The Larval Development of the Crab, Cyclograpsus cinereus Dana, under Laboratory Conditions¹

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EARLY DESCRIPTIONS of larvae of the Grapsidae, based largely on material from the plankton and frequently limited to the first zoeal stage, suggested considerable uniformity in the morphological characteristics of larvae of this group of crabs (Hyman, 1924). Subsequent descriptions, based on plankton material as well as on material obtained from rearing the larvae in the laboratory, have served to point out certain differences which do exist in the larvae of this group (Aikawa, 1929; Hart, 1935). To date, however, a very limited number of larvae of crabs belonging to the family Grapsidae have been described.

Within the subfamily Sesarminae larvae of two species of the genus Sesarma have been described from rearing under laboratory conditions (Costlow and Bookhout, 1960, 1962). These two species, S. cinereum and S. reticulatum, while relatively common along the east coast of North America and even extending as far as Venezuela, are not known from the west coast of North or South America.

On the west coast of Chile, crabs of the subfamily Sesarminae are limited to two species of *Cyclograpsus*: *C. cinereus* Dana and *C. punctatus* Milne Edwards (Garth, 1957). The larvae of these species have not been described, either from rearing or from the plankton, and nothing is known about the effect of environmental factors on the development of the larval stages.

The present study has had two main objectives: one, to rear the larvae of *Cyclograpsus cinereus* Dana and provide a description of all developmental stages; and two, to determine if salinity and temperature affect the survival and duration of the larval stages.

METHODS

Ovigerous Cyclograpsus cinereus females were obtained in the vicinity of the Marine Biological Station, Montemar, University of Chile, and flown by air to the Duke University Marine Laboratory, Beaufort, North Carolina. The crabs were transported in sea water, salinity 34.4 ppt, and extreme temperature changes were avoided by packing them in thermos containers. On arrival at Beaufort, the females were retained at 35 ppt, 20°C. At the time of hatching the larvae were removed, segregated into series of 50 or 100 larvae, and maintained at the temperature-salinity combinations shown in Table 1. Within each temperature-salinity series the larvae were further subdivided, 10 zoeae per bowl, and were fed Artemia nauplii and Arbacia eggs. Each day the larvae were moved to freshly filtered sea water in clean bowls and fresh food was added. At this time the bowls were examined for exuviae, the dead larvae were removed, and the number was recorded. When the megalops stage was reached the larvae were maintained individually in plastic compartmented boxes and fed only Artemia nauplii.

From mass cultures the larvae and exuviae were preserved in 5% formalin at known stages of development. Drawings were made to scale with the aid of a camera lucida and the chromatophore pattern was determined from living larvae.

RESULTS

Larval Stages

There are five zoeal stages and one megalops stage in the complete development of *C. cine*reus. The major characteristics of each larval stage are as follows:

FIRST ZOEA (Fig. 1, A-I): The cephalothorax has a gibbose dorsal spine which curves caudally (Fig. 1, A). The rostral spine is short and the carapace is devoid of lateral spines.

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TABLE 1

Comparison of Original Number of Larvae of Cyclograpsus cinereus, Maintained at Different Combinations of Salinity and Temperature, Survival to Megalops and Crab Stage, and Time Required for Development Through All Larval Stages

SALINITY (ppt)	TEMP. °C	ORIGINAL NUMBER	PERCENT TO MEGALOPS	PERCENT TO CRAB	TIME OF DEVELOPMENT (DAYS)		
					HATCH TO MEGALOPS	MEGALOPS DURATION	HATCH TO CRAB
30	20	100	70.0	45.0	24–33 25.7	15-31 20.3	40-57 45. 7
35	20	100	61.0	38.0	25–29 26.0	15–29 22.0	40-56 47.7
30	25	50	30.0	2.0	19–24 20. 7	13	30
35	25	50	44.0	10.0	1821 19.7	14–16 15.0	33-35 34.2
35	30	50	0.0	0.0	-		

^{*} Average figures given in bold type.

The eyes are not stalked. The ventrolateral edge of the carapace bears 8 small spines. The abdomen (Fig. 1, B) consists of 5 segments plus the telson. The second abdominal segment has a short lateral hook directed anteriorly. The telson formula is 3 plus 3 spines and the furcal rami are denticulate.

The antennule (Fig. 1, C) bears 2 long aesthetes and 2 shorter, unequal setae. The antennal peduncle (Fig. 1, D) is unsegmented and terminates as a large, denticulate spine. The exopodite is shorter and terminates as 2 unequal spines. The bisegmented endopodite of the maxillule (Fig. 1, F) bears 4 terminal setae, 1 subterminal seta on the second segment and a single seta on the first segment. The basipodite has 5 terminal plumose spines and the coxopodite bears 4 terminal and 1 subterminal setae. Four unequal soft, plumose setae fringe the distal border of the scaphognathite of the maxilla (Fig. 1, G), and the apical tip terminates as 1 plumose hair. The bilobate endopodite bears 2 plumose setae on each lobe and its margins are covered with numerous fine hairs. The bilobed coxopodite and basipodite bear 5-4 and 2-4 plumose setae respectively. The basopodites and exopodites of maxillipeds one and two are as shown in Figure 1, H and I. The 5-segmented endopodite of the first maxilliped has a setation of 2,1,1,2,5 (Fig. 1, H). The 3-segmented endopodite of the second maxilliped (Fig. 1, I) has a setation of 0,1,5.

The pattern of chromatophores is consistent for all five zoeal stages. The location of melanophores in the carapace is as follows: (a) 1, median and dorsal to eyes; (b) 1 pair, ventrolateral border; (c) 1 pair, median-lateral, posterior margin. Melanophores of the zoeal appendages are as follows: 1 at basis of the antenna; 1 in mandible; 1 in labrum; and 1 in basipodite of first maxilliped. In the abdominal segments 1 melanophore is found dorsal to the gut in segments one through four, 1 in the midventral region of segments two through five (in first and second zoea), and through six (in third to fifth zoea), and 1 pair in the posterior-lateral corner of segment five.

SECOND ZOEA (Fig. 2, A-I): The eyes are stalked, the dorsal spine is no longer gibbose, and the lateral spines are present (Fig. 2, A). The ventrolateral borders of the carapace bear 6 small spines plus 6 setae and there are 2 spines on the posterior, middorsal margin. Antennule now bears 4 aesthetes, approximately equal in length (Fig. 2, C). Changes in setation of the appendages are limited to the following: basipodite of maxillule has 5 spines

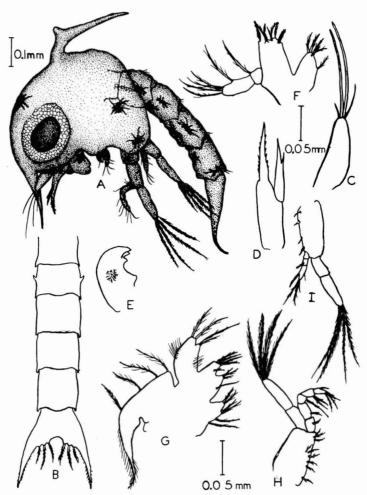


Fig. 1. Side view (A) of first zoeal stage of Cyclograpsus cinereus Dana. B, Ventral view of abdomen; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped.

plus 2 setae and a spine projects from the protopodite (Fig. 2, F). Scaphognathite of maxilla (Fig. 2, G) has 5 proximal and 3 distal plumose setae. Setation of the exopodite of the first and second maxillipeds has increased to 6 (Fig. 2, H and I). Setation of the endopodite of the first maxilliped is now 2,2,1,2,5, and of the second maxilliped, 0,1,6.

THIRD ZOEA (Fig. 3, A-I): Small spines on the ventrolateral borders of the carapace have decreased to 5 and setae increased to 10 (Fig. 3, A). The sixth abdominal segment is added and the number of telson spines has increased to 8 on the inner surface (Fig. 3, B). Changes in setation of the appendages are limited to the

following: 1 small spine is added on the lateral margin of basopodite of maxillule (Fig. 3, F); scaphognathite of maxilla has 8 proximal and 6 distal plumose setae and each lobe of basopodite bears 5 setae (Fig. 3, G); 1 seta has been added to lateral margin of coxopodite of maxilla (Fig. 3, G). Setation of exopodite of first and second maxillipeds has increased to 8 (Fig. 3, H and I). Setation of endopodite of first maxilliped is now 2,2,2,2,5.

FOURTH ZOEA (Fig. 4, A-I): Small spines on ventrolateral borders of carapace decreased to 4 and setae increased to 14. Rudiments of pereiopods present under carapace (Fig. 4, A). Dorsal surface of first abdominal segment now

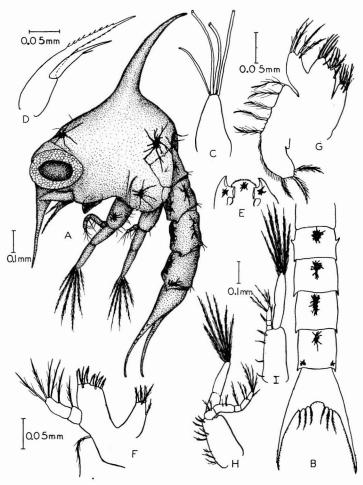


Fig. 2. Side view of (A) of second zoeal stage of Cyclograpsus cinereus Dana. B, Ventral view of abdomen; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped.

bears 5 spines and pleopod buds are present on segments two through six (Fig. 4, B). Setation of the appendages is as follows: antennule (Fig. 4, C) bears 5 terminal and 1 subterminal aesthetes; the unsegmented endopodite bud of the antenna (Fig. 4, D) is approximately half the length of the antennal spine. Setation of basopodite of maxillule has increased to 11 (Fig. 4, F). Scaphognathite of maxilla (Fig. 4, G) has 16 proximal and 9 distal plumose setae and setation of coxopodite has increased to 9. Setation of exopodite of first and second maxillipeds (Fig. 4, H-I) has increased to 10. Setation of endopodite of first maxilliped is now 2,2,2,2,6 (Fig. 4, I).

FIFTH ZOEA (Fig. 5, A-I): Minute spines on ventrolateral borders of carapace increased to approximately 10, and 18 setae are present (Fig. 5, A). Rudiments of unsegmented pereiopods now visible under carapace. Pleopods of abdominal segments two through six partially segmented (Fig. 5, B). Changes in setation of the appendages are as follows: swollen basal region of antennule (Fig. 5, C) bears 2 small, plumose setae, endopodite bud is present and subterminal aesthetes have increased to 4. Endopodite of antenna (Fig. 5, D) partially segmented and longer than exopodite. Setation of basopodite of maxillule (Fig. 5, F) increased to 13 and coxopodite now bears 9 setae.

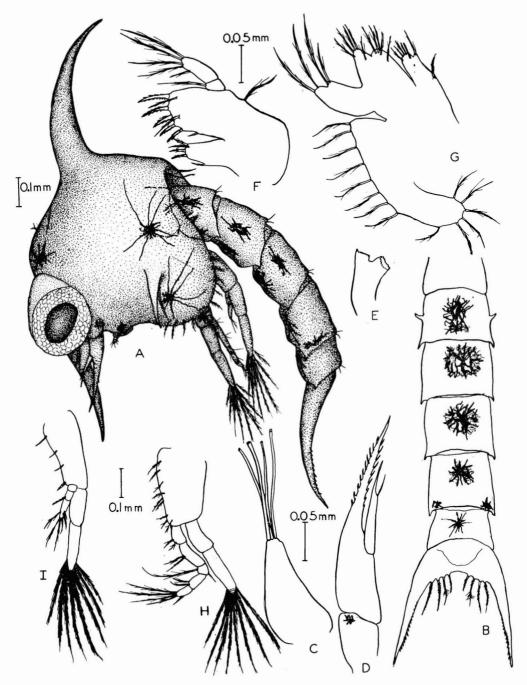


Fig. 3. Side view (A) of third zoeal stage of Cyclograpsus cinereus Dana. B, Ventral view of abdomen; C, antennule; D, antenna; E, mandible; F_i maxillule; G_i maxilla; H_i first maxilliped; I_i second maxilliped.

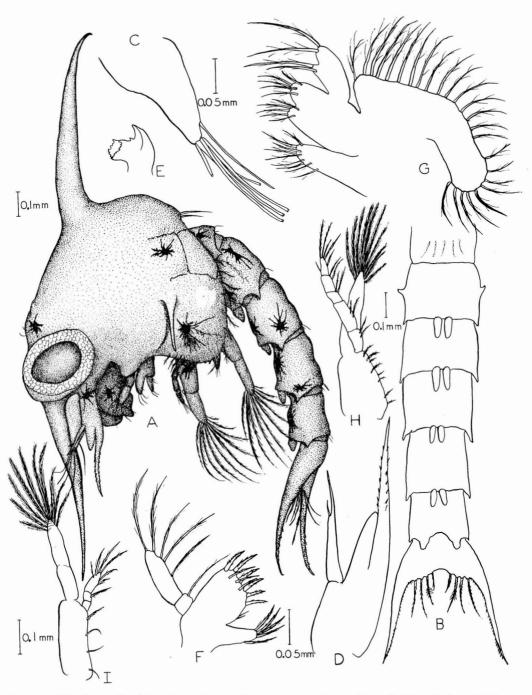


Fig. 4. Side view (A) of fourth zoeal stage of Cyclograpsus cinereus Dana. B, Ventral view of abdomen; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped.

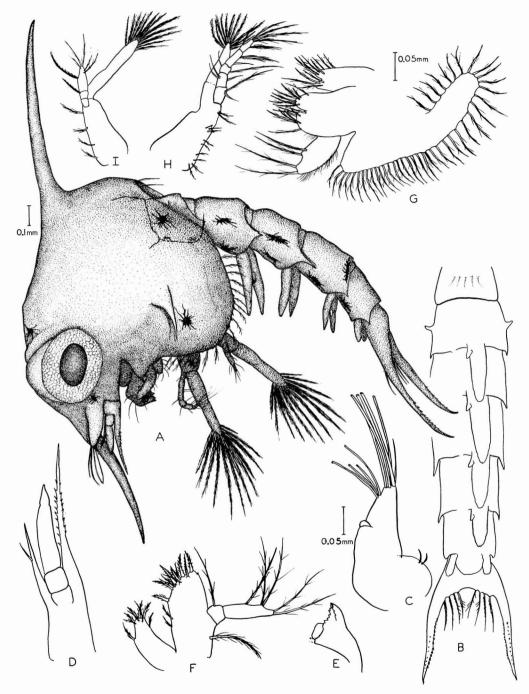


Fig. 5. Side view (A) of fifth zoeal stage of Cyclograpsus cinereus Dana. B, Ventral view of abdomen; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped.

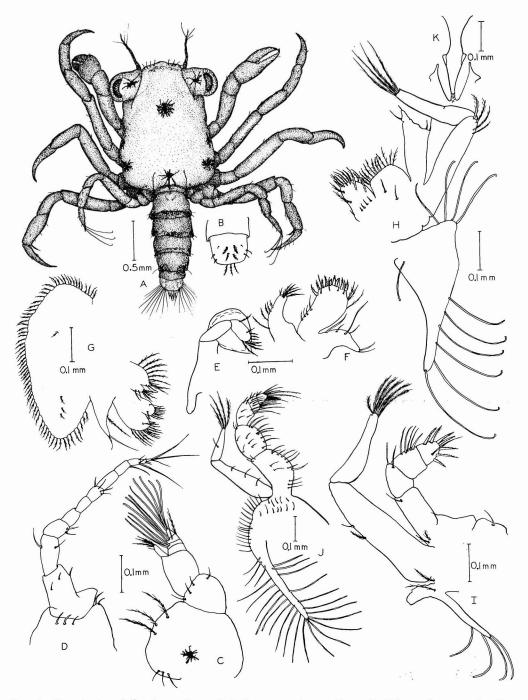


Fig. 6. Dorsal view (A) of megalops of Cyclograpsus cinereus Dana. B, Telson; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, third maxilliped; K, pleopods.

Scaphognathite of maxilla (Fig. 5, *G*) has approximately 30 proximal and 12 distal plumose setae, setation of basopodite increased to approximately 16, and the coxopodite now bears 11 setae. Setation of exopodite of first and second maxillipeds (Fig. 5, *H–I*) has increased to 12. Setation of endopodite of first maxilliped is now 2,3,2,2,6.

MEGALOPS (Fig. 6, A-K): Cephalothorax without rostral spines and provided with hairs at lateral edges (Fig. 6, A). Abdomen 6-segmented, with telson (Fig. 6, B) bearing 4 dorsal and 3 terminal plumose setae. Antennule (Fig. 6, C) with 2 flagella on second segment. Unsegmented flagellum with 3 terminal setae and 1 subterminal seta. The 4-segmented flagellum bears 3 aesthetes on the second segment, 4 aesthetes plus 1 seta on the third segment, and 5 aesthetes on the terminal segment. Antenna (Fig. 6, D) with 11 segments and setation as shown in Figure 6, D. Mandible (Fig. 6, E) with 2-segmented palp bearing 9 plumose setae on terminal segment. Unsegmented endopodite of maxillule (Fig. 6, F) with 2 terminal and 4 lateral setae. Basopodite with approximately 21 spines and setae and the coxopodite with 6 terminal and 5 lateral setae. Scaphognathite of maxilla (Fig. 6, G) fringed with approximately

70 plumose setae (Fig. 6, G). Unsegmented endopodite bearing 2 unequal terminal setae and 1 subterminal plumose seta. Lobes of basopodite bearing 13 and 11 plumose setae, respectively, and lobes of coxopodite with 6 and 12 setae. The first, second, and third maxillipeds are as shown in Figure 6, H, I, and J. Setation of exopodites of pleopods of abdominal segments two to five varies from 17 to 20. Endopodites of all pleopods have 3 median hooks (Fig. 6, K). Uropods bisegmented with 1 seta on first segment and 10 setae on second segment.

Chromatophore pattern of carapace as follows: one, dorsomedian surface, one on each median-lateral border, a pair on ventral surface of rostrum, joined at the median line, and one at each posteriolateral corner. Chromatophore pattern of appendages: one on each eyestalk, one on basopodite of antennule, one on basopodite of cheliped, mandibles, and labrum. Within the abdominal segments melanophores are located as follows: one in first segment, dorsal to gut, extending into cephalothorax; one at posterioventral margin of segments two through five, the chromatophore of segment five extending into proximal region of segment six.

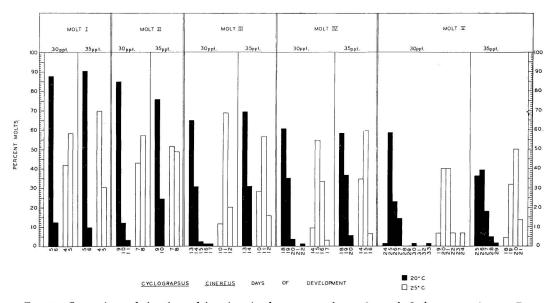


Fig. 7. Comparison of the time of larval molts for zoeae and megalops of Cyclograpsus cinereus Dana reared in the laboratory at different salinities and temperatures. Black, 20°C; white, 25°C.

Larval Development

The frequency of molting during the five zoeal and one megalops stages is shown in Figure 7. The first and second molts of most larvae were confined to two days at all four salinity-temperature combinations. By the time of the third molt, however, the uniformity was not as apparent and the later molts were spread over three, four, and five days. Figure 8 shows the time required for development of the five zoeal stages and megalops of *C. cinereus* when maintained at combinations of two salinities and two temperatures. At 20°C, the duration of all larval stages is longer than that observed

for larvae reared at 25°C. This difference is more pronounced as development continues and is quite apparent for the megalops stage. Within the two salinities used, 30 and 35 ppt, there is no apparent difference in the time required for development of the larval stages (Fig. 8). The average time for total development to the first crab (Fig. 8) at 25°C was 30 days at 30 ppt and 34.2 days at 35 ppt. At 20°C and 30 ppt, 45.7 days were required and at the same temperature and 35 ppt comparable development required 47.7 days.

Mortality of the individual larval stages is shown in Figure 9. Although larvae were main-

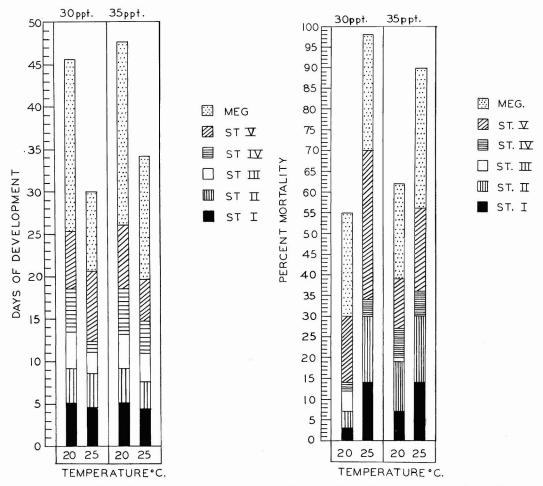


Fig. 8. Comparison of the duration of five zoeal stages and megalops of *Cyclograpsus cinereus* Dana reared in the laboratory at different salinities and temperatures.

Fig. 9. Comparison of the mortality of the five zoeal stages and megalops stage of *Cyclograpsus cinereus* Dana reared in the laboratory at different salinities and temperatures.

tained at 30 and 35 ppt, 30°C, all died within the first two days following hatching and are not included in Figure 9. Mortality of most larval stages was higher at 25°C than at 20°C. Mortality of any one zoeal stage at 20°C does not exceed 16%, while at 25°C mortality within one stage (Stage V) was as high as 36%. At 25°C, there was a tendency for the mortality to be higher in the later larval stages than in the early zoeal stages. Survival to the crab ranged from 2 to 10% at 25°C and from 38 to 45% at 20°C.

DISCUSSION

Larval Stages

A comparison of the larvae among species of the same subfamily as Cyclograpsus cinereus is limited to descriptions of Sesarma cinereum (Hyman, 1924; Costlow and Bookhout, 1960), Sesarma reticulatum (Hyman, 1924; Costlow and Bookhout, 1962) and Sesarma picta (Aikawa, 1937). The number of zoeal stages varies considerably within those species of Sesarminae which have been described. C. cinereus has five zoeal stages, S. cinereum has four zoea (Costlow and Bookhout, 1960) and S. reticulatum has three zoeal stages (Costlow and Bookhout, 1962). Aikawa (1937), while describing the first stage zoea of S. picta from the plankton, does not indicate the total number of larval stages of this species. The first zoea of C. cinereus is quite distinctive in that the dorsal spine is gibbose. In all subsequent zoeal stages, when the dorsal spine is straight only C. cinereus has lateral spines. All the larval stages of C. cinereus may be further differentiated from zoeae of the three species of Sesarma by the absence of a knob on each lateral surface of the third abdominal segment of larvae of C. cinereus.

Among the Chilean species of the family Grapsidae the larvae of only one, *Grapsus grapsus* L., have been described to date (Aikawa, 1937). Only the first zoea was described and may be differentiated from the first zoeal stage of *C. cinereus* by the presence of the lateral knob on the third abdominal segment of *G. grapsus* as well as by the gibbose dorsal spine of *C. cinereus*.

The megalops of C. cinereus differs from the

megalops of S. cinereum and S. reticulatum in several respects. The main differences can be observed in the rostrum, telson, antennule, and second maxilliped. The rostrum of C. cinereus megalops is not depressed as in S. cinereum (Costlow and Bookhout, 1960), and does not have a rostral spine as in S. reticulatum (Costlow and Bookhout, 1962). The telson of C. cinereus bears only 3 setae on the distal margin, while the telsons of S. cinereum and S. reticulatum bear 8 setae and 6 setae, respectively, plus lateral spines. In C. cinereus the unsegmented flagellum of the antennule is present, while in S. cinereum and S. reticulatum the unsegmented flagellum is absent and replaced by a single seta. The epipodite of the second maxilliped is present in the megalops of C. cinereus but absent in S. cinereum and in S. reticulatum.

Of all the other megalops of the family Grapsidae which have been described to date, none are found in Chilean waters. However, it should be noted that the megalops of *C. cinereus* bears a greater resemblance to megalops of *Hemigrapsus nudus* and *H. oregonesis*, which belong to the subfamily Varuninae and were described from the Pacific coast of Canada by Hart (1935), than to megalops of the subfamily Sesarminae.

A more detailed comparison of the morphology of larvae of *C. cinereus* with larvae of other closely related forms in Chilean waters must await additional descriptions.

Larval Development

The adults of C. cinereus are normally confined to the area from Ancon, Peru to Calbuco, Chile on the western coast of South America (Garth, 1957). One extra limital locality, Panama, has also been recorded (Rathbun, 1910, 1918). The habitat of the adults is in the upper level of the intertidal region, where they live under stones in the coarse sand. Ovigerous females have been observed in the Montemar region throughout the year with the exception of February. The principal spawning period, however, appears to be from July through November, when more than 60% of the population is ovigerous. During this period the water temperature increases from 12°C to 14°C. The salinity of the water in which larval development occurs is quite stable, ranging

from 34.1 ppt to 34.5 ppt (Antezana, Fagetti, and Lopez, 1965).

In the experimental conditions of the laboratory, duration of the five zoeal stages and one megalops stage appears to be relatively unaffected by the limited range of salinity used. The larvae did develop to the crab faster at 25°C than at 20°C, as would have been expected. Survival, however, was consistently higher at 20°C than at 25°C or at 30°C. The larval development of certain other species of Brachyura, normally considered to be estuarine, has been shown to be directly affected by salinity (Costlow and Bookhout, 1962; Costlow, Bookout, and Monroe, 1960, 1966). The results of the present study, however, suggest that the development of larvae of C. cinereus is not strongly influenced by the relatively small salinity fluctuations to which the larvae would be subjected during their planktonic existence in the waters off the western coast of Chile and Peru.

SUMMARY AND CONCLUSIONS

The larval stages of *Cyclograpsus cinereus* Dana have been reared in the laboratory from hatching to the first-stage crab. The larvae were maintained in combinations of three temperatures, 20°C, 25°C, and 30°C, and two salinities, 30 ppt and 35 ppt, and were fed recently hatched *Artemia* nauplii and fertilized *Arbacia* eggs.

There are five zoeal stages and one megalops under laboratory conditions. The larvae, as well as the setation of the functional appendages, have been described and figured. Descriptions of larvae of closely related species from Chilean waters are not available, but the larvae of *C. cinereus* Dana can be differentiated from the other grapsid larvae described to date.

Approximately 46 days were required for development to the crab at 20°C. At 25°C, development was completed in 30 to 34 days.

Larvae completed development to the first crab in salinity-temperature combinations other than 35 ppt, 30°C. A higher percentage of the larvae survived at 20°C than at 25°C. Survival at 30 ppt and 35 ppt was simliar, suggesting that development under natural conditions is not affected by minor fluctuations in salinity.

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