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LEIDEN E. J. BRILL

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A DESCRIPTION OF THE LABORATORY-REARED LARVAE OF CANCER GRACILIS DANA, 1852 (DECAPODA, BRACHYURA) ¹)

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J. R. RAYMOND ALLY

Department of Biology California State University, Long Beach, California 90801, U.S.A.²)

INTRODUCTION

Knowledge of the larval development of the nine species of *Cancer* which occur on the Pacific coast of North America is scarce. Mir (1961) described the first zoeal stage of *C. magister* Dana, *C. antennarius* Stimpson, and *C. anthonyi* Rathbun. Poole (1966) was the first to describe and figure all larval stages, except the prezoeal stage, of *C. magister*. Trask (1970) fully described and figured all larval stages, except the prezoeal stage, of *C. productus*.

The larval stages of *C. gracilis* Dana, a species of no commercial value, are presented is this paper. This work is a continuation of the study of *Cancer* larvae from the Pacific coast of North America.

MATERIALS AND METHODS

On September 17, 1971, an ovigerous *C. gracilis* was captured in San Pedro Bay, near Seal Beach, California, and transported to a temperature-controlled room at California State University, Long Beach, California. The room had simulated day and night conditions and was kept at a constant 17° C. This temperature approximated the ambient temperature of the collecting area. The egg mass of the female was removed and placed into an aerated three liter container. Sea water was obtained from Seal Beach and transported to the laboratory in 19 liter plastic carboys. The water was then filtered through number one Whatman qualitative filter paper of two thicknesses and kept in the temperature controlled room. The salinity of the water varied from 33.5 to $33.6^{0}/_{00}$.

On September 23, most of the eggs had hatched and some prezoeae were found. Twenty-six first zoeae were placed in each of twelve 226 ml plastic cups. The water in these cups was not aerated. The larvae were transferred daily, by means of a pipette, into clean cups containing new sea water. The juvenile crabs were kept in aerated 532 ml plastic containers with fine grain sand on the bottom and transferred weekly into clean receptacles containing new sea water and fine grain sand.

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²) Present address: Department of Fish and Game, Operations Research Branch, 350 Golden Shore, Long Beach, California 90802, U.S.A.

Nourishment for the zoeae was provided in the form of freshly-hatched Artemia salina (L.) nauplii. The megalopae were fed 2 to 4 day old A. salina nauplii, and the juveniles were fed adult brine shrimp obtained commercially in large frozen packages.

In order to avoid mortality due to bacterial infection, a commercial preparation of penicillin and streptomycin was used. The volume of sea water used each day was treated with 0.3 cc of the preparation per liter of sea water.

Larvae and exuviae of the various stages were preserved in a 5% solution of formalin. From 5 to 15 specimens were used to study external anatomical variation within each larval stage. Fine insect pins were used to dissect the larval appendages. Zoeal appendages were mounted in glycerin for study, and megalopal appendages were mounted in glycerin-gel. All figures were drawn with the aid of a camera lucida.

RESULTS

The larval stages of *Cancer gracilis* consist of a prezoeal stage, five zoeal stages, and a megalopal stage. Each successive stage shows a progressive increase in size and complexity. Percent survival, time of development, and duration of the larval stages and first juvenile stage are summarized in table I.

TABLE I

Survival (%), time of development (days), and duration (days) of the larval stages and first juvenile stage of *Cancer gracilis* Dana reared in the laboratory

	Zoea 1	Zoea 2	Zoea 3	Zoea 4	Zoea 5	Megalopa	Juvenile Stage 1
Survival in each stage Survival from first zoeal stage	65	84	87	92	91	48	82
to successive stages Time of development (from batching):		65	55	47	43	40	19
range		511	1017	16-21	22-25	28	42-47
mean		6.8	12.2	18.0	23.2	29.1	44.6
Duration of							
each stage:							
range	511	512	510	58	6—8	1217	
mean	6.8	7.2	7.0	6.2	7.1	14.6	

In the description, all series of armature are listed from proximal to distal. Also, due to the type of armature distribution, some of the appendages figured do not show their full armature complement.

Prezoea

The mean of the distance between the front of the head (the carapace portion between the eyes) and the middle of the posterior edge of the carapace of the prezoea (fig. 1, A) is 0.39 mm. Lateral spines on the carapace and lateral hooks on the second abdominal somite can clearly be seen through the embryonic membrane. None of the appendages is well developed. In some specimens, the antennules and antennae bear long hairy sheaths (not shown in the figure). When this situation exists, similar ornamentation is found on the telson (fig. 1, B), originating from 4 of the 6 elements projecting from each furca.



Fig. 1. Prezoea of Cancer gracilis Dana. A, lateral view; B, telson. Scale = 0.1 mm.

First Zoea

The carapace of the first zoea (fig. 2, A) has a rostral and dorsal spine, and a pair of lateral spines. These spines are found throughout the zoeal stages. The mean of the perpendicular distance between the tip of the rostral spine and the tip of the dorsal spine is 1.12 mm. There is a setule present above each lateral spine. The eyes are not stalked. The abdomen (fig. 2, B) consists of 5 somites and a bifurcated telson. The posterolateral edges of each somite extend caudally, overlapping the adjacent somite. These extensions are in the form of spines on somites 2 through 5 and increase in size with each successive zoeal stage. The second somite bears a pair of lateral hooks. A pair of setules is present on the posterodorsal border of somites 2 through 5. Each furca of the telson has 3 plumose setae on the inner margin, a smooth spine on the outer margin, and another similar spine on the dorsal side posterior to the latter one. The smooth spines of the telson are constant throughout the zoeal stages. The antennule (fig. 2, C) bears 2 long, unequal aesthetes and 3 shorter, unequal setae. The protopodite of the antenna (fig. 2, D) is drawn out as a long denticulate spine, and the shorter



Fig. 2. First Zoea of *Cancer gracilis* Dana. A, lateral view; B, ventral view of abdomen; C, antennule; D, antenna; E-1 and E-2, right and left mandibles respectively; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped. Scale = 0.1 mm.

exopodite bears 2 unequal, terminal setae. The right and left mandibles (fig. 2, E-1 and E-2, respectively) differ slightly in structure, the right one showing more denticulation. This difference is essentially constant in all zoeal stages. The twosegmented endopodite of the maxillule (fig. 2, F) has 1 naked seta on the first segment and 5 naked setae on the terminal segment. This relationship is constant throughout the zoeal stages. The armature of the basipodite is 5 and there are 7 setae on the coxopodite, some of which are plumose. Four naked setae fringe the distal border of the scaphognathite of the maxilla (fig. 2, G). The bilobed endopodite has 3 naked setae on each lobe and this is constant throughout the zoeal stages. The bilobed basipodite and coxopodite bear 5-4 and 3-3 naked setae respectively. The protopodite of the first maxilliped (fig. 2, H) has a naked setae arrangement of 2-2-3-2, which is constant through the fifth zoeal stage. The five-segmented endopodite has a formula of 2, 2, 1, 2, 5, which is constant through the third zoeal stage. The formula of the protopodite of the second maxilliped (fig. 2, I) is 1-1-1-1, and that of the three-segmented endopodite, 1, 1, 5. The latter two formulae are constant through the fifth zoeal stage. The distal segment of the two-segmented exopodite of the first and second maxillipeds bears 4 long plumose setae.

Second Zoea

The mean of the distance from rostral spine to dorsal spine of the second zoea (fig. 3, A) is 1.45 mm. This is an increase of 30% over the previous stage. Setules on the carapace have increased to a total of 6. There are 3 to 5 setules on the dorsal spine, but 4 is most common. There are 3 to 4 plumose setae on the ventrolateral margin of the carapace. The eyes are now stalked, as they are in the remaining larval stages. The antennule (fig. 3, C) bears 4 unequal aesthetes and 2 shorter, unequal setae. The armature of the basipodite of the maxillule (fig. 3, F) has increased to 7, and there is now a lateral seta on the protopodite. The setation of the exopodite of the first and second maxillipeds (fig. 3, H, I) has increased to 6. At a magnification of 150, buds representing the third maxillipeds, chelipeds, and walking legs are visible under the carapace.

Third Zoea

The mean of the distance between rostral and dorsal spines of the third zoea (fig. 4, A) is 1.87 mm. This is an increase of 67% and 29% over the first and second zoeae respectively. The carapace now bears a total of 10 setules. The dorsal spine has 6 to 8 setules, but 8 is most common. Five to 7 plumose setae fringe the ventrolateral margin of the carapace. The abdomen (fig. 4, B) has added the sixth somite, and the number of dorsal setules on each somite is now 1, 2, 2, 2, 2, 0. The telson has added a naked seta on each side of the furcal angle. The armature of the antennule (fig. 4, C) is unchanged. The antenna (fig. 4, D) bears a bud representing the developing endopodite. The armature of the basi-



Fig. 3. Second Zoea of *Cancer gracilis* Dana. A, lateral view; B, ventral view of abdomen; C, antennule; D, antenna; E-1 and E-2, right and left mandibles respectively; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped. Scale = 0.1 mm.



Fig. 4. Third Zoea of *Cancer gracilis* Dana. A, lateral view; B, ventral view of abdomen; C, antennule; D, antenna; E-1 and E-2, right and left mandibles respectively; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped. Scale = 0.1 mm.

podite of the maxillule (fig. 4, F) has increased to 8. The scaphognathite of the maxilla (fig. 4, G) has 17 to 19 plumose setae. The setae on the bilobed basipodite and coxopodite have changed to a 5-5 and 3-4 arrangement respectively, some of which are plumose. The plumose setae of the exopodite of the first and second maxillipeds (fig. 4, H, I) have increased to 8. Buds representing the third maxillipeds, chelipeds, and walking legs are visible in the zoea (fig. 4, A).

Fourth Zoea

The mean of the distance between the rostral and dorsal spines of the fourth zoea (fig. 5, A) is 2.49 mm. This is an increase of 122% and 33% over the first and third zoeal stages respectively. The setules on the carapace have increased to a total of 12. There are 10 to 12 setules on the dorsal spine and 2 at the beginning of the rostral spine. Seven to 11 plumose setae fringe the ventrolateral margin of the carapace. Pleopod buds are now present on abdominal somites 2 through 6 (fig. 5, B). The telson has added another naked seta on each side of the furcal angle. Aesthetes on the antennule (fig. 5, C) are on two tiers: 2 on the lower tier and 5 on the terminal tier. There is also a very small seta on the terminal tier. The bud on the antennule is another developing flagellum. The endopodite of the antenna (fig. 5, D) is now nearly as long as the exopodite. The armature of the basipodite of the maxillule (fig. 5, F) has increased to 12, and the coxopodite now has 8 setae. The protopodite has 1 (occasionally 2) plumose setae on the lateral border. The scaphognathite of the maxilla (fig. 5, G) is fringed with 23 to 27 plumose setae, and the setation of the bilobed basipodite is 6-5. The setae on the terminal segment of the endopodite of the first maxilliped (fig. 5, H) have increased to 6. Setation of the exopodite of the first and second maxillipeds has increased to 10. A biramous development is beginning to appear in the third maxilliped (fig. 5, A). Also, segmentation is beginning to appear in the chelipeds and first walking legs.

Fifth Zoea

The mean of the distance between the rostral and dorsal spines of the fifth zoea (fig. 6, A) is 3.30 mm. This is an increase of 195% and 33% over the first and fourth zoeal stages respectively. There are a total of 16 setules on the carapace. The dorsal spine has 11 to 15 setules, and there are still 2 setules at the beginning of the rostral spine. The number of plumose setae on the ventrolateral border of the carapace is 12 to 14. The pleopod buds on the abdomen (fig. 6, B) have increased considerably in size. There is a variation in the number of dorsal setules on three abdominal somites, and the formula is now 1 (occasionally 3), 4, 2 (occasionally 4), 2 (occasionally 4), 2, 0. The antennule (fig. 6, C) now has an armed flagellum of three tiers and a smaller, unarmed flagellum. The first tier of the armed flagellum has 6 aesthetes, the second, 7 to 9 and the third, 3 to 4. The basal segment of the antennule has 2 naked setae. The endopodite of the antennua (fig. 6, D) is now articulated and is considerably larger than the



Fig. 5. Fourth Zoea of *Cancer gracilis* Dana. A, lateral view; B, ventral view of abdomen; C, antennule; D, antenna; E-1 and E-2, right and left mandibles respectively; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped. Scale = 0.1 mm.



Fig. 6. Fifth Zoea of *Cancer gracilis* Dana. A, lateral view; B, ventral view of abdomen; C, antennule; D, antenna; E-1 and E-2, right and left mandibles respectively; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, third maxilliped. Scale = 0.1 mm.

exopodite. A palp is developing on the mandibles (fig. 6, E-1, E-2). The armature of the basipodite and coxopodite is 15 and 10 respectively. The protopodite has 2 plumose setae. The scaphognathite of the maxilla (fig. 6, G) has 33 to 36 plumose setae. The bilobed basipodite has a setal arrangement of 8-7 (occasionally 7-7), and the number of setae on the bilobed coxopodite is 4-4. The number of plumose setae on the exopodite of the first maxilliped (fig. 6, H) has increased to 11, and there is no change in the setal formula of the endopodite. The exopodite of the second maxilliped (fig. 6, I) bears 12 plumose setae. The developing endopodite of the third maxilliped (fig. 6, J) has 4 segments. The developing cheliped and walking legs (fig. 6, A) are now all segmented, and the dactylopodite is segmented from the chela.

Megalopa

The rostral and dorsal spines on the carapace of the megalopa (fig. 7, A) are relatively smaller than those of the zoeal stages, and there are no lateral spines. The mean of the distance between the tip of the rostral spine and the midposterior edge of the carapace is 2.21 mm. The number of setules on the carapace, as well as the number of plumose setae on the ventrolateral margin, has increased considerably over that of the previous stage. This ornamentation is not shown in the figure. There are 9 (occasionally 8) setae on the inflated basal segment of the antennule (fig. 7, B), most of which are plumose. This segment is followed by another bearing 4 (occasionally 3) naked setae, and a third bearing 1 naked seta. A four-segmented flagellum and an unsegmented flagellum arise from the third segment. The latter flagellum has 4 terminal and 2 sub-terminal naked setae. The former flagellum has no armature on the first segment; 12 to 14 aesthetes on the second; 9 aesthetes and 2 plumose setae on the third; 5 sub-terminal aesthetes, 1 sub-terminal naked seta, and 1 terminal plumose seta on the distal segment. The antenna (fig. 7, C) consists of 11 segments, but a ten-segmented antenna was observed. On two different specimens examined, the seventh and ninth segments were missing on one antenna. The antennal formula is 5, 2 (occasionally 3), 4 (occasionally 5), 0, 0, 4 (occasionally 3 and 5), 0, 5, 0 (occasionally 1), 4, 5. Unlike the zoeal stages, the right and left mandibles of the megalopa are similar (fig. 7, D). The mandibular palp is now three-segmented with a formula 0, 0, 8 (occasionally 7 and 9). The two-segmented endopodite of the maxillule (fig. 7, E) has 1 plumose seta on the first segment and 2 naked setae on the terminal segment. The armature of the basipodite and coxopodite is 26 and 15 (occasionally 14) respectively, and the protopodite has 2 (occasionally 3) setae. The scaphognathite of the maxilla (fig. 7, F) is fringed with 53 to 59 plumose setae and there are 4 elements on the ventral surface. The now singlelobed endopodite bears 3 to 4 (occasionally 2) plumose setae on the outer lateral margin of the basal portion, and the terminal portion is either armed with a very small naked seta, or unarmed. The armature of the bilobed basipodite is 9-9, occasionally 8-9 and 9-8, and rarely 8-8. The setal formula of the bilobed coxo-

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Fig. 7. Megalopa of *Cancer gracilis* Dana. A, dorsal view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxillal. Scale = 0.1 mm.



Fig. 8. Megalopa of *Cancer gracilis* Dana. A, first maxilliped; B, second maxilliped; C, third maxilliped; D, ventral view of abdomen. Scale = 0.1 mm.

podite varies considerably. The most frequent combination is 2-7, followed by 3-7, 4-6, 3-6, 4-7, and 2-8. The protopodite of the first maxilliped (fig. 8, A) is bilobed. The armature of the smaller lobe is 14 and that of the larger lobe, 20 to 23. The well developed epipodite bears 2 (occasionally 3) naked setae on the outer margin of the upper triangular-shaped portion and 8 to 11 naked setae on the outer margin of the lower ribbon-like portion. The endopodite is a single flattened process bearing 1 naked seta on the inner side towards the base and generally 3 naked setae on the truncate distal end. One specimen had an armature of 6 on the truncate distal end and another had 4. The two-segmented exopodite bears 2 to 4 plumose setae on the outer distal portion of the first segment and 5 plumose setae on the terminal end of the following segment. The protopodite of the second maxilliped (fig. 8, B) bears 1 to 2 naked setae, and there are 4 (occasionally 3) naked setae at the distal end of the epipodite. The formula of the five-segmented endopodite is 1, 1 (occasionally 0), 1, 6 to 7 (occasionally 5), and 9 (occasionally 8). The two-segmented exopodite has 1 (occasionally 2) elements on the proximal segment and 5 plumose setae on the terminal portion of the distal segment. The protopodite of the third maxilliped (fig. 8, C) has an armature of 16 to 20. There are 3 to 4 plumose setae near the proximal end of the long epipodite, and distal to these are 12 to 15 naked setae. The formula of the five-segmented endopodite is 23 to 27, 13 (occasionally 12), 10 to 12, 10 to 13, and 9. The two-segmented exopodite bears 2 to 4 elements on the first segment and 5 terminal plumose setae on the distal segment. There are numerous setules (not shown in the fig.) on the chelipeds and walking legs (figs. 7, A). The chelipeds possess a hook (not shown in the fig.) on the ventral side of the basi-ischiopodite. The dactylopodite of the fourth walking leg has 3 long setae. The number of setules (not shown in the fig.) on the dorsal side of the abdomen (fig. 8, D) has increased over that of the previous stage. The pleopods of somites 2 through 5 of the abdomen are biramous. The protopodites bear no armature. The exopodites of the first two pairs have 17 to 19 plumose setae, those of the third pair have 17 to 18, and those of the fourth pair possess 14 to 16. All endopodites have 3 (occasionally 2) hooks at the distal end. The two-segmented uropods bear 1 plumose seta on the first segment and 7 to 9 plumose setae on the distal segment. The telson is now a flat plate with a rounded posterior margin.

DISCUSSION

Although I observed a prezoeal stage in C. gracilis, I was not able to ascertain whether this is a "normal" stage in its life history. Of those individuals which hatched, I observed approximately 5% as prezoeae and the remaining percentage as first zoeae. If the prezoeae is a "normal" stage in this species, it is of very short duration.

A prezoeal stage was reported as a "normal" stage in *C. amoenus* Herbst (= *C. irroratus* Say) (Conolly, 1923), *C. pagurus* Linnaeus (Williamson, 1911; Lebour, 1928), and *C. magister* Dana (MacKay, 1942). However, Mir (1961) was of the

opinion that the prezoeal stage in C. magister, C. antennarius, and C. anthonyi was an imperfect stage. Poole (1966) believed that the prezoea previously reported in C. magister was merely a prematurely ruptured egg.

Buchanan & Millemann (1969) established that the prezoea previously reported in *C. magister* was a "normal" stage in its larval development, and that it was of very short duration. In view of this, it seems probable that the prezoea which I observed in *C. gracilis* is a "normal" stage in its life history.

Not all prezoeae examined possessed the hairy sheaths of the antennules, antennae, and telson. It may be that this ornamentation is lost in some even before the embryonic cuticle is shed.

The two most critical stages in the larval development of *C. gracilis* are the first zoeal stage and the megalopal stage (table I). The high mortality in the first zoeal stage might be due to an initial critical feeding period. There may be a very short period of time, after molting into the first zoeal stage, when the larvae must find food or die. The high mortality in the megalopal stage might be due to the inability of many megalopae to free themselves completely from the fifth zoeal exoskeleton.

Thirteen percent of the individuals died in molting from the fifth zoeal stage to the megalopa. This percentage, however, is biased because I teased the fifth zoeal exoskeleton off of 14 megalopa, which could not free themselves from it. Nine of the 14 later died in the megalopal stage. Therefore, without interference the percentage might have been approximately 35. Seven percent of the individuals died in molting from the megalopa to the first juvenile stage. Sixteen percent of the initial number of individuals reached the second juvenile stage. Only one individual had reached the third juvenile stage when the study was ended.

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résumé

Les larves du crabe *Cancer gracilis* Dana ont été élevées en laboratoire à partir des œufs d'une femelle ovigère capturée dans la baie de San Pedro, Californie. Les stades larvaires comprennent un stade prézoé, cinq stades zoé, et un stade mégalope. Dans l'expérience, les larves ont été soumises à une température de 17° C et à des salinités variant de 33,5 à $33,6^{0}/00$, et le jour et la nuit ont été simulés. Il s'est écoulé en moyenne 29 jours de l'éclosion des œufs jusqu'au stade mégalope. Tous les stades larvaires sont décrits et figurés.

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