DEVELOPMENT OF LARVAE OF THE GOLDEN KING CRAB LITHODES AEQUISPINUS (ANOMURA: LITHODIDAE) REARED AT DIFFERENT TEMPERATURES

A. J. Paul and J. M. Paul

ABSTRACT

Unfed lecithotrophic larvae of the golden king crab Lithodes aequispinus were reared at 3, 6, and 9°C in darkness and 33–34 ppt salinity. This study was done to improve our understanding of larval development time and the ability of the larvae to survive under different seasonal thermal conditions. The survival rates and intermolt duration was observed for the first zoeal molt (ZI), second molt (ZII), third molt (ZIII), and glaucothoe (G). The duration from hatching to the start of the first nonlarval stage (crab I) averaged 148, 94, and 75 days at 3, 6, and 9°C, respectively. Development rate for ZI to Crab I versus the rearing temperature was described by the equation: Development period (days) = -35.82 (Rearing Temperature °C) + 1.96 (°C²) + 238.6; $r^2 = 0.99$. Regardless of stage, every degree increase in temperature reduced the length of the development period by approximately 9%.

Survival rates of ZI larvae were typically >97% regardless of temperature. By the completion of the ZII molt 83-87% were still surviving. Survival rates to the end of the ZIII molt at 3° and 6°C were 77% and 75%, but only 65% at 9°C. Within stages there was no significant difference in survival rates for ZI, ZII, or ZIII at the 3 test temperatures. The survival rate through the glaucothoe stage was 47% and 51% for larvae reared at 3° and 6°C, respectively, while only 16% of those at 9°C survived to Crab I. There was no significant difference in the percentage of glaucothoe surviving at 3, 6, and 9°C.

The golden king crab Lithodes aequispinus Benedict accounts for about 50% of all king crab landings in western Alaska (Otto, 1990) and because of its value there is interest in developing a sound biological basis for management (Shirley and Zhou, 1997; Adams and Paul, 1999). The larvae are large (ZI = 7 mm) nonfeeding organisms that in captivity exhibit both planktonic and benthic habits (Shirley and Zhou, 1997; Adams and Paul, 1999). Since juveniles are found geographically separated from adults, it has been hypothesized that the larvae are planktonic (Hiramoto, 1985; Sloan, 1985; Blau et al., 1996). Much of their habitat is in remote sites where temperatures of the water column are not monitored. In the bays of the North Pacific, juveniles live at <100 m depth (Sloan, 1985). One site in the northern Gulf of Alaska, where there is a long-term water-column thermal record, is Resurrection Bay near Seward, Alaska. That thermal record suggests that the larvae could encounter 3-11°C depending on when they hatched and the depths they selected (Fig. 1; data from Paul et al., in press). Resurrection Bay is only 100 km downstream from the western side of Prince William Sound where brood females were

captured for this study. Recently Shirley and Zhou (1997) provided information on the intermolt duration of the larval stages, but they did not control temperature during rearing. In this study larvae were reared under controlled temperature conditions at 3, 6, and 9°C to improve our understanding of development time and determine the potential effects of seasonal thermal conditions on survival.

MATERIALS AND METHODS

Individual brooding females from western Prince William Sound, Alaska (N = 8), were placed in separate 800-l tanks which were monitored each day for the presence or absence of larvae. During captivity, and prior to egg hatch, females were held at $6^{\circ}C (\pm 0.8)$ and the seawater exchange rate was 100% per hour. The thermal conditions under which the brood had developed in situ were unknown. Females were fed to excess every other day. The food alternated between the tissues of Pacific herring (Clupea pallasi Valenciennes, 1847) and Octopus dofleini (Wulker, 1910). On the first day when a large hatch of larvae was seen in a tank the female was moved to a fresh tank. The following morning <24-h-old larvae were collected for this study, if there were at least 30 new larvae. If there were <30 larvae in the tank, the female was moved to a new tank; this was done repeatedly until the day arrived when ≥30 ZI were present. A total of 240 larvae were used in the study, 30 collected from each of the 8 females. The 30 larvae from each female were divided into 3 lots of 10 each. Each lot of 10 larvae was

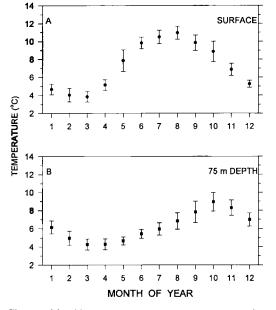


Fig. 1. Monthly average sea-water temperature at the sea surface (A) and at 75-m depth (B) in Resurrection Bay, Gulf of Alaska, during 1986–1996 (Data from Paul *et al.*, in press). Data = \bar{x} , SD.

placed in a 4-l jar filled with 25- μ m filtered sea water (33-34 ppt). The jars were then placed in an incubator to control the rearing temperature. Larvae were reared at 3° (±0.5), 6° (±0.4), and 9°C (±0.4) in darkness. Ten larvae from every female were reared at each test temperature. Every day 16% of the water in the rearing jar was replaced. No food was offered to the larvae since they do not feed (Shirley and Zhou, 1997).

Each day the rearing jars were examined for exuviae or mortalities, both of which are easily observable (Shirley and Zhou, 1997). This species hatches as a ZI. In all the culture jars, enough exuviae were recovered to account for only 3 molts per individual before the molt to the glaucothoe. This observation of only 3 molts prior to attaining the glaucothoe stage is in agreement with growth patterns reported by Shirley and Zhou (1997), and Adams and Paul (1999). Drawings of the three morphological types observed are shown in Adams and Paul (1999). However, Haynes (1982) reported that there were 4 zoeal stages. Shirley and Zhou (1997) discussed the propensity of ZII golden king crab larvae to molt to either ZIII or ZIV and the existence of intermediate morphological types. In this study, we assigned the first molt ZI status, second molt ZII, third molt ZIII, and then glaucothoe for simplicity. Since we did not stage the third molt as ZIII or ZIV, the term ZIII in this report should be viewed as merely indicating the third larval molt, not the morphological stage.

Survival rates for the larvae versus temperature were analyzed for statistical differences using a Kruskal-Wallis ANOVA on ranks. This nonparametric test was used because the equal variance test failed when the data were analyzed prior to running ANOVA. A Mann-Whitney Rank Sum test (MWRS) was used to compare survival

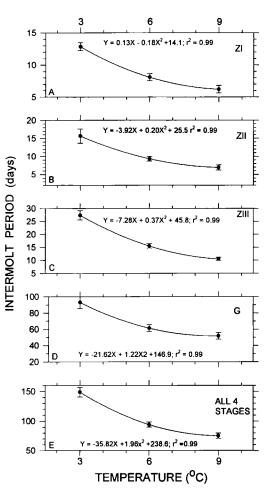
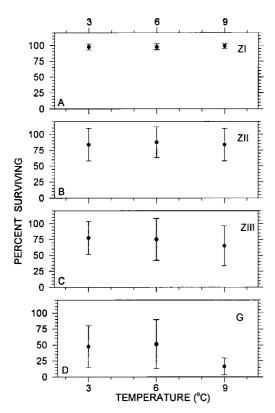


Fig. 2. The intermolt period of larvae of the golden king crab for the first zoeal molt ZI (A), second molt ZII (B), third molt called ZIII (C), glaucothoe G (D), and the total length of time needed to reach the first crab stage (E) relative to rearing temperature. Data = \bar{x} , SD.

rates of glaucothoe reared at 3° versus 6° and 6° versus 9°C. The data were not transformed for analysis.

RESULTS

The duration to the end of the various larval molts (\bar{x} , SD) relative to temperature is portrayed in Fig. 2. The ZI intermolt period averaged 12.8 (±0.4) days at 3°, 8.1 (±0.5) days at 6°, and 6.2 (±0.5) days at 9°C (Fig. 2A). The ZII intermolt ended after 15.8 (±1.9) to 6.9 (±0.7) days at 3 to 9°C, respectively (Fig. 2B). The time required to complete the ZIII molt varied from 27 (±1.7) days at 3° to 10 (±0.6) days at 9°C (Fig. 2C). The glaucothoe stage lasted a total of 93 (±7.5) days at 3° compared to 52 (±4.2) days at 9°C (Fig.



The survival rate of larvae of the golden king Fig. 3. crab through the first zoeal molt ZI (A), second molt ZII (B), third molt called ZIII (C), and molting from the glaucothoe G to the first crab stage (D) relative to rearing temperature. Data = \bar{x} , SD.

2D). All the larval forms responded similarly to increasing temperature by reducing the duration of the intermolt period. Every degree of increase in temperature reduced the length of the development period by approximately 9% for all larval forms. Development rate of individual stages was described by regression equations with r^2 values = 0.99 (Fig. 2). The total development time from ZI to Crab I at 3-9°C was described by the equation: Development period (days) = -35.82 (Rearing Temperature °C) + 1.96 (°C²) + 238.6; r^2 = 0.99 (Fig. 2E).

Survival rates to the end of the first larval molt were 97–98% at 3, 6, and 9°C with no significant difference in ZI survival rates at the three temperatures (Fig. 3A; P = 0.79). By the end of the second molt the average percentage of larvae surviving was 84% at 3°, 87% at 6°, and 83% at 9°C (Fig. 3B), with no significant difference in survival rates (P = 0.89). By the end of the third molt (Fig. 3C)

77%, 75%, and 65% of the original 80 larvae that were reared at 3, 6, and 9°C, respectively, were still alive. There was no significant difference in survival rates of those ZIII groups (P = 0.56). The survival rate of glaucothoe to Crab I was 47% (±32), 51% (± 30) , and 16% (± 13) , for groups reared at 3, 6, and 9°C (Fig. 3D). There was no significant difference (KW-ANOVA, P = 0.1) in survival rates to Crab I among the three groups portrayed in Fig. 3D. The differences in the median survival rate values for glaucothoe reared at 3° versus 6° (MWRS, P = 0.96) were not significantly different. A similar comparison for survival of glaucothoe reared at 6° versus 9°C also determined that there was not a statistically significant difference between the two groups (MWRS, P = 0.83).

DISCUSSION

The survival rate to Crab I for larvae held at $9^{\circ}C$ (16%, Fig. 3D) is similar to the 17% obtained for unfed larvae reared by Shirley and Zhou (1997) at 7.0°-9.5°C. The survival rates for larvae reared to Crab I at 3° and 6°C (Fig. 3D) were nearly three times higher than for larvae reared by both ourselves at 9°C and Shirley and Zhou (1997) at fluctuating temperatures of 7.0°–9.5°C. The larval durations obtained by them were also similar to our results at 9°C. From a purely thermal perspective, larvae that hatched during the colder period of the year would seem to have better survival potential than in warmer months. However, development at 3°C to Crab I takes about twice as long as it does at 9°C, and the \Im longer the larval period lasts the more opportunity predators would have to kill a larva. Currently the relative importance of predation, and thermal moderation of survival rates, to the recruitment process in larvae of the golden king crab is unknown. We did not rear larvae at temperatures $>9^{\circ}C$ and it is possible that some larvae could survive warmer conditions. If juveniles live at 50-100 m (Sloan, 1985), they must be able to tolerate temperatures up to 10°C in northern Gulf of Alaska fjords during the fall (Fig. 1B). However, this idea needs to be tested.

It is not known whether larvae of the golden king crab are pelagic or benthic in nature, since there are no reports of them occurring in plankton or benthic samples. This may be the result of the rarity of these larvae at any given time. Female golden king crabs carry ≤27,000 eggs, only about onetenth the number of eggs in a clutch of the red king crab Paralithodes camtschaticus (Tilesius, 1815) (see Jewett et al., 1985). Female golden king crabs are found in all reproductive stages throughout the year (Otto and Cummiskey, 1985; Sloan, 1985) and hatching can occur in any month (Hiramoto, 1985). All eight females in this study had protracted hatching durations, with 16-26 days passing from release of first to last larvae. The eggs from these eight females hatched during six different months. With low fecundity, asynchronous hatching, and protracted hatching periods one might expect larvae of the golden king crab to be relatively rare in routine plankton sampling programs.

In the fjords of British Columbia, Canada, Sloan (1985) observed that juvenile ξ , lden king crabs were common at depths of 50-100 m, while females with hatching eggs were caught at >200-m depth. He hypothesized that pelagic larvae are moved inshore by upper water-column currents, like many other estuarine meroplankton. All the zoeal stages of the golden king crab are positively phototrophic (Adams and Paul, 1999), like larvae of the red king crab, which are known to be pelagic (Shirley and Shirley, 1988). This study demonstrated that larvae of the golden king crab can tolerate temperatures typical of the upper 100 m in the Gulf of Alaska during most months. The zoeal stages seem to be especially tolerant of a wide range of temperatures. This would be consistent with the theory that they rise to the temporarily warm surface waters for dispersal (Sloan, 1985). Perhaps the separate larval stages have different depth preferences. Since the larvae do not feed (Shirley and Zhou, 1997), they are not obligated to select their vertical position based on prey behavior. Their swimming abilities may allow them to seek the thermal conditions in the water column most suitable for survival. These results show that the larvae can survive at temperatures typical of the upper water column in the Gulf of Alaska. It would, therefore, be prudent to include both benthic and pelagic sampling when seeking larvae of the golden king crab in situ.

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Address: Seward Marine Center Laboratory, Institute of Marine Science, University of Alaska, Seward, Alaska 99664, U.S.A. (e-mail: ffajp@uaf.edu)