

LECITHOTROPHIC DEVELOPMENT OF THE GOLDEN KING CRAB *LITHODES AEQUISPINUS* (ANOMURA: LITHODIDAE)

Thomas C. Shirley and Shijie Zhou

ABSTRACT

Larvae of the golden king crab *Lithodes aequispinus* were reared in individual chambers in the laboratory from hatching to the first crab stage (C1). The experiment included 2 treatments: 1 group was fed live nauplii of *Artemia* daily, while the other group was unfed. A total of 4 molts were observed for all larvae from hatching to C1. One larval stage, either zoea III or zoea IV, was skipped by all larvae. No significant difference existed for the duration of development of each stage between fed and unfed treatments. The mean durations were ZI (ZI = zoeal stage I, ZII = zoeal stage II, etc.) = 6.6 days (± 0.71 SD), ZII_u (molted to ZIII) = 7.0 d (± 0.65 SD), ZII_f (molted to ZIV) = 8.8 d (± 0.95 SD), ZIII (skipped ZIV) = 12.0 d (± 1.33 SD), ZIV (skipped ZIII) = 9.3 d (± 1.63 SD), and glaucothoe = 41.3 d (± 2.65 SD). The total larval duration was approximately 67 d. The survival rate of the fed group was significantly lower than that of the unfed group. Seventeen percent of unfed larvae developed to C1, but only 0.7% of fed larvae did so. The longest duration of survival from hatching was 191 d for an unfed crab. The dry weights of unfed larvae decreased 10% from hatching to C1. Our results indicate that the larval development of the golden king crab is fully lecithotrophic, i.e., larvae can successfully develop to juvenile crabs without eating.

The golden king crab *Lithodes aequispinus* Benedict is a commercially important species in the North Pacific Ocean and the Bering Sea. Before 1983 golden king crabs were harvested only incidentally, but since the dramatic declines of red and blue king crabs in the early 1980s, the golden king crab harvest has increased rapidly. By 1988 golden king crabs represented 50% of all king crab landings in the East Bering Sea and Aleutian Islands (Otto, 1990). The continued exploitation and management needs for this species warrant additional studies of adult and larval biology.

Larval processes may determine the distribution and abundance of adult populations (Olson and Olson, 1989). Little is known about the larval biology of the golden king crab other than a single larval morphological description (Haynes, 1982). Because golden king crabs do not have seasonal reproduction (Somerton and Otto, 1986; Sloan, 1985) and have much larger eggs than those of red and blue king crabs (Sasakawa, 1975; Haynes, 1982; Matsuura and Takeshita, 1985; Somerton and Otto, 1986) we assumed that they would have different patterns of larval development from red and blue king crabs. Somerton and Otto (1986) suggested that the larger size of golden king crab larvae might allow them to withstand starvation for a

longer period. Furthermore, in a preliminary experiment, one of us (TCS) previously had reared a small number of golden king crab larvae to the C1 stage without feeding them. In this paper, we applied fed and unfed treatments to explore the following questions: (1) Are golden king crab larvae lecithotrophic, and can they develop through all larval stages without feeding? (2) What is the developmental pattern for the larvae? What is the duration of each larval stage and the entire larval period? and (3) What is the mortality during larval development?

MATERIALS AND METHODS

Thirteen ovigerous females were collected in Chatham Strait, southeastern Alaska (58°10'N, 135°00'W). They were reared in a 200-l fiberglass tank with flow-through sea water at the Auke Bay Fisheries Laboratories, National Marine Fisheries Service, beginning in March 1992. The larvae were collected the day after hatching and transferred with large-bore pipettes into numbered 100-ml glass culture jars, one larva per jar. The jars were filled with 80–90 ml of filtered sea water and placed in a rectangular fiberglass tank with flowing sea water to maintain the experimental temperature the same as that of ambient sea water at –30 m, the depth of the sea water intake at our laboratory. The water inside and outside of the culture jars remained at the same level. The experiment included 2 treatments: one with food and one without food. We refer to these treatments as “fed” and “unfed” throughout the paper, but do not imply that larvae in the

Table 1. The numbers of larvae of *Lithodes aequispinus* at the beginning of each trial and the number of larvae surviving to crab stage I (C1) for fed and unfed treatments. The water temperature is the range during that culture period.

Trial	Hatching date	Fed		Unfed		T(°C)
		Initial	C1	Initial	C1	
1	19 May	42	1	42	18	7.0–8.5
2	30, 31 May	95	0	30	8	8.0–9.0
3	8 June	56	1	30	2	8.0–9.0
4	20, 21 June	30	0	32	1	8.0–9.0
5	30 June	62	0	61	5	8.0–9.5

“fed” treatment consumed food. The larvae in the fed treatment were provided with newly hatched *Artemia* with 5–18 nauplii ml⁻¹, but the larvae in the unfed treatment were not provided food. The water in the jars was changed every 2–4 days. Water temperature was recorded daily, and salinity was constant at 32 ppt. The tank was partially covered to maintain a dim light condition inside the tank with natural photoperiod. Five groups of larvae totaling 480 individuals were reared (Table 1).

Larvae were checked daily for survival and exuviae. Larvae were considered dead when their body color changed to white or when no movements could be observed. The morphology and behavior of larvae were observed with a magnifying glass and microscope. The larval stages were identified with the description of Haynes (1982). Larvae of each zoeal stage were sacrificed at the beginning of the instar for dry-weight determinations. The dry body weight of each stage was measured with a Kahn electrobalance. To prepare the sample for dry weight, the larvae were rinsed with fresh water and then blotted dry with a paper towel. Each larva was wrapped in an untouched aluminum foil and dried in an oven at 55–60°C for 24 h.

The molts and mortality of each individual larva were recorded. The data were statistically analyzed with 1- and 2-way analysis of variance to detect the difference between fed and unfed treatments and among the larval stages. Tukey multiple comparisons and Fisher Least Significant-difference test were applied as a posteriori tests.

RESULTS

Hatching

Most of the hatching of eggs from 13 female golden king crabs occurred over a few weeks. However, the total duration of hatching was 123 d. The first larva was observed on 2 April 1992 and the last larva on 3 August 1992. One female died on 15 May as a result of gill damage caused by a fish brooding eggs in her gill chamber (Love and Shirley, 1993). Peak hatching occurred between 8–17 July. By 17 July, approximately 99% of the

eggs of 11 females had hatched, but one female hatched only about 50% of its eggs.

Molting and Development

Four molts were observed for each larva from hatching (H) to juvenile crab (C1), i.e., Zoea I (ZI), Zoea II (ZII), Zoea III (ZIII) or Zoea IV (ZIV), and glaucothoe (G). Times of molting generally were similar for both the fed and unfed treatments. The peak molting time after hatching was 6 d for the first molt, 14 or 18 d for the second molt, 25–27 d for the third molt, and 62–71 d for the fourth molt (Fig. 1). All larvae skipped one zoeal stage, either Zoea III or Zoea IV. Sixty-one % of larvae molted from ZII to ZIII (ZII_a stage), then to glaucothoe, and 39% of larvae molted from ZII to ZIV (ZII_b stage), then to glaucothoe (Fig. 2). The identification of some Zoea III and Zoea IV was confounded because a few larvae were more advanced than Zoea III but less developed than Zoea IV, i.e., their external morphological structures were between ZIII and ZIV.

There was no significant difference for the duration of development (total larval period from hatching to first crab stage) between the fed and unfed treatments (two-way ANOVA,

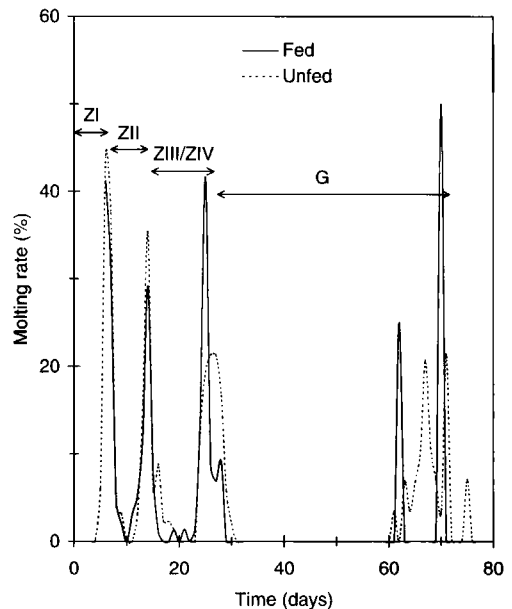


Fig. 1. Molting rate of fed and unfed golden king crab larvae from hatching to the first crab stage ($N = 480$).

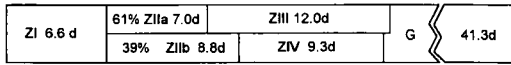


Fig. 2. Mean duration (days) of each larval stage and percentage of golden king crab larvae which molted from ZII to ZIII or from ZII to ZIV. ZI to ZIV = zoeal stage I to IV, G = glaucothoe. Total larval period from hatching until metamorphosis to the C1 averaged 67 days.

$N = 30, d.f. = 1, P = 0.701$), but there were significant differences for the duration between stages (ANOVA, $N = 30, d.f. = 5, P < 0.001$; Table 2). The average intermolt period increased with larval stage. The a posteriori test using Tukey multiple comparison demonstrated that the duration of both Zoea III and glaucothoe differed from all other zoeal stages. Both the duration of each stage and the duration of molting (duration over which larvae from the same brood molted) increased with larval development (Table 2). Zoeae molting from ZII to ZIV ($ZII_b = 8.8 \text{ d} \pm 0.95 \text{ SD}$ for both fed and unfed larvae) required a longer time than zoeae molting from ZII to ZIII ($ZII_a = 7.0 \text{ d} \pm 0.65 \text{ SD}$). However, these larvae had compensation or decompensation during the subsequent molt: zoeae molting from ZIV to glaucothoe took a shorter time ($9.3 \text{ d} \pm 1.63 \text{ SD}$) than zoeae molting from ZIII to glaucothoe ($12.0 \text{ d} \pm 1.33 \text{ SD}$). The total duration from the second molt (ZII) to the third molt (glaucothoe) for both types of

larvae was comparable, averaging 18.9 d for ZII → ZIII → glaucothoe and 18.2 d for ZII → ZIV → glaucothoe.

Survival Rate

No relationship between daily mortality and molt cycle could be detected (Fig. 3). Because larvae molted from ZII to either ZIII or ZIV, and ZIII and ZIV were not clearly distinct for some individuals, mortalities in these two stages were combined. The mean survival rates differed significantly between fed and unfed groups (two-way ANOVA, $N = 39, d.f. = 1, P = 0.016$) and among stages (two-way ANOVA, $N = 39, d.f. = 4, P = 0.019$). The mean survival rates of the fed group, which varied from 14.4% for glaucothoe to 57.8% for zoea I, were lower than those of the unfed treatment, which varied from 49.2% for glaucothoe to 68.3% for zoea I (Fig. 4). Glaucothoes had the lowest survival rate in both fed and unfed treatments. However, because glaucothoes experienced a longer duration, they had a lower mean daily mortality than other larval stages. Because the survival rates in the fed treatment were lower than in the unfed treatment for all stages, the difference in the total survival rate between the two treatments became greater as larvae developed (Fig. 5). At the end of larval development, 17.4% of the unfed larvae survived to the first crab stage (C1), but only 0.7% of fed larvae molted to C1 (Table 1).

Table 2. Duration (days) of development of each larval stage of *Lithodes aequispinus*. N = total number of larvae molted. ZII_a = zoea molting from ZII to ZIII, ZII_b = zoea molting from ZII to ZIV, G = glaucothoe.

Stage	Treatment	N	Duration (days)											Mean (d)			
			5	6	7	8	9	10	11	12	13	14	15				
ZI	Fed	125		69	46	7	3										6.6
	Unfed	84	3	38	36	4	3										6.6
ZIIa	Fed	31	2	3	20	6											7.0
	Unfed	28		5	20	3											6.9
ZIIb	Fed	6				4	2										8.3
	Unfed	8				2	3	2	1								9.3
ZIII	Fed	22					1	1	9	4	2	4	1				12.0
	Unfed	20						1	5	9	2	3					12.1
ZIV	Fed	5			1		2	1	1		1						9.8
	Unfed	28		1	5	5	7	6	3	1							8.9
G	Fed	2													1		41.5
	Unfed	34	1	2	2	6	6	2	5	3	2	3	1				41.2

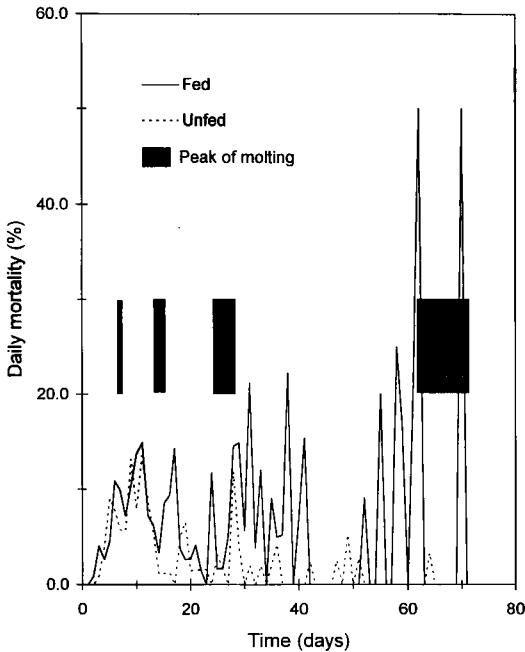


Fig. 3. Daily mortality of fed and unfed golden king crab larvae from hatching to the first crab stage. The gray blocks indicate the peak periods of molting.

Mortality of Juvenile Crabs

After an average of 67 d of larval development, a total of 34 unfed larvae molted to C1, of which 25 were used for further culture. These juvenile crabs were divided into two treatments: 11 were fed with newly hatched brine shrimp and chopped mussel tissue (*Mytilus trossulus* Gould), and 14 were unfed. Crabs in the fed treatment actively consumed brine shrimp and mussel tissue. The body color changed from a transparent white to the golden color of field-collected juveniles (TCS, unpublished observations) soon after the crabs began eating. The body color of unfed crabs remained transparent.

Mortality was distinctly different between the two treatments. The first death occurred in the fed treatment 12 d after an individual molted to C1 and started feeding. All juveniles in the fed treatment died within 30 d after molting to C1, which was 98 d since hatching. The first death in the unfed treatment was observed 46 d after the crab molted to C1 (117 days from hatching), and the last one died 125 d after it had molted to C1 (191 d from hatching) (Fig. 6). The duration of survival of C1 in fed and unfed treatments

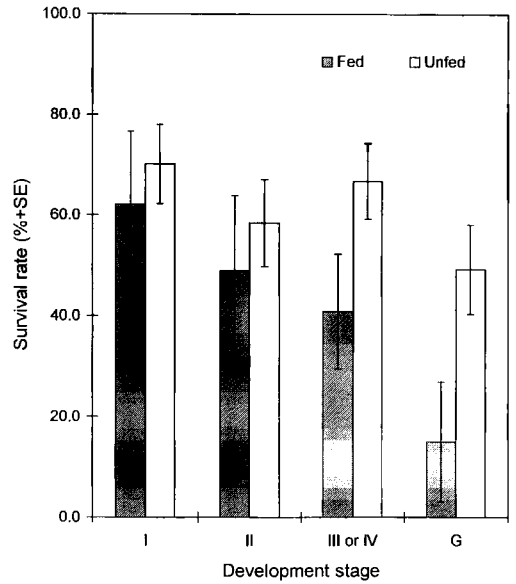


Fig. 4. Mean survival rates of fed and unfed golden king crab larvae by stages (Zoea I to glaucothoe). Vertical bars represent ± 1 standard error of the mean.

averaged 22 d (± 6 SD) and 89 d (± 28 SD), respectively.

Change in Body Weight

Because larvae were weighed at the beginning of each stage, ZI had the same weight

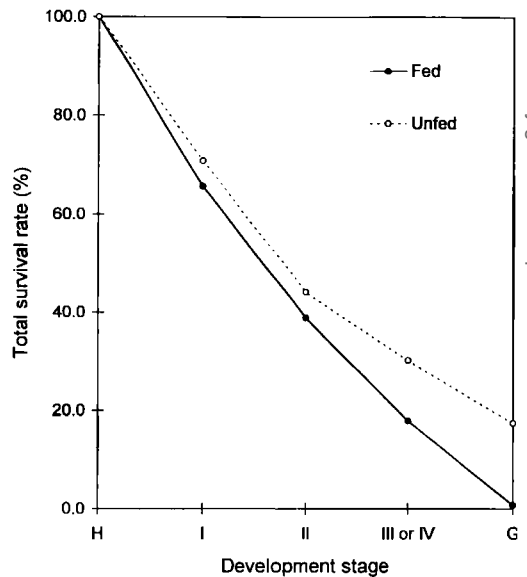


Fig. 5. Total survival rates of fed and unfed golden king crab larvae after each molt. H = hatch, I to IV = zoea I to IV, G = glaucothoe.

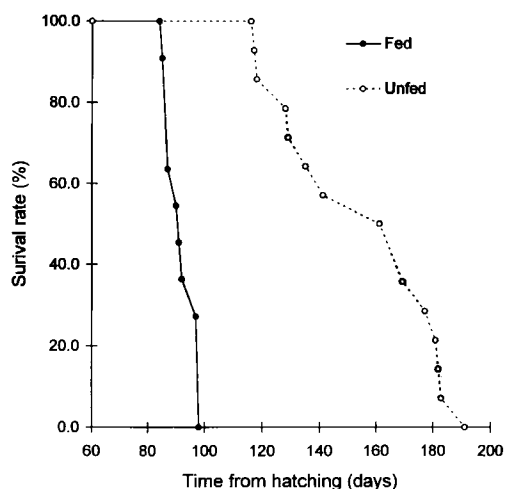


Fig. 6. Survival rate of stage 1 juvenile golden king crabs in fed ($N = 11$) and unfed ($N = 14$) treatments.

for both fed and unfed treatments. ZIII and ZIV larvae were treated as the same stage. To examine the effect of treatment, the variable of larval stage consisted of three levels (ZII, ZIII/ZIV, and glaucothoe). No significant difference was found in dry weight between fed and unfed treatments (ANOVA, $N = 34$, $d.f. = 1$, $P = 0.173$). To examine the difference between stages, one-way ANOVA with four stages (ZI, ZII, ZIII/ZIV, and glaucothoe) was applied to the fed treatment, and with five stages (the above four plus C1) to the unfed treatment. Significant differences existed between zoal stages of the unfed treatment ($N = 39$, $d.f. = 4$, $P = 0.031$) but not the fed treatment ($N = 36$, $d.f. = 3$, $P = 0.101$, statistical power = 0.52). The dry weights of unfed larvae decreased slightly with development, from an average of 1.55 mg for ZI to 1.42 mg for glaucothoe and 1.39 for C1 (Fig. 7). The total decrease in dry weight from ZI to C1 represented 10%.

We observed larvae regularly with a magnifying glass or a dissecting microscope. They usually rested quietly on the bottom. In earlier zoal stages, the zoeae swam from time to time. When brine shrimp nauplii were added, most larvae became more active, and moved backward to escape the prey rather than to feed on them. Unhatched and dead brine shrimp and detritus were seen adhering to the bodies of larvae even though the water was changed frequently. Brine shrimp

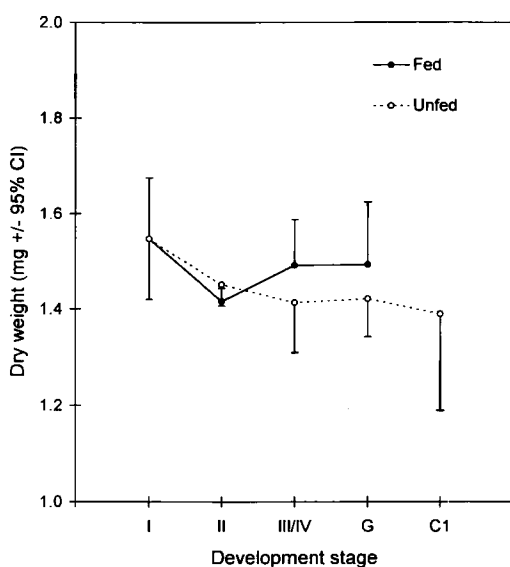


Fig. 7. Mean dry body weights of fed and unfed golden king crab larvae and stage 1 crab at the beginning of each stage. Vertical bars represent $\pm 95\%$ confidence interval.

swam near the larval mouth and among the pereopods, but no feeding responses were observed during any larval stages. Although the larvae occasionally caught brine shrimp with their chelae, they released the prey rather than ate them. The bodies of these larvae were translucent and no food was observed in the gut. As soon as larvae molted to C1, they began to feed actively, catching brine shrimp with their chelae and transferring the prey to their mouths. The food inside the digestive tract was visible, and the larval body color changed from transparent to gold. The body color of unfed C1 crabs remained translucent.

DISCUSSION

Golden king crab larvae successfully developed from hatching to the first benthic instar without feeding. The development, therefore, was lecithotrophic. This larval trophic type is in distinct contrast to the planktivorous larvae of the red king crab *Paralithodes camtschaticus* (Tilesius). If red king crab larvae were deprived of food for four days, they lost feeding capability and could not molt to the next zoal stage, even if they were provided food again (Kurata, 1959; Paul and Paul, 1980).

In addition, golden king crab larvae are fully lecithotrophic, compared to some "partially" lecithotrophic or facultative feeding (Strathmann, 1987) crustacean larvae. For example, Rice and Provenzano (1965) reported that the hermit crab *Paguristes sericeus* A. Milne Edwards was lecithotrophic. However, starved zoeae of *P. sericeus* molted to the glaucothoe only at an optimal temperature (25°C). At lower temperatures they required food to complete development. Starvation delayed metamorphosis and none of the starved larvae of *P. sericeus* molted to the crab stage, while 85% of fed glaucothoe developed to the third crab stage.

The lecithotrophic nature of golden king crab larvae is suggested by their larger eggs. The mean external egg lengths of golden king crab (2.2 mm, Otto and Cummiskey, 1985; Somerton and Otto, 1986) is more than twice as large as the egg lengths of red king crab (0.88–1.03 mm, Matsuura and Takeshita, 1985) and blue king crab (1.2 mm, Sasakawa, 1975). The total length of ZI of golden king crabs (7.3 mm TL, Haynes, 1982) hatching from these large eggs is much larger than that of red king crabs (4.6 mm TL, Sato and Tanaka, 1949) and blue king crabs (4.9 mm TL, Hoffman, 1968). Larger eggs and first stage larvae are common characteristics of lecithotrophic crustaceans (Rabalais and Gore, 1985).

Lecithotrophy may have adaptive significance related to the deeper habitat of golden king crabs. A survey in northern British Columbia fjords reported that adult golden king crabs predominated from 200–400-m depths. Females usually mated and extruded eggs at <150 m, then incubated eggs at 150–200 m (Sloan, 1985). Early juvenile stages (0–1 year class) of golden king crabs have been found in depths as shallow as 174 m (F. Blau, Alaska Department of Fish and Game, personal communication), but the highest catch rates of juveniles near the Aleutian Islands was >800 m (Blau *et al.*, 1996). This habitat is much deeper than the average depths for red and blue king crabs (Somerton and Otto, 1985; Sloan, 1985).

The depth distribution of larvae of golden king crabs in Alaskan waters is unknown, since none have been reported from plankton samples despite extensive sampling (S. Shirley and T. Shirley, 1989). A study of crab larvae in the upper 50 m near the edge of the

eastern Bering Sea continental shelf reported that, although both red and blue king crab larvae were found, golden king crab larvae were not present (Somerton and Otto, 1986). They may occur in deeper water, perhaps near the benthos, where they would not be sampled by typical plankton tows. The relative inactivity of the golden king crab larvae in our cultures contrasts sharply with the active swimming of cultured larvae of red king crabs (S. Shirley and T. Shirley, 1988; T. Shirley and S. Shirley, 1989) and suggests that they may occur near the benthos, since nonswimming larvae sink. Jewett *et al.* (1985) also reported the behavior of recently hatched golden king crab larvae was more benthic than planktonic. The larvae of *Lithodes antarcticus* Jacquinet under culture conditions also demonstrated a strong demersal behavior (Vinuesa *et al.*, 1985). Support for a deeper distribution of golden king crab larvae also comes from the depth distribution of early benthic stages discussed previously, in which the highest abundance of juveniles occurred at the greatest depths.

Distinct rhythms of feeding that coincide with diel vertical migrations, with feeding occurring in shallow waters during the day, were reported for the larvae of red king crabs (S. Shirley and T. Shirley, 1990). Laboratory growth rate (Paul *et al.*, 1989, 1990) and survival rate in the field (S. Shirley and T. Shirley, 1989) of red king crab larvae have been related to quantity and quality of prey items. Somerton and Otto (1986) also suggested that which our results imply: golden king crab larvae might not need to ascend to the photic zone to feed. Our results demonstrate that they can develop through all larval stages in deeper water via lecithotrophy.

The hatching of golden king crabs was not synchronous. The total duration of hatching among the 13 ovigerous females was 123 days, extending from 2 April until 3 August. Hatching among red king crabs is considerably more synchronous (Shirley *et al.*, 1990), with peak hatching usually coinciding with the spring phytoplankton bloom (S. Shirley and T. Shirley, 1989; T. Shirley and S. Shirley, 1990). Golden king crabs in the Bering Sea (Somerton and Otto, 1985) and in British Columbia fjords (Sloan, 1985) were reported to have eggs in all stages of development. Although most female *Lithodes aequispinus* hatch their eggs in late spring and early sum-

mer in waters of central Japan, eggs in all stages of development have been reported throughout the year (Hiramoto, 1985). Because of their lecithotrophic development, the hatching of golden king crabs need not coincide with the spring phytoplankton bloom for successful larval recruitment, and reproduction can be asynchronous.

Skipping of larval stages is common in decapod development (Gore, 1985; Rabalais and Gore, 1985; Wehrmann, 1991), and has been reported in other anomuran species (Provenzano, 1962a, b; Gore and Scotto, 1983). In our experiments, all golden king crab larvae skipped one stage, either ZIII or ZIV. Since environmental variables often play an important role in abbreviated development (Gore, 1985), we conjecture that the rearing temperature in our laboratory culture (Table 1), being higher than ambient temperature at 200–400-m depth (approximately 2–4°C), may have contributed to the skipped larval stages. In British Columbia, golden king crab larvae are thought to hatch in deep water (>200 m), where water temperatures may be somewhat colder than our rearing temperatures (Sloan, 1985). In central Japan, the ambient sea-water temperatures where ovigerous female golden king crabs are found varies between 1–5°C. Alternately, the skipping of larval stages may represent common abbreviated development for golden king crabs.

The highest mortality of cultured decapod larvae often occurs during molting, since ecdysis is a critical period in larval development (Rabalais and Gore, 1985). This phenomenon was not present in our study. No relationship was evident between daily mortality and the molting cycle, although some larvae died while molting.

Mortality of fed larvae was higher than that of unfed larvae in all larval stages, and juvenile crabs in the fed treatment survived a shorter time than in unfed treatment. This phenomenon has not been reported for other decapods, even if they were lecithotrophic (Dobkin, 1963, 1968; Rice and Provenzano, 1965; Campodonica and Guzman, 1981; McConaughy, 1985; Wehrmann, 1991). The survival rate of fed larvae was either higher or equal to that of unfed larvae in all other reports. However, increased mortality of fed adult crabs in comparison to unfed crabs following a starvation period has been reported (Paul *et al.*, 1994). We suggest that golden

king crab larvae are fully lecithotrophic compared to some “partially” lecithotrophic animals. External food is not necessary as a nutritional source for their larval development; food may even be harmful to larvae. In our study, food might contribute to higher mortality in three ways. First, the continuously swimming brine shrimp surrounding crab larvae might disturb them. We observed that larvae in the fed treatment were more active than larvae in the unfed treatment. Golden king crab larvae in the fed treatment became agitated and tried to avoid brine shrimp which became entangled in their pereopods. This disturbed environment might stress larvae and result in higher mortality in the fed treatment. Second, the dead brine shrimp and detritus adhering to the setae might hinder larval respiration. And third, we cannot refute that water quality in the fed treatment might have been poorer than that in the unfed treatment.

Starvation prolongs duration of larval development in some decapods (Rice and Provenzano, 1965; Anger and Dawirs, 1981; Anger *et al.*, 1981; Dawirs, 1984), but not in others (Campodonica and Guzman, 1981; Farrelly and Sulkin, 1988; Wehrmann, 1991). For golden king crabs, duration of development did not differ between larvae in fed and unfed treatments.

It is understandable that the body weight of unfed larvae declined with larval development. The lack of significant differences in dry weight between the fed and unfed treatments was also expected if feeding did not occur. However, the reason that body weight did not change significantly with development in the fed treatment remains unclear. Size-selective mortality of larvae in the fed treatment may help explain the lack of a significant decline in average dry weight; larger individuals may have had higher survival. We cannot test this hypothesis, because we did not weigh dead larvae; biases could have been introduced due to weight loss caused by decomposition. Another explanation is that the larvae did feed. However, no feeding behavior was observed during any larval stages. In addition, the total length of the larvae suggested that they did not grow. The mean total lengths of fed larvae from zoea I to glaucothoe were 7.3, 7.5, 7.6, 6.8, 5.9 mm, respectively (Haynes, 1982), with a growth factor of less than 1 from ZI to ZIV. This distinctly contrasts to an overall mean larval

growth factor of about 1.14 for Caridea, about 1.25 for Anomura, and about 1.30 for lobsters and for Brachyura (Gore, 1985).

An alternate explanation for the lack of feeding in our cultures, which we do not support, is that feeding did not occur because the food provided was not appropriate. We provided newly hatched nauplii of *Artemia* to the golden king crab larvae. The digestive tracts of early zoeal stages of red king crabs collected in the plankton contained primarily phytoplankton (S. Shirley and T. Shirley, 1990; T. Shirley and S. Shirley, 1990) and the early zoeal stages had high growth rates and molting success in laboratory culture when provided only phytoplankton (Paul *et al.*, 1989, 1990). However, laboratory cultures of red king crab zoeae also fed on nauplii of *Artemia* and each other and had high survival when provided only *Artemia* (Paul and Paul, 1980; S. Shirley and T. Shirley, 1988; T. Shirley and S. Shirley, 1989). The zoeae of golden king crabs are considerably larger than the zoeae of red king crabs and should have been able to feed on nauplii of *Artemia*, particularly since the smaller first crab stage of golden king crabs readily fed upon the same prey. Studies of the histological and morphological attributes of the larval gut might provide additional insights into the feeding capabilities of golden king crab larvae.

Larvae survived as long as 191 days without feeding, from hatching through molting to the first benthic crab instar. Only a few larvae of golden king crabs have been collected in plankton samples, despite the widespread distribution of the adults, but we believe the larvae generally occur at depths greater than 200 m and remain near the benthic substrate. If the larvae occur at these greater depths, the larval period might be longer due to the colder temperatures (2–4°C) commonly encountered at the greater depths. We do not suggest that the instar duration or larval periods that we measured approximate those in nature. However, the high survival rates of golden king crabs in laboratory conditions without food demonstrate the lecithotrophic capabilities of the species.

ACKNOWLEDGEMENTS

We thank T. Koeneman for collecting and C. Botelho for transporting the ovigerous golden king crabs. We also thank D. Love for maintaining the crabs, providing the larvae, and collecting larval hatching data. Dr. B. Stevens

provided a meaningful critique of the manuscript. This work was supported in part by Alaska Sea Grant with funds from the National Oceanic and Atmospheric Administration, Office of Sea Grant, Department of Commerce, under grant no. NA 90AA-D-SG066, project E/70-10, and from the University of Alaska with funds appropriated by the state.

LITERATURE CITED

- Anger, K., and R. R. Dawirs. 1981. Influence of starvation on the larval development of *Hyas araneus* (Decapoda, Majidae).—*Helgoländer Meeresuntersuchungen* 34: 287–311.
- , ———, V. Anger, and J. D. Costlow. 1981. Effects of early starvation periods on zoeal development of brachyuran crabs.—*Biological Bulletin* 161: 199–212.
- Blau, S. F., D. Penguilly, and D. A. Tracy. 1996. Distribution of golden king crabs by sex, size, and depth zones in the eastern Aleutian Islands, Alaska.—*In*: Proceedings of the international symposium on biology, management, and economics of crabs from high latitude waters. Lowell Wakefield Symposium Series, pp. 167–185. Alaska Sea Grant College Program Report No. 96-02, University of Alaska Fairbanks.
- Campodonico, I., and L. Guzman. 1981. Larval development of *Paralomis granulosa* (Jacquinot) under laboratory conditions (Decapoda, Anomura, Lithodidae).—*Crustaceana* 40: 272–285.
- Dobkin, S. 1963. The larval development of *Palaemonetes paludosus* (Gibbes, 1850) (Decapoda, Palaemonidae) reared in the laboratory.—*Crustaceana* 6: 41–61.
- . 1968. The larval development of a species of *Thor* (Caridea, Hippolytidae) from south Florida, U.S.A.—*Crustaceana*, supplement 2: 1–18.
- Dawirs, R. R. 1984. Influence of starvation on larval development of *Carcinus maenas* L. (Decapoda: Portunidae).—*Journal of Experimental Marine Biology and Ecology* 80: 47–66.
- Farrelly, C., and S. D. Sulkin. 1988. Effect of starvation on megalopal development in the brachyuran crab *Hemigrapsus oregonensis*.—*Journal of Crustacean Biology* 8: 614–617.
- Gore, R. H. 1985. Molting and growth in decapod larvae.—*In*: F. R. Schram, gen. ed., *Crustacean issues* 2. A. M. Wenner, ed., Larval growth. Pp. 1–65. A. A. Balkema, Rotterdam, The Netherlands.
- , and L. E. Scotto. 1983. Studies on decapod crustacea from the Indian River region of Florida XXVII. *Phimochirus holthuisi* (Provenzano, 1961) (Anomura: Paguridae): the complete larval development under laboratory conditions, and the systematic relationships of its larvae.—*Journal of Crustacean Biology* 3: 93–116.
- Haynes, E. 1982. Description of larvae of the golden king crab, *Lithodes aequispina*, reared in the laboratory.—*Fishery Bulletin*, United States 80: 305–313.
- Hiramoto, K. 1985. Overview of the golden king crab, *Lithodes aequispina*, fishery and its fisheries biology

- in the Pacific waters of Central Japan.—Proceedings of the International King Crab Symposium. Lowell Wakefield Symposia Series. University of Alaska, Alaska Sea Grant Report 85-12. Pp. 297-317.
- Hoffman, E. G. 1968. Description of laboratory-reared larvae of *Paralithodes platypus* (Decapoda, Anomura, Lithodidae).—Journal of the Fisheries Research Board of Canada 25: 439-455.
- Jewett, S. C., N. A. Sloan, and D. A. Somerton. 1985. Size at sexual maturity and fecundity of the fjord-dwelling golden king crab *Lithodes aequispina* Benedict from northern British Columbia.—Journal of Crustacean Biology 5: 377-385.
- Kurata, H. 1959. Studies on the larva and post-larva of *Paralithodes camtschatica* (T.). Rearing of the larvae, with special reference to the food of the zoea.—Bulletin of Hokkaido Region Fishery Research Laboratory 20: 76-83.
- Love, D. C., and T. C. Shirley. 1993. Parasitism of the golden king crab, *Lithodes aequispinus* Benedict, 1895, by a liparid fish.—Crustaceana 65: 97-104.
- McConaughy, J. R. 1985. Nutrition and larval growth.—In: F. R. Schram, gen. ed., Crustacean issues 2. A. M. Wenner, ed., Larval growth. Pp. 127-154. A. A. Balkema, Rotterdam, The Netherlands.
- Matsuura, S., and K. Takeshita. 1985. Development and decrease in number of eggs attached to pleopods of laboratory-reared king crab, *Paralithodes camtschatica* (Tilesius).—Proceedings of the International King Crab Symposium. Lowell Wakefield Symposia Series. University of Alaska, Alaska Sea Grant Report 85-12. Pp. 155-165.
- Olson, R. R., and M. H. Olson. 1989. Food limitation of planktotrophic marine invertebrate larvae: does it control recruitment success?—Annual Reviews of Ecology and Systematics 20: 225-247.
- Otto, R. S. 1990. An overview of eastern Bering Sea king and Tanner crab fisheries.—Proceedings of the International Symposium on King and Tanner Crabs. Alaska Sea Grant College Program No. 90-04, Lowell Wakefield Symposium Series, pp. 9-26.
- , and P. A. Cumiskey. 1985. Observation on the reproductive biology of golden king crab (*Lithodes aequispinus*) in the Bering Sea and Aleutian Islands.—Proceedings of the International King Crab Symposium. Lowell Wakefield Symposia Series. University of Alaska, Alaska Sea Grant Report 85-12. Pp. 123-135.
- Paul, A. J., and J. M. Paul. 1980. The effect of early starvation on later feeding success of king crab zoeae.—Journal of Experimental Marine Biology and Ecology 44: 247-251.
- , ———, and K. O. Coyle. 1989. Energy sources for first-feeding zoeae of king crab *Paralithodes camtschatica* (Tilesius) (Decapoda, Lithodidae).—Journal of Experimental Marine Biology and Ecology 130: 55-69.
- , ———, and ———. 1990. Growth of stage I king crab larvae *Paralithodes camtschatica* (Tilesius) (Decapoda, Lithodidae) in natural communities.—Journal of Crustacean Biology 10: 175-183.
- Paul, J. M., A. J. Paul, and A. Kimker. 1994. Compensatory feeding capacity of two brachyuran crabs, Tanner and Dungeness, after starvation periods like those encountered in pots.—Alaska Fisheries Research Bulletin 1: 184-187.
- Provenzano, Jr., A. J. 1962a. The larval development of *Calcinus tibicen* (Herbst) (Crustacea, Anomura) in the laboratory.—Biological Bulletin 123: 179-202.
- . 1962b. The larval development of the tropical land hermit *Coenobita clypeatus* (Herbst) in the laboratory.—Crustaceana 4: 207-228.
- Rabalais, N. N., and R. H. Gore. 1985. Abbreviated development in decapods.—In: F. R. Schram, gen. ed., Crustacean issues 2. A. M. Wenner, ed., Larval growth. Pp. 67-126. A. A. Balkema, Rotterdam, The Netherlands.
- Rice, A. L., and A. J. Provenzano. 1965. The zoeal stages and the glaucothoe of *Paguristes sericeus* A. Milne-Edwards (Anomura, Diogenidae).—Crustaceana 8: 239-254.
- Sasakawa, Y. 1975. Studies on blue king crab resources in the western Bering Sea. III. Ovarian weights, egg numbers carried and diameters.—Bulletin of Japanese Society of Science Fisheries 41: 941-944.
- Sato, S., and S. Tanaka. 1949. Study on the larval stage of *Paralithodes camtschatica* (Tilesius) I. Morphological research.—Hokkaido Fishery Experimental Station Research Report 1: 7-24.
- Shirley, S. M., and T. C. Shirley. 1988. Behavior of red king crab larvae: phototaxis, geotaxis and rheotaxis.—Marine Behavior and Physiology 13: 369-388.
- , and ———. 1989. Interannual variability in density, timing and survival of Alaska red king crab (*Paralithodes camtschatica*) larvae.—Marine Ecology Progress Series 54: 51-59.
- , and ———. 1990. Diel feeding periodicity of larvae of the red king crab, *Paralithodes camtschatica*.—Proceedings of the International King and Tanner Crab Symposium. Alaska Sea Grant College Program Report No. 90-04, Lowell Wakefield Symposia Series, pp. 233-244.
- Shirley, T. C., and S. M. Shirley. 1989. Temperature and salinity tolerances and preferences of red king crab larvae.—Marine Behavior and Physiology 16: 19-30.
- , and ———. 1990. Planktonic survival of red king crab larvae in a subarctic ecosystem, 1985-1989.—In: APPRISE - Interannual variability and fisheries recruitment. D. A. Ziemann and K. W. Fulton-Bennett, eds. The Oceanic Institute, Honolulu, Hawaii. Pp. 263-286.
- , ———, and S. D. Korn. 1990. Incubation period, molting and growth of female red king crabs: effects of temperature.—Proceedings of the International King and Tanner Crab Symposium. Alaska Sea Grant College Program Report No. 90-04, Lowell Wakefield Symposia Series, pp. 51-63.
- Sloan, N. A. 1985. Life history characteristics of fjord dwelling golden king crab *Lithodes aequispina*.—Marine Ecology Progress Series 22: 219-228.
- 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.
- Strathmann, R. R. 1987. Larval feeding.—In: Reproduction of marine invertebrates. Vol. 9. Pp. 465–550. A. C. Giese and J. S. Pearse, eds. Blackwell Scientific Publications and Boxwood Press, Palo Alto and Monterey, California.
- Vinuesa, J. H., L. Ferrari, and R. J. Lombardo. 1985. Effect of temperature and salinity on larval development of southern king crab (*Lithodes antarcticus*).—Marine Biology 85: 83–87.
- Wehrmann, I. S. 1991. How important are starvation periods in early larval development for survival of *Cragon septemspinosa* larvae?—Marine Ecology Progress Series 73: 183–190.

RECEIVED: 18 June 1996.

ACCEPTED: 29 October 1996.

Address: Juneau Center, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 11120 Glacier Highway, Juneau, Alaska 99801, U.S.A. (e-mail: fflcs@aurora.alaska.edu)

ANNOUNCEMENT

“Atlas des Crustacés marins profonds de Polynésie française—Récoltes du navire Marara (1986/1996)” has been published (1996) by the Service Mixte de Surveillance Radiologique et Biologique (SMSRB), France. Over a period of 10 years, the fishing boat *Marara* has investigated the deep-sea crustacean fauna around the polynesian islands by the use of traps set at depths ranging from 20–1,050 m. The carcinological material, mainly decapods, has been studied by carcinologists and 180 species have been inventoried, of which 71 are recognized as new taxa.

Colored photographs of 154 species—39 shrimps, 10 lobsters, 39 hermit crabs and galatheids, 65 crabs, 1 stomatopod, and 1 amphipod—are presented, with indication of depth and location of capture.

An introduction, history of deep-sea investigations in French Polynesia, and presentations of the carcinologists involved are in French, followed by 20 colored plates. Studies devoted to the deep-sea crustacean fauna of French Polynesia are listed in the bibliographic section. A station list, with English summary, is given and a map of the area is provided.

Free copies of this work are still available at the following address:

SMSRB (% J. Poupin)
B.P. 208
91311 Montlhéry Cedex
France