The Larval Development of the Sand Crab *Emerita rathbunae* Schmitt (Decapoda, Hippidae)[1]

MARGARET D. KNIGHT

TWO SPECIES of the sand crab *Emerita* have been found on the western coasts of North and South America. *Emerita analoga* (Stimpson) has been recorded from Vancouver Island, British Columbia (Butler, 1959) to Magdalena Bay, Baja California, and from Salavery, Peru to Eden Harbor, Territory of Aysen, Chile (Haig, 1955). Dr. Ian Efford (personal communication of unpublished observations) has found that the northern limit of the species may be Kodiak Island, Alaska, and that the southern limit of its range in South America is the Strait of Magellan. *E. rathbunae* Schmitt has been found from La Paz, Baja California to Capon, Peru (Schmitt, 1935). Specimens of *E. rathbunae* have also been collected at San Francisquito Bay, on the east coast of Baja California above La Paz (Steinbeck and Rickets, 1941).

The larvae of *Emerita analoga* were described by Johnson and Lewis (1942). The first zoea was obtained from eggs hatched in the laboratory and one individual molted to the second stage. Later stages were described from preserved plankton samples. Larvae of the species have subsequently been cultured from egg to megalopa by Dr. Ian Efford (personal communication). During the present study, larvae of the tropical species *Emerita rathbunae* were cultured in the laboratory and compared with specimens from the plankton to provide a detailed description of the sequence of larval development and a means of differentiating the larvae from those of the amphi-tropical species *E. analoga.*

The larvae of three other species of *Emerita* have been investigated. Menon (1933) obtained five zoeal stages of *E. emerita* (L.) from the plankton, the larvae of *E. talpoida* (Say) have been described both from laboratory cultures (Rees, 1959) and from the plankton (Smith, 1877), and larvae of *E. holthuisi* Sankolli have been studied in the laboratory by Sankolli (1965).

METHODS

An ovigerous female of *Emerita rathbunae* was collected from a sandy beach near La Playa, Mazatlan, Mexico, on 20 September 1963 during a cruise in the Gulf of California aboard R/V "Alexander Agassiz" of the Scripps Institution of Oceanography. The female was held aboard ship in a 3-gallon aquarium. Hatching of the eggs began 12 hours after capture. The larvae were maintained in groups of 10–25 in 4-inch glass finger bowls of 1200 cc capacity or in plastic containers of 400 cc capacity. They were transferred daily to fresh sea water and fed newly hatched nauplii of *Artemia salina* (L.). All larvae molted once during the six days' culture period aboard ship. In addition, one second zoea of the species was sorted from a plankton tow taken earlier near shore below Cape Corrientes, Mexico (19° 22′ N, 105° 03′ W), and was maintained in isolated culture aboard ship for 11 days. A surface temperature of 29.6° C and salinity of 33.9‰ were recorded for the water from which the larva was taken. The salinity of water used for cultures was 33.8–33.9‰. As the ship returned north from the collecting area, the temperature of the water held in the cultures dropped from 29° to 23° C, subjecting the larvae to considerable cooling during the early zoeal stages.

At the conclusion of the cruise, the approximately 100 larvae hatched aboard ship (then in stages II and III), and the single larva taken from the plankton were transferred to the laboratory and isolated either in compartmented plastic trays holding 50 cc per compartment, or in plastic boxes of 400 cc capacity. They were transferred daily to sea water filtered through

[1] Contribution from Scripps Institution of Oceanography, University of California, San Diego. Manuscript received January 18, 1966.

glass wool, and fed newly hatched *Artemia* nauplii. The laboratory cultures were maintained at room temperature which, because of seasonal cooling, decreased gradually from 22° to 19° C, with daily fluctuations of 1° C or less. The salinity range during the culture period was 33.5–33.8‰. The larvae were kept under natural illumination but away from direct sunlight.

Both aboard ship and in the laboratory, all exuviae and some specimens of each developmental stage were removed and preserved in 5% formaldehyde buffered with hexamethylene tetramine. The casts were transferred to glycerine for study. The cultures, the preserved specimens, and the exuviae were maintained in such a way that the individual history of each larva could be followed. In the course of the study, 328 exuviae and 50 specimens of reared larvae were examined and dissected.

In order to compare zoeal stages occurring naturally in the plankton with those obtained in the laboratory, 143 zooplankton samples (taken in August–September and November–December in the area between Cape San Lucas and Cape Corrientes, north into the Gulf of California to Tiburon Island, and along the west coast of Baja California north to Magdalena Bay) were examined. The majority of samples were taken with a 1-meter net towed obliquely from 140 m to the surface, filtering approximately 500 m^3, during cruises 5612 (SIO Ref. 61-22, 1961), 6108 (SIO Ref. 62-16, 1962), 6208-9, Azul II and El Golfo (Snyder and Fleminger, 1965). A total of 150 specimens were obtained for comparison with cultured larvae. In addition, 70 larvae of *Emerita analoga* were sorted from zooplankton samples taken off Point Conception, on cruises 32 (SIO Ref. 52-1, 1952*a*) and 33 (SIO Ref. 52-7, 1952*b*) and off the Coronado Islands, for detailed comparison of the two species.

Larvae were dissected in glycerine. Drawings of whole specimens and appendages were prepared with the aid of a camera lucida. Young stages were stained with lignin pink to facilitate dissection and study.

RESULTS

The cultured larvae molted 7, 8, or 9 times before metamorphosis to megalopa, with the majority passing through 8 zoeal stages. The stages became progressively longer and the duration of the last stage was twice that of the preceding one (Table 1). Of the larvae cultured 42% completed zoeal development and molted successfully to megalopa. The highest mortality (20%) occurred in the terminal stage.

Within stages I, II, and III morphological development was similar for all individuals. In subsequent stages, slight variation was found among individuals that completed development in seven zoeal molts, but larvae passing through eight or nine stages showed considerable individual variation in relative growth and setation of appendages, so that the number of stages through which an individual had progressed could be positively ascertained, beyond stage IV, only by a study of its molting history. Despite this variability, the order of developmental events was similar for all larvae. The degree of growth attained with each molt beyond stage III decreased with an increase in the number of zoeal stages in the larval period, but the terminal zoeas were alike in development of appendages (addition of pleopods, growth of thoracic appendages and flagellum of second antenna, etc.) and differed mainly in details of setation and size. No larvae intermediate between the terminal zoea and megalopa were observed.

The variation among the cultured larvae in number of zoeal stages, and in morphology of individuals with similar molting histories, prompted detailed examination of specimens from preserved plankton samples. The ratios of carapace length to rostrum length (Table 2), together with study of appendages, were used for identification of planktonic specimens. The stage of development was determined by examination of the natatory setation of the first and second maxillipeds and of relative change in other appendages. The cultured larvae, hatched with four natatory setae on the exopodites of the first and second maxillipeds, added two setae with each molt through stage III. Either one or two setae were added with each successive molt. Rees (1959:368) and Sankolli (1965:39) found similar patterns of progressive increase in setation in cultured larvae of *E. talpoida* and *E. holthuisi*. Planktonic larvae of *E. rathbunae*, with rare exceptions, had only

TABLE 1

DURATION AND NUMBER OF ZOEAL STAGES FOR LARVAE COMPLETING THE MOLT TO MEGALOPA
(Means given for isolated cultures only)

NO. OF ZOEAL STAGES	NO. OF LARVAE		DAYS IN STAGE I	II	III	IV	V	VI	VII	VIII	IX
Cultured larvae											
7	4	mean	–	–	–	5.3	9.3	11.5	31.8		
		range	5	5–6	4–6	5–6	8–10	10–13	22–43		
8	22	mean	–	–	5.3	6.5	9.0	8.9	12.4	30.7	
		range	5	5–6	4–6	5–8	7–11	7–12	11–16	22–43	
9	3	mean	–	–	–	7	8	9.7	9.7	13.3	29.3
		range	5	5–6	4–6	7	7–9	8–12	9–10	11–16	27–31
Planktonic larva											
8					3	3	7	8	14	?30	
Duration megalopa stage for 6 individuals:			mean 12.5 days								
			range 10–13 days								

an even number of setae on the exopodites of the maxillipeds. This setation, therefore, appeared to be a reliable indication of the number of molts through which an individual had progressed.

In samples examined, 67% of the planktonic larvae of *E. rathbunae* apparently would have molted to megalopa after six zoeal stages, 33% after seven zoeal molts. This represents, on the average, an abbreviation of the zoeal development observed in the laboratory-reared animals. Comparatively few differences were observed between individuals in comparable zoeal stages.

There were no detectable morphological differences between cultured and planktonic larvae within stages I, II, and III. In intermediate instars IV–VI, a detailed comparison of the larval cycle of seven zoeal stages, common to both cultured and planktonic forms, showed that cultured larvae were less advanced in growth and setation of some appendages than were planktonic larvae in equivalent stages. The terminal zoeas again were similar. The cultured larvae were smaller than planktonic larvae at comparable stages of development beyond stage I (Fig. A), but the distinctive proportions of the carapace and its rostral and lateral spines were consistent in both cultured and planktonic forms throughout zoeal development.

The second zoea of *E. rathbunae*, sorted from living plankton, was cultured for 7 of the 11 days aboard ship under conditions comparable with its natural environment. During this period it molted three times, following exactly the pattern of growth and setation observed in planktonic specimens preserved from the same area. The larva was transferred to the laboratory in stage V and died in stage VIII, before the molt to megalopa (indicated by segmentation of postlarval appendages visible beneath the cuticle). In stages V–VII, the rate of development of appendages was retarded in relation to the regular progressive setation (2 setae per molt) of the first and second maxillipeds. This larva developed more rapidly than did larvae hatched and cultured aboard ship which had been subjected to environmental change at an earlier age, but it was less advanced in the late instars than were larvae studied from the plankton. Although the evidence for modification of molt cycle midway in zoeal development is based on

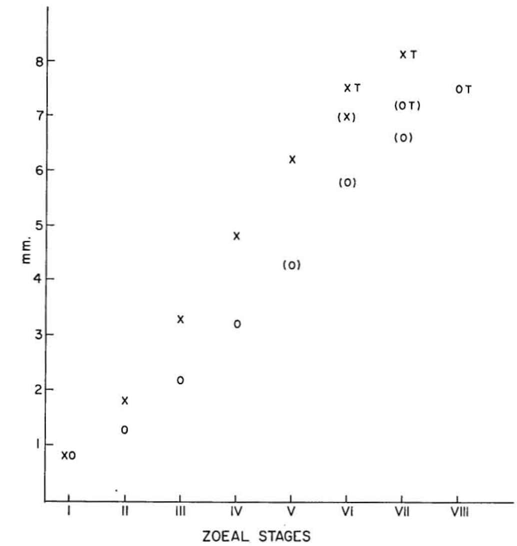


FIG. A. Average length of carapace (posterior margin to tip of rostral spine) for zoeal stages of cultured and planktonic larvae of *Emerita rathbunae*. *X*, Planktonic larvae; *O*, cultured larvae; *T*, terminal zoeal stage; ( ), average based on less than 10 specimens.

only a single specimen, it provides a link between the cultured and planktonic forms as well as an indication of the potential variability in the larval development of *E. rathbunae*.

Description of Larval Stages

To facilitate identification of the larvae of *E. rathbunae* in the plankton, the descriptions of intermediate stages IV and V are based upon planktonic specimens rather than upon the variable forms obtained in the laboratory. The descriptions of stages I–III and the terminal zoea are based upon both cultured and planktonic larvae for structure and development of appendages; the setation is based upon zoeal stages from the plankton. Measurements of the zoeal stages are given in Table 2. Average figures are based upon measurements of 10 or more specimens, except for zoea VI (not terminal), for which only 5 specimens were available. The length of rostrum and carapace were measured from the posterior margin of eyestalk. The length of telson excludes telson processes.

ZOEA I (Fig. 1): The zoea is colorless and translucent, the rounded carapace has a short,

TABLE 2

MEASUREMENTS (IN MM) OF ZOEAL STAGES OF *Emerita rathbunae*, AND OF STAGES I–IV AND THE TERMINAL ZOEA OF *E. analoga* (IN ITALICS)

	CARAPACE				ROSTRUM		LATERAL SPINES		TELSON				CARAPACE LENGTH / ROSTRUM LENGTH
	LENGTH		WIDTH		LENGTH		LENGTH		LENGTH		WIDTH		
STAGE	MEAN	RANGE	MEAN	RANGE	MEAN	RANGE	MEAN	RANGE	MEAN	RANGE	MEAN	RANGE	
I	0.56	(0.54–0.60)	0.43	(0.42–0.44)	0.20	(0.18–0.20)			0.36	(0.34–0.38)	0.36	(0.34–0.38)	2.80
	0.68	*(0.66–0.68)*	*0.54*	*(0.52–0.56)*	*0.20*				*0.43*	*(0.40–0.48)*	*0.45*	*(0.42–0.48)*	*3.40*
II	0.67	(0.62–0.72)	0.62	(0.58–0.68)	1.10	(1.00–1.20)	0.56	(0.48–0.62)	0.50	(0.48–0.54)	0.49	(0.46–0.52)	0.61
	0.83	*(0.80–0.84)*	*0.77*	*(0.74–0.78)*	*1.21*	*(1.16–1.28)*	*0.65*	*(0.60–0.68)*	*0.64*	*(0.62–0.66)*	*0.64*	*(0.62–0.68)*	*0.68*
III	0.97	(0.90–1.10)	0.84	(0.78–0.94)	2.28	(2.04–2.64)	1.46	(0.90–1.70)	0.69	(0.64–0.74)	0.67	(0.62–0.72)	0.43
	1.27	*(1.20–1.32)*	*1.15*	*(1.12–1.16)*	*2.13*	*(2.04–2.20)*	*1.23*	*(1.16–1.24)*	*0.92*	*(0.86–0.96)*	*0.88*	*(0.82–0.92)*	*0.60*
IV	1.33	(1.28–1.44)	1.10	(1.04–1.20)	3.45	(3.16–3.84)	2.32	(2.12–2.72)	0.98	(0.96–1.02)	0.89	(0.86–0.92)	0.39
	1.64	*(1.52–1.80)*	*1.40*	*(1.32–1.48)*	*3.08*	*(2.84–3.40)*	*1.86*	*(1.72–2.08)*	*1.31*	*(1.20–1.36)*	*1.15*	*(1.08–1.20)*	*0.53*
V	1.75	(1.60–2.04)	1.43	(1.32–1.60)	4.41	(4.04–4.80)	3.03	(2.60–3.28)	1.34	(1.18–1.50)	1.17	(1.10–1.30)	0.39
VI	2.07	(1.96–2.16)	1.71	(1.52–1.76)	4.90	(4.80–5.06)	3.14	(3.00–3.24)	1.60	(1.52–1.66)	1.38	(1.30–1.44)	0.42
VI TERMINAL ZOEA	2.21	(1.92–2.68)	1.77	(1.52–2.16)	5.27	(4.40–5.64)	3.39	(3.00–3.88)	1.78	(1.48–2.04)	1.45	(1.24–1.66)	0.42
VII TERMINAL ZOEA	2.48	(2.24–2.64)	2.02	(1.76–2.20)	5.64	(5.40–5.89)	3.53	(3.28–3.80)	2.09	(2.06–2.14)	1.69	(1.66–1.70)	0.44
? TERMINAL ZOEA	*3.45*	*(3.20–3.80)*	*2.54*	*(2.36–2.80)*	*4.88*	*(4.68–5.39)*	*2.16*	*(1.96–2.88)*	*2.81*	*(2.64–3.00)*	*2.04*	*(1.96–2.24)*	*0.71*

FIGS. 1–5. *Emerita rathbunae.* Zoea I–V.

broad rostral spine; the lateral spines characteristic of later stages are absent. The large eyes are stalked.

The first antenna (antennule) (Fig. 11) is conical and unsegmented, tapering distally to a blunt tip which bears 3 aesthetes and 2 hairlike setae.

The protopodite of the second antenna (Fig. 17) is produced into a strong lateral spine and bears a slender inner spine of approximately the same length. A small spine is situated ventrally at the base of the medial spine.

The mandibles (Fig. 23) are armed with strong ventral teeth, short triangular teeth, and slender spines. The ventral tooth of the left mandible is split shallowly at the tip. There is little change except growth during zoeal development.

The coxal endite of the first maxilla (maxillule) (Fig. 24) bears 3 terminal setae with 1 small seta subterminally on the inner margin. The basal endite bears 2 strong curved spines armed with tiny spines, the small unsegmented endopodite bears a single long seta.

The protopodite of the second maxilla (Fig. 26) is triangular, bearing 3 setae on the blunt anterior margin, 1 set slightly apart toward the scaphognathite, and 1 small seta subterminally on the inner margin. In later stages, the anterior tip becomes more pointed and the 3 setae more evenly spaced (Fig. 27). The scaphognathite bears 7–8 plumose setae on the anterior-outer margin; one-third of the specimens dissected, from both hatching and plankton, had 7 setae.

The short coxopodite of the first maxilliped (Fig. 29) is unarmed. The basipodite bears 7 setae along the medial margin in groups of 1–1–2–3 progressing distally. The endopodite is 4-segmented; the first three segments are armed along the inner margin as follows: first segment with a group of 3 setae, one conspicuously stronger than others and armed with tiny spines; second segment with 2 setae, again one being stout and armed with spinules; third segment with 2 setae spaced around the distal margin of the segment. The fourth segment bears 4 terminal setae; the outer 2 setae are quite long and armed with spinules on the inner margin. There is also a short hairlike seta placed subterminally on the outer margin which frequently curves in between the terminal setae and is difficult to see without high magnification. The exopodite consists of 2 segments; the very short, often weakly delineated, terminal segment bears 4 long plumose natatory setae.

The coxopodite of the second maxilliped (Fig. 28) is unarmed, the basipodite bears 3 setae on the inner margin in groups of 1–2 progressing distally. The endopodite consists of 4 segments. Along the medial margin, the first segment bears 3 setae distally, the second segment bears 1 seta, and the third segment has 2 setae around the distal margin of the segment. The fourth segment bears 4 terminal setae and 1 small subterminal seta on the outer margin as described for the first maxilliped. The exopodite is 2-segmented, the small terminal segment bears 4 plumose natatory setae.

The abdomen consists of 5 segments. The first is very weakly differentiated. The sixth segment is consolidated with the telson, as shown by the position of the uropods in subsequent stages.

The telson (Fig. 34) is rounded, slightly concave, and usually about as wide as long, occasionally slightly longer than wide. There are 2 prominent posterior-lateral spines notched near the tip on the outer margin. Between the lateral spines there are 25–27, usually 26, spines around the posterior margin of the telson, with a series of very small denticles between the spines. The eighth spine from either side is somewhat longer and more prominent than the remaining spines; all are armed near the base with small spinules. There is little change throughout zoeal development except for an increase in number of denticles between the terminal spines.

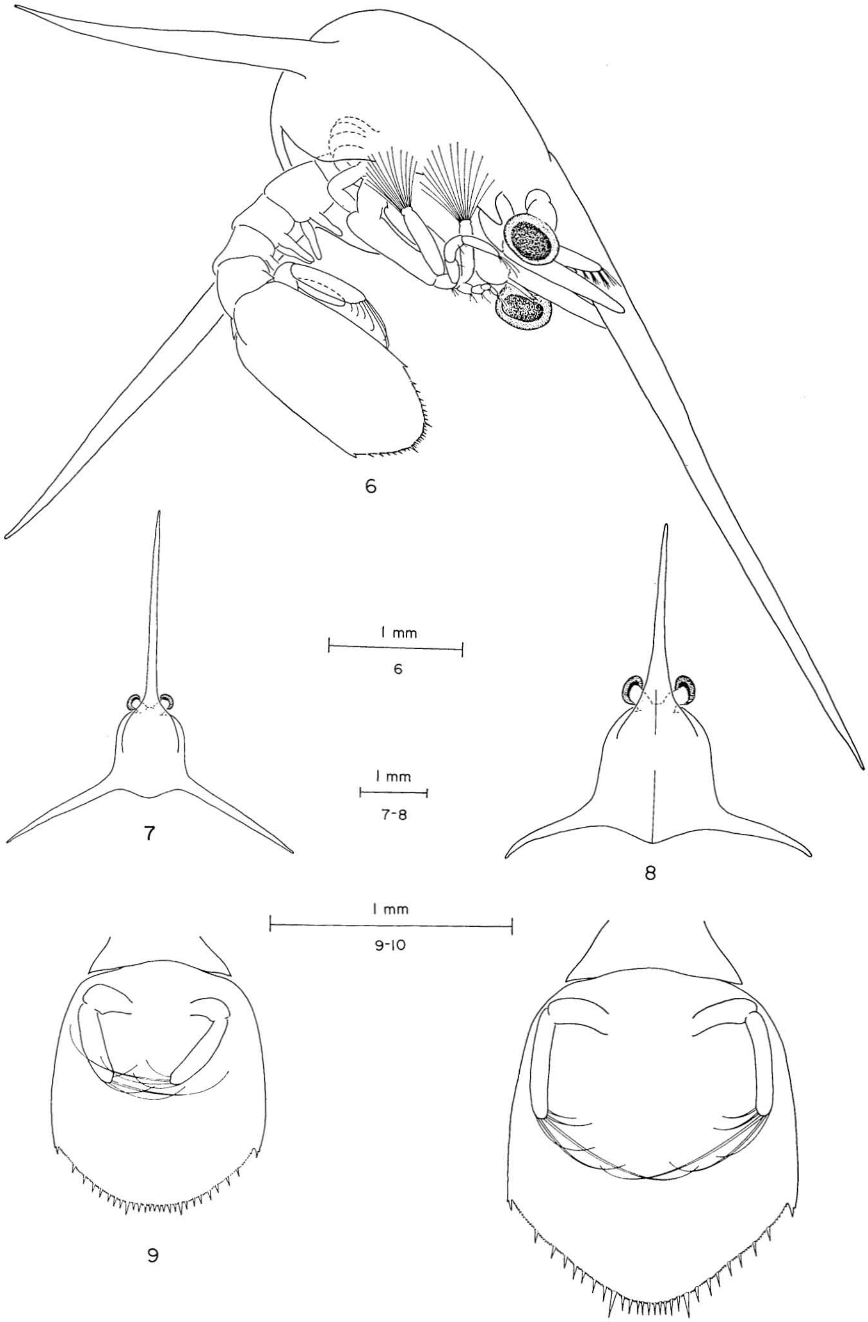
In the following stages, unless noted, there is no change in setation and form of appendages described and figured for zoea I.

ZOEA II (Fig. 2): There is now a pair of short lateral spines on the carapace.

The first antenna (Fig. 12) terminates with 1 large aesthete and approximately 3 small hairlike setae.

The second antenna (Fig. 18) bears a small subterminal spine on the medial margin of the lateral spine.

The basal endite of the first maxilla (Fig. 25), with the addition of 1 spine, now bears 3 strong curved spines armed with spinules;



FIGS. 6–10. *Emerita rathbunae*. *6,* Zoea VI; *7,* zoea IV, dorsal; *9,* zoea IV, telson. *Emerita analoga*. ***8,*** Zoea IV, dorsal; *10,* zoea IV, telson.

the inner two spines are articulated at the base. There is no other change and the first maxilla maintains this form throughout zoeal development.

The scaphognathite of the second maxilla bears usually 8, occasionally 9, plumose setae on the anterior-outer margin.

The exopodites of the first and second maxillipeds bear 6 plumose natatory setae.

ZOEA III (Fig. 3): The first antenna (Fig. 13) bears 3 aesthetes and 3 small setae on the tip. One aesthete is slightly larger and set apart from the other two in the terminal grouping found throughout further zoeal development.

Small spines have been added distally on both lateral and medial spines of the second antenna (Fig. 19).

The scaphognathite of the second maxilla may have 9 or 10, rarely 11, plumose setae on the anterior-outer margin.

The exopodites of the first and second maxillipeds bear 8 plumose natatory setae.

A pair of uniramous, 2-segmented uropods (Fig. 31) are now present on the anterior-ventral portion of the telson. Each of the distal segments bears 2 slender curving terminal setae armed with tiny spines distally; the inner seta is longest.

ZOEA IV (Figs. 4, 7): The first antenna (Fig. 14) now bears a subterminal tier of 2 aesthetes on the medial margin.

The flagellum of the second antenna (Fig. 20) appears in this stage as a slight rounded prominence to a small bud.

The number of plumose setae along the outer margin of the scaphognathite of the second maxilla ranged from 15 to 21; most specimens had 17–20.

The exopodites of the first and second maxillipeds bear 10 natatory setae, and the basipodite of the first maxilliped may have 8 setae along the inner margin in groups of 1–2–2–3 progressing distally.

Small buds of the third maxilliped and thoracic appendages are present beneath the carapace, posterior to the second maxilliped.

The exopodites of the uropods (Fig. 32) now bear 4 terminal setae of varying lengths; the third seta is the longest. The endopodite may appear in this stage as a rudiment or a small bud.

The telson (Fig. 9) has become somewhat longer than wide and remains so in subsequent zoeal stages.

ZOEA V (Fig. 5): The first antenna (Fig. 15) bears usually 2, occasionally 3, subterminal groups of aesthetes along the medial margin; only one-fourth of the specimens dissected had 3 tiers of aesthetes. The majority of larvae had 4 subterminal aesthetes in groups of 2–2; rarely an additional aesthete was added to form groups of 2–3 progressing distally. Those larvae with 3 subterminal tiers of aesthetes added them in groups of 2–2–3, rarely 1–2–3.

The flagellum of the second antenna (Fig. 21) is now slightly shorter than to slightly longer than the 2 spines of the protopodite.

The scaphognathite of the second maxilla bears 24–39 plumose setae along the outer margin; most individuals had between 30 and 34 setae.

The exopodites of the first and second maxillipeds bear 12, rarely 11, natatory setae. The basipodite of the first maxilliped now bears 8 setae along the medial margin in groups of 1–2–2–3 progressing distally.

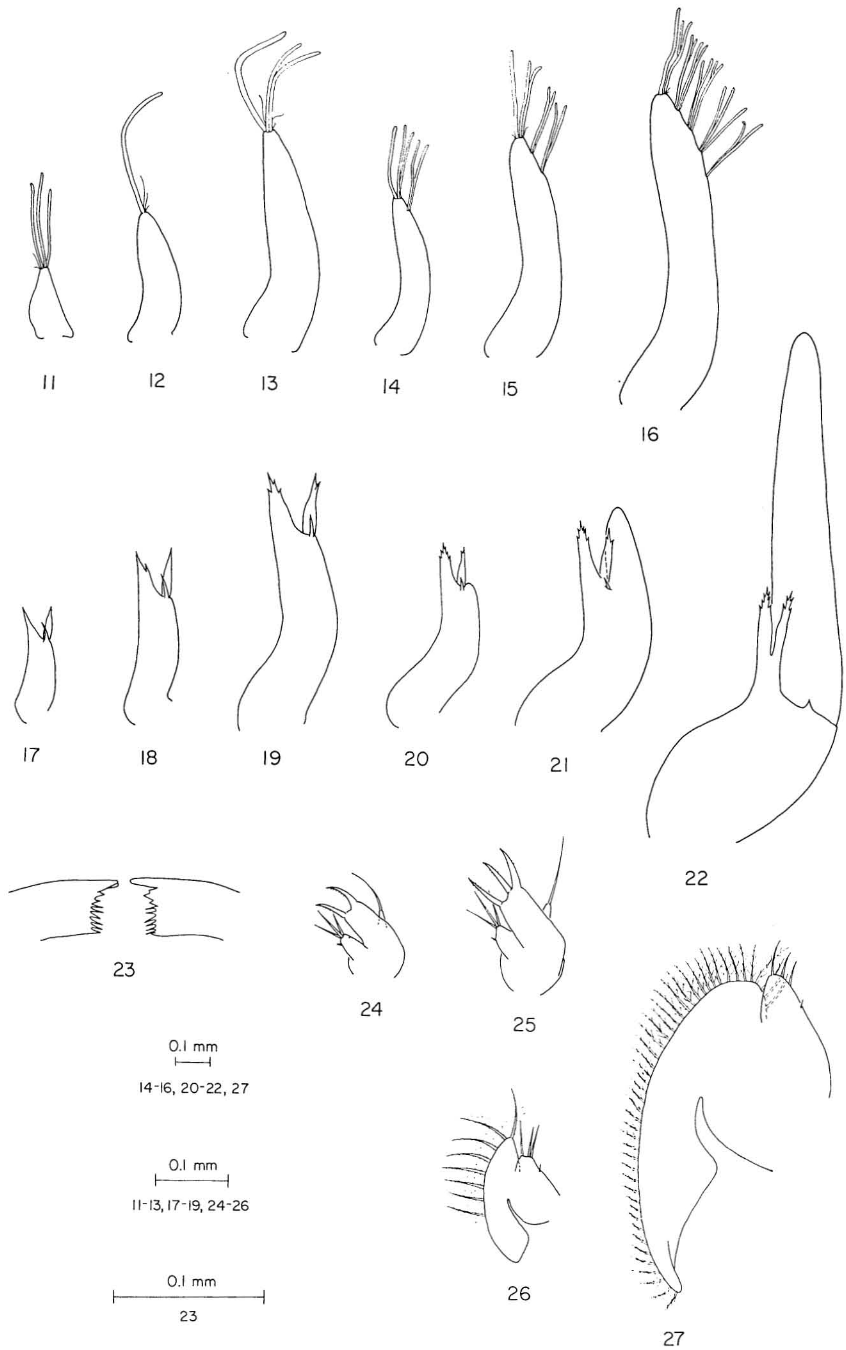
The third maxilliped and thoracic appendages have increased in size, curving under toward the thorax.

The exopodites of the uropods (Fig. 33) now bear 5 or 6 setae of unequal length; the third seta is very long. More larvae had 5 than 6 setae, a few had 5 on one side and 6 on the other. The endopodite now varies in size from a small to prominent bud approximately 1/3 the length of the exopodite.

ZOEA VI (Fig. 6): Now the first antenna (Fig. 16) usually has 4 subterminal tiers of aesthetes in groups of 2–3–4–4 or 2–2–4–4 progressing distally. Of 19 specimens 5 had only 3 tiers in groups of 2–3–4 or 2–4–4.

The flagellum of the second antenna (Fig. 22) has increased greatly in length and now dwarfs the spines on the protopodite. In specimens close to molting to megalopa, the segmentation of postlarval peduncle and flagellum can be seen beneath the cuticle.

The scaphognathite of the second maxilla



FIGS. 11–27. *Emerita rathbunae. 11–16,* First antenna, zoea I–VI; *17–22,* second antenna, zoea **I–VI;** *23,* mandible, zoea I; *24–25,* first maxilla, zoea I and II; *26–27,* second maxilla, zoea I and VI.

(Fig. 27) has 43–55 plumose setae along the outer margin.

The exopodites of the first and second maxillipeds now bear 14 plumose natatory setae.

The third maxilliped and thoracic legs (Fig. 30) have increased greatly in size; the fifth leg, curved up and behind the first four, is slightly bifid at the tip.

Now each of the segments 2, 3, 4, and 5 of the abdomen bears a pair of uniramous, unsegmented pleopods.

The exopodites of the uropods (Fig. 35) bear 7 or 8 setae of varying lengths; twice as many larvae had 7 as had 8 setae; a few had both 7 and 8 setae. The endopodites are quite long, usually 3/4 the length of the exopodites.

ALTERNATE ZOEAL STAGES: Of the larvae of *Emerita rathbunae* studied from preserved samples, 49 had at least 14 setae on the exopodites of the first and second maxillipeds. While 33 of these larvae were in the described stage VI, with pleopods on abdominal somites, and were, in many cases, close to molting to megalopa, sixteen of the larvae seemed to have prolonged the larval cycle to seven zoeal stages. Five larvae with 14 natatory setae on the maxillipeds did not have pleopods on abdominal segments. They had only 6 setae on the exopodites of the uropods, 3 tiers of aesthetes on the first antenna, and in all other respects (measurements, development of appendages, etc.) were intermediate between the forms described as zoea V and zoea VI. The remaining 11 larvae had 16 setae on the exopodites of the maxillipeds (one had only 15), had pleopods on abdominal somites, and were slightly larger and more advanced than the form described as zoea VI.

Two zoea IV and two zoea V were found which corresponded with the described stages in over-all proportions and in setation. They were slightly smaller, however, and some appendages were somewhat less developed (flagellum of second antenna and thoracic legs), which suggests that they might be the early stages of such an extended larval cycle.

The variation in development and setation of some appendages of cultured larvae within stage VI is summarized in Table 3.

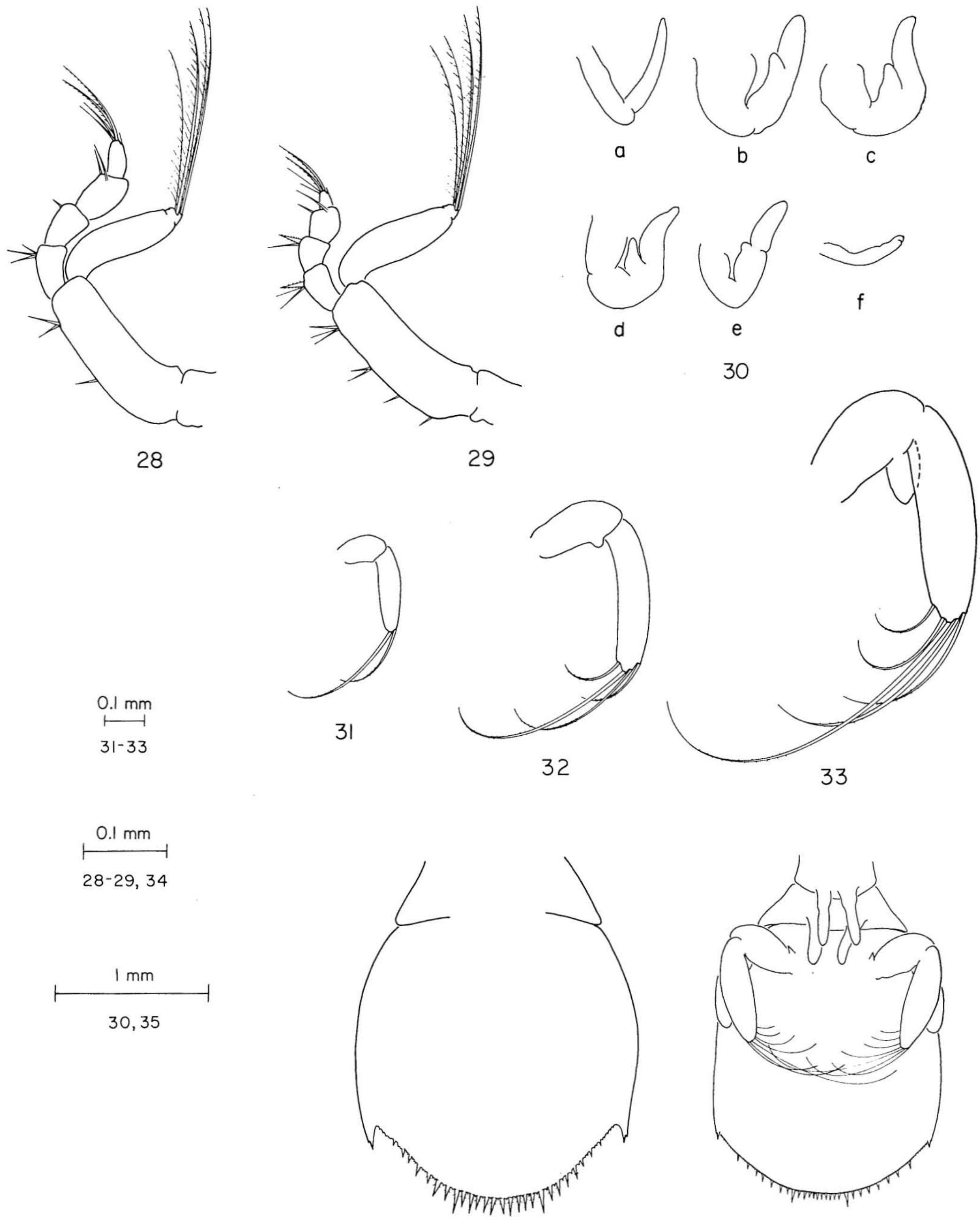
MEGALOPA (Fig. 36): The megalopa is colorless, slightly translucid and very much like the adult in form. The most noticeable differences are presence of setose pleopods on abdominal segments and relatively large eyes. The average size of carapace in reared individuals was: length, 2.65 mm; width, 1.98 mm. No specimens from the plankton were available.

The first antenna (Fig. 37) consists of a 3-segmented peduncle and a flagellum. The second and third segments of the peduncle have small ventral processes armed with setae and that of the third segment is 2-segmented. The flagellum usually consists of 10 segments armed

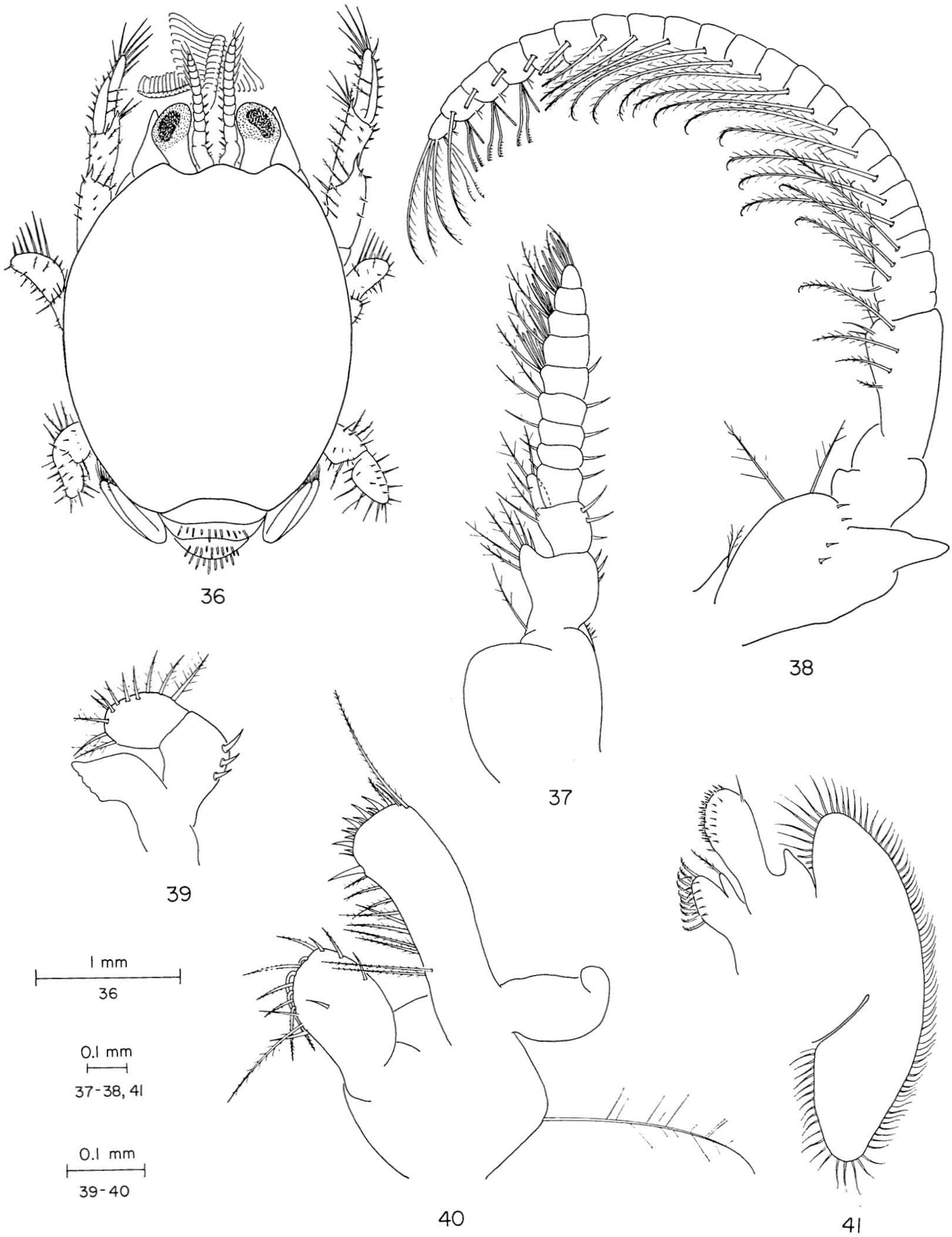
TABLE 3

COMPARISON OF SOME FEATURES OF CULTURED LARVAE IN STAGE VI FROM SERIES WITH 7, 8, AND 9 ZOEAL STAGES

FEATURE		HATCHED LARVAE 7 STAGES	HATCHED LARVAE 8 STAGES	HATCHED LARVAE 9 STAGES	PLANKTONIC LARVA 8 STAGES
First antenna: No. of subterminal tiers of aesthetes	range	2	1–2	1–2	
	majority	2	2	1 and 2	3
Second antenna: Development of flagellum in relation to spines on protopodite	range	= spines	rudiment to = spines	0 to rudiment	
	majority	= spines	= ½ spines	0	= spines
First and second maxillipeds: Natatory setae	range	13–14	11–14	12–14	
	majority	14	13 and 14	12 and 13	14
Uropods: Exopod setae	range	6–7	5–7	5–7	
	majority	6	6	6	6 and 7



FIGS. 28–35. *Emerita rathbunae. 28,* Second maxilliped, zoea I; *29,* first maxilliped, zoea I; *30a,* third maxilliped, *b–f,* thoracic legs 1–5, zoea VI; *31–33,* uropod, zoea III–V; *34–35,* telson, zoea I and VI.



FIGS. 36–41. *Emerita rathbunae*. Megalopa. *36,* Dorsal; *37,* first antenna; *38,* second antenna; *39,* mandible; *40,* first maxilla; *41,* second maxilla.

laterally and ventrally with strong setae. The distal 5 segments bear aesthetes between the ventral setae.

The basal segments of the second antenna (Fig. 38) are similar to those of the adult. The flagellum consists of 23–25 segments each bearing 7 processes: 2 long plumose filtering setae, 2 strong setae armed with comblike spines, and 3 shorter unarmed setae.

The mandible (Fig. 39) consists of a light gnathal lobe and a palp of 2 segments. The first segment of the palp has 3, rarely 2, stout setae on the lateral margin, and the terminal segment bears setae along the medial and anterior margins.

The basal endite of the first maxilla (Fig. 40) is armed with short, stout teeth and numerous setae; 1 long plumose seta is conspicuous on the anterior-outer corner. On the coxal endite, a series of long setae curve sharply down toward the mouth region. The endopod is unsegmented and saclike. There is 1 long seta on the lateral angle of the protopodite below the endopodite.

The scaphognathite of the second maxilla (Fig. 41) has a dense fringe of approximately 95 setae along the outer margin. The coxal endite is now bilobed; the small distal lobe bears 1 long seta. The proximal lobe and the basal endite bear many setae. The small triangular endoped is unarmed.

The anterior portion of the protopodite of the first maxilliped (Fig. 42) is produced into a flat blade armed with rows of small setae and a series of long plumose setae on the basal portion. The exopodite consists of 2 segments; the bladelike terminal segment is fringed with plumose setae. The rudimentary endopod is unarmed.

The exopodite of the second maxilliped (Fig. 43) is 2-segmented; the first segment bears 3–4 strong setae on the lateral margin and the small oval terminal segment is fringed with plumose setae. The endopodite consists of 4 segments with setation as figured.

The meropodites of the third maxilliped (Fig. 44) are broad and opercular. The 3 slender terminal segments bear plumose and bristle setae; the inner surfaces are covered with dense rows of setae to form a brushlike structure.

The pereiopods are like those of the adult in form, with the first three pairs directed forward and the fourth pair directed posteriorly. The fifth legs, slender and chelate, are curved up beneath the carapace.

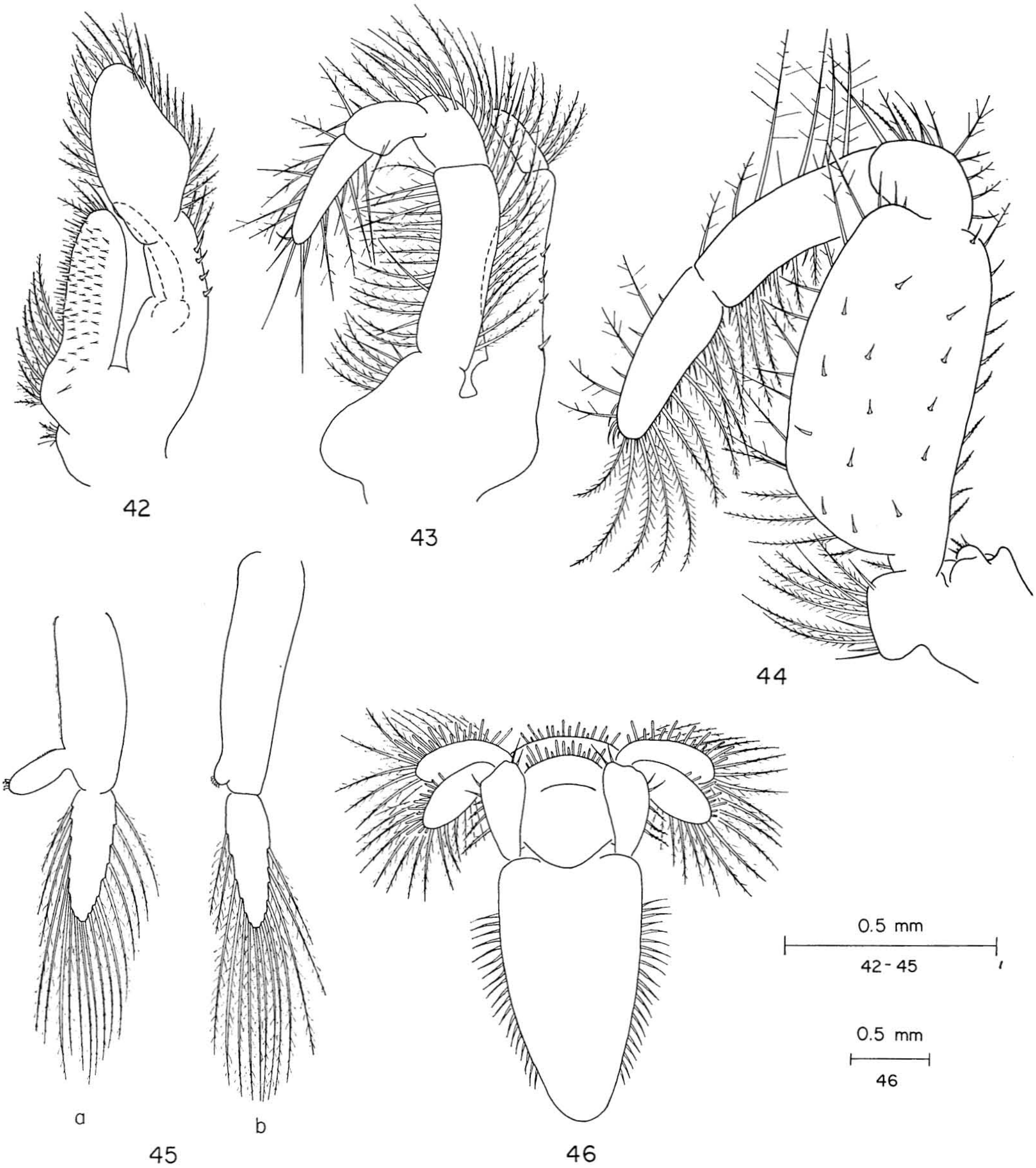
The abdomen now consists of 6 segments; segments 2, 3, 4, and 5 bear biramous pleopods and segment 6 carries biramous uropods. The pleopods (Fig. 45) decrease in length posteriorly. The exopodites bear plumose setae; the first pair has 14–15 setae, the second pair bears 15–16 setae, and the third and fourth pairs have 17–18 setae. The knoblike endopodites increase in length from the first to the fourth pair and have tiny median hooks which interlock with those of the opposite pleopod to form a single swimming unit of the pair.

The oval exopodites and endopodites of the uropods (Fig. 46) are fringed with plumose and small unarmed setae. The triangular telson (Fig. 46) has plumose setae along the lateral margins.

Comparison of Species

Among larvae of *Emerita analoga* studied from preserved plankton samples, the early stages, I–IV (the "low stage IV" described by Johnson and Lewis (1942:79) with usually 10, occasionally 9 or 11, setae on the first and second maxillipeds), were found to be consistent in detail and degree of development, but later stages showed such variation in setation and development of appendages that the number of molts through which any individual had progressed could not be ascertained with confidence. The terminal zoeas, with indications of postlarval appendages beneath the cuticle, were consistent in possession of pleopods, an extremely long flagellum on the second antenna, and 5 tiers of subterminal aesthetes on the first antenna, as described by Johnson and Lewis. From 16–19 setae were found on the exopodites of the maxillipeds. Groupings of the late stage larvae by size and relative growth of appendages suggested that there were at least 7 zoeal instars in the planktonic larval life of the species.

No differences in morphological detail were detected between larvae of *Emerita rathbunae* and *E. analoga* in stages I and II. In stage III, the uropods of *E. analoga* may bear 3 setae but 7 out of 10 specimens examined had only 2



FIGS. 42–46. *Emerita rathbunae.* Megalopa. *42,* First maxilliped; *43,* second maxilliped; *44,* third maxilliped; *45,* pleopods (*a,* fourth, *b,* first); *46,* uropods and telson.

setae as found in the equivalent stage of *E. rathbunae.* In stage IV, the setation of the exopodites of the uropods becomes consistent and a useful character for differentiation of the species: larvae of *E. analoga* have 5 setae and those of *E. rathbunae* have 4 setae on this appendage. In all subsequent instars, the setation of the coxal endite of the first maxilla may be used. The larvae of *E. analoga* develop a strong fifth seta subterminally on the proximal margin, while larvae of *E. rathbunae* apparently maintain 4 setae throughout zoeal development.

Differences in terms of size of carapace, ratio of length of carapace to rostral spine, and proportions of the telson increase between larvae of *E. analoga* and *E. rathbunae* as zoeal development proceeds. The larvae of *E. anologa* become progressively larger than those of *E. rathbunae,* and the carapace spines are considerably shorter in relation to the length of the carapace. The posterior margin of the telson of *E. analoga* larvae becomes increasingly pointed and triangular between the prominent eighth marginal spines, while that of *E. rathbunae* remains smoothly rounded. Measurements of the first four stages and of the terminal stage of larvae of *E. analoga* are given in Table 2 for comparison with equivalent stages of *E. rathbunae*. The carapace and telson of both species in stage IV are shown in Figures 7–10.

The larvae of *Emerita emerita,* described by Menon (1933), and *E. talpoida,* described by Rees (1959) and Smith (1877), and those of *E. rathbunae* and *E. analoga* appear to be very similar in structure of appendages and in form of carapace and telson. The pattern of development may be common for all species through stage III, and through stage IV (with specific variation in setation) for those species described from the plankton. Larvae of *E. emerita,* and *E. talpoida* apparently pass directly from zoea IV to terminal zoea in the plankton. Those of *E. talpoida* in the laboratory and of *E. rathbunae* and *E. analoga* in both laboratory and field have a variable series of intermediate instars between stage IV and the terminal zoea in which there is progressive growth and setation without addition of appendages. The zoeal stages which appear to be common to all larvae of the genus are as follows:

1. Uropods absent
   a. Lateral spines on carapace absent, 4 natatory setae on maxillipeds . . . . Stage I
   b. Lateral spines on carapace present, 6 natatory setae on maxillipeds . . . . Stage II
2. Uropods present
   a. Pleopods absent, 8 natatory setae on maxillipeds . . . . Stage III
   b. Pleopods absent, 10 natatory setae on maxillipeds . . . . Stage IV
   c. Pleopods present, 12 or more natatory setae on maxillipeds . . . . Terminal Stage

Distribution of Larvae

The locations of zooplankton samples examined and the distribution of *Emerita* larvae are given in Figure 47. Larvae of *E. analoga* were found in samples taken near Magdalena Bay, and those of *E. rathbunae* usually in samples taken south and east of Cape San Lucas. A group of stage I larvae were found in nearshore samples from the west coast of Baja California below Magdalena Bay. From measurements, they appeared to be larvae of *E. rathbunae,* but lack of morphological features with which to differentiate stage I larvae of the two species makes identification tentative. In addition, 16 larvae of *E. rathbunae,* ranging from zoea II to terminal zoea VI, were found just south of Magdalena Bay. It seems likely, inasmuch as the range of developmental stages was found in the sample, that the larvae were hatched locally and that populations of the species might be found in the sandy beaches between Cape San Lucas and Magdalena Bay.

Twenty larvae were found in samples taken in November and December in the Gulf of California, the majority north of La Paz, which, although slightly smaller, were almost identical with those of the coastal *E. analoga* in morphological detail and proportions. Only late stages were obtained. These showed variation in setation and development of appendages similar to that found in larvae of *E. analoga.* During August to December, the movements of surface water along the western coast of Baja California are predominantly offshore and westerly (Wyrtki, 1965). It therefore seems unlikely that the larvae could have been carried into the Gulf from breeding populations near Magdalena Bay. The appearance of the *analoga*-like larvae in a series of samples suggests that either *Emerita analoga* or a closely related species may be found in the warm temperate zone of the Gulf of California, extending north from Aqua Verde Bay on the west coast and Puerto San Carlos on the east (Garth, 1955, 1960).

DISCUSSION

This study of planktonic and cultured larvae of *Emerita rathbunae* has shown that the number of zoeal stages in the larval period is vari-

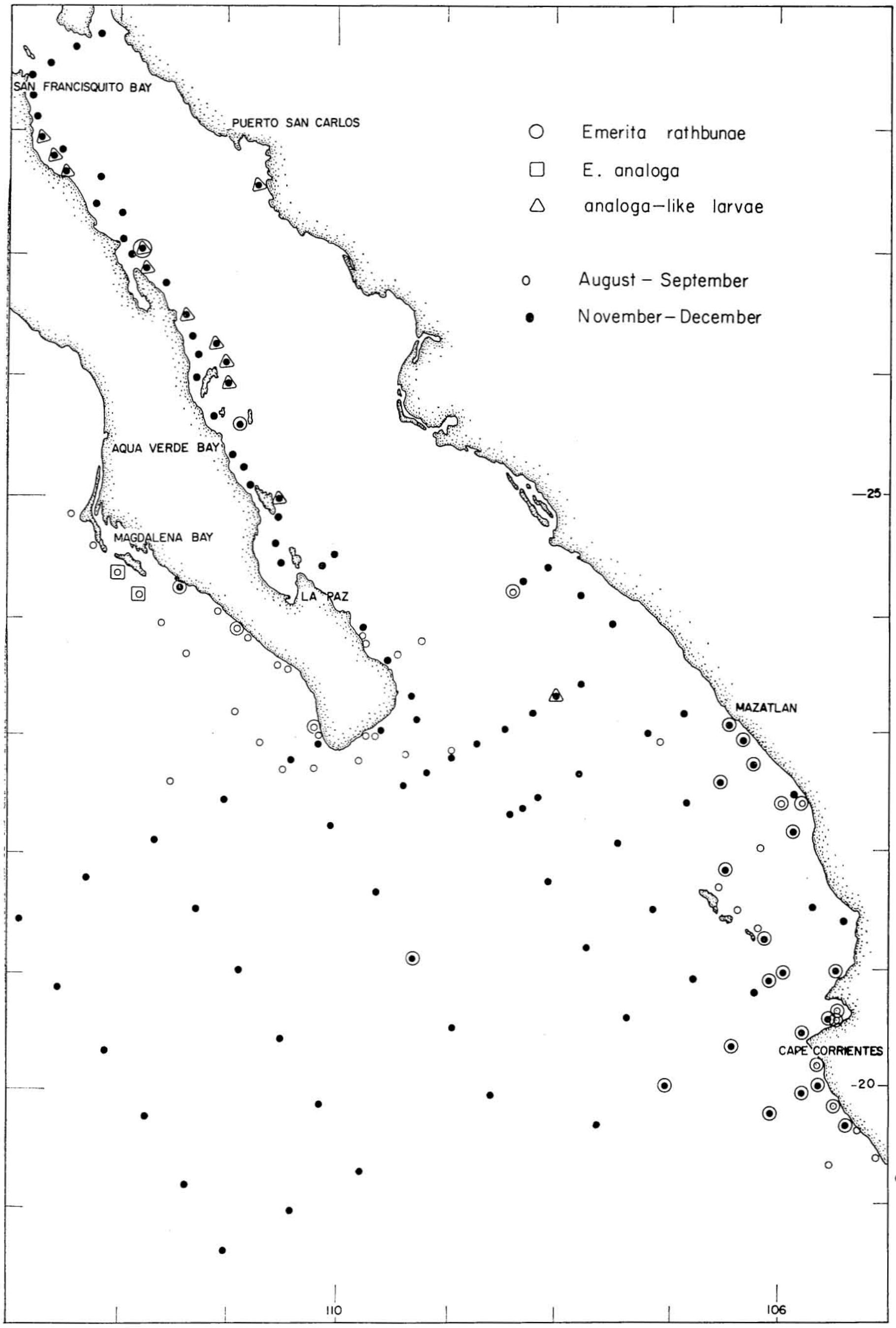


FIG. 47. Location of zooplankton samples examined and distribution of *Emerita* larvae.

able, both in nature and under conditions of laboratory culture. In the laboratory, although the larvae retained their specific proportions and pattern of development, as many as three intermediate instars could be added to the larval sequences usually observed in specimens from the plankton. Variability between individuals at comparable stages of development increased with an increase in the number of zoeal molts in the larval period.

A variable number of zoeal stages has been found in the laboratory culture of two other species of *Emerita*. Dr. Ian Efford (personal communication) has noted 9–11 zoeal molts among reared larvae of *E. analoga*, and larvae of *E. talpoida* cultured by Rees (1959) passed through 6 or 7 zoeal stages before the molt to megalopa. Rees, using setation of the maxillipeds as an indication of the stage of development, compared the zoeal stages observed in the laboratory with those described by Smith (1877) from the plankton and found that larvae from the plankton which molted to megalopa in the laboratory were apparently only in stage V. Rees noted as well that "zoea from nature possess features (appearance of thoracic limb buds, pleopods, etc.) which show them to be farther advanced in development than the corresponding laboratory stages." This relation between cultured and "natural" larvae was also observed in the present study.

Some indication of seasonal variation in number of zoeal stages was found in specimens of *E. rathbunae* examined from the plankton. Most (94%) of the late-stage larvae taken in August and September appeared ready to molt to megalopa after six zoeal stages; in the December samples only 32% would metamorphose after six stages and 68% after seven stages.

Differences in setation and development of appendages between individuals in comparable intermediate stages were not noted by Rees in cultured larvae of *E. talpoida* and were rare in larvae of *E. rathbunae* from the plankton. Individual variation became more pronounced among reared larvae of *E. rathbunae* with an increase in the number of zoeal stages, and might be related to rate of development. Larvae of *E. rathbunae* subjected at an early age to low temperatures (and perhaps other variables) of the laboratory environment had a larval span of 81–94 days. *E. talpoida* completed zoeal development in 23–33 days at 30°C. The molting frequency of the planktonic larva of *E. rathbunae* cultured through two instars at 27°–30°C was consistent with that found by Rees for *E. talpoida,* and it appears likely that *E. rathbunae* would have a much shorter larval life at the higher temperatures in its natural environment. Perhaps culture of *Emerita* larvae over a range of controlled temperatures would show a relation between duration and number of zoeal stages and degree of individual variability. The consistent difference in size found between cultured and planktonic specimens suggests that larvae of this species are restricted in over-all size by the conditions of laboratory culture.

Costlow (1965) has reviewed accounts in the literature of variability within larvae of Crustacea and has discussed effects of environmental factors (light, diet, temperature, salinity, etc.) on frequency and variability in molting, as well as current investigations of endocrine mechanisms related to molting in larvae of brachyuran decapods. Variation in number of zoeal intermolts has been noted in the laboratory culture of several anomuran decapods by Provenzano (1962*a, b*) for two species of pagurid crabs, and by Boyd and Johnson (1963) for the galatheid, *Pleuroncodes planipes,* but apparently such variation is rare among brachyurans. Gurney (1942) suggested that artificial rearing might give misleading results, and stated that, while stages I–III in the development of larval decapods seemed to be relatively fixed, the natural course of development after that might be disturbed with addition of stages not found in nature. He noted as well that there is no certainty that all stages observed in nature are passed through by all individuals of a species. The use of only laboratory-reared material to investigate the growth patterns of a species with such capacity for variability in larval development as that shown by *E. rathbunae* would indeed have been misleading unless supplemented by a study of the larvae taken from their natural environment.

ACKNOWLEDGMENTS

This work was supported by the Marine Life Research Program, the Scripps Institution of

Oceanography's component of the California Cooperative Oceanic Fisheries Investigations, a project sponsored by the Marine Research Committee of the State of California.

I would like to thank Dr. M. W. Johnson, Dr. E. W. Fager, Dr. J. A. McGowan, and Dr. W. A. Newman for their valuable criticism of the manuscript.

REFERENCES

BOYD, CARL M., and M. W. JOHNSON. 1963. Variations in the larval stages of a decapod crustacean, *Pleuroncodes planipes* Stimpson (Galatheidae). Biol. Bull. 124(3):141–152.

BUTLER, T. H. 1959. A record of the anomuran crustacean *Emerita analoga* (Stimpson) from British Columbia. J. Fisheries Research Board Canada 16(5):761.

COSTLOW, JOHN D., JR. 1965. Variability in larval stages of the blue crab, *Callinectes sapidus*. Biol. Bull. 128(1):58–66.

GARTH, JOHN S. 1955. The case for a warm-temperate marine fauna on the west coast of North America. Essays in the Natural Sciences in Honor of Captain Allan Hancock, pp. 19–27. Univ. Southern Calif. Press, Los Angeles.

——— 1960. Distribution and affinities of the brachyuran crustacea. Systematic Zool. 9(3): 105–123.

GURNEY, ROBERT. 1942. Larvae of Decapod Crustacea. Ray Society, London. 306 pp.

HAIG, JANET. 1955. The Crustacea Anomura of Chile. Rept. Lund Univ. Chile Expedition 1948–49, no. 20. 68 pp.

JOHNSON, MARTIN W., and W. M. LEWIS. 1942. Pelagic larval stages of the sand crabs *Emerita analoga* (Stimpson), *Blepharipoda occidentalis* Randall and *Lepidopa myops* Stimpson. Biol. Bull. 83(1):67–87.

MENON, M. KRISHNA. 1933. The life-histories of decapod crustacea from Madras. Bull. Madras Govt. Mus., New Series, Nat. Hist. Section 3(3):1–45.

PROVENZANO, ANTHONY J., JR. 1962*a*. The larval development of the tropical land hermit *Coenobita clypeatus* (Herbst) in the laboratory. Crustaceana 4(3):207–228.

——— 1962*b*. The larval development of *Calcinus tibicen* (Herbst) (Crustacea, Anomura) in the laboratory. Biol. Bull. 123(1):179–202.

REES, GEORGE H. 1959. Larval development of the sand crab *Emerita talpoida* (Say) in the laboratory. Biol. Bull. 117(2):356–370.

SANKOLLI, K. N. 1965. Laboratory study on the life history of mole crab, *Emerita holthuisi* Sankolli. Abstracts of Papers, Symposium on Crustacea, Marine Biol. Assoc. India. 85 pp.

SCHMITT, WALDO L. 1935. Crustacea Macrura and Anomura of Porto Rico and the Virgin Islands. Scientific Survey of Porto Rico and the Virgin Islands, New York Acad. Sci., Vol. 15, pt. 2, pp. 124–227.

SMITH, SIDNEY I. 1877. The early stages of *Hippa talpoida*, with a note on the structure of the mandible and maxillae in *Hippa* and *Remipes*. Trans. Connecticut Acad. Sci. 3:311–342.

SNYDER, H. GEORGE, and A. FLEMINGER. 1965. A catalogue of zooplankton samples in the marine invertebrate collections of Scripps Institution of Oceanography. Univ. California, Scripps Institution of Oceanography, SIO Ref. 65–14.

STEINBECK, JOHN, and E. F. RICKETTS. 1941. The Sea of Cortez. Viking Press, New York. 598 pp.

UNIVERSITY OF CALIFORNIA, SCRIPPS INSTITUTION OF OCEANOGRAPHY. 1952*a*. Preliminary report of temperature, salinity and current measurements, cruise 32, 25 November to 9 December, 1951. SIO Ref. 52–1.

——— 1952*b*. Preliminary report of temperature, salinity and current measurements, cruise 33, 8–28 January, 1952. SIO Ref. 52–7.

——— 1961. Physical and chemical data report, CCOFI cruise 5612, 24 November to 21 December 1956. SIO Ref. 61–22.

——— 1962. Physical and chemical data report, CCOFI cruise 6108, 13–28 August 1961. SIO Ref. 62-16.

WYRTKI, KLAUS. 1965. Surface currents of the Eastern Tropical Pacific Ocean. Inter-American Tropical Tuna Commission, Bull. 9(5): 271–304.