

PHOTOTAXIS AND GEOTAXIS OF LIGHT-ADAPTED ZOEAE OF THE GOLDEN KING CRAB *LITHODES AEQUISPINUS* (ANOMURA: LITHODIDAE) IN THE LABORATORY

C. F. Adams and A. J. Paul

ABSTRACT

Phototaxis and geotaxis of light-adapted zoeae of the golden king crab *Lithodes aequispinus* Benedict were investigated in the laboratory. Stages I, II, and III zoeae were positively phototactic to white-light intensities of $1.5 \times 10^{15} \text{ q s}^{-1} \text{ cm}^{-2}$ and $3.1 \times 10^{13} \text{ q s}^{-1} \text{ cm}^{-2}$. No significant response was observed in zoeae of any stage to $7.3 \times 10^{11} \text{ q s}^{-1} \text{ cm}^{-2}$. Negative geotaxis was observed in all three stages, although this response was significantly diminished in stages II and III. These behaviors are similar to those seen in stage I larvae of the red king crab *Paralithodes camtschaticus*, as well as in later zoeal stages of several brachyuran crabs.

Commercial harvest of the golden king crab *Lithodes aequispinus* Benedict began in Alaska during the 1981/1982 season and is currently the fourth largest shellfish fishery in the state (Blau *et al.*, 1996). To provide information that may help to conserve stocks, several aspects of its biology are under study.

The depth distribution of zoeae of the golden king crab is unknown. Larvae of the related red king crab *Paralithodes camtschaticus* (Tilesius) are planktonic (Somerton and Otto, 1986; Shirley and Shirley, 1989), and consume phytoplankton and zooplankton in the upper water column (Paul *et al.*, 1990). Shirley and Shirley (1988) found that light-adapted stage I zoeae of the red king crab are positively phototactic to high intensities of white light and negatively phototactic to lower intensities. They also found that these zoeae are negatively geotactic. We decided to observe the response of light-adapted zoeae of *L. aequispinus* to the range of intensities used by Shirley and Shirley (1988), as well as the response to gravity.

MATERIALS AND METHODS

General Methods.—Adult golden king crabs, caught in Prince William Sound in November 1996 and May 1997, were held in the Seward Marine Center laboratory (Institute of Marine Science, University of Alaska). Crabs were fed an alternating diet of squid and fish twice weekly.

Three ovigerous females began hatching in April 1997, 1 in June 1997, and 2 in February 1998. Each female was individually housed in a 380-l tank that received flowing sea water from a depth of 80 m in Resurrection Bay. Daily incoming temperatures ranged from 4.0°–6.7°C. Salinity remained constant throughout the study

period at 33 ppt. A natural photoperiod was simulated with overhead lights by increasing them weekly from 9.5 h light/14.5 h dark in mid-February to 19.5 h light/4.5 h dark in mid-June. Since zoeae of *L. aequispinus* are lecithotrophic (Shirley and Zhou, 1997), we did not feed our zoeae.

Haynes (1982) described 4 zoeal stages for *L. aequispinus*. Similarly, Shirley and Zhou (1997) reported 4 stages, although "All larvae skipped one zoeal stage." We observed only 3 zoeal morphotypes. For this study, stage I zoeae were identified by the absence of setae on the third maxilliped (Fig. 1A), stage II was characterized by setae on the third maxilliped and paired limb buds on the abdominal segments (Fig. 1B), and stage III zoeae were identified by the paired swimming legs on the abdominal segments (Fig. 1C).

All experiments were conducted with light-adapted zoeae ($1.25 \times 10^{14} \text{ q s}^{-1} \text{ cm}^{-2}$, measured with a LICOR 188B quantum sensor) during photophase, between 0900 and 1700 h. As an indicator of health, only active zoeae were chosen for observation. Zoeal stage of every subject was determined microscopically immediately before testing according to the criteria described above. A total of 15 zoeae from at least 2 different females were used per treatment for each zoeal stage in every experiment. No zoea was used more than once. Zoeae were tested individually to eliminate any possible confounding effects that might result from larval interactions, such as chemical signaling, avoidance responses, etc.

The observational chambers were 5 cm (diameter) transparent coring tubes cut to 1 m in length. A transparent piece of Plexiglas® was glued to one end with acrylic cement. The tube was then filled with filtered (25 μm) sea water from the other end and capped. The tubes were marked into 10-cm sections so that zoeal positions could be rapidly identified.

All experiments were conducted in a temperature-controlled room without windows or lights, sealed by a door with a gasket that shut out all exterior light. The stimulus light source was a fiber-optic light (Fiber Light 180).

Phototaxis.—The experimental tube was aligned horizontally with a level. The fiber-optic light was directed at the transparent Plexiglas® end, and a neutral density filter (Edmund 53212) was used to control the intensity

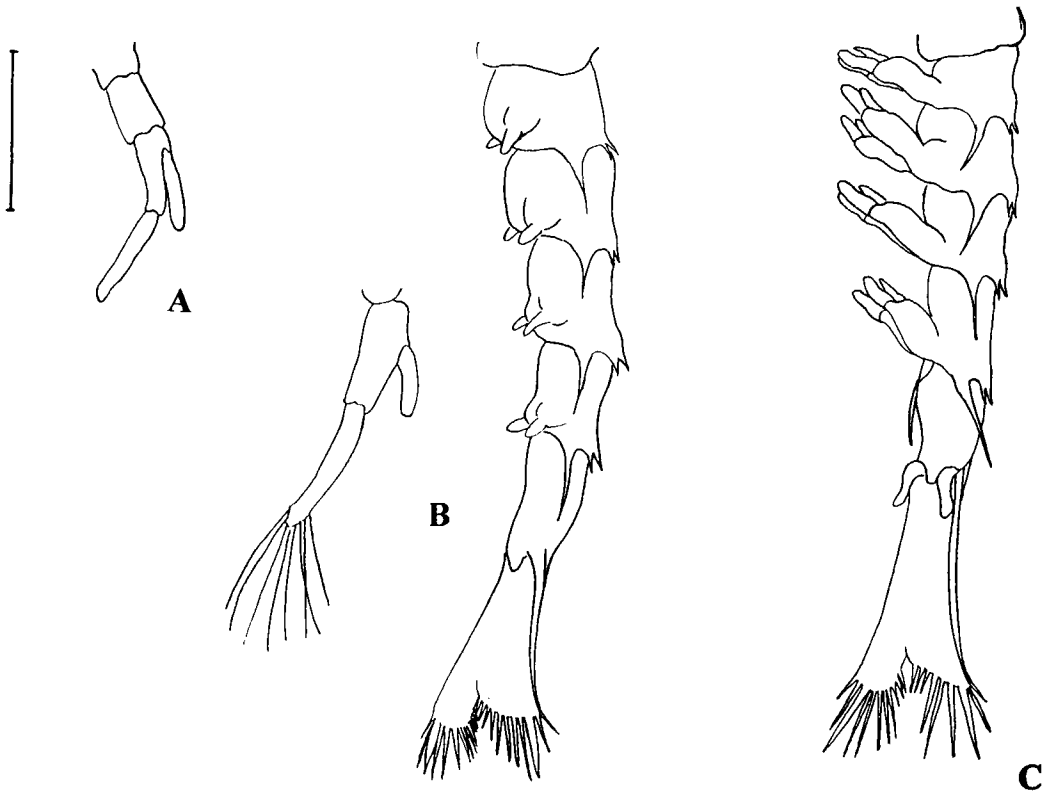


Fig. 1. Characteristics used to identify zoeal stages I-III of *Lithodes aequispinus*: A, absence of setae on the third maxilliped; B, paired limb buds on the abdominal segments and setae on the third maxilliped; C, paired swimming legs on the abdominal segments. Scale bar = 1 mm.

of light from 400–700 nm. Intensities of 1.5×10^{15} , 3.1×10^{13} , and 7.3×10^{11} $q\ s^{-1}\ cm^2$ were used, approximating the same range described by Shirley and Shirley (1988) for their experiments on zoea I of *P. camtschaticus*. A hole drilled into the midpoint of the tube served as an entry port for the individual zoea, thus allowing for both positive and negative photoresponses. After 5 min, the location of the zoea in the tube was determined with the aid of a flashlight. Movement was scored from –50 to 50 cm, with the latter being assigned to individuals at the end of the tube closest to the light source. Controls were tested in darkness.

Geotaxis.—The experimental tube was aligned vertically with a level. A zoea was placed in the top of the tube and then drawn to the bottom with the fiber-optic light. Once the subject was at the bottom, the fiber-optic light was shut off. After 5 min in darkness, the location of the zoea in the tube was determined with the aid of a flashlight. Movement was scored from 0–90 cm, ranging from the bottom to top sections of the tube, respectively.

Adapting the methods of Sulkin *et al.* (1980), controls were tested by positioning the tube horizontally. A hole at one end of the tube served as an entry port for the individual zoea. Once the subject was in the tube, it was drawn to the other end with the fiber-optic light. The fiber-optic light was then shut off. After 5 min in darkness, the location of the zoea in the tube was determined

with the aid of a flashlight. Movement was scored from 0 to 90 cm, with 0 corresponding to the end of the tube to which the zoea had been drawn by the fiber-optic light.

Statistics.—Data were analyzed with the Kruskal-Wallis *H* test for each of the different light intensities and geotaxis (3 stages \times 2 treatments). The Newman-Keuls test was used to detect differences between treatment and control groups at each zoeal stage. All results are presented graphically as the mean \pm SE.

RESULTS

Phototaxis

All zoeal stages had positive phototactic responses to the two highest intensities. Significant effects of treatment were found for light intensities of 1.5×10^{15} $q\ s^{-1}\ cm^2$ (Fig. 2A; Kruskal-Wallis, $H = 70.9$, $d.f. = 5$, $P < 0.0001$) and 3.1×10^{13} $q\ s^{-1}\ cm^2$ (Fig. 2B; Kruskal-Wallis, $H = 61.8$, $d.f. = 5$, $P < 0.0001$), with significant differences at each stage as compared with its respective control (Newman-Keuls, $P < 0.05$). There was no significant effect of 7.3×10^{11} $q\ s^{-1}\ cm^2$ (Fig.

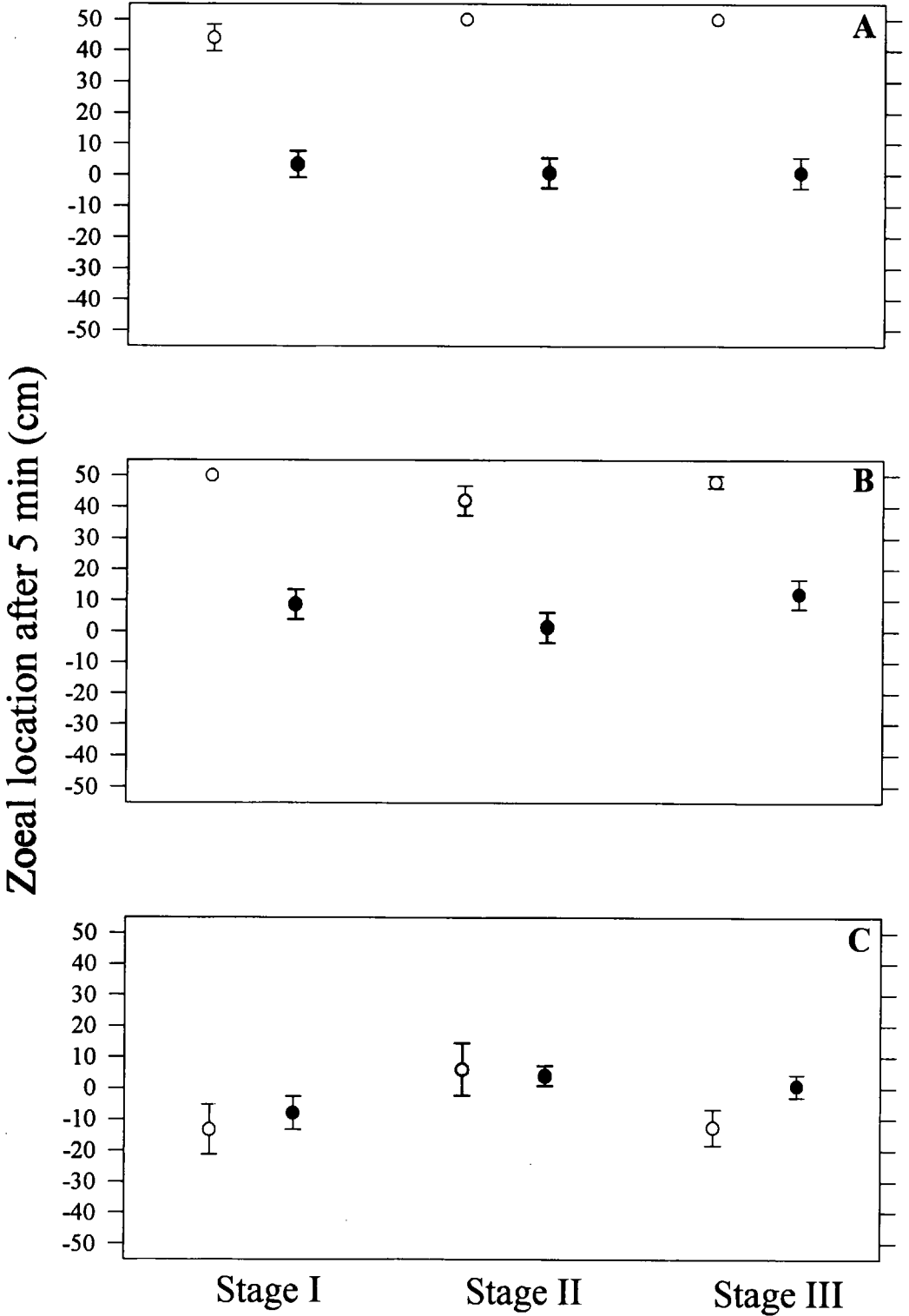


Fig. 2. Mean \pm SE response of light-adapted zoeae of the golden king crab to white light of (A) $1.5 \times 10^{15} q\ s^{-1} cm^{-2}$, (B) $3.1 \times 10^{13} q\ s^{-1} cm^{-2}$, and (C) $7.3 \times 10^{11} q\ s^{-1} cm^{-2}$. ○ = treatment, ● = control. $N = 15$ for each light intensity.

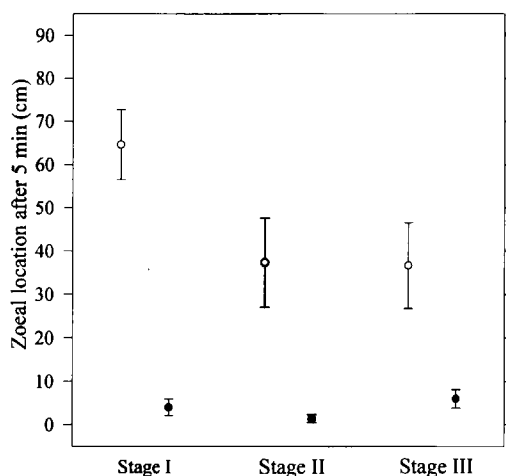


Fig. 3. Mean \pm SE response of light-adapted zoeae of the golden king crab to gravity. \circ = treatment, \bullet = control. $N = 15$.

2C; Kruskal-Wallis, $H = 10.1$, $d.f. = 5$, $P = 0.07$).

Geototaxis

All zoeal stages had a negative georesponse. Significant effects of treatment and zoeal stage were found (Fig. 3; Kruskal-Wallis, $H = 37.6$, $d.f. = 5$, $P < 0.0001$). Each zoeal stage was significantly different compared with its respective control (Newman-Keuls, $P < 0.05$), and both stages II and III were significantly different from stage I (Newman-Keuls, $P < 0.05$).

DISCUSSION

Haynes (1982) described four zoeal stages for *L. aequispinus*. Shirley and Zhou (1997) also reported four stages, although they stated that "All larvae skipped one zoeal stage, either Zoea III or Zoea IV." We raised 20 zoeae of *L. aequispinus* in individual beakers prior to the start of our experiments. All of them shed three exuviae before molting to the glaucothoe. Our drawings, presented in Fig. 1, were based on this preliminary study. The 360 zoeae we subsequently used in our experiments also conformed to this development pattern, and no deviation from our drawings in Fig. 1 were observed. Since skipping of zoeal stages is common when decapods are reared in captivity, the larval morphology reported from laboratory studies may not occur in nature. Obviously, field collection of zoeae of *L. aequispinus* is needed to better

understand larval development. Regardless of developmental pattern, however, our findings demonstrate that light-adapted zoeae of *L. aequispinus* respond to light and gravity prior to molting to the glaucothoe in a manner similar to that in stage I zoeae of *P. camtschaticus*.

All three stages of light-adapted zoeae of *L. aequispinus* had a positive photoresponse to light intensities of 1.5×10^{15} $q\ s^{-1}\ cm^{-2}$ and 3.1×10^{13} $q\ s^{-1}\ cm^{-2}$, and no significant response to 7.3×10^{11} $q\ s^{-1}\ cm^{-2}$ (Fig. 2). Shirley and Shirley (1988) reported that stage I zoeae of *P. camtschaticus* are positively phototactic to white light ranging from 5.1×10^{15} $q\ s^{-1}\ cm^{-2}$ to 5.1×10^{12} $q\ s^{-1}\ cm^{-2}$, and that threshold occurs at 1.63×10^{12} $q\ s^{-1}\ cm^{-2}$. Since we found no response to 7.3×10^{11} $q\ s^{-1}\ cm^{-2}$, zoeae of *L. aequispinus* may have a lower threshold than stage I zoeae of *P. camtschaticus*. Obviously, additional experiments are needed at lower light intensities to explore this possibility. Our objective here, however, was not to determine the threshold of zoeae of *L. aequispinus*, but to observe the response of these animals to the range of light intensities used by Shirley and Shirley (1988) in their study of stage I zoeae of *P. camtschaticus*, and to compare our results. No previous work has been published on phototaxis in later zoeal stages of other anomuran species. The positive photoresponse that we saw in stages II and III of *L. aequispinus* is similar to that reported for later stages of several brachyuran crabs (Sulkin, 1975; Bigford, 1979).

Light-adapted stage I zoeae of *L. aequispinus* had a negative georesponse (Fig. 3). This is identical to that reported for stage I zoeae of *P. camtschaticus* by Shirley and Shirley (1988). Again, no previous work has been published on geotaxis in later zoeal stages of other anomuran species. The decline of this response in stages II and III of *L. aequispinus* is similar to that described for later stages of several brachyuran crabs (Sulkin, 1973; Bigford, 1979; Sulkin *et al.*, 1980).

While stage I zoeae of *P. camtschaticus* move up to the euphotic zone to feed (Somerton and Otto, 1986; Shirley and Shirley, 1989; Paul *et al.*, 1990), such a migration may not be necessary in lecithotrophic zoeae of *L. aequispinus* (see Shirley and Zhou, 1997). Although zoeae of *L. aequispinus* show a similar response to light and gravity in the lab-

oratory as stage I zoeae of *P. camtschaticus*, this does not mean that zoeae of *L. aequispinus* ascend to the photic zone in nature. Forward (1986) demonstrated that positive phototaxis is an artifact of unnatural laboratory lighting conditions, and that normal behavior occurs only when the natural angular light distribution is simulated. Nevertheless, our results demonstrate that light-adapted zoeae of *L. aequispinus* have a response to light and gravity similar to stage I zoeae of *P. camtschaticus* in the laboratory. These findings provide a basis for further investigations of phototaxis and geotaxis in zoeae of *L. aequispinus*, both in the laboratory and under natural conditions.

ACKNOWLEDGEMENTS

This work is a result of research sponsored by the Alaska Sea Grant College Program, cooperatively supported by NOAA, Office of Sea Grant and Extramural Programs, Department of Commerce, under grant number NA46RG0104 project number R/06-36 and the University of Alaska with funds appropriated by the state. Facilities were provided by the Seward Marine Center laboratory of the University of Alaska Institute of Marine Science. This is contribution number 2517 from the Institute of Marine Science, University of Alaska. C. Trowbridge of the Alaska Department of Fish and Game, Cordova Office, supplied the experimental animals. Drawings were done by J. M. Paul. We thank J. J. Kelley (IMS) for the use of the LICOR quantum sensor.

LITERATURE CITED

- Bigford, T. E. 1979. Ontogeny of light and gravity responses in rock crab larvae (*Cancer irroratus*).—*Marine Biology* 52: 69–76.
- Blau, S. F., D. Pengilly, and D. A. Tracy. 1996. Distribution of golden king crabs by sex, size, and depth zones in the eastern Aleutian Islands, Alaska.—*In: High latitude crabs: biology, management, and economics*. Pp. 167–185. Alaska Sea Grant College Program Report 96-02, University of Alaska Fairbanks.
- Forward, Jr., R. B. 1986. A reconsideration of the shadow response of a larval crustacean.—*Marine Behaviour and Physiology* 12: 99–113.
- Haynes, E. 1982. Description of larvae of the golden king crab, *Lithodes aequispina*, reared in the laboratory.—*Fishery Bulletin*, United States 80: 305–313.
- Paul, A. J., J. M. Paul, and K. O. Coyle. 1990. Growth of stage I king crab larvae of *Paralithodes camtschatica* (Tilesius) (Decapoda: Lithodidae) in natural communities.—*Journal of Crustacean Biology* 10: 175–183.
- Shirley, S. M., and T. C. Shirley. 1988. Behavior of red king crab larvae: phototaxis, geotaxis and rheotaxis.—*Marine Behaviour and Physiology* 13: 369–388.
- , and ———. 1989. Interannual variability in density, timing and survival of Alaskan red king crab *Paralithodes camtschatica* larvae.—*Marine Ecology Progress Series* 54: 51–59.
- Shirley, T. C., and S. Zhou. 1997. Lecithotrophic development of the golden king crab *Lithodes aequispinus* (Anomura: Lithodidae).—*Journal of Crustacean Biology* 17: 207–216.
- Somerton, D. A., and R. S. Otto. 1986. Distribution and reproductive biology of the golden king crab, *Lithodes aequispina*, in the eastern Bering Sea.—*Fishery Bulletin*, United States 84: 571–584.
- Sulkin, S. D. 1973. Depth regulation of crab larvae in the absence of light.—*Journal of Experimental Marine Biology and Ecology* 13: 73–82.
- . 1975. The influence of light in the depth regulation of crab larvae.—*Biological Bulletin* 148: 333–343.
- , W. Van Heukelem, P. Kelly, and L. Van Heukelem. 1980. The behavioral basis of larval recruitment in the crab *Callinectes sapidus* Rathbun: a laboratory investigation of ontogenetic changes in geotaxis and barokinesis.—*Biological Bulletin* 159: 402–417.

RECEIVED: 16 July 1997.

ACCEPTED: 11 March 1998.

Address: Institute of Marine Science, University of Alaska, Box 730, Seward, Alaska 99664, U.S.A.