LARVAL DEVELOPMENT OF THE SPIDER CRAB, *LIBINIA EMARGINATA* (MAJIDAE)[1]

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ABSTRACT

Larval development of the spider crab, *Libinia emarginata*, consists of two zoeal stages and megalopa. Laboratory-reared larvae (South Carolina and Rhode Island) are described and compared with planktonic larvae from Narragansett Bay, R.I. No significant variations in morphology were found between laboratory-cultured larvae and "wild" larvae from plankton catches; first stage zoea from South Carolina were smaller than Rhode Island specimens. Using *Artemia* diets, the best percentage survival in culture was found to be 20°C for Rhode Island larvae and 25°C for South Carolina larvae. Zoeal stages show little difference from larvae of *L. dubia*; however, the megalopae of the two species can be differentiated by the number of protuberances on the cardiac region of the carapace.

Larval stages have previously been described for a number of species from the family Majidae (Sandifer and Van Engel 1971, 1972). For the genus *Libinia* only two complete descriptions have been published. Boschi and Scelzo (1968) described larval stages of *L. spinosa* from Mar del Plata Harbor, Argentina; and Sandifer and Van Engel (1971) described the larval stages of *L. dubia* from Chesapeake Bay. Larvae of *L. erinacea* have been described by Yang (1967), but the results remain unpublished. In all cases, the larval development consists of two zoeal stages and a megalopa.

Adult *Libinia emarginata* Leach range from Windsor, Nova Scotia, to the western Gulf of Mexico and are found in nearshore waters down to a depth of 29 m (Williams 1965). Although the larvae of *L. emarginata* have not been formally described, they have been successfully reared (J. D. Costlow, pers. commun.). Grassle (1968) studied heterogeneity of hemocyanins during ontogeny, but no attempt was made to describe development. In support of ongoing studies using *Libinia* larvae at this laboratory, the present study was undertaken to: 1) describe the larval stages, 2) compare morphology of laboratory cultured and field collected larvae, and 3) determine successful temperature-salinity rearing parameters and development times. Characteristics which distinguish *L. emarginata* larvae from the larvae of *L. dubia* and *L. erinacea* were also noted.

METHODS AND MATERIALS

Ovigerous females of *L. emarginata* were collected off Charleston, S.C., during fall 1975 and spring 1976, and in Narragansett Bay, R.I., during summer 1976. Females were isolated in chambers at 25°C (in South Carolina) or 20°-22°C (in Rhode Island) and 30‰. After hatching, zoeae were isolated into compartmentalized plastic boxes. Larvae were fed day old *Artemia* every other day following a change of water. Larvae reared at salinities other than 30‰ were brought to the appropriate levels (15, 20, 40, or 45‰) using increment changes of 2.5‰ every 30 min. Larvae reared at temperatures other than hatching temperature were brought to the test temperature (15°, 20°, or 30°C) by placing larvae in environmental chambers and allowing them to equilibrate to these temperatures.

Field samples were obtained from surface plankton tows collected in Narragansett Bay during July and August 1976.

Drawings were made with the aid of camera lucida using exuviae and larvae fixed in 10% Formalin.[4] Carapace and total lengths were made with an ocular micrometer. Dry weights were determined with a Cahn Electrobalance on larvae

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that were dried in an 80°C oven for 24 h. The weights for each stage were calculated from three samples of five zoeae each.

One-way analysis of variance was computed on carapace length measurements taken on larval stages from South Carolina reared, Rhode Island reared, and field samples. If significant differences (at $P = 0.05$) were found within stages, a Scheffe Posterior comparison was used to determine where the differences lay (Nie et al. 1975).

The following abbreviations were used in all descriptions: AN1 = antennule, AN2 = antenna, MN = mandible, MAX1 = maxillule, MAX2 = maxilla, MXP1 = first maxilliped, MXP2 = second maxilliped, MXP3 = third maxilliped, P1 to P5 = pereopods 1 to 5, PL2 to PL6 = pleopods on abdominal somites 2 to 6. Types of setae specified are as described by Bookhout and Costlow (1974).

RESULTS

Development

Development times in both the South Carolina and Rhode Island reared larvae vary with temperature and salinity. In the South Carolina larvae, optimal and most advanced development occurred at 25°C and 30‰. At these conditions, the second stage appeared at day 3, megalopa at day 6 and first crab at day 14. In other conditions tested, development did not continue past the megalopa (Table 1).

In the Rhode Island reared larvae, complete development occurred only at 20°C and 30‰ with the second zoeal stage appearing at day 5, megalopa at day 8, and first crab at day 14. With other conditions tested, development was varied (Table 1).

South Carolina reared larvae tended to be smaller than both Rhode Island reared and field samples (Table 2). With statistical analysis, this difference is significant in stage I ($P<0.05$) but only between South Carolina reared and Rhode Island reared. At no other stage were the size variations found to be significant.

TABLE 1.—Time to various developmental stages (in days) for the spider crab, *Libinia emarginata*, reared at various temperature-salinity combinations in both South Carolina and Rhode Island.

Rearing site	Temperature-salinity combination	No. of larvae	Stage		
			II	Megalopa	1st crab
South Carolina	15°C-30‰	36	12	27	(1)
	20°C-30‰	36	7	12	(1)
	25°C-15‰	54	(1)		
	25°C-20‰	54	3	8	(1)
	25°C-30‰	54	3	6	14
	25°C-40‰	54	3	7	(1)
	25°C-45‰	54	4	8	(1)
	30°C-30‰	36	(1)		
Rhode Island	15°C-30‰	60	(2)		
	20°C-30‰	60	5	8	14
	25°C-30‰	60	4	(1)	

[1]All larvae had died prior to this stage.
[2]Second stage was not reached by day 15.

TABLE 2.—Comparison of carapace lengths for South Carolina reared, Rhode Island reared, and field sample larvae of *Libinia emarginata*.

Stage	Item	South Carolina reared	Rhode Island reared	Field samples
Zoea I*	$\bar{x}$ (mm)	[1]0.75	[1]0.78	0.775
	SD (mm)	0.019	0.020	0.028
	N	10	10	13
Zoea II	$\bar{x}$ (mm)	0.94	0.94	0.96
	SD (mm)	0.02	0.038	0.035
	N	7	14	11
Megalopa	$\bar{x}$ (mm)	1.16	1.21	1.20
	SD (mm)	0.049	0.064	0.001
	N	4	3	4

*Indicates significant differences within a stage by one-way analysis of variance ($P = 0.05$).
[1]Significant differences exist between the two means, according to Scheffe's Posterior comparison.

Larval Description

Two zoeal stages and one megalopa were obtained during the rearing period. Mandibles of the zoea are without palps and have a complex triangular biting surface. Since, in these stages, mandibles appear to have little diagnostic value and are difficult to accurately portray, they have been omitted from the following description.

Zoea I

Size and weight—Average carapace length, 0.78 mm (range 0.76-0.80 mm), average total length 2.19 mm (range 2.00-2.30 mm). Average dry weight 0.0214 mg (range 0.0200-0.0224 mg).

Carapace (Figure 1A, B) with dorsal and rostral spines; lateral spines absent. Dorsal spine long and slightly curved posteriorly; rostral spine nearly as long as antennule and slightly curved inward. Carapace large and somewhat rounded; 7 small plumose setae along the ventrolateral margin of carapace. Eyes sessile.

Abdomen (Figure 1C) with 5 somites; 6th somite fused to telson. Somite 2 with small anteriorly curved knobs on each side of lateral surface; somites 3-5 with pair of small posterolateral spines. Bifurcate telson; each furca bearing 1 spine. Inner

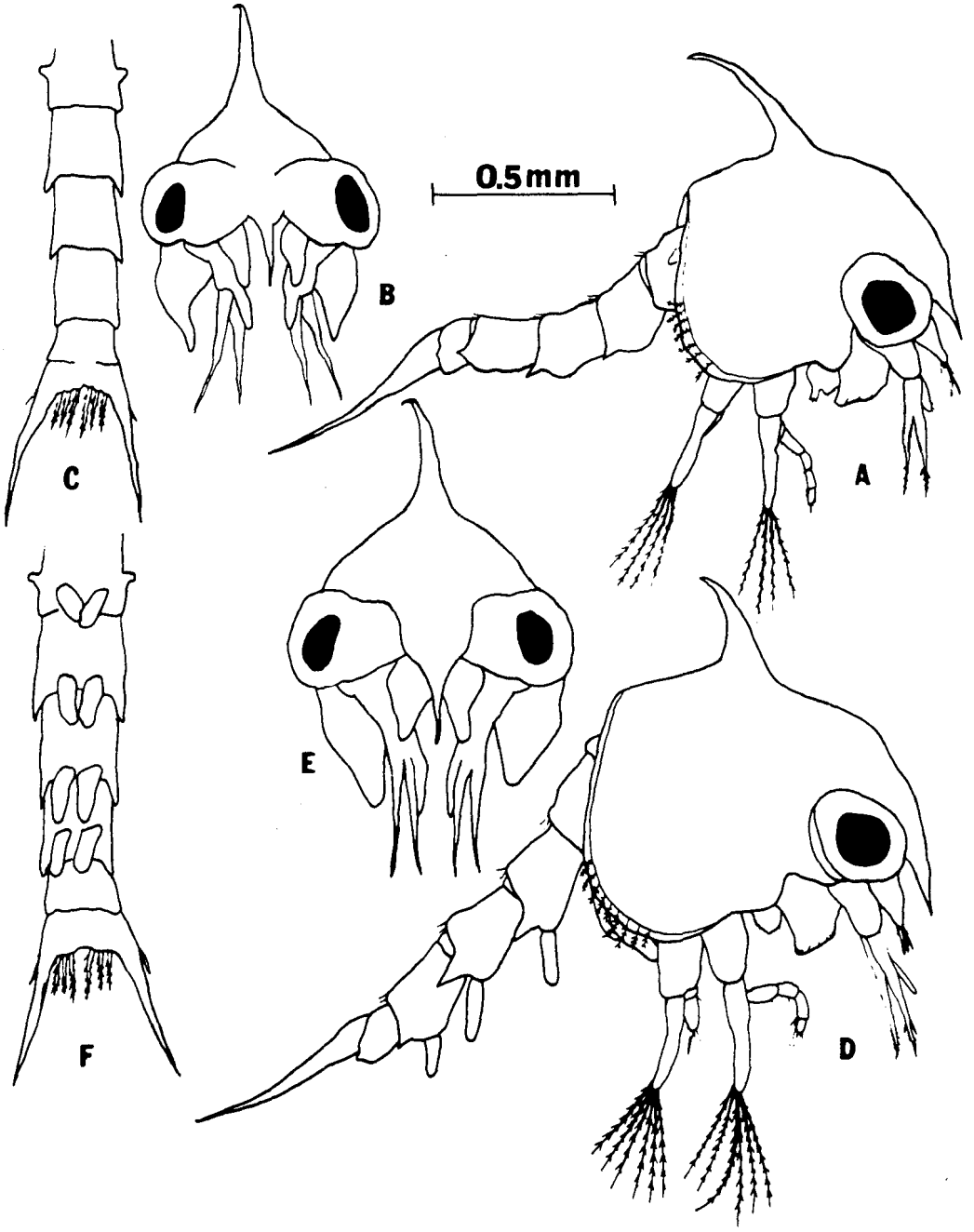

FIGURE 1.—*Libinia emarginata* zoea I and II. (A) lateral view of stage I, (B) front view of stage I, (C) dorsal view of abdomen at stage I, (D) lateral view of stage II, (E) front view of stage II, (F) dorsal view of abdomen at stage II. All unmarked scales = 0.1 mm.

margin of telson fork bearing 6 spines of approximately the same length.

AN1 (Figure 2C)—Uniramous, unsegmented, and conical with 2 long aesthetascs, 2 smaller aesthetascs, and one simple setae on the terminal end.

AN2 (Figure 2D)—Protopodite long, ending in a point with 2 rows of spinules distally, small endopodite bud near base. Exopodite long, spinulose distally; 2 small spines just subterminal, innermost spinulose.

MAX1 (Figure 2F)—Endopodite 2-segmented; proximal segment with 1 long simple or sparsely plumose seta, distal segment with 4 terminal setae (2 plumose, 2 plumodenticulate) and 1 subterminal plumose seta. Basal endite with 4 plumodenticulate cuspidate and 2 plumodenticulate terminal setae and 1 subterminal plumose seta; smaller coxal endite with 5 plumose setae and 2 simple setae.

MAX2 (Figure 2E)—Scaphognathite with 9 plumose marginal setae and a plumose apical tip. Endopodite simple with 4 (rarely 5) terminal plumodenticulate setae and 1 simple seta. Basal endite slightly bilobed; 4-5 plumodenticulate setae on distal lobe and 5 (rarely 4) plumodenticulate setae on proximal lobe. Coxal endite bilobed; 3-4 plumose setae on distal lobe and 4 plumose setae on proximal lobe.

MXP1 (Figure 2A)—Exopodite with 4 long, plumose natatory setae. Endopodite 5-segmented; setation formulae (proximal to distal): 3, 2, 1, 2, 5. Terminal segment with 5 setae (4 multidenticulate and 1 short, simple). Basiopodite with up to 9 setae.

MXP2 (Figure 2B)—Exopodite with 4 plumose

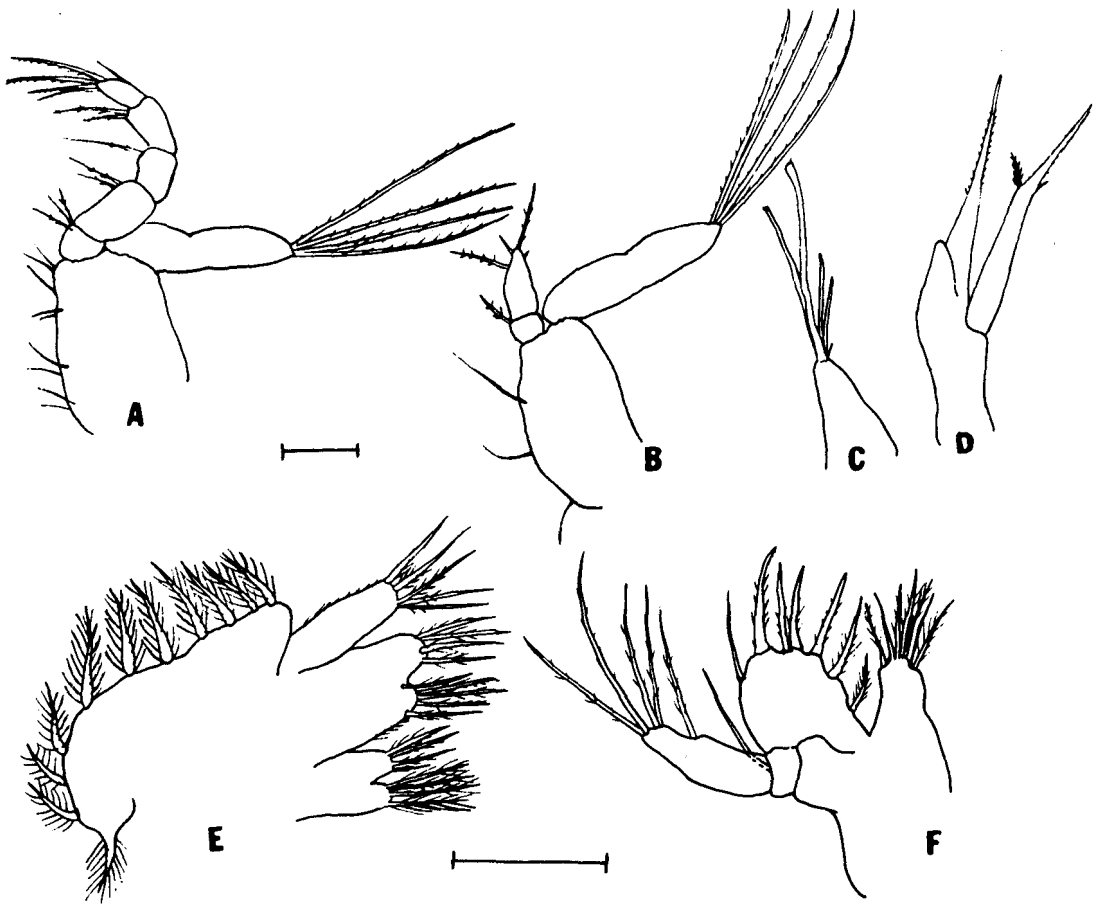

FIGURE 2.—*Libinia emarginata*. Appendages of stage I zoea. (A) first maxilliped, (B) second maxilliped, (C) antennule, (D) antenna, (E) maxilla, (F) maxillule. All unmarked scales = 0.1 mm.

natatory setae. Endopodite 2-segmented; terminal segment with 4 setae (2 plumodenticulate and 2 simple). Basiopodite with 3 setae.

Zoea II

Size and weight—Average carapace length, 0.94 mm (range 0.89-0.98 mm), average total length 2.69 mm (range 2.56-2.82 mm). Average dry weight, 0.0654 mg (range 0.0613-0.0712 mg).

Carapace (Figure 1D) same as for stage I. Dorsal spine proportionately shorter and stouter than before. Ventrolateral margin now with 8-10 small plumose setae. Eyes stalked.

Abdomen (Figure 1F) with 6 somites. Somite 2 with small anteriorly curved knobs as before. Somites 2-5 with 2 pleopod buds ventrally. Telson as in stage I.

AN1 (Figure 3C)—With 2 long, thick aesthetascs, 4 smaller aesthetascs, and 1-2 simple setae or thin aesthetascs on terminal end.

AN2 (Figure 3D)—Protopodite same as before, endopodite bud at least half length of protopodite. Exopodite same as before.

MAX1 (Figure 3F)—Endopodite same as before. Basal endite with 8 terminal setae (5 denticulate cuspidate and 3 plumodenticulate), and 2 subterminal plumose setae; coxal endite with 8 setae (5 plumose and 3 simple).

MAX2 (Figure 3E)—Scaphognathite with 16 (in South Carolina reared) or 20 (in Rhode Island reared and field samples) plumose marginal setae. Endopodite with basal endite and coxal endite same as in stage I.

MXP1 (Figure 3A)—Exopodite with 6 large plumose natatory setae. Endopodite same as before. Basiopodite with up to 10 setae.

MXP2 (Figure 3B)—Exopodite with 6 large,

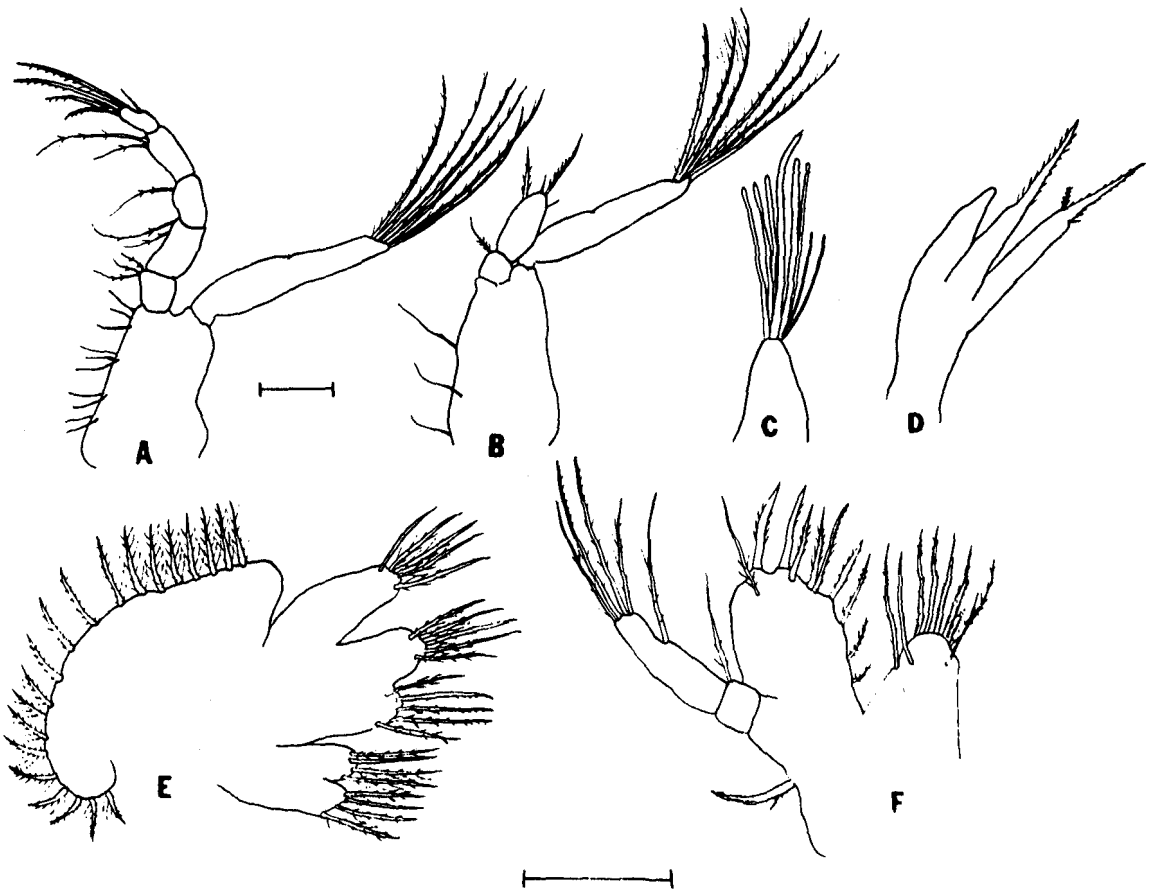

FIGURE 3.—*Libinia emarginata*. Appendages of stage II zoea. (A) first maxilliped, (B) second maxilliped, (C) antennule, (D) antenna, (E) maxilla, (F) maxillule. All unmarked scales = 0.1 mm.

plumose natatory setae. Endopodite and basiopodite same as before.

Megalopa

Size and weight—Average carapace length, 1.21 mm (range 1.16-1.28 mm), average total length 2.14 mm (range 2.07-2.17 mm). Average dry weight 0.205 mg (range 0.145-0.259 mg).

Carapace (Figure 4A, B) without spines; short rostrum tapers to blunt tip. Median line of carapace depressed between eyes with 2 partially connected protuberances along gastric region, paired protuberances at cardiac region and slight protuberance at posterior border. Lateral carapace region with 3 paired protuberances, surface somewhat expanded over posterolateral area.

Abdomen (Figure 4B) with 6 somites plus telson.

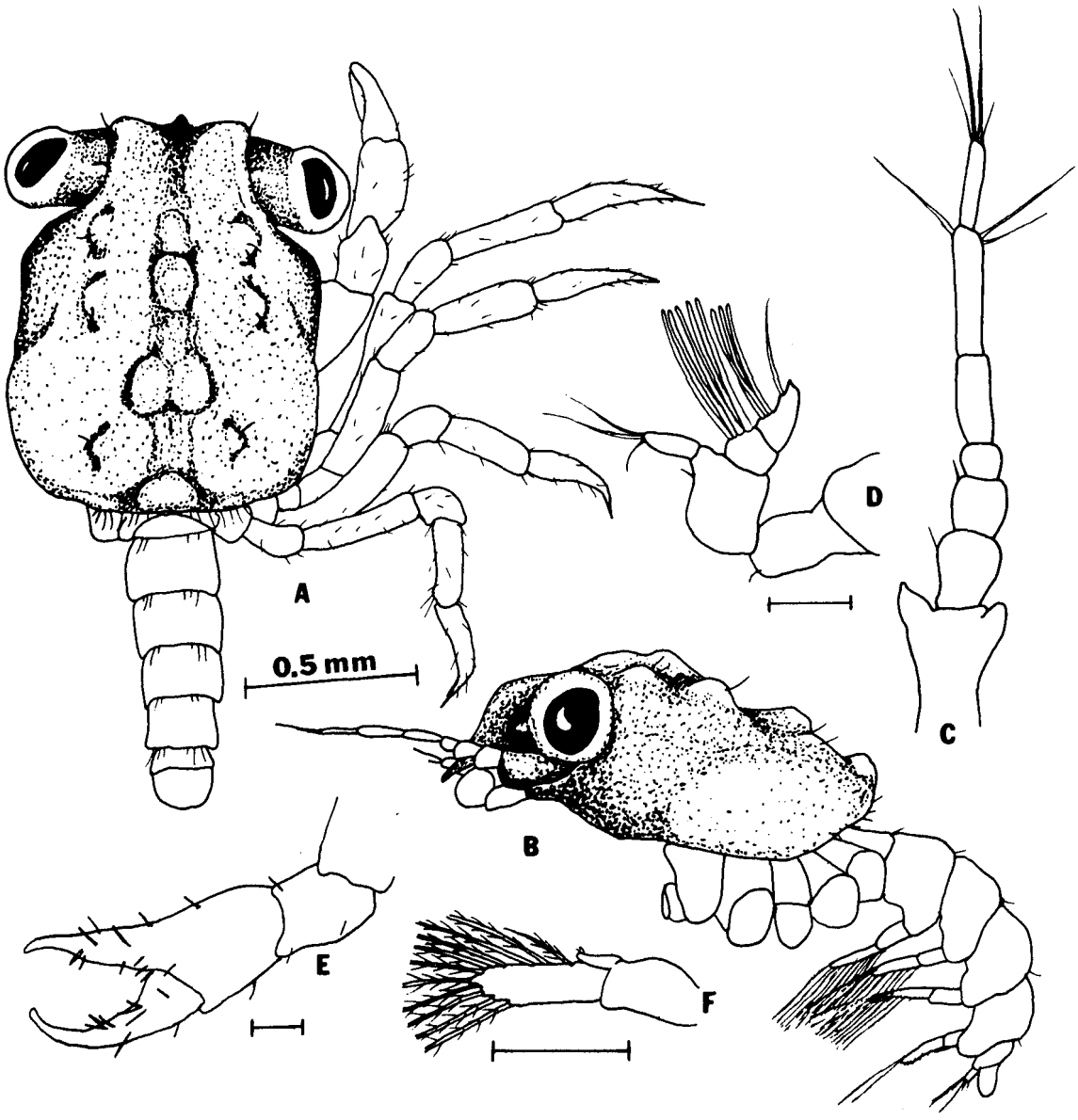

FIGURE 4.—*Libinia emarginata* megalopa. (A) dorsal view, (B) lateral view, (C) antenna, (D) antennule, (E) cheliped, (F) pleopod. All unmarked scales = 0.1 mm.

AN1 (Figure 4D)—Peduncles 3-segmented; basal segment bare, second and third segment with 1 short seta each. Inner flagellum unsegmented with 3 terminal simple setae; dorsal flagellum 2-segmented proximal segment with 5 aesthetascs; distal with 3 aesthetascs and 1 subterminal simple seta.

AN2 (Figure 4C)—Peduncle 3-segmented. Flagellum 4-segmented, with 2 distal segments having 3 subterminal and 4 terminal simple setae, respectively.

MN (Figure 5A)—Palp 3-segmented with 5 terminal setose setae.

MAX1 (Figure 5B)—Endopodite unsegmented with 2-3 terminal simple setae. Basal endite with 14 processes (6 plumodenticulate cuspidate, 6 plumodenticulate, 2 short multidenticulate) and 2-3 marginal plumose setae; coxal endite with 3 plumodenticulate and 3 simple terminal setae and 4 subterminal plumose setae.

MAX2 (Figure 5C)—Scaphognathite with 31-33 (in South Carolina reared) or 33-35 (in Rhode Island reared and field samples) plumose marginal setae. Endopodite with 0-1 seta. Basal endite bilobed; distal portion and proximal portion with 6-7 plumodenticulate or plumose setae each. Coxal endite bilobed; distal portion with 3 plumose setae and proximal portion with 4 plumose and 1 simple setae.

MXP1 (Figure 5D)—Exopodite 2-segmented, proximal segment with 1 plumose seta; distal segment with 5 plumose and 1 simple setae. Endopodite unsegmented with 1-3 terminal setae. Basal endite with 8-10 plumodenticulate setae; coxal endite with 6 plumodenticulate and 1 plumose setae. Epipodite with 4 long simple setae.

MXP2 (Figure 5E)—Exopodite 2-segmented; distal segment with 5-6 long plumose setae. Endopodite 4-segmented; setation formulae (proximal to distal) 0, 1, 3, 6. Distal setae, 5 plumodenticulate cuspidate, 1 simple.

MXP3 (Figure 5F)—Exopodite 2-segmented; terminal segment with 3-4 long plumose and 2 small simple terminal setae. Endopodite 5-segmented; setation formulae (proximal to distal) 9-10, 7-8, 4, 6, 4, mostly plumodenticulate or serrate plumose setae. Epipodite with 3 terminal and 3 subterminal multidenticulate setae.

P1 to P5 (Figure 4A, E)—Moderately setose, cheliped similar to adult form.

PL2 to PL6 (Figure 4F)—Exopodite 2-segmented; plumose natatory setae on distal segment varies from 11 (PL2) to 8 (PL5). Endopodite small with 2 small hooks.

Zoeal Chromatophores

Libinia emarginata larvae are sparsely pigmented in freshly sacrificed specimens. Chromatophore color ranges from orange to a dark brown-red. Distinctive pigment areas with little individual variation include an orange spot at the posterior dorsal spine base, a deep red area posterior to the eye base, a large distinctive red spot on the posterolateral carapace region near the carapace setae and red pigmentation of the mandibles. The abdomen is pigmented in the central ventral area of each segment juncture. Additional pigment spots occur on the carapace and appendages but do not appear consistent in location or occurrence.

DISCUSSION

There is only a narrow range of temperature-salinity conditions at which the larvae successfully develop in the laboratory. With South Carolina larvae, these conditions are 25°C and 30‰, while with Rhode Island larvae, maximum development occurs at 20°C and 30‰. The difference in these temperatures possibly reflects the influence of latitudinal separation on larval development, however, until critical experiments are undertaken, this cannot be confirmed (Vernberg 1962; Vernberg and Costlow 1966; Sastry 1970; Sastry and Vargo 1977). The larvae develop best in temperatures that represent the mean temperature during the larval season. Gravid *L. emarginata* were collected from May to September in South Carolina in coastal waters that had a mean water temperature near 25°C. In Rhode Island, gravid crabs were collected from July to August in bay and coastal waters that had a mean water temperature near 20°C.

The narrowness of successful rearing conditions may reflect inadequate rearing variables such as diet, substrate, water circulation, etc. (Roberts 1972; Sulkin 1975; Sulkin and Norman 1976), or reflect the habitat of *L. emarginata*. With larvae that develop entirely in bay or coastal waters, there follows a characteristic inability of larvae to develop successfully over wide ranges of temperature and salinity, while larvae from estuarine waters usually develop in a much wider range of temperatures and salinity. In the offshore

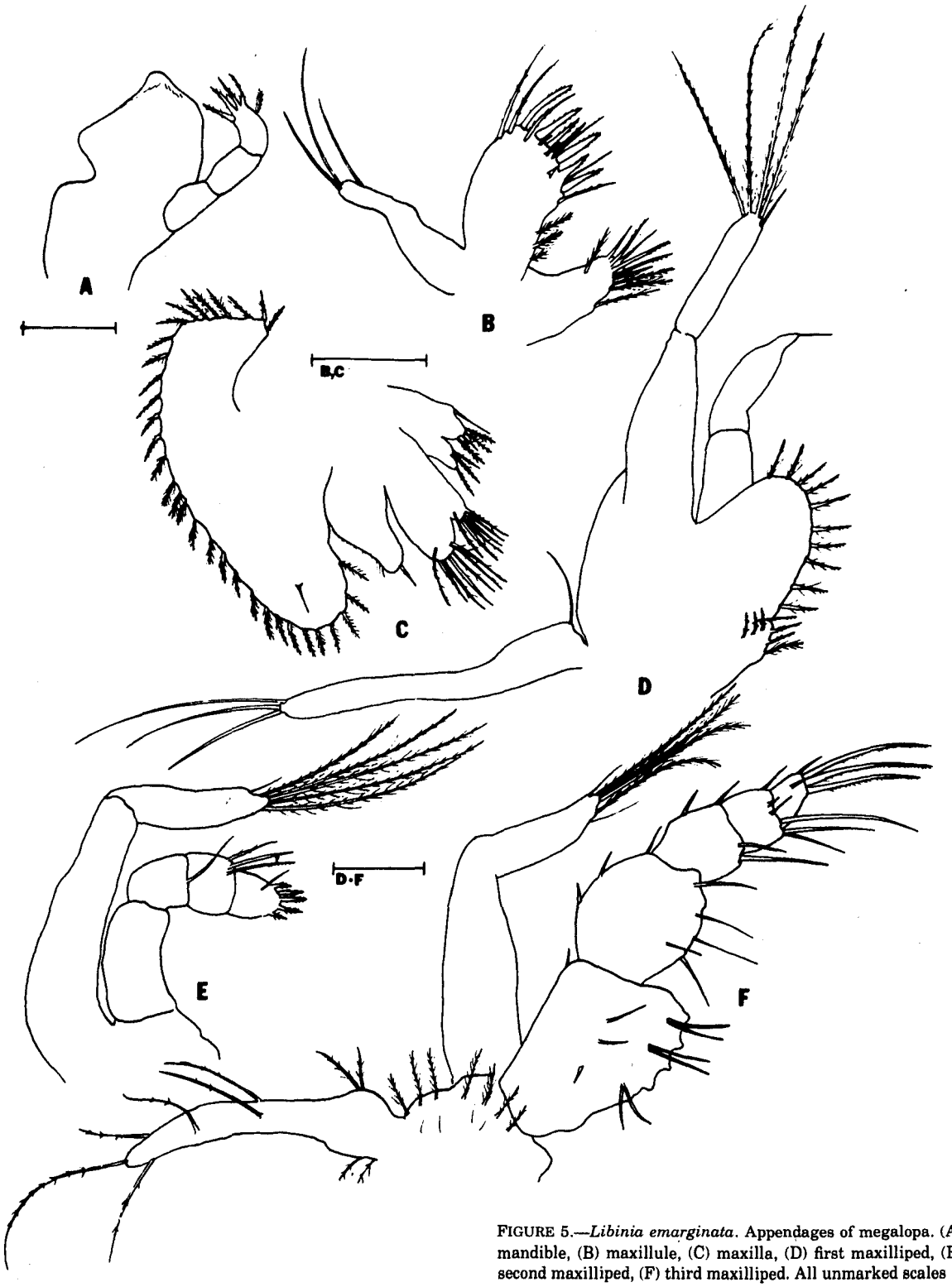

FIGURE 5.—*Libinia emarginata*. Appendages of megalopa. (A) mandible, (B) maxillule, (C) maxilla, (D) first maxilliped, (E) second maxilliped, (F) third maxilliped. All unmarked scales = 0.1 mm.

spawner, *Callinectes sapidus*, for example, larvae will complete early development only at 25°C and 31.1‰ (Costlow and Bookhout 1959) while an estuarine xanthid, *Rhithropanopeus harrisii*, completes development at temperatures of 20°, 25°, and 30°C and salinities between 2.5 and 40‰ (Costlow et al. 1966). Throughout this study, all gravid females were collected in near coast bay or open coastal waters >30‰ salinity).

The duration of development within the genus *Libinia* also varies. Boschi and Scelzo (1968) reported that development for *L. spinosa* required 20-30 days (at 20°C) or an average of 8-10 days per stage. *Libinia erinacea* required 14 days (at 20°C) or 9 days (at 25°C) to reach first crab stage (Yang 1967). Sandifer and Van Engel (1971) reported that *L. dubia* needed only 9 days (at 25.5°-28.5°C) for larval development. *Libinia emarginata* is intermediate with at least 14 days needed to reach first crab stage. As pointed out by Sandifer and Van Engel (1971), these differences in development times may be explained, in part, by rearing temperatures. For *L. erinacea*, total development time is reduced by 5 days with a 5°C increase in temperature. However, other factors must also play a role in development for *L. spinosa* and *L. erinacea* reared at the same temperature (20°C) and given the same food source (*Artemia*) still showed a 6- to 16-day difference in development times.

The number of larval stages for *L. emarginata* is typical for the family Majidae (Gurney 1942; Hart 1960). Larvae from the three sources examined showed few differences. South Carolina larvae tended to be slightly smaller than Rhode Island and field samples (Table 2). Morphology of larvae was virtually identical in all cases, except for the scaphognathite setal number being consistently lower in South Carolina larvae. In this case, reared larvae appear to represent accurate "mimics" of wild larvae, even to specific setal types. However, it is unknown if this similarity also pertains to physiological or behavioral parameters.

In comparing larval descriptions of *L. erinacea, L. dubia, L. spinosa,* and *L. emarginata*, we have found that carapace setation and armature of the abdominal somites are the most useful zoeal characters (Table 3). *Libinia erinacea* and *L. spinosa* may be distinguished by the presence of lateral spines on abdominal somite 2, as opposed to small knobs for *L. dubia* and *L. emarginata*. *Libinia spinosa* may be differentiated from *L. erinacea* by the lack of setation on the ventrolateral margin of the carapace. The first zoea of *L. dubia* and *L. emarginata* show no differences in general morphology and setal numbers. The second zoea of *L. emarginata* usually has 10 setae on the ventrolateral margin while *L. dubia* has 8 setae but as in stage I there appears to be no ready

TABLE 3.—Comparison of diagnostic characteristics for zoeal stages of *Libinia erinacea, L. spinosa, L. dubia,* and *L. emarginata*.

Species and stage	Dorsal spine	Abdominal somites		Carapace setation
		Somite 2	Somites 3-5	
L. erinacea:[1]				
Zoea I	Single, long, curved posteriorly, sometimes ending in short hook	Two lateral spines, one on each side, pointing posteriorly	Two medium spines, one on each side, pointing posteriorly	6 setae on ventrolateral margin
Zoea II	Same as zoea I	Same as in zoea I, but with pair of pleopod buds per somite	Same as in zoea I, but with pair of pleopod buds per somite	8 setae on ventrolateral margin
L. spinosa:[2]				
Zoea I	Same as in *L. erinacea*	Same as in *L. erinacea*	Two long spines, one on each side, pointing posteriorly	No setation on ventrolateral margin
Zoea II	Same as in *L. erinacea*	Same as in *L. erinacea*	Same as in zoea I, but with pair of pleopod buds per somite	No setation on ventrolateral margin
L. dubia:[3]				
Zoea I	Single, fairly long, curved posteriorly	Two small curved knobs, one on each side	Two small spines, one on each side, pointing posteriorly	6-7 setae on ventrolateral margin
Zoea II	Same as zoea I	Same as in zoea I, but with pair of pleopod buds per somite	Same as in zoea I, but with pair of pleopod buds per somite	7-8 setae on ventrolateral margin
L. emarginata				
Zoea I	Single, long, slightly curved posteriorly	Same as in *L. dubia*	Same as in *L. dubia*	7 setae on ventrolateral margin
Zoea II	Short and stout	Same as in *L. dubia*	Same as in *L. dubia*	8-10 setae on ventrolateral margin

[1]From Yang (1967).
[2]From Boschi and Scelzo (1968).
[3]From Sandifer and Van Engel (1971).

TABLE 4.—Average carapace lengths, total lengths and dry weights for the larval stages of *Libinia emarginata, L. dubia, L. erinacea,* and *L. spinosa.*

Species	Carapace length (mm)			Total length (mm)			Dry weight (mg)		
	Zoea I	Zoea II	Megalopa	Zoea I	Zoea II	Megalopa	Zoea I	Zoea II	Megalopa
L. emarginata	0.78	0.94	1.21	2.19	2.69	2.14	0.0214	0.0654	0.205
L. dubia[1]	0.81	0.97	1.16	2.35	2.78	2.11	—	—	—
L. erinacea[2]	0.88	1.03	1.24	—	—	—	—	—	—
L. spinosa[3]	0.80	0.96	1.30	2.30	2.80	3.10	—	—	—

[1]From Sandifer and Van Engel (1971).
[2]From Yang (1967).
[3]From Boschi and Scelzo (1968).

means to distinguish the species. *Libinia dubia* zoea, as described by Sandifer and Van Engel (1971), are larger than *L. emarginata* zoea (Table 4), but statistical analysis of various samples would be needed to determine if a consistent size difference exists. Differences in setal types may also occur, but these have not been described for *L. dubia*. As with larvae of various species of *Uca* (Hyman 1920), a rapid, reliable means to distinguish *L. emarginata* and *L. dubia* larvae to species does not exist.

Megalopae of all four species, however, are distinguishable. *Libinia spinosa* has a distinct dorsal spine which curves posteriorly (Boschi and Scelzo 1968) while the dorsal spine of *L. erinacea* is long and upright (Yang 1967). *Libinia dubia* and *L. emarginata* megalopae both lack a dorsal spine. The median cardiac protuberance of the *L. dubia* megalopa is single but is paired in *L. emarginata*. This difference is relatively easy to observe, thus unlike zoeal stages, *L. dubia* and *L. emarginata* megalopae may be identified to species.

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