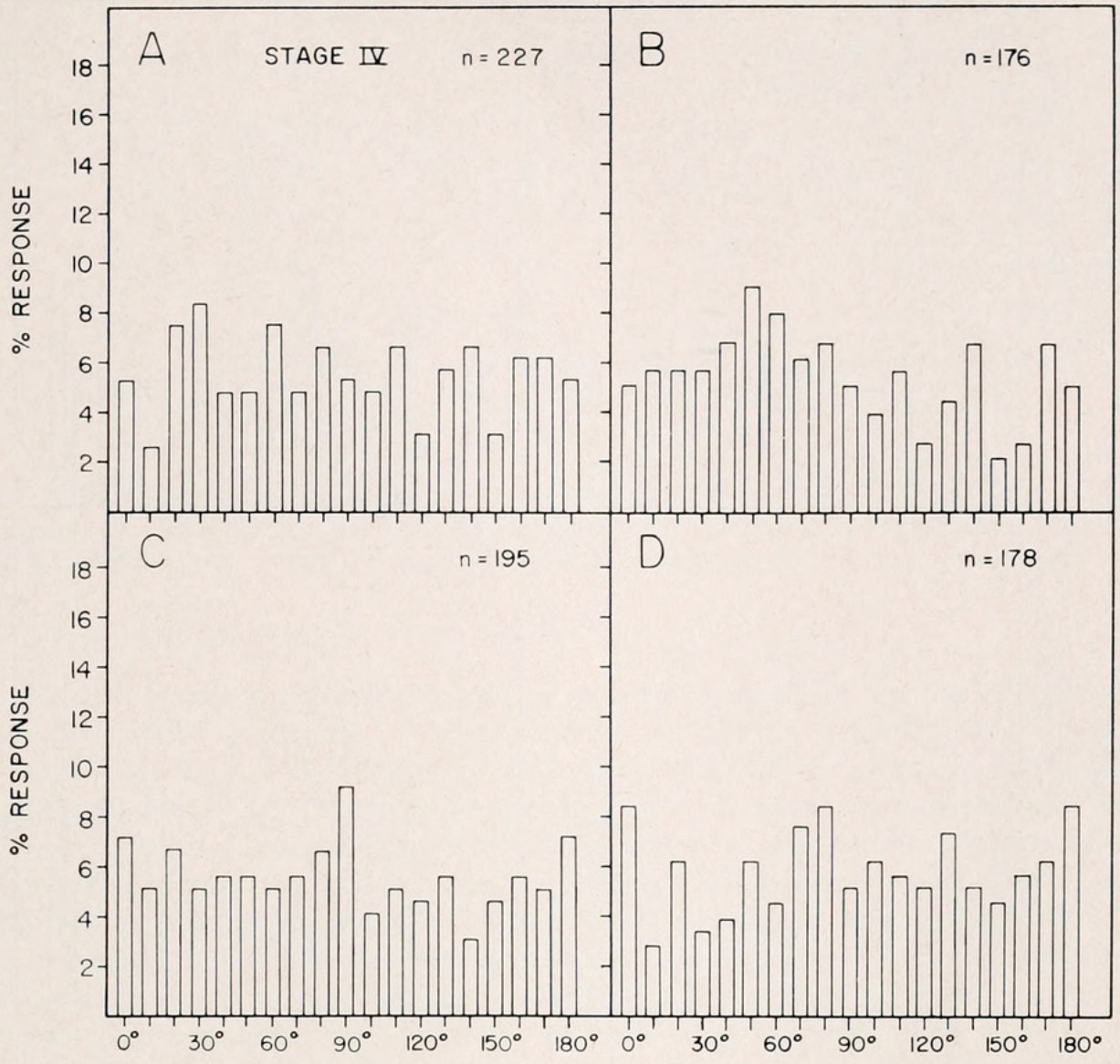

FIGURE 5. Angular distributions of swimming directions in stage IV zoeae under polarized light at 499 nm at intensities of 2×10^{-1} W/m^2 (A), 10^{-1} W/m^2 (B), 10^{-2} W/m^2 (C) and 10^{-3} W/m^2 (D). Treatment and presentation of data are the same as in Figure 2. The χ^2 values for the overall distributions (A. 17.130, B. 14.898, C. 9.640, and D. 12.357) indicate none of the distributions differ from random.

TABLE I

χ^2 values for swimming distributions under depolarized light in control experiments.

	Stimulus intensity (W/m^2)			
	10^{-3}	10^{-2}	10^{-1}	2×10^{-1}
Stage I	20.843	23.773	26.150	13.881
Stage II	—	12.724	9.245	15.941
Stage III	19.517	16.312	22.727	13.683
Stage IV	11.407	17.271	14.077	15.014
Dark adapted stage II	18.992	31.993	14.479	15.894

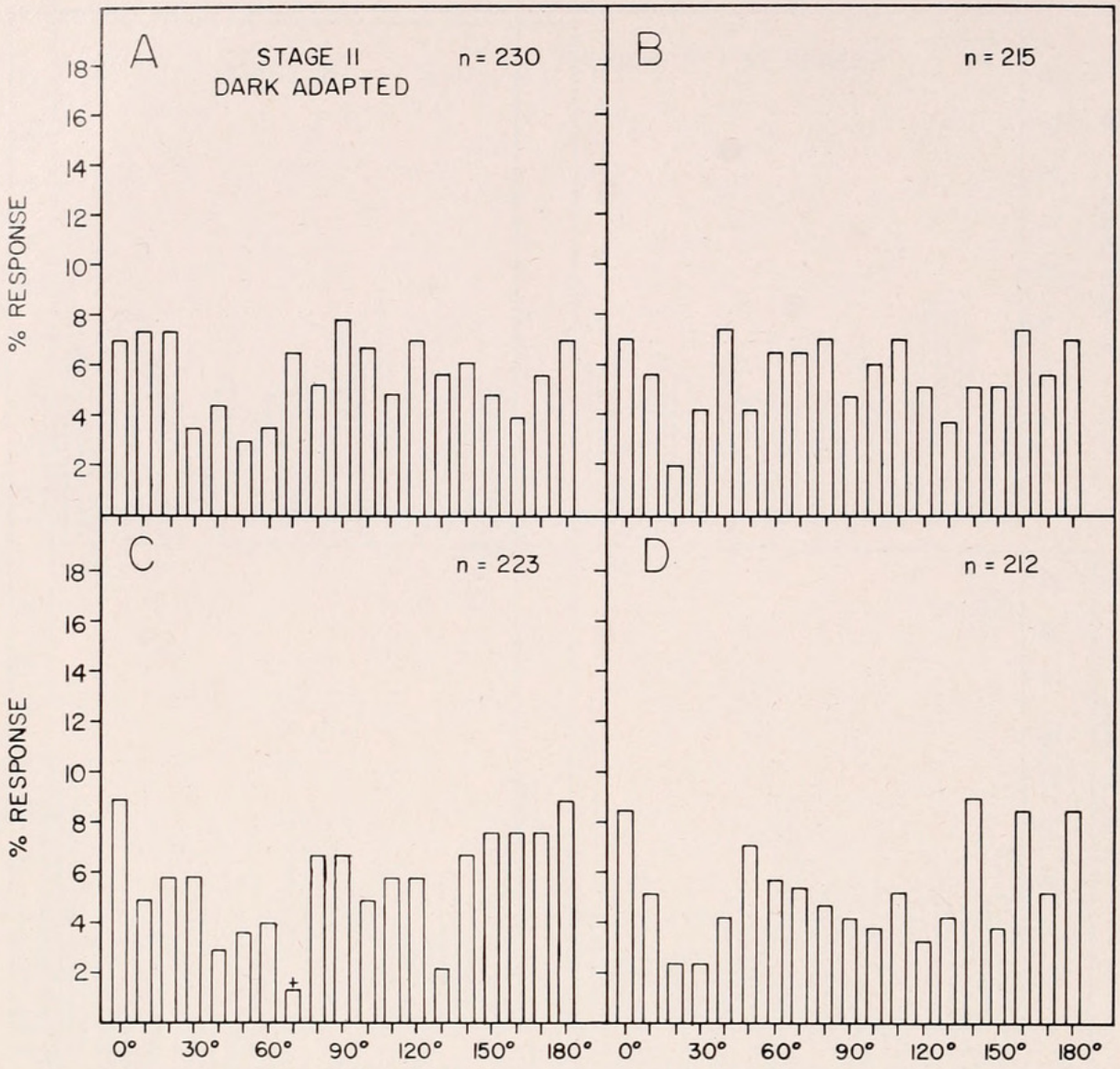

FIGURE 6. Angular distributions of swimming directions for dark adapted stage II zoeae under polarized light at 499 nm of intensities 2×10^{-1} W/m² (A), 10^{-1} W/m² (B), 10^{-2} W/m² (C) and 10^{-3} W/m² (D). Treatment and presentation of data are the same as in Figure 2. The overall distributions in A ($\chi^2 = 15.984$), B ($\chi^2 = 14.479$) and D ($\chi^2 = 18.992$) do not differ from random while that in C ($\chi^2 = 31.993$) is significantly different ($P < 2.5\%$).

Spectral sensitivity

When tested under various wavelengths, stage II larvae from females collected locally showed maximum responsiveness to 499-nm light (Fig. 7). In fact, this is the only wavelength at which significant ($P < 0.005$) perpendicular swimming occurred. The angular distribution for 420 nm was significantly different from a random distribution ($P < 0.05$) but the 9.7% response at 90° was not significant. This suggests that another maximum in the near ultraviolet might become apparent if shorter wavelengths could be tested. For all other wavelengths, the angular distributions were random, and the percent response fell close to the expected 5.5% for totally random swimming. It should be noted that the responsiveness of these larvae was 11.8% at 499 nm, as opposed to the 19.5% shown under the same experimental conditions by the larvae from crabs from Florida (Fig. 3c). This difference may indicate that responses may vary between populations.

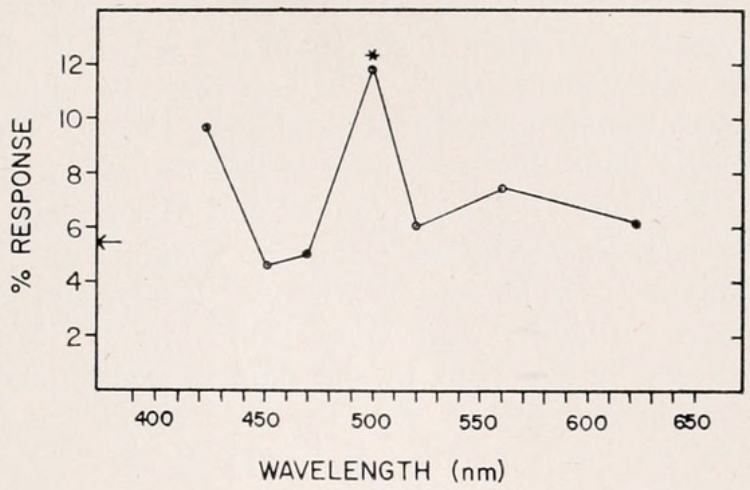

FIGURE 7. Spectral sensitivity for polarotaxis. Points represent the percentage of swimming perpendicular to the e-vector (ordinate) at the stimulus wavelengths (abscissa). The horizontal arrow shows the expected percentage response for random swimming.

Phototaxis vs. *polarotaxis*

In these tests the experimental vessel was surrounded by a collar of alternating black and white quadrants. Under depolarized light, a significantly greater ($P < 0.005$) number of light adapted stage II larvae (62%) swam in the direction of the light quadrants than toward the dark quadrants of the experimental vessel (36%). Under polarized light with the e-vector parallel to the white quadrants, this positive phototaxis was reduced since nearly equal numbers of animals swam toward the dark quadrants (48%) as toward the white quadrants (52%). In this experimental situation the centers of the dark quadrants are perpendicular to the e-vector which is the dominant polarotactic orientation direction for stage II larvae. Since positive phototaxis is reduced, this suggests that a polarotactic response which is independent of phototaxis contributes to directional swimming.

DISCUSSION

It is clear from these results that marked changes occur in polarotaxis during the larval development of the crab *Rhithropanopeus harrisi*. While stage II and III zoeae are significantly polarotactic (stage II perpendicular and stage III parallel to the e-vector), larvae of stages I and IV are unresponsive. Because polarized light perception is a function of precision in anatomical dimensions, the onset of polarotaxis in stage II may result from functional alterations associated with the morphological change between the sessile eyes of stage I and the stalked eyes of stage II (see Costlow and Bookhout, 1971, for diagram). There are no such externally obvious changes between stages III and IV which could account for the altered responsiveness there, however, only an ultrastructural examination could reveal definitively what dimensional changes occur within the eye. Responsiveness may also be altered by developmental changes in higher order neural anatomy.

Both the magnitude and the direction of the response of *R. harrisi* larvae are in good agreement with previous studies on adults of other crustacean species. Considering the absolute percent response at a particular angle of orientation as opposed to the "degree of orientation" [defined as $o_{max} = d_{max} - d_{min}/d_{max} + d_{min}$,

where d = observed counts in a particular direction (Forward and Waterman, 1973)], the 19.5% response of stage II zoea is in fact one of the highest percentages published to date for a laboratory study. The best response obtained elsewhere was 20% for the copepod *Cyclops vernalis* (Umminger, 1968). Other values, which appear slightly lowered since they represent responses within 5° rather than 10° sectors, range from 16% for *Daphnia* (Jander and Waterman, 1960), to 8% for the ghost crab *Ocypode ceratophalma* (Daumer, Jander and Waterman, 1963), 6% for *Mysidium gracile* (Jander and Waterman, 1960), and even as low as 4% for the mite *Arrenurus* (Jander and Waterman, 1960). Measurement of behavior in the laboratory rather than in the natural conditions of the field may explain the rather low percentages of even the most significant of these responses. Concerning direction, the perpendicular and parallel swimming of *R. harrisi* in relation to the e-vector are typical polarotactic responses (see Waterman, 1974, for a summary of previous work).

It is important to consider whether the observed polarotaxis is an independent behavior from a phototaxis to light intensity distribution patterns created by the interaction of polarized light with the experimental vessel. The experiments with the collar of alternating white-dark quadrants surrounding the experimental vessel strongly suggests that the two behaviors are independent.

Comparison of the two responses under similar laboratory conditions (Forward, 1974; Forward and Costlow, 1974) provides further evidence for their independence. While the phototactic behavior itself and the spectral and intensity sensitivity for phototaxis were almost identical at all four zoeal stages, polarotaxis varied dramatically. Stages I and IV showed no responses. Even though stages II and III showed polarotaxis, the orientation direction is different, since stage II swims perpendicular to the e-vector while stage III swims parallel. The difference between the consistent phototaxis at all zoeal stages versus the variation in polarotaxis is a good indication that the two responses are actually different.

A difference in the optimal intensities for phototaxis and polarotaxis also suggests that they are separate responses. Polarotaxis is at a maximum at 10^{-2} W/m^2, which falls between the intensity that initiates maximum positive phototaxis by light-adapted animals (7 W/m^2, stage II; 10^{-1} W/m^2, stage III) and that for negative phototaxis ($10^{-2} - 10^{-4}$ W/m^2; Forward and Costlow, 1974). It may be significant that 10^{-2} W/m^2 is an intensity of transition for phototaxis at which not only are positive and negative phototaxes reduced, but random swimming increases (R. B. Forward, Jr., unpublished), while polarotaxis is maximal at this intensity.

Comparison of the spectral sensitivity curves for polarotaxis and phototaxis shows that both are maximal at 500 nm (Forward and Costlow, 1974). The response spectrum for phototaxis has another smaller maximum at 400 nm, and it appears from the rise seen at 420 nm in the sensitivity spectrum for polarotaxis (Fig. 7) that it may also have a secondary maximum in this region. Unfortunately, neither the tungsten light source nor the polaroid utilized in these experiments permitted the examination of wavelengths below 420 nm. While a dual pigment system is suggested by two maxima in the spectral sensitivity curve, further experiments utilizing selective wavelength bleaching and/or pigment extractions are necessary for positive verification. Nevertheless, the spectral maxima shown here for *R. harrisi* are consistent with those for other adult brachyuran crustaceans

with dual pigment systems (Wald, 1968; Wasserman, 1974), as well as with those for animals which have only one pigment, *e.g., Callinectes sapidus,* 505 nm (Goldsmith and Fernandez, 1969) and *Carcinus maenus,* 508 nm (Horridge, 1967).

Although *R. harrisi* may possess a mutliple pigment system, the identity of the spectral characteristics of phototaxis and polarotaxis provides no evidence for a functional separation of pigments for these responses, as has been suggested for some terrestrial arthropods, *e.g.,* the ant *Cataglyphis bicolor* (Duelli and Wehner, 1973) and the bee *Apis mellifera* (Menzel and Snyder, 1974), in which polarization sensitivity is restricted to ultraviolet sensitive cells.

The suppression of polarotaxis in *R. harrisi* following dark adaptation is in marked contrast to the phototactic response, in which positive phototactic intensity sensitivity is increased by 1–2 log units in dark adapted animals (Forward, 1974; Forward and Costlow, 1974). One potentially viable explanation, based on a model of an insectan fused rhabdom, concerns electrical coupling between retinula cells (Snyder, Menzel and Laughlin, 1973). If cells with perpendicular microvilli were coupled in dark adaptation only, as Shaw (1969a) suggests is possible, then Snyder *et al.* (1973) assert that the resulting overall sensitivity increase would be at the expense of spectral and polarization sensitivity. While Muller (1973) suggests that only parallel tubules are coupled in the crustacean-type rhabdom, thereby increasing rather than eliminating polarization sensitivity, Mote (1974) argues against this interpretation. Although he refutes the theory of parallel coupling, it is still unclear whether the coupling of perpendicular tubules is possible given the interdigitating microvilli of the crustacean rhabdom. Although such a case could explain both the increased sensitivity in phototaxis and the elimination of polarotaxis with dark adaptation, our data offer no basis for an assertion of this mechanism in *R. harrisi.*

In interpreting these results, it must be remarked that due to a certain degree of artificiality, laboratory experimentation approaches the question of behavior in terms of *capability,* not *actuality.* While these experiments therefore do not result in a description of behavior in the field, our demonstration of larval polarotaxis does reveal that the larvae can perceive and orient to linearly polarized light. Only experimentation in the natural conditions of the field, however, can definitively answer questions of actual behavior, and although submarine patterns of polarization are well described (Waterman, 1954; Waterman and Westell, 1956), actual field experimentation on underwater polarotaxis has been minimal. The detailed studies which do exist concern fish (Waterman and Forward, 1970, 1972), and so except for a preliminary study by Bainbridge and Waterman (1957), the field behavior of aquatic arthropods including plankton and larval forms remains entirely unexamined.

However, results of field studies performed on the orientation of terrestrial arthropods (*e.g.,* von Frisch, 1967; Duelli and Wehner, 1973) strongly suggest a major role for polarization within the mechanism of sun compass orientation. For example, in the desert ant, *Cataglyphis bicolor,* Duelli and Wehner (1973) found solar location to be unimportant relative to sky polarization. This result confirms, for the terrestrial case at least, that polarization cues are used in the field.

The lack of comparable information for the underwater case has created a disjunction between laboratory and field behavior of aquatic arthropods which is critical to the creation of a general theory of the use of polarized light. This

problem arises from the fact that there are basically three avenues of investigation of polarized light: perception, behavioral capability and normal field behavior.

Although studies within each of the areas can clearly yield useful and necessary information, their integration is precluded because the nature of the links between the area is unclear. Specifically, we neither know how the electrical signal from the retinula cells is analyzed and converted into behavior, nor if polarized light underwater is even used by animals in nature. Laboratory studies of orientation behavior are therefore separated from both polarized light reception and its use in nature by the lack of knowledge about central nervous system information processing and behavior in the field.

By preventing the formulation of a unified theory, these gaps reduce the utility of information within the three areas of investigation. We therefore feel that investigations into the areas of information processing and field behavior are critical at this stage in the study of polarized light and navigation by aquatic arthropods.

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Summary

1. To determine the ontogeny plus the intensity and spectral characteristics of polarotaxis in larvae of the crab, *Rhithropanopeus harrisi,* swimming paths in relation to the e-vector direction of linearly polarized light were monitored and recorded with a closed circuit video system.

2. All four zoeal stages were examined. Only stages II and III responded with significant directional swimming (stage II, perpendicular to the e-vector, stage III, parallel to the e-vector; Figs. 3 and 4). Stages I and IV appeared indifferent to the polarization plane (Figs. 2 and 5). Swimming under unpolarized light was consistently random (Table I).

3. Polarotaxis disappeared following dark adaptation of stage II larvae (Fig. 6).

4. The lower intensity threshold at 499-nm light for polarotaxis was found to be between 10^{-4} and 10^{-3} W/m^2, while the upper threshold is in the range 10^{-1} to 2×10^{-1} W/m^2 (Figs. 3 and 4).

5. Examination of selected wavelengths from 420–620 nm yielded greatest responsiveness at 499 nm (Fig. 7). A rise evident at 420 nm suggests a secondary maximum in the violet.

6. Stage II larvae showed significant positive phototaxis under depolarized light when a collar of alternating black and white quadrants surrounded the experimental vessel. With the e-vector of polarized light aligned parallel to the white sectors, phototaxis was reduced by polarotactic swimming into the black sectors (approximately perpendicular to the e-vector).

7. A comparison with phototaxis (Forward and Costlow, 1974) provides two items of evidence that polarotaxis and phototaxis are indeed separate responses.

First, phototaxis is essentially unchanged during larval development, while polarotaxis appears only at stages II and III. Secondly, the responses have different optimum intensities.

LITERATURE CITED

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