# LARVAL DEVELOPMENT IN TWO POPULATIONS OF THE GHOST SHRIMP CALLICHIRUS MAJOR (DECAPODA: THALASSINIDEA) UNDER LABORATORY CONDITIONS

## Karen M. Strasser and Darryl L. Felder

## ABSTRACT

Zoeal and first postlarval stages of the Gulf of Mexico and Florida Atlantic populations of the ghost shrimp *Callichirus major* were obtained from laboratory cultures. Forty to sixty larvae from each parental female (8 from the Gulf population, and 4 from the Florida Atlantic population) were reared individually to obtain stage-duration data, while morphological studies were based on animals from mass cultures. Durations of larval stages were similar in larvae from different females and different populations. The Florida Atlantic population of *C. major* passed through 4 or 5 zoeal stages before molting to the decapodid stage. In contrast, the Gulf populations, duration for each of the first 3 zoeal stages was about 2 days. Duration of the fourth zoeal stage was, as in the decapodid stage, typically 3-4 days. When present, the fifth zoeal stage was usually 3-4 days in duration. Larvae from these populations were morphologically similar, with the persistent exception of the outermost spines on the posterior margin of the telson and the dorsal spine on abdominal segment 2, both of which were longer in the Gulf of Mexico population. Comparisons with other species in the genus *Callichirus* showed that the 2 populations of *C. major* were morphologically closer to the Brazilian *Callichirus* sp. (formerly referred to as *C. major*) than to *C. islagrande* and *C. garthi.* 

The genus Callichirus Stimpson, 1866, redefined by Manning and Felder (1986), includes the species Callichirus major (Say, 1818), C. islagrande Schmitt, 1935, C. seilacheri Bott, 1955, C. garthi Retamal, 1975, and C. adamas Kensley, 1974. At least one more undescribed species of Callichirus (previously reported as C. major) is known from the coast of Brazil (Staton and Felder, 1995; DLF, personal observation). Larval descriptions are available only for C. garthi from the coast of Chile (Aste and Retamal, 1983), C. islagrande from the northern Gulf of Mexico (Strasser and Felder, in press b), and the first three stages of Callichirus sp. from Brazil (as C. major in Rodrigues, 1976). Although Callichirus major has been well studied (Felder and Griffis, 1994; Staton and Felder, 1995; Strasser and Felder, 1998; Strasser and Felder, in press a, b), the larval development of this species has not been described.

The range of *C. major* as traditionally treated extends in the northern Gulf of Mexico from South Padre Island, Texas, to Horn Island, Mississippi, and on the east coast of the United States from Beaufort Inlet, North Carolina, to Cape Canaveral, Florida (Williams, 1984). The distribution breaks on both sides of the Florida peninsula. Since *C.* 

major typically prefers quartzite sands, the calcareous sands of the southern Florida peninsula may serve as a barrier to its distribution (Staton and Felder, 1995). Flow patterns of the Gulf stream and the Florida current may also inhibit gene flow between the Gulf and Atlantic populations, as postulated for other coastal marine invertebrates (Reeb and Avise, 1990). Gulf of Mexico and Atlantic Coast populations have been shown to be genetically divergent (Staton and Felder, 1995) and to have different intertidal distributions (Felder and Griffis, 1994). The Florida Atlantic population of C. major prefers middle to high intertidal of beaches and inlet margins, while the Gulf of Mexico population appears to prefer low intertidal to subtidal substrates along bayward sides and inlet margins of barrier islands. In the Gulf, C. major is typically replaced in the high intertidal by C. islagrande, which is not found in the Atlantic. The Florida Atlantic population lives at a relatively stable 30-35 ppt salinity, while the Gulf of Mexico population often experiences lower and more fluctuating salinities ranging from 12-30% (Felder and Griffis, 1994).

Differing qualities of the habitats in these populations have led us to examine differences in their responses to settlement stimuli (Strasser and Felder, in press a). The present work was undertaken to determine whether there are also morphological differences in their developmental stages. This has additionally facilitated morphological comparisons between the two populations of *C. major* and other species of *Callichirus* for which larval descriptions are available.

#### MATERIALS AND METHODS

Ovigerous females were collected from the bayward side of a barrier island (Isles Dernières, Louisiana) in July, August, and September, 1996; and from a sand flat on the north side of Sebastian Inlet (Florida) in May, June, and July 1997, by previously described methods (Felder, 1978). Adult females were maintained in 20-cm diameter finger bowls with daily water changes until eggs hatched. Animals from the Atlantic population of C. major were maintained at 35 ppt salinity, approximately 27-29°C, while those from the Gulf population were kept at 25 ppt salinity, 27°C. Sea water was taken from well offshore of Florida and Louisiana, filtered, and aerated before use in culture of animals from the Atlantic and Gulf populations, respectively. To determine stage durations, 40-60 larvae from each parental female (8 from the Gulf of Mexico population, 4 from the Atlantic population) were reared individually through the first juvenile stage (J1). ZI (first zoeal stage) larvae were moved to individual compartments upon hatching and maintained at 27°C, in filtered sea water, on a 12:12 light:dark cycle. Each day larvae were moved to containers with new sea water, fed freshly hatched nauplii of Artemia (Great Salt Lake), and examined to determine their stage of development. Observations were terminated when animals reached the first juvenile stage (J1).

Animals used for morphological comparisons were obtained from mass cultures. Larvae (typically 100-200 at ZI) were maintained in 20-cm diameter finger bowls with daily water changes under conditions mentioned above. Animals were fixed in 70% ethanol, stained with chlorozol black, and transferred to glycerine prior to dissection. At least 10 animals were dissected for each stage, with both right and left appendages used for setal counts. Line illustrations were made on a Nikon inverted microscope fitted with a camera lucida. Appendages were also examined under an Olympus compound microscope equipped with differential interference contrast (Nomarski) optics. Illustrations of the Florida Atlantic population of Callichirus major were provided for only those features that differed distinctly in morphology from the Gulf population. Measurements were made with a calibrated ocular micrometer. Carapace length (CL) was measured from the rostral tip to the posterior midpoint of the carapace, and total length (TL) was measured from the rostral tip to the posterior midpoint of the telson. Arrangement of setae is listed sequentially from proximal to distal margin as in Nates et al. (1997) and Konishi (1989). Setal groups on successive segments are separated with a comma (,). Groups of setae on the same segment, or on different lobes of the same segment, article or endite, are separated with a plus (+). A question mark (?) designates questionable distinctions between setae and aesthetascs. Roman numerals are used to describe the pattern of processes on the posterior margin of the telson.

### RESULTS

Eggs changed in color from bright orangered to a translucent brown in the days prior to hatching in both populations of C. major. Ovigerous females from the Gulf of Mexico were maintained for up to 22 days before the eggs hatched, while one female from the Atlantic coast of Florida held her eggs for 17 days before they hatched. Eggs typically hatched at night in both populations. Larvae that hatched as prezoeae were not fully formed, and were not viable. These animals were unable to swim and twitched on the bottom of the bowl until they died. Late stage eggs that were dropped by the female before hatching were also not viable, even when aeration was provided.

Zoeal stages (ZI–ZV, at maximum) consumed nauplii of *Artemia* as well as each other. While the decapodid stage (D) was also observed to feed, it fed much less than did the preceding zoeal stage. The first three zoeal stages (ZI–ZIII) exhibited strong positive phototaxis. While the fourth zoeal stage (ZIV) also was attracted to light, many individuals in the mass cultures reacted indifferently. At the decapodid stage, animals did not exhibit obvious phototaxis.

The Gulf of Mexico population passed through four zoeal stages (ZI-ZIV) before molting to D. In rare instances, some larvae passed through a ZV or molted directly from ZIII to D. In contrast, larvae of the Florida Atlantic population of C. major regularly passed through four or five zoeal stages and no larvae passed directly from ZIII to D (Tables 1, 2, Fig. 1). Survival to J1 was typically higher in animals that molted directly from ZIV to D than in those that molted from ZIV to ZV (Table 2). Durations of the zoeal stages were similar in larvae from different females, and from different populations (Table 1). Mean survival to J1 was also similar between populations (80.3% in the Gulf of Mexico population, 79.4% in the Florida Atlantic population).

### DESCRIPTION OF ZOEAL AND DECAPODID STAGES

Morphological descriptions of the Gulf of Mexico and Florida Atlantic populations of *Callichirus major* are provided for stages ZI-ZIV and D. ZV was variable, with appendages like those of ZIV, D, or some gra-

Table 1. Mean duration in days ( $\pm 95\%$  CI) of the first to fifth zoeal stages (ZI to ZV), and the decapodid stage (D) in Gulf of Mexico and Florida Atlantic populations of the ghost shrimp *Callichirus major*. Each batch consists of larvae from a different parental female. Only animals that survived to J1 (first juvenile stage) (N) were used to calculate mean durations for each stage; N<sub>0</sub> indicates the starting number of ZI larvae.

Batch	N	N <sub>o</sub>	ZI	ZII	ZIII	ZIV	ZV	D
Gulf	of Me	xico po	pulation					
1	29	60	2.21 (±0.21)	1.97 (±0.12)	2.24 (±0.17)	3.34 (±0.18)		2.93 (±0.14)
2	36	40	2.50 (±0.19)	2.14 (±0.20)	2.19 (±0.16)	3.53 (±0.21)	*4	3.00 (±0.0)
3	59	60	1.92 (±0.07)	1.52 (±0.13)	2.20 (±0.11)	3.88 (±0.15)		3.00 (±0.0)
4	57	60	2.07 (±0.07	2.00 (±0.09)	2.26 (±0.12)	3.44 (±0.17)		3.09 (±0.08)
5	48	60	2.08 (±0.10)	2.00 (±0.08)	2.02 (±0.07)	3.65 (±0.15)		2.98 (±0.07)
6	38	60	2.52 (±0.17)	2.00 (±0.15)	2.76 (±0.28)	3.66 (±0.19)		3.05 (±0.07)
7	51	60	2.22 (±0.12)	2.04 (±0.11)	2.43 (±0.15)	3.78 (±0.14)		2.96 (±0.06)
8	33	40	2.12 (±0.12)	2.36 (±0.21)	2.52 (±0.25)	3.31 (±0.17)		3.00 (±0.0)
Mear	durati	ions	2.18 (±0.05)	1.97 (±0.05)	2.31 (±0.06)	3.60 (±0.06)		3.01 (±0.02)
Flori	la Atla	ntic po	opulation					
1	24	40	2.04 (±0.09)	2.17 (±0.16)	3.00 (±0.28)	3.92 (±0.25)	4.17 (±0.17)	3.33 (±0.24)
2	38	40	$2.00 (\pm 0.0)$	2.03 (±0.0)	2.08 (±0.10)	3.67 (±0.20)		3.34 (±0.16)
3	32	40	$2.03 (\pm 0.0)$	1.97 (±0.10)	2.06 (±0.12)	3.75 (±0.22)	3.06 (±0.14)	3.53 (±0.24)
4	36	40	1.61 (±0.17)	1.78 (±0.14)	2.08 (±0.12)	3.44 (±0.17)	3.05 (±0.08)	3.22 (±0.14)
Mear	durati	ions	1.91 (±0.06)	1.97 (±0.06)	2.25 (±0.09)	3.67 (±0.09)	3.16 (±0.11)	3.35 (±0.09)

\* 1 individual molted from ZIV to ZV.

dation between the two. Illustrations for the Atlantic population of *C. major* are presented for only structures that differ from those of the Gulf population. For each appendage, setal patterns are given from proximal to distal segments. Carapace length (CL) and total length (TL) are given as the mean  $\pm 95\%$  CI in mm, followed by the range of measurements from 10 specimens.

Larvae from both populations had two or three red chromatophores on each lateral margin of the carapace, often forming a red line when expanded. Two other red chromatophores, usually fused, were centered near the mandibles. These chromatophores were present on all larval stages and the decapodid.

### **Gulf Population**

### Zoea I

### Figs. 2a, 3a-j, 12a

Size.—CL =  $1.7 \pm 0.11$  mm, 1.35-1.84 mm; TL =  $3.99 \pm 0.20$  mm, 3.49-4.36 mm.

Table 2. Fate and survivorship of larval *Callichirus major* that molted from the fourth zoeal stage (ZIV) to the fifth zoeal stage (ZV) or directly to the decapodid stage (D) in larval cultures from eight ovigerous females from the Gulf of Mexico population and four from the Florida Atlantic population. Each culture consists of larvae from a different parental female.  $N_0$  = number surviving beyond ZIV;  $N_1$  = number molting ZIV to ZV;  $P_{1J}$  = percentage of  $N_1$  surviving to J1;  $N_2$  = number molting ZIV to D;  $P_{21}$  = percentage of  $N_2$  surviving to J1 (first juvenile stage).

Culture number	From ZIV $N_0$	To ZV $N_1$	Then to D and JI $P_{ij}$	To D N <sub>2</sub>	Then to J1 $P_{2J}$	
Gulf of Mexico population						
1	30			30	96.7	
2	36	1	100.0	35	100.0	
3	59			59	100.0	
4	58			58	98.3	
5	58	1	0.0	57	84.2	
6	*39			39	89.7	
7	**52			52	96.2	
8	**33			33	97.0	
Florida Atlantic population						
1	30	11	54.6	19	95.0	
2	39			39	100.0	
3	40	26	53.9	14	92.9	
4	40	23	82.6	17	100.0	

\* 4 animals molted directly from ZIII to D. \*\* 1 animal molted directly from ZIII to D.



Fig. 1. Mean proportion of larvae at each stage during development of (A) the Gulf of Mexico and (B) the Florida Atlantic populations of *Callichirus major*. Mean proportions are derived from the individual rearings of 8 parental females for the Gulf population and 4 parental females of the Atlantic population. The first through fifth zoeal stages (ZI to ZV), the decapodid stage (D), and all juvenile stages passed D (J) are labeled under the peak of each line.



Fig. 2. *Callichirus major* from the Gulf of Mexico population, dorsal view of larvae: a, ZI stage; b, ZII stage; c, ZIII stage; d, ZIV stage; e, decapodid stage. Scale = 1 mm.

*Carapace* (Fig. 2a).—Shorter than abdomen, with pterygostomial spine; rostrum well developed, smooth, sometimes with serrations at distal end; eyes sessile.

Abdomen (Figs. 2a, 12a).—Somite 2 with strong anterolateral projections, weakly developed on somite 1; somites 2–5 with posterolateral projections and posterodorsal spines; dorsal spine elongate on somite 2, sometimes reaching posterior margin of somite 5; dorsal spine on somite 3 much shorter than that of 2; somites 4 and 5 with short distal spines.

Antennule (Fig. 3a).—Elongate, exopodal and endopodal lobes not distinct; 6 terminal aesthetascs, 3 elongate and thick, 3 short and thin; 1 long, plumose seta on future endopodal lobe.

Antenna (Fig. 3b).—Protopod with 1 distal spine between rami; endopod with 1 long, plumose seta distally, 0 or 1 smaller seta; scaphocerite (exopod) armed with 1 strong dis-



Fig. 3. *Callichirus major* from the Gulf of Mexico population, ZI stage: a, antennule; b, antenna; c, right mandible; d, left mandible; e, maxillule; f, maxilla (plumose condition not shown); g, maxilliped 1; h, maxilliped 2; i, maxilliped 3; j, telson. Scales = 0.2 mm.

tolateral spine, 11–13 plumose setae on inner margin, and 1 plumose seta on outer margin.

*Mandible* (Fig. 3c, d).—Asymmetrically dentate; incisor process with 7 or 8 teeth on right mandible, 8 or 9 teeth on left mandible; molar process denticulate on both mandibles.

Maxillule (Fig. 3e).—Coxal endite with 9–13 marginal setae; basal endite with 3 plumose setae, 5 large dentate spines, and 5 or 6 smaller dentate spines, inner margin with 1 plumose seta; endopod bisegmented, distinction between segments sometimes obscure, with 2, 2+4 setae; protopod without setae.

Maxilla (Fig. 3f).—Coxal endite bilobed, 12–16 setae on proximal lobe, 4 or 5 on dis-

tal lobe; basal endite bilobed, 7–10 setae on each lobe; endopod with 5 lobes, (2 or 3)+2+2+2+3 setae; scaphognathite with 22–29 setae; all setae plumose.

Maxilliped 1 (Fig. 3g).—Coxa with 4-8 setae; basis with 4 submarginal, 9-15 marginal setae; endopod 4-segmented, 4, (1 or 2), 2, 4 setae; exopod with 2 articulated segments, proximal segment without setae, distal segment with 7 setae on distal margin; bilobed epipod without setae; all setae plumose.

*Maxilliped 2* (Fig. 3h).—Coxa with 2 or 3 setae; basis with 5 setae; endopod 4-segmented, 4, 1, 2, 3–5 setae; exopod unsegmented, 7–9 setae on distal margin; all setae plumose. *Maxilliped 3* (Fig. 3i).—Coxa with 0 or 1 seta; basis with 2 setae; endopod 4-segmented, 2, 2, (3 or 4), 3 setae; exopod unsegmented, 8 or 9 setae on distal margin; all setae plumose.

Pereiopods.—Not developed.

Pleopods.—Not developed.

Telson (Fig. 3j).—Triangular, narrow anterior part not differentiated from abdominal segment 6; processes on posterior margin arranged as (I, II, III, IV, III, II, I), (I) outermost process a long naked spine, (II) second process "anomuran hair," (III) 19-22plumodenticulate setae, (IV) center process a naked spine, longer than process III, shorter than process I.

### Zoea II

#### Figs. 2b, 4a–l, 12b

Size.—CL =  $2.01 \pm 0.06$  mm, 1.84-2.12 mm; TL =  $4.49 \pm 0.11$  mm, 4.17-4.67 mm.

*Carapace* (Figs. 2b, 12b).—Rostrum elongate and serrated; eyes separated from carapace.

Abdomen (Figs. 2b, 12b).—No marked change from ZI.

Antennule (Fig. 4a).—Elongate, weakly bilobed; peduncle with 1 long plumose, 0 or 1 short seta; endopodal bud with 1 terminal plumose seta; exopod with 7–10 terminal, 1 subterminal aesthetascs.

Antenna (Fig. 4b).—Protopod with 1 distal spine between rami; endopod without setae; scaphocerite armed with 1 strong distolateral spine, 12–14 plumose setae on inner margin, 1 plumose seta on outer margin.

*Mandible* (Fig. 4c, d).—No marked change from ZI.

Maxillule (Fig. 4e).—Coxal endite with 11-13 marginal plumose setae; basal endite with 3 plumose setae, 5 or 6 large dentate spines, and 5 or 6 smaller dentate spines, inner margin with 1 plumose seta; endopod bisegmented, distinction between segments sometimes obscure, 2, 2+(3-5) setae; protopod without setae.

*Maxilla* (Fig. 4f).—Coxal endite bilobed, 11–17 setae on proximal lobe, 4 or 5 on distal lobe; basal endite bilobed with 7–10 setae on each lobe; endopod with 5 lobes, 3+2+2+2+3 setae; scaphognathite with 21–29 setae; all setae plumose.

Maxilliped 1 (Fig. 4g).—Coxa with 4-8 setae; basis with 4 submarginal, 12-16 marginal setae; endopod 4-segmented, (3 or 4), (1 or 2), 2, 4 setae; exopod bisegmented, proximal segment without setae, distal segment with 6 or 7 setae on distal margin; bilobed epipod without setae; all setae plumose.

Maxilliped 2 (Fig. 4h).—Coxa with 0-3 setae on inner margin; basis with 5 setae; endopod 4-segmented, (4 or 5), 1, 3, (3-5) setae; exopod unsegmented, 8-10 setae on distal margin; all setae plumose.

*Maxilliped 3* (Fig. 4i).—Coxa with 0 or 1 seta; basis with 1 or 2 setae; endopod 4-segmented, 2, (2 or 3), (3–5), 4 setae; exopod unsegmented, 9 or 10 setae on distal margin; all setae plumose.

*Pereiopods* (Fig. 4j, k).—First and second pereiopods present, both without setae.

*Pleopods.*—Not developed.

Telson (Fig. 41).—No change from ZI.

### Zoea III Figs. 2c, 5a-h, 6a-h, 12c

Size.—CL =  $2.30 \pm 0.11$  mm, 2.09-2.55 mm; TL =  $5.17 \pm 0.09$  mm, 4.98-5.42 mm.

Carapace (Figs. 2c, 12c).—No marked change from ZII.

Abdomen (Figs. 2c, 12c).—No marked change from ZII.

Antennule (Fig. 5a).—Biramous, peduncle bisegmented; proximal segment with (0 or 1)+(2 or 3) short setae; distal segment with 2 or 3 plumose setae on inner margin, 1 plumose seta and 0-4 short setae on distal end; endopod with 0 or 1 plumose seta; exopod with 7–10 terminal, 2 subterminal aesthetascs.



Fig. 4. *Callichirus major* from the Gulf of Mexico population, ZII stage: a, antennule; b, antenna; c, right mandible; d, left mandible; e, maxillule; f, maxilla (plumose condition not shown); g, maxilliped 1; h, maxilliped 2; i, maxilliped 3; j, pereiopod 1; k, pereiopod 2; 1, telson. Scales = 0.2 mm.

Antenna (Fig. 5b).—Protopod with 1 distal spine between rami; endopod without setae; scaphocerite armed with 1 strong distolateral spine, 12–15 plumose setae on inner margin, 1 plumose seta on outer margin.

*Mandible* (Fig. 5c, d).—Asymmetrically dentate; incisor process with 7–9 teeth on right mandible, 8 or 9 teeth on left mandible; molar process denticulate on both mandibles; palps present as buds. *Maxillule* (Fig. 5e).—Coxal endite with 11–14 marginal plumose setae; basal endite with 3 plumose setae, 5 or 6 large dentate spines, and 5-7 smaller dentate spines, inner margin with 1 plumose seta; endopod bisegmented, distinction between segments sometimes obscure, 2, 2+(3 or 4) setae; protopod without setae.

*Maxilla* (Fig. 5f).—Coxal endite bilobed, 15–18 setae on proximal lobe, 5 on distal lobe; basal endite bilobed, 8–10 setae on each



Fig. 5. *Callichirus major* from the Gulf of Mexico population, ZIII stage: a, antennule; b, antenna; c, right mandible; d, left mandible; e, maxillule; f, maxilla (plumose condition not shown); g, maxilliped 1; h, maxilliped 2. Scales = 0.2 mm.

lobe; endopod with 5 lobes, 3+2+2+2+3 setae; scaphognathite with 26-32 setae; all setae plumose.

*Maxilliped 1* (Fig. 5g).—Coxa with 5–8 setae; basis with 4 submarginal, 13–16 marginal setae; endopod 4-segmented, (3 or 4), (1 or 2), (1 or 2), (2–4) setae; exopod bisegmented, proximal segment without setae, distal segment with 6 or 7 setae on distal margin; bilobed epipod without setae; all setae plumose. Maxilliped 2 (Fig. 5h).—Coxa with 1–3 setae on inner margin; basis with 4 or 5 setae; endopod 4-segmented, (4 or 5), 1, 3, (3–5) setae; exopod unsegmented, 7–9 setae on distal margin; all setae plumose.

Maxilliped 3 (Fig. 6a).—Coxa with 0 or 1 seta; basis with 0-2 setae; endopod 4-segmented, (1 or 2), (1 or 2), (4 or 5), (4 or 5) setae; exopod unsegmented, 8 or 9 setae on distal margin; all setae plumose.



Fig. 6. *Callichirus major* from the Gulf of Mexico population, ZIII stage: a, maxilliped 3; b, pereiopod 1; c, pereiopod 2; d, pereiopod 3; e, pereiopod 4; f, pereiopod 5; g, pleopods from fourth abdominal somite; h, telson and uropods. Scales = 0.2 mm.

*Pereiopod 1* (Fig. 6b).—Chelate, biramous; coxa without setae; basis with 1 plumose seta on distal margin; endopod 4-segmented, 0, 2, (1-4), (2 or 3) setae; exopod with 7 or 8 setae on distal margin.

*Pereiopod 2* (Fig. 6c).—Chelate, biramous; coxa without setae; basis with 0 or 1 plumose seta on distal margin; endopod 4-segmented, 0, (1 or 2), (0-4), 2 setae; exopod with 5–7 setae on distal margin.

Pereiopods 3-5 (Fig. 6d-f).—Without setae.

*Pleopods* (Figs. 2c, 6g, 12c).—Bilobed buds on abdominal segments 3–5.

Telson and Uropods (Fig. 6h).—Triangular, narrow anteriorly, separated by suture from abdominal segment 6; processes on posterior margin arranged as (I, II, III, IV, V, VI, V, IV, III, II, I), (I) outermost process a long naked spine, (II) second process "anomuran hair," (III) 1 plumodenticulate seta, (IV) naked spine, (V) 15–19 plumodenticulate setae, (VI) center process a naked spine; uropods biramous, endopod without setae, exopod with 9–12 marginal plumose setae.

# Zoea IV

# Figs. 2d, 7a-h, 8a-h, 12d

Size.—CL = 2.73 ± 0.09 mm, 2.58–2.91 mm; TL = 5.89 ± 0.19 mm, 5.67–6.29 mm.



Fig. 7. *Callichirus major* from the Gulf of Mexico population, ZIV stage: a, antennule; b, antenna; c, right mandible; d, left mandible; e, maxillule; f, maxilla (plumose condition not shown); g, maxilliped 1; h, maxilliped 2. Scales = 0.2 mm.

*Carapace* (Figs. 2d, 12d).—No marked change from ZIII.

Abdomen (Figs. 2d, 12d).—Similar to previous stages, dorsal spines on somites 2 and 3 reduced in size.

Antennule (Fig. 7a).—Biramous, peduncle bisegmented; proximal segment with (0 or 1)+(2 or 3) short setae on outer margin, 0 or 1 seta on inner margin; distal segment with

2-4 plumose setae on inner margin, 1 plumose seta, 0-4 short setae on distal end; endopod with 1 plumose seta; exopod with 4-7 terminal, 0-2 subterminal aesthetascs.

Antenna (Fig. 7b).—Protopod with 1 distal spine between rami, spine reduced in some; endopod with 0 or 1 small seta; scaphocerite armed with 1 strong distolateral spine, 14–17 plumose setae on inner margin, and 1 plumose seta on outer margin.



Fig. 8. *Callichirus major* from the Gulf of Mexico population, ZIV stage: a, maxilliped 3; b, pereiopod 1; c, pereiopod 2; d, pereiopod 3; e, pereiopod 4; f, pereiopod 5; g, pleopods from fourth abdominal somite; h, telson and uropods. Scales = 0.2 mm.

*Mandible* (Fig. 7c, d).—Asymmetrically dentate; incisor process with 7 or 8 teeth on right mandible, 8 or 9 teeth on left mandible; molar process denticulate on both mandibles; palps present.

*Maxillule* (Fig. 7e).—Coxal endite with 13–16 marginal plumose setae; basal endite with 3 plumose setae, 5 or 6 large dentate spines, and 7 or 8 smaller dentate spines, inner margin with 1 plumose seta; endopod bisegmented, distinction between segments sometimes obscure, 2, 2+4 setae; protopod without setae.

*Maxilla* (Fig. 7f).—Coxal endite bilobed, 16– 19 setae on proximal lobe, 5 on distal lobe; basal endite bilobed with 8–10 setae on proximal lobe, 9–12 setae on distal lobe; endopod with 5 lobes, 3+(1 or 2)+(1 or 2)+2+(2-4)setae; scaphognathite with 27–35 setae; all setae plumose.

Maxilliped 1 (Fig. 7g).—Coxa with 5–9 setae; basis with 3–6 submarginal, and 13–16 marginal setae; endopod 4-segmented, (3 or 4), (1 or 2), 2, (3 or 4) setae; exopod bisegmented, proximal segment without setae, distal segment with 7 setae on distal margin; bilobed epipod without setae; all setae plumose.

*Maxilliped* 2 (Fig. 7h).—Coxa with 2 or 3 setae on inner margin; basis with 4 or 5 setae; endopod 4-segmented, (4-6), (0 or 1), (2-4), (3-5) setae; exopod unsegmented, 8 or 9 setae on distal margin; all setae plumose.

*Maxilliped 3* (Fig. 8a).—Coxa with 0 or 1 seta; basis with 2 or 3 setae; endopod 4-segmented, 2, (1 or 2), (3-5), (2-4) setae; exopod unsegmented, 7–10 setae on distal margin; all setae plumose.

Pereiopod 1 (Fig. 8b).—Biramous, cheliform; coxa with 0 or 1 seta; basis with 0 or 1 seta; endopod 4-segmented, (0-2), (1 or 2), (2-4), (1-4) setae; exopod with 7 or 8 setae on distal margin.

Pereiopod 2 (Fig. 8c).—Biramous, cheliform; coxa without setae; basis with 0 or 1 seta; endopod 4-segmented, (0-2), (1 or 2), (3-5), (2-4) setae; exopod with 6-8 setae on distal margin.

Pereiopod 3 (Fig. 8d).—Uniramous and 6-segmented, 0, 0, (0 or 1), (1 or 2), (2-5), (1-3) setae; propodus bladelike.

Pereiopod 4 (Fig. 8e).—Uniramous and 6-segmented, 0, 0, (0 or 1), (1 or 2), (1-4), (2 or 3) setae.

Pereiopod 5 (Fig. 8f).—Uniramous and 6-segmented, 0, 0, 0, (1 or 2), (2-4), (2 or 3) setae.

*Pleopods* (Figs. 2d, 8g, 12d).—Larger than those at ZIII, without setae.

Telson and Uropods (Fig. 8h).—Triangular, narrow anteriorly; processes on posterior margin arranged as (I, II, III, IV, V, VI, V, IV, III, II, I), (I) outermost process a long naked spine, (II) second process "anomuran hair," (III) 1 plumodenticulate seta, (IV) naked spine, (V) 16–18 plumodenticulate setae, (VI) center process a naked spine; uropods biramous, endopod with 7–10 marginal plumose setae, exopod with 1 naked distolateral spine, 12–15 marginal plumose setae.

> Decapodid (first postlarva) Figs. 2e, 9a-h, 10a-h

Size.—CL =  $1.31 \pm 0.04$  mm, 1.23-1.41 mm; TL =  $4.29 \pm 0.16$  mm, 3.86-4.49 mm.

*Carapace* (Fig. 2e).—About one-third length of abdomen; rostrum reduced, often deflected ventrally; eyes stalked.

Abdomen (Fig. 2e).—Abdominal segments wider than long; no posterodorsal spines; 0–5 setae on lateral margin of each segment.

Antennule (Fig. 9a).—Peduncle 3-segmented; proximal segment with 16-20 setae, 13 or 14 of these associated with statocyst; second segment of peduncle with 2 vertical rows of 2-5 setae each, 3-8 setae on outer dorsal margin; third segment of peduncle with 2 vertical rows of 6-10 setae each, 1-3 additional setae on outer margin, 3-5 short setae on distal margin; endopod 4-5-segmented, (0-2), (1 or 2), (2 or 3), (3 or 4), (2-5) setae; exopod 3 to 5-segmented, (2-4), (1-3), (3 or 4) setae + 2 aesthetascs, (4-6) aesthetascs (?).

Antenna (Fig. 9b).—Peduncle with 0 or 1 seta on proximal segment, 5–7 plumose setae on STRASSER AND FELDER: LARVAL DEVELOPMENT IN CALLICHIRUS MAJOR



Fig. 9. *Callichirus major* from the Gulf of Mexico population, decapodid stage: a, antennule; b, antenna. c, right mandible; d, left mandible; e, maxillule; f, maxilla (plumose condition not shown); g, maxilliped 1; h, maxilliped 2. Scales = 0.2 mm.

distal segment, spine between rami reduced to small nub; flagellum of 13-18 segments, setation (1-3), (2-4), variable region (2-6 articles, usually without setae), (3-5), (0-4), (3-6), (1-3), (4-6), (1-4), (4-6), (4-7), (4-7); exopod typically reduced to small naked bud.

*Mandible* (Fig. 9c, d).—Right and left mandibles similar, incisor process with 4–7 teeth; molar process smooth or with small

ridges; palp 3-segmented, 13–23 setae on distal segment.

*Maxillule* (Fig. 9e).—Coxal endite with 18–24 marginal setae, and 0 or 1 submarginal seta; basal endite with 7–11 plumose setae and 19–25 dentate spines, 1 or 2 plumose setae on inner margin; endopod reduced, with 0–8 setae; protopod with 0 or 1 seta on outer margin.

*Maxilla* (Fig. 9f).—Coxal endite trilobed, (16-19)+(8-14)+(5-12) setae on proximal to



Fig. 10. *Callichirus major* from the Gulf of Mexico population, decapodid stage: a, maxilliped 3; b, pereiopod 1; c, pereiopod 2; d, pereiopod 3; e, pereiopod 4; f, pereiopod 5; g, pleopods from fourth abdominal somite; h, telson and uropods. Scales = 0.2 mm.

distal lobes; basal endite bilobed with (9-13)+(17-29) setae; endopod reduced, with 4-9 setae; scaphognathite with 36-49 setae; all setae plumose.

Maxilliped 1 (Fig. 9g).—Coxa with 8-15 setae; basis highly setose, with 50-100 setae; endopod reduced, with 0-5 setae; exopod unsegmented, 9-24 setae; bilobed epipod without setae.

*Maxilliped* 2 (Fig. 9h).—Coxa partially fused to basis, with 2–6 setae; basis with 5–10 setae; endopod 4-segmented, (23-39), (0 or 1), (8-16), (6-12) setae; exopod unsegmented, 0-16 setae; epipod present, without setae.

Maxilliped 3 (Fig. 10a).—Coxa with 2–5 setae; basis with 2–6 setae; endopod 5-segmented, (17-35), (7-14), (11-24), (15-32), (6-10) setae; exopod usually reduced and without setae, occasionally with 4–8 setae; epipod bilobed distally, without setae.

Pereiopod 1 (Fig. 10b).—Chelate, 7-segmented; coxa with 1-4 setae; basis with 1-3 setae; ischium with 0-4 setae; merus with 3-6 setae; carpus with 7-18 setae; propodus with 26-41 setae, 2 or 3 spines on inner margin of immovable finger; dactylus with 17-30 setae; exopod usually reduced, without setae (with 7 setae on 1 specimen).

Pereiopod 2 (Fig. 10c).—Chelate, 7-segmented; coxa with 0-5 setae; basis with 1-4setae; ischium with 2-10 setae; merus with 8-31 setae; carpus with 9-19 setae; propodus with 21-47 setae, 2-4 spines on inner margin of immovable finger; dactylus with 20-27setae; exopod usually reduced, without setae (with 7 setae on 1 specimen).

Pereiopod 3 (Fig. 10d).—7-segmented; coxa with 1–5 setae; basis with 0–2 setae; ischium with 0–5 setae; merus with 2–7 setae; carpus with 5–13 setae; propodus bladelike with 28–79 setae, 1 spine on inner distal margin; dactylus with 6–26 setae; exopod usually reduced to small nub.

Pereiopod 4 (Fig. 10e).—7-segmented; coxa with 1-6 setae; basis with 0-3 setae; ischium with 1-7 setae; merus with 2-8 setae; carpus with 2-7 setae; propodus with 20-46 setae, 1 spine on inner distal margin; dactylus

with 10-20 setae; exopod usually reduced to small nub.

Pereiopod 5 (Fig. 10f).—Cheliform, 7-segmented; coxa with 0-4 setae; basis with 0 or 1 seta; ischium with 1-4 setae; merus with 2-7 setae; carpus with 2-6 setae; propodus with 12-24 setae; 1 spine on immovable finger; dactylus with 5-9 setae; exopod usually reduced to small nub.

*Pleopods* (Figs. 2e, 10g).—Present on abdominal segments 3-5, all pairs biramous and morphologically similar; coxa without setae; basis with 4-9 marginal plumose setae; endopod with 14-21 plumose marginal setae, and 0-3 naked submarginal setae, 4-10hooked setae on appendix interna; exopod with 35-63 marginal plumose setae and 2-7submarginal naked setae.

Telson and Uropods (Fig. 10h).—Subquadrate, broadest posteriorly, processes on posterior margin usually reduced to 1–3 setae on each end; uropods biramous, endopod with 16–23 plumose setae, exopod with 56–108 plumose setae, protopod with 3–5 setae.

# Florida Atlantic Population Zoea I Figs. 11a, 12e

Size.—CL =  $1.82 \pm 0.04$  mm, 1.75-1.90 mm; TL =  $4.65 \pm 0.06$  mm, 4.55-4.80 mm.

*Carapace* (Fig. 12e).—Shorter than abdomen, with pterygostomial spine; rostrum well developed, smooth, sometimes with serrations at distal end; eyes sessile.

Abdomen (Fig. 12e).—Somite 2 with strong anterolateral projections, weakly developed on somite 1; somites 2–5 with posterolateral projections and posterodorsal spines; dorsal spine elongate on somite 2, sometimes reaching posterior margin of somite 5; dorsal spine on somite 3 much shorter than that of somite 2; somites 4 and 5 with short distal spines.

Antennule.—Elongate, exopodal and endopodal lobes not distinct; 6 terminal aesthetascs, 3 elongate and thick, 3 short and thin; 1 long, plumose seta on future endopodal lobe; 0-3 short setae on peduncle.



Fig. 11. *Callichirus major* from the Florida Atlantic population, ventral view of telson: a, ZI stage; b, ZII stage; c, ZIII stage; d, ZIV stage; Scale = 1 mm.

Antenna.—Protopod with 1 distal spine between rami; endopod with 1 long plumose seta distally; scaphocerite (exopod) armed with 1 strong distolateral spine, 13–15 plumose setae on inner margin, 1 plumose seta on outer margin.

*Mandible.*—Asymmetrically dentate; incisor process with 6–8 teeth on right mandible, 9 teeth on left mandible; molar process denticulate on both mandibles.

*Maxillule.*—Coxal endite with 11–13 marginal setae; basal endite with 3 plumose setae, 5 or 6 large dentate spines, and 6 or 7 smaller dentate spines, inner margin with 1 plumose seta; endopod bisegmented, distinction between segments sometimes obscure, 2, 2+(3 or 4) setae; protopod without setae.

*Maxilla.*—Coxal endite bilobed, 15–18 setae on proximal lobe, 5 on distal lobe; basal endite bilobed, 9–11 setae on proximal lobe, 8– 11 on distal lobe; endopod with 5 lobes, (2-4)+2+2+2+3 setae; scaphognathite with 26–31 setae; all setae plumose.

Maxilliped 1.—Coxa with 3–8 setae; basis with 4 submarginal, 14–16 marginal setae; endopod 4-segmented, 4, (1 or 2), 2, 4 setae; exopod bisegmented, proximal segment without setae, distal segment with 7 setae on distal margin; bilobed epipod without setae; all setae plumose.

860



Fig. 12. *Callichirus major*, lateral view of abdomen. a–d, Gulf of Mexico population: a, ZI stage; b, ZII stage; c, ZIII stage; d, ZIV stage; e–h, Florida Atlantic population: e, ZI stage; f, ZII stage; g, ZIII stage; h, ZIV stage. Scale = 1 mm.

Maxilliped 2.—Coxa with 1–3 setae; basis with 5 setae; endopod 4-segmented, (3-5), (1 or 2), 2, (4 or 5) setae; exopod unsegmented, 9 setae on distal margin; all setae plumose.

*Maxilliped 3.*—Coxa with 0 or 1 seta; basis with 1 or 2 setae; endopod 4-segmented, 2, 2, (2-4), 3 setae; exopod unsegmented, 8 or 9 setae on distal margin; all setae plumose.

Pereiopods.-Not developed.

Pleopods (Fig. 12e).-Not developed.

Telson (Fig. 11a).—Triangular, narrow anteriorly not differentiated from abdominal segment 6; processes on posterior margin arranged as (I, II, III, IV, III, II, I), (I) outermost process a long naked spine, (II) second process "anomuran hair," (III) 18–21 plumodenticulate setae, (IV) center process a naked spine, usually equal in length to process I.

### Zoea II Figs. 11b, 12f

*Size.*—CL = 1.97 ± 0.08 mm, 1.84–2.06 mm; TL = 4.98 + 0.13 mm, 4.80–5.30 mm.

*Carapace.*—Shorter than abdomen, with pterygostomial spine; rostrum elongate and serrated; eyes separated from carapace.

Abdomen (Fig. 12f).—No marked change from ZI.

Antennule.—Elongate, weakly bilobed; peduncle with 1–3 long plumose, 0–3 short setae; endopodal bud with 1 terminal plumose seta; exopod with 6-10 terminal, 0 or 1 sub-terminal aesthetascs.

Antenna.—Scaphocerite armed with 1 strong distolateral spine, 15 or 16 plumose setae on inner margin, 1 plumose seta on outer margin; endopod with 0 or 1 plumose seta; protopod with 1 distal spine between rami.

Mandible.—Incisor process with 8 or 9 teeth on right mandible, 8–10 teeth on left mandible; molar process denticulate on both mandibles.

*Maxillule.*—Coxal endite with 11-14 marginal plumose setae; basal endite with 3 plumose setae, 5 or 6 large dentate spines, and 6-8 smaller dentate spines, inner margin with 1 plumose seta; endopod bisegmented, distinction between segments sometimes obscure, 2, 2+4 setae; protopod without setae.

*Maxilla.*—Coxal endite bilobed, 17–20 setae on proximal lobe, 5 on distal lobe; basal endite bilobed, 9–12 setae on proximal lobe, 10-13 on distal lobe; endopod with 5 lobes, 3+2+(1 or 2)+2+3 setae; scaphognathite with 25-35 setae; all setae plumose.

Maxilliped 1.—Coxa with 4–9 setae; basis with 4 submarginal, 15 or 16 marginal setae; endopod 4-segmented, 4, 2, 2, 4 setae; exopod bisegmented, proximal segment without setae, distal segment with 7 setae on distal margin; bilobed epipod without setae; all setae plumose.

*Maxilliped* 2.—Coxa with 1–3 setae on inner margin; basis with 4 or 5 setae; endopod 4-segmented, (4 or 5), (1 or 2), (2 or 3), 5 setae; exopod unsegmented, 9 or 10 setae on distal margin; all setae plumose.

Maxilliped 3.—Coxa with 1 seta; basis with 1 or 2 setae; endopod 4-segmented, (1 or 2), (2 or 3), 5, (3 or 4) setae; exopod unsegmented, 9 or 10 setae on distal margin; all setae plumose.

*Pereiopods.*—First and second pereiopods present, both without setae.

Pleopods (Fig. 12f).-Not developed.

Telson (Fig. 11b).—No change from ZI.

### Zoea III Figs. 11c, 12g

Size.—CL =  $2.20 \pm 0.08$  mm, 2.02-2.39 mm; TL =  $5.52 \pm 0.19$  mm, 5.05-5.86 mm.

Carapace (Fig. 12g).—No marked change from ZII.

Abdomen (Fig. 12g).—No marked change from ZII.

Antennule.—Biramous, peduncle bisegmented; proximal segment with (0 or 1)+(2-4) short setae; distal segment with 2 or 3 plumose setae on inner margin, 1 plumose seta and 0-4 short setae on distal end; endopod with 0 or 1 plumose seta; exopod with 7-10 terminal, 1 or 2 subterminal aesthetascs.

Antenna.—Protopod with 1 distal spine between rami; endopod with 0 or 1 short seta; scaphocerite armed with 1 strong distolateral spine, 14–16 plumose setae on inner margin, 1 plumose seta on outer margin.

*Mandible.*—Asymmetrically dentate; incisor process with 8 teeth on right mandible, 9 or 10 teeth on left mandible; molar process denticulate on both mandibles; palps present as buds.

*Maxillule.*—Coxal endite with 13-16 marginal plumose setae; basal endite with 3 plumose setae, 5 or 6 large dentate spines, and 7–9 smaller dentate spines, inner margin with 1 plumose seta; endopod bisegmented, distinction between segments sometimes obscure, 2, 2+(3 or 4) setae; protopod without setae.

Maxilla.—Coxal endite bilobed, 17–20 setae on proximal lobe, 5 on distal lobe; basal endite bilobed, 10–12 setae on proximal lobe, 9–12 on distal lobe; endopod with 5 lobes, 3, 2, 2, 2, 3 setae; scaphognathite with 29–34 setae; all setae plumose.

Maxilliped 1.—Coxa with 6–9 setae; basis with 4 submarginal, 15–18 marginal setae; endopod 4-segmented, (3 or 4), 2, 2, 4 setae; exopod bisegmented, proximal segment without setae, distal segment with 7 setae on distal margin; bilobed epipod without setae; all setae plumose.

862

Maxilliped 2.—Coxa with 2-4 setae; basis with 4 or 5 setae; endopod 4-segmented, (4 or 5), (1 or 2), 3, 5 setae; exopod unsegmented, 9 or 10 setae on distal margin; all setae plumose.

Maxilliped 3.—Coxa with 1 seta; basis with 1 or 2 setae; endopod 4-segmented, (1-3), 2, (4 or 5), (3 or 4) setae; exopod unsegmented, 9 or 10 setae on distal margin; all setae plumose.

Pereiopod 1.—Chelate, biramous; coxa without setae; basis with 1 plumose seta on distal margin; endopod 4-segmented, 0, 2, (1-4), (1 or 2) setae; exopod with 7–9 setae on distal margin.

Pereiopod 2.—Chelate, biramous; coxa without setae; basis with 0 or 1 plumose seta on distal margin; endopod 4-segmented, 0, (0-2), (1-4), (1 or 2) setae; exopod with 7 or 8 setae on distal margin.

Pereiopods 3-5.—Without setae.

*Pleopods* (Fig. 12g).—Bilobed buds on abdominal segments 3–5.

Telson and Uropods (Fig. 11c).—Triangular, narrow anteriorly, separated by suture from abdominal segments; processes on posterior margin arranged as (I, II, III, IV, V, VI, V, IV, III, II, I), (I) outermost process a long naked spine, (II) second process "anomuran hair," (III) 1 plumodenticulate seta, (IV) naked spine, (V) 16–20 plumodenticulate setae, (VI) center process a naked spine; uropods biramous, endopod without setae, exopod with 9–14 marginal plumose setae.

### Zoea IV Figs. 11d, 12h

Size.—CL =  $2.50 \pm 0.05$  mm, 2.42-2.61 mm; TL =  $6.12 \pm 0.12$  mm, 5.79-6.29 mm.

Carapace (Fig. 12h).—No marked change from ZIII.

Abdomen (Fig. 12h).—Similar to previous stages, dorsal spines on somites 2 and 3 reduced in size.

Antennule.—Biramous, peduncle bisegmented; proximal segment with (0-2)+(3 or 4) short setae on outer margin, and 0 or 1 seta on inner margin; distal segment with 4-6plumose setae on inner margin, 1 plumose seta, 0-4 short setae on distal end; endopod with 1 or 2 plumose setae; exopod with 4-8terminal, 2 subterminal aesthetascs.

Antenna.—Protopod with 1 distal spine between rami, spine reduced in some; endopod without setae; scaphocerite armed with 1 strong distolateral spine, 13–16 plumose setae on inner margin, 1 plumose seta on outer margin.

Mandible.—Asymmetrically dentate; incisor process with 7 or 8 teeth on right mandible, 8 or 9 teeth on left mandible; molar process denticulate on both mandibles; palps present.

*Maxillule.*—Coxal endite with 15-17 marginal plumose setae; basal endite with 3 or 4 plumose setae, 6 or 7 large dentate spines, and 7–9 smaller dentate spines, inner margin with 1 plumose seta; endopod bisegmented, distinction between segments sometimes obscure, 2, 2+(3 or 4) setae; protopod without setae.

*Maxilla.*—Coxal endite bilobed, 17-23 setae on proximal lobe, 5 on distal lobe; basal endite bilobed, 10-12 setae on proximal lobe, 11-14 on distal lobe; endopod with 5 lobes, 3+2+2+(1 or 2)+3 setae; scaphognathite with 31-39 setae; all setae plumose.

Maxilliped 1.—Coxa with 6-9 setae; basis with 4-6 submarginal, and 15-20 marginal setae; endopod 4-segmented, 4, 2, 2, 4 setae; exopod bisegmented, proximal segment without setae, distal segment with 7 setae on distal margin; bilobed epipod without setae; all setae plumose.

Maxilliped 2.—Coxa with 2 or 3 setae on inner margin; basis with 4 or 5 setae; endopod 4-segmented, (4 or 5), (1 or 2), (2–4), (4 or 5) setae; exopod unsegmented, 9 or 10 setae on distal margin; all setae plumose.

Maxilliped 3.—Coxa with 1 seta; basis with 0-3 setae; endopod 4-segmented, (2 or 3), 2, (4 or 5), (3-5) setae; exopod unsegmented, 9 or 10 setae on distal margin; all setae plumose.

Pereiopod 1.—Biramous, cheliform; coxa with 0 or 1 seta; basis with 1 or 2 setae; en-

dopod 4-segmented, (0-2), (1 or 2), (3-5), (1 or 3) setae; exopod with 7–9 setae on distal margin.

*Pereiopod* 2.—Biramous, cheliform; coxa without setae; basis with 0-2 setae; endopod 4-segmented, (0-2), (1 or 2), (3-5), (2 or 3) setae; exopod with 7 or 8 setae on distal margin.

*Pereiopod 3.*—Uniramous and 6-segmented, 0, 0, (0 or 1), 2, (2–5), 2 setae; propodus bladelike.

Pereiopod 4.—Uniramous and 6-segmented, 0, 0, (0 or 1), 2, (1-4), 2 setae.

*Pereiopod 5.*—Uniramous and 6-segmented, 0, 0, 0, (1 or 2), (2–5), 2 setae.

Pleopods (Fig. 12h).—Larger than those at ZIII, without setae.

Telson and Uropods (Fig. 11d).—Triangular, narrow anteriorly; processes on posterior margin arranged as (I, II, III, IV, V, VI, V, IV, III, II, I), (I) outermost process a long naked spine, (II) second process "anomuran hair," (III) 1 plumodenticulate seta, (IV) naked spine, (V) 17–21 plumodenticulate setae, (VI) center process a naked spine; uropods biramous, endopod with 7–11 marginal plumose setae, exopod with 1 naked distolateral spine, 13–16 marginal plumose setae.

Decapodid (first postlarva)

Size.—CL =  $1.60 \pm 0.10$  mm, 1.35-1.81 mm; TL =  $5.07 \pm 0.11$  mm, 4.80-5.36 mm.

*Carapace.*—About one-third length of abdomen; rostrum reduced, often deflected ventrally; eyes stalked.

Abdomen.—Abdominal segments wider than long; no posterodorsal spines; 0–5 setae on lateral margin of each segment.

Antennule.—Peduncle 3-segmented; proximal segment with 16-27 setae, 11-14 of these associated with statocyst; second segment of peduncle with 2 vertical rows of 3-5 setae each, 4-10 setae on outer dorsal margin; third segment of peduncle with 2 vertical rows of 7-10 setae each, 2 or 3 additional setae on outer margin, 3-5 short setae on distal mar-

gin; endopod 4-segmented, (0-2), (2 or 3), (2 or 3), (3-6) setae; exopod 4-segmented, (0-4), (1-3), (1-5) setae + 2 aesthetascs, (4-8) aesthetascs (?).

Antenna.—Peduncle with 0 or 1 seta on proximal segment, 5–8 plumose setae on distal segment, spine between rami reduced to small nub; flagellum of 14–17 segments; setation (1-3), (2-4), variable region (2-4 articles,usually without setae), (0-4), variable region (0 or 1 article, with 0 or 1 seta), (3-5), (0-2), (4-6), (1-4), (5 or 6), (1-5), (5 or 6), (5 or6), (5-8); exopod typically reduced to small naked bud.

*Mandible.*—Right and left mandibles similar, incisor process with 4–8 teeth; molar process smooth or with small ridges; palp 3-segmented, 17–25 setae on distal segment.

*Maxillule.*—Coxal endite with 21-28 marginal setae, and 0 or 1 submarginal seta; basal endite with 6-11 plumose setae and 21-27 dentate spines, 1 or 2 plumose setae on inner margin; endopod reduced, with 0-8 setae; protopod with 0 or 1 seta on outer margin.

*Maxilla.*—Coxal endite trilobed, (18-25)+(9-15)+(6-12) setae; basal endite bilobed with (11-16)+(22-41) setae; endopod reduced, with 4-11 setae; scaphognathite with 33-48 setae; all setae plumose.

Maxilliped 1.—Coxa with 11-20 setae; basis highly setose, with 50-100 setae; endopod reduced, with 0-8 setae; exopod unsegmented, with 0-22 setae; bilobed epipod without setae.

*Maxilliped* 2.—Coxa partially fused to basis, with 2–6 setae; basis with 4–14 setae; endopod 4-segmented, (25-42), (0 or 1), (9-17), (9-15) setae; exopod unsegmented, with 0–14 setae; epipod present, without setae.

Maxilliped 3.—Coxa with 2–6 setae; basis with 2–7 setae; endopod 5-segmented, (21–36), (12–20), (19–25), (18–32), (8–13) setae; exopod usually reduced and without setae, occasionally with 3–9 setae; epipod bilobed distally, without setae.

Pereiopod 1.—Chelate, 7-segmented; coxa with 1-4 setae; basis with 1-3 setae; ischium

with 2-5 setae; merus with 3-7 setae; carpus with 11-22 setae; propodus with 31-46setae, 2-4 spines on inner margin of immovable finger; dactylus with 20-32 setae; exopod usually reduced, without setae, occasionally with 2-8 setae.

Pereiopod 2.—Chelate, 7-segmented; coxa with 1-4 setae; basis with 1-4 setae; ischium with 5-10 setae; merus with 19-28 setae; carpus with 10-16 setae; propodus with 31-49 setae, 2 or 3 spines on inner margin of immovable finger; dactylus with 20-30 setae; exopod usually reduced, without setae, occasionally with 7 or 8 setae.

Pereiopod 3.—7-segmented; coxa with 2 or 3 setae; basis with 1 or 2 setae; ischium with 3-6 setae; merus with 4-8 setae; carpus with 9-19 setae; propodus bladelike with 42-87 setae, 1 spine on inner distal margin; dacty-lus with 17-35 setae; exopod usually reduced to small nub.

Pereiopod 4.—7-segmented; coxa with 2–5 setae; basis with 1 or 2 setae; ischium with 3–6 setae; merus with 3–7 setae; carpus with 4–8 setae; propodus with 28–47 setae, 1 spine on inner distal margin; dactylus with 12–21 setae; exopod usually reduced to small nub.

Pereiopod 5.—Cheliform, 7-segmented; coxa with 1-3 setae; basis with 1 or 2 setae; ischium with 1-3 setae; merus with 3-5 setae; carpus with 5-7 setae; propodus with 13-33 setae, 1 spine on immovable finger; dactylus with 8-13 setae; exopod usually reduced to small nub.

*Pleopods.*—Present on abdominal segments 3-5, all pairs biramous and morphologically similar; coxa without setae; basis with 6-10 marginal plumose setae; endopod with 12-28 plumose marginal setae, and 0-2 naked submarginal setae, 5-11 hooked setae on appendix interna; exopod with 41-54 margin plumose setae and 0-9 submarginal naked setae.

*Telson.*—Subquadrate, broadest posteriorly, processes on posterior margin usually reduced to 1-5 setae, but occasionally with up to 21 setae on each end; uropods biramous, endopod with 20-27 plumose setae, exopod with 31-103 plumose setae, protopod with 2-5 setae.

### DISCUSSION

Although there is some variation between different species of Callichirus, several common characters are unique and support their congeneric status (Tables 3-7). Most significantly, they differ from larvae of all other known callianassid genera in that they have numerous processes on the posterior margin of the telson during the four or five zoeal stages that each species passes through. The combination of these characters prevents placing larvae of Callichirus in either larval Type I or II described by Gurney (1942). Larvae of Callichirus may also differ from other callianassids by their retention of the anomuran hair during the late zoeal stages. The second process on the posterior margin of the telson does not become a spine at ZIII or ZIV in C. islagrande and both populations of C. major. In addition, there is no mention of a loss of the anomuran hair at the late zoeal stages of other congeneric species and illustrations show its retention at ZIII for Callichirus sp. and ZV for C. garthi (Rodrigues, 1976: fig. 35; Aste and Retamal, 1983: fig. 80). The second process becomes a spine in the callianassids Neotrypaea uncinata (H. Milne Edwards) at ZV and Callianassa petalura Stimpson at ZIV (Aste and Retamal. 1984: Konishi et al., 1990).

While dissection of specimens allows detailed structural characters to be examined, the stage of animals could in our study be distinguished from intact, live material. At ZI, the rostrum was long, thin, and generally smooth, except for some serrations at the distal end, eyes were sessile, and pereiopods were absent. ZII resembled ZI, except that the rostrum was wider with lateral serrations, the eyes were stalked, and the first and second pereiopods were present (Table 4). As in many other decapod crustaceans (Williamson, 1982), uropods flanked the telson at the third zoeal stage. The exopod of the uropod had marginal setae but no unarticulated distolateral spine, and the endopods were without setae (Table 5). At ZIV, a distolateral spine was present on the exopod of the uropods and pleopods were present on the abdomen (Table 6). It should be noted that C. islagrande, the two populations of C. major, and the Brazilian Callichirus sp. had pleopods at ZIII, while C. garthi was reported to develop pleopods at ZIV. ZV was a variable stage in C. major

Table 3. Comparison of morphological characters for ZI larvae of *Callichirus major* (Gulf of Mexico), *C. major* (Florida Atlantic), *Callichirus* sp. (Brazil; as *C. major*, Re driques, 1976), *C. islagrande* (Gulf of Mexico; Strasser and Felder, in press b), and *C. garthi* (Chile; Aste and Retamal, 1983). Symbols represent: presence (P); absence (A aesthetascs (I); counts of setae and spines (ct); and no record in description or record obtained from illustration (?). Setal counts are listed from proximal to distal. Groups of setae on the same segment, or on different lobes of the same endite, are separated with a plus (+). Setal groups on successive segments are separated with a comma (,). A sem colon (;) is used to separate groups of setae on different segments in which the distinction between segments is sometimes obscure. Total length and carapace length are presented as mean (mm)  $\pm$  95% CI.

	Callie	chirus major			
	Gulf of Mexico	Florida Atlantic	Callichirus sp.	C. islagrande	C. garthi
Carapace length	$1.7 \pm 0.11$	$1.82 \pm 0.04$		$1.23 \pm 0.06$	1.80
Total length	$3.99 \pm 0.20$	$4.65 \pm 0.06$	4	$3.26 \pm 0.07$	5.31
Antennule					
Endopod ct	1	1	1	1	
Exopod ct	61	61	3	4–6I	3+3
Antenna					
Flagellum	Α	Α	Α	Α	Α
Endopod ct	1+(0 or 1)	1	2	2	2
Exopod ct	1+1+(11-13)	1+1+(13-15)	1+1+13	1+1+8	1+1+8
Protopod ct	1	1	1	1	1
Maxillule					
Coxal endite ct	9–13	11–13	4	8–10	10
Basal endite ct	3+5+(5 or 6)+1	3+(5 or 6)+(6 or 7)+1	7	3+(3  or  4)+(4  or  5)+1	5+3
Endopod ct	2; 2+4	2; 2+(3 or 4)	2+2+3	2; 2; (3 or 4)	2, 2, 4
Maxilla					
Coxal endite ct	(12–16)+(4 or 5)	(15-18)+5	7+2	(11 or 12)+(4 or 5)	13+5
Basal endite ct	(7-10)+(7-10)	(9-11)+(8-11)	3+3	(6-9)+(6-9)	9+10
Endopod ct	(2  or  3)+2+2+2+3	(2-4)+2+2+2+3	2+2+2+2+2	3+2+2+2+(2  or  3)	3, 2, 2, 2, 3
Scaphognathite ct	22-29	26-31	19	16–19	23
Maxilliped 1					
Coxa ct	4-8	3–8	7	4-8	8
Basis ct	4+(9-15)	4+(14-16)	12	13–17	15
Endopod ct	4, (1 or 2), 2, 4	4, (1 or 2), 2, 4	1, 1, 5	(3  or  4), (1  or  2), (1-3), (3  or  4)	4, 2, 2, 4
Exopod ct	0, 7	0, 7	7	0, (5 or 6)	7
Epipod	P	P	Р	P	Р
Maxilliped 2					
Coxa ct	2 or 3	1–3	3	1 or 2	3
Basis ct	5	5	5	3-6	5
Endopod ct	4, 1, 2, (3-5)	(3-5), (1 or 2), 2, (4 or 5)	4, 1, 3, 4	(4 or 5), (0 or 1), (1 or 2), (3-6)	4, 2, 2, 5
Exopod ct	7-9	9	8 or 9	7 or 8	9
Maxilliped 3					
Coxa ct	0 or 1	0 or 1	1	0 or 1	0
Basis ct	2	1 or 2	2	1 or 2	2

	Callichi	rus major			
	Gulf of Mexico	Florida Atlantic	Callichirus sp.	C. islagrande	C. garthi
Endopod ct	2, 2, (3 or 4), 3	2, 2, (2–4), 3	1, 1, 3, 4	(0 or 1), (0–2), (2 or 3), (3–5)	1, 2, 3, 5
Exopod ct	8 or 9	8 or 9	7 or 8	6-8	10
reiopods	A	Α	A	Α	Α
eopods Ison	A	Υ	Υ	А	V
Processes ct	(21-24)+1+(21-24)	(20-23)+1+(20-23)	(21-24)+1+(21-24)	(12–14)+1+(13 or 14)	18+1+19
Process 2 as hair	Д	, d	, d	Ĺ Ĺ	Ч
Median process	Ч	Ч	Р	Р	Р
ropods	A	Α	A	Α	Α

Table 3. Continued.

and C. islagrande in which characters resembled those of ZIV, the decapodid stage, or some gradation between the two. In the decapodid stage, the abdomen was wider, flattened dorsally, had no dorsal spines, and had fanlike pleopods lined with marginal plumose setae (Table 7). The telson metamorphosed from the triangular shape of the zoeal stages to a subquadrate form. Decapodids could also be identified by their swimming behavior. While zoeae often swam backward and frequently made backward jerking motions, decapodids usually swam or crawled forward. Durations of these stages were consistent, at least until the decapodid stage was reached.

### Morphological Comparisons among Congeneric Populations

Individuals from the same population varied in setal counts, and ranges between populations typically overlapped (Tables 3-7). While setal counts were similar between species, two groups may be formed on the basis of larval morphology, with the greatest difference between them being the number of pleopod pairs in the late zoeal stages. *Callichirus garthi* and *C. islagrande* had pleopods on abdominal segments 2–5, while the two populations of *C. major* and the Brazilian *Callichirus* sp. had pleopods only on abdominal segments 3–5 (Tables 6, 7).

There were also consistent differences in the triangular telson of these groups, the posterior margin usually being straight in the two populations of C. major and the Brazilian Callichirus sp., but being concave in C. islagrande and  $\overline{C}$ . garthi. The arrangement of processes also differed between the two groups. In C. major and the Brazilian Callichirus sp. the outermost process was an unarticulated spine, while it was a plumodenticulate seta in C. garthi and  $\overline{C}$ . islagrande. In ZIII larvae of the first group the fourth process was a naked spine, unarticulated in the Gulf and Florida Atlantic populations of C. major, articulated as illustrated in the Brazilian Callichirus sp. (Rodrigues, 1976: fig. 35). In C. islagrande and C. garthi, the fourth process was a plumodenticulate seta. At ZIV both C. islagrande and C. garthi also had a ventral spine on the protopod of each uropod, and this character was absent in C. major and the Brazilian Callichirus sp.

The telson may also be used to separate two populations of *C. major* from one an-

Table 4. Comparison of morphological characters for ZII larvae of *Callichirus major* (Gulf of Mexico), *C. major* (Florida Atlantic), *Callichirus* sp. (Brazil; as *C. major*, Red driques, 1976), *C. islagrande* (Gulf of Mexico; Strasser and Felder, in press b), and *C. garthi* (Chile; Aste and Retamal, 1983). Symbols represent: presence (P); absence (A aesthetascs (I); counts of setae and spines (ct); and no record in description or record obtained from illustration (?). Setal counts are listed from proximal to distal. Groups of setae on the same segment, or on different lobes of the same endite, are separated with a plus (+). Setal groups on successive segments are separated with a comma (.). A sem colon (;) is used to separate groups of setae on different segments in which the distinction between segments is sometimes obscure. Total length and carapace length are prosented as mean (mm)  $\pm$  95% CI.

	Callichirus major				
	Gulf of Mexico	Florida Atlantic	Callichirus sp.	C. islagrande	C. garthi
Carapace length	$2.01 \pm 0.06$	$1.97 \pm 0.08$		$1.44 \pm 0.03$	2.13
Total length	$4.49 \pm 0.11$	$4.98 \pm 0.13$	4.6	$3.64 \pm 0.06$	6.12
Antennule					
Peduncle	1+(0 or 1)	(1-3)+(0-3)	1	(0-3), 2+(0-3)	0
Endopod ct	1	1	1	1	1
Exopod ct	1I+(8-10I)	(0 or 1I)+(6–10I)	4	6-8	5+4
Antenna					
Flagellum	Α	Α	Α	А	Α
Endopod ct	0	0 or 1	0	0	0
Exopod ct	1+1+(12-14)	1+1+(15  or  16)	1+1+16	1+1+(10 or 11)	1+1+9
Protopod ct	1	1	1	2	1
Maxillule					
Coxal endite ct	11-13	11-14	4	8-10	9 or 10
Basal endite ct	3+(5 or 6)+(5 or 6)+1	3+(5  or  6)+(6-8)+1	7	3+(4  or  5)+(4  or  5)+(0  or  1)	3+7
Endopod ct	2; 2+(3-5)	2; 2+4	2+2+3	2; 2; (4 or 5)	2, 2, 4
Maxilla					
Coxal endite ct	(11–17)+(4 or 5)	(17–20)+5	7+2	(12–15)+(4 or 5)	13+5
Basal endite ct	(7-10)+(7-10)	(9-12)+(10-13)	3+3	(6-8)+(5-9)	9+10
Endopod ct	3+2+2+2+3	3+2+(1  or  2)+2+3	2+2+2+2+2	(2  or  3)+2+2+2+3	3, 2, 2, 2, 3
Scaphognathite ct	21-29	25-35	19	19–24	28
Maxilliped 1					
Coxa ct	4-8	4–9	7	4-8	8
Basis ct	4+(12-16)	4+(15 or 16)	12	13–17	16
Endopod ct	(3 or 4), (1 or 2), 2, 4	4+2+2+4	1, 1, 5	(3 or 4), 2, (1 or 2), 4	4+2+2+4
Exopod ct	0, (6 or 7)	0, 7	7	0, (6 or 7)	8
Epipod	Р	Р	Р	Р	Р
Maxilliped 2					
Coxa ct	0-3	1–3	3	0–2	3
Basis ct	5	4 or 5	5	4–6	5
Endopod ct	(4 or 5), 1, 3, (3–5)	(4 or 5), (1 or 2), (2 or 3), 5	4, 1, 3, 4	(4-6), 1, (2 or 3), (4-6)	4, 2, 2, 5
Exopod ct	8-10	9 or 10	8 or 9	7 or 8	10
Maxilliped 3					
Coxa ct	0 or 1	1	1	0	0

	Callic	hirus major			
	Gulf of Mexico	Florida Atlantic	Callichirus sp.	C. islagrande	C. garthi
Basis ct	1 or 2	1 or 2	2	0-2	2
Endopod ct	2, (2 or 3), (3–5), 4	(1 or 2), (2 or 3), 5, (3 or 4)	1, 1, 3, 4	(1  or  2), (1-3), (2-4), (3-6)	1, 2, 4, 6
Exopod ct	9 or 10	9 or 10	7 or 8	6-8	10
Pereiopods	Ъ	Ъ	Ъ	Ρ	Ъ
Pleopods Telson	A	Α	A	Α	Α
Processes ct	(21-24)+1+(21-24)	(20-23)+1+(20-23)	(21-24)+1+(21-24)	(12-14)+1+(13  or  14)	18+1+17
Process 2 as hair	Р	Р	Р	Р	Р
Median process	Р	Р	Ъ	Ъ	Р
Uropods	¥	A	А	Α	Α

Table 4. Continued.

other, since the outermost process in the Gulf population was over two times longer than the median process (Figs. 3j, 4l, 6h, 8h). In contrast, the outer process was about equal in length to the median process in both the Florida Atlantic population of C. major (Fig. 11) and Brazilian Callichirus sp. (Rodrigues, 1976: figs. 22, 35). The dorsal spine on the second abdominal segment was also longer in the Gulf population than in the Florida Atlantic specimens (Fig. 12). While these characters can be used to distinguish zoeae of these disjunct geographic stocks, they are lost at the decapodid stage, which is very similar among the populations compared. A similar trend has also been reported for brachyuran species such as Panopeus herbstii H. Milne Edwards and P. bermudensis Benedict and Rathbun, which differ in morphology during the zoeal phase, but are very similar at the decapodid and first crab stages (Martin et al., 1984). The increased length of spines found in zoeae from the Gulf population may serve to compensate for reduced buoyancy at decreased salinities or as armor to ward off increased predation at lower salinities. However, C. islagrande, which is found in much the same habitat as the Gulf C. major, does not have long spines on the telson or second abdominal segment (Strasser and Felder, in press b).

There are also characters that separate both the Gulf and Florida Atlantic populations of *C. major* from the Brazilian *Callichirus* sp. In both populations of *C. major*, the endopod of the first maxilliped was 4-segmented, while it was 3-segmented in the Brazilian *Callichirus* sp. At ZI, the exopod of the first maxilliped appears to be 2-segmented in the two populations of *C. major*, while it is represented as unsegmented in fig. 17 of the Brazilian *Callichirus* sp. (Rodrigues, 1976). However, segmentation of this appendage is sometimes difficult to discern and its interpretation may vary depending on illumination techniques used.

### Number of Zoeal Stages

The occurrence of ZV varied between the Florida Atlantic and Gulf populations of C. *major*. In the Gulf population, molting to ZV was rare, and animals more commonly molted directly from ZIII to D than ZIV to ZV in this population (Table 2). In contrast, the presence of ZV was common in larvae from three out

Table 5. Comparison of morphological characters for ZIII larvae of *Callichirus major* (Gulf of Mexico), *C. major* (Florida Atlantic), *Callichirus* sp. (Brazil; as *C. major*, Ro driques, 1976), *C. islagrande* (Gulf of Mexico; Strasser and Felder, in press b), and *C. garthi* (Chile; Aste and Retamal, 1983). Symbols represent: presence (P); absence (A aesthetascs (I); counts of setae and spines (ct); and no record in description or record obtained from illustration (?). Setal counts are listed from proximal to distal. Groups of setae on the same segment, or on different lobes of the same endite, are separated with a plus (+). Setal groups on successive segments are separated with a comma (,). A sem colon (;) is used to separate groups of setae on different segments in which the distinction between segments is sometimes obscure. Total length and carapace length are prosented as mean (mm)  $\pm$  95% CI.

	Callichirus major				
	Gulf of Mexico	Florida Atlantic	Callichirus sp.	C. islagrande	C. garthi
Carapace length	$2.30 \pm 0.11$	$2.20 \pm 0.08$		$1.65 \pm 0.03$	2.57
Total length	$5.17 \pm 0.09$	$5.52 \pm 0.19$	5	$4.13 \pm 0.09$	6.90
Antennule					
Peduncle	(2-4), (3-8)	(2–5), (3–8)	0, 3	(3-5), (2-8)	(1 or 2), 2
Endopod ct	0 or 1	0 or 1	1	0 or 1	1
Exopod ct	2I+(7–10I)	(1 or 2I), (7–10I)	1+(7 or 8)	(0-2I)+(6  or  7I)	5+4
Antenna					
Flagellum	Α	Α	Α	Α	Α
Endopod ct	0	0 or 1	0	0 or 1	0
Exopod ct	1+1+(12-15)	1+1+(14-16)	1+1+15	1+1+(11-13)	1+1+11
Protopod ct	1	1	1	1	1
Maxillule					
Coxal endite ct	11–14	13-16	12	10-12	11
Basal endite ct	3+(5  or  6)+(5-7)+1	3+(5 or 6)+(7–9)+1	16	3+(4 or 5)+(4 or 5)+1	3+7?
Endopod ct	2; 2+(3 or 4)	2; 2+(3 or 4)	2, 2+4	2; 2; 4	2, 2, 4
Maxilla					
Coxal endite ct	(15-18)+5	(17-20)+5	14+3	(14-17)+(4-6)	14+6
Basal endite ct	(8-10)+(8-10)	(10-12)+(9-12)	4+4	(7-10)+(6-9)	10+10
Endopod ct	3+2+2+2+3	3+2+2+2+3	2+2+2+2+3	3+2+2+2+(2  or  3)	3, 3, 2, 2, 3
Scaphognathite ct	26-32	29-34	34	21-26	31
Maxilliped 1					
Coxa ct	5-8	6–9	7	4–9	8?
Basis ct	4+(13-16)	4+(15–18)	12	14–18	17
Endopod ct	(3 or 4), (1 or 2), (1 or 2), (2–4)	(3 or 4), 2, 2, 4	1, 1, 5	(3 or 4), 2, 2, (3 or 4)	5, 2, 2, 4
Exopod ct	0, (6 or 7)	0, 7	7	0, (5–7)	8
Epipod	Р	Р	Р	Р	Р
Maxilliped 2					
Coxa ct	1–3	2-4	3	0–2	3
Basis ct	4 or 5	4 or 5	5	5 or 6	5
Endopod ct	(4 or 5), 1, 3, (3–5)	(4 or 5), (1 or 2), 3, 5	4, 1, 3, 4	(4-6), 1, 3, (4-6)	3, 2, 3, 6
Exopod ct	7-9	9 or 10	8 or 9	7 or 8	10
Maxilliped 3					
Coxa ct	0 or 1	1	1	0 or 1	0 or 1?

Table 5. Continued.

	Callici	hirus major				
	Gulf of Mexico	Florida Atlantic	Callichirus sp.	C. islagrande	C. garthi	
Basis ct	0-2	1 or 2	2	1–3	2	
Endopod ct	(1 or 2), (1 or 2), (4 or 5), (4 or 5)	(1-3), 2, (4 or 5), (3 or 4)	1, 1, 3, 4	(1 or 2), 2, (2–4), (4 or 5)	1, 2, 4, 6	
Exopod ct	8 or 9	9 or 10	7 or 8	7 or 8	10	
Pereiopod 1						
Coxa ct	0	0	0	0	0	
Basis ct	1	1	0	0 or 1	1	
Endopod ct	0, 2, (1–4), (2 or 3)	0, 2, (1-4), (1  or  2)	0, 1, 3, 1?	0, (1 or 2), (2-4), 2	0, 2, 3, 2	
Exopod ct	7 or 8	7–9	5-7	6 or 7	8	
Pereiopod 2						
Coxa ct	0	0	0	0	0	
Basis ct	0 or 1	0 or 1	0	0 or 1	0	
Endopod ct	0, (1 or 2), (0-4), 2	0, (0-2), (1-4), (1  or  2)	0, 2, 3, 2?	0, (0-2), (0-4), 2	0, 2, 2, 2	
Exopod ct	5–7	7 or 8	5–7	5-7	8	
Pereiopods 3–5	Р	Р	Р	Р	Р	
Pleopods	on somites 3-5	on somites 3–5	on somites 3-5	on somites 2–5	Α	
Telson						
Processes ct	(19–23)+1 +(19–23)	(20-24)+1+(20-24)	22+1+22?	(12–14)+1+(13 or 14)	18+1+18	
Process 2 as hair	Р	Р	Р	Р	Р	
Process 4 as strong spine	e P	Р	Р	Α	Α	
Median process	Р	Р	Р	Р	Р	
Uropods						
Endopod ct	0	0	0	0	0	
Exopod ct	9-12	9–14	10 or 11	10 or 11	12	

Table 6. Comparison of morphological characters for ZIV larvae of *Callichirus major* (Gulf of Mexico), *C. major* (Florida Atlantic), *C. islagrande* (Gulf of Mexico; Strasse and Felder, in press b), and *C. garthi* (Chile; Aste and Retamal, 1983). Symbols represent: presence (P); absence (A); aesthetascs (I); counts of setae and spines (ct); and n record in description or record obtained from illustration (?). Setal counts are listed from proximal to distal. Groups of setae on the same segment, or on different lobes of th same endite, are separated with a plus (+). Setal groups on successive segments are separated with a comma (,). A semicolon (;) is used to separate groups of setae on different segments in which the distinction between segments is sometimes obscure. Total length and carapace length are presented as mean (mm)  $\pm$  95% CI.

	Callichi	rus major		
	Gulf of Mexico	Florida Atlantic	C. islagrande	C. garthi
Carapace length	$2.73 \pm 0.09$	$2.50 \pm 0.05$	$1.92 \pm 0.09$	3.11
Total length	$5.89 \pm 0.19$	$6.12 \pm 0.12$	$4.82 \pm 0.25$	7.88
Antennule				
Peduncle	(2-5), (3-9)	(3-7), (5-11)	(2-6), (4-9)	7, 5
Endopod ct	1	1 or 2	1 or 2	1+2
Exopod ct	(0-2I)+(4-7I)	2I+(4-8I)	2I+(6 or 7I)	2+5
Antenna				
Endopod ct	0 or 1	0	0-2	0
Exopod ct	1+1+(14-17)	1+1+(13-16)	1+1+(12-14)	1+1+14
Protopod ct	1	1	1	1
Maxillule				
Coxal endite ct	13–16	15-17	12-14	13
Basal endite ct	3+(5 or 6)+(7 or 8)+1	(3  or  4)+(6  or  7)+(7-9)+1	3+(5 or 6)+(5 or 6)+1	3+7?
Endopod ct	2; 2+4	2; 2+(3 or 4)	2; 2; (3 or 4)	2, 2, 4
Maxilla				
Coxal endite ct	(16–19)+5	(17-23)+5	(14–19)+5	15+6
Basal endite ct	(8-10)+(9-12)	(10-12)+(11-14)	(6–10)+(8 or 9)	10+10
Endopod ct	3+(1  or  2)+(1  or  2)+2+(2-4)	3+2+2+(1 or 2)+3	3+(2  or  3)+2+2+3	3, 2, 2, 3, 3
Scaphognathite ct	27–35	31–39	27–32	37
Maxilliped 1				
Coxa ct	5–9	6–9	2-8	8?
Basis ct	(3-6)+(13-16)	(4-6)+(15-20)	16-19	20
Endopod ct	(3 or 4), (1 or 2), 2, (3 or 4)	4, 2, 2, 4	(3 or 4), 2, 2, 4	4, 2, 2, 4
Exopod ct	0, 7	0, 7	0, 6 or 7	8
Epipod	Р	Р	Р	Р
Maxilliped 2				
Coxa ct	2 or 3	2 or 3	0-3	3
Basis ct	4 or 5	4 or 5	4-6	6
Endopod ct	(4-6), (0 or 1), (2-4), (3-5)	(4 or 5), (1 or 2), (2–4), (4 or 5)	(5–8), 1, (3–5), (4 or 5)	3, 4, 5, 6
Exopod ct	8 or 9	9 or 10	7 or 8	10
Maxilliped 3				
Coxa ct	0 or 1	1	0 or 1	0 or 1?
Basis ct	2 or 3	0–3	2-4	3
Endopod ct	2, (1 or 2), (3–5), (2–4)	(2 or 3), 2, (4 or 5), (3–5)	(1 or 2), 2, (3–5), (3 or 4)	2, 3, 7, 5

Table 6. Continued.

	Callichiru	s major		
	Gulf of Mexico	Florida Atlantic	C. islagrande	C. garthi
Exopod ct	7–10	9 or 10	7 or 8	10
Pereiopod 1				
Coxa ct	0 or 1	0 or 1	0	1
Basis ct	0 or 1	1 or 2	0-2	1
Endopod ct	(0-2), $(1  or  2)$ , $(2-4)$ , $(1-4)$	(0-2), $(1  or  2)$ , $(3-5)$ , $(1-3)$	(0 or 1), (1 or 2), (2–4), (1 or 2)	1, 2, 6, 1
Exopod ct	7 or 8	7–9	5–7	10
Pereiopod 2				
Coxa ct	0	0	0	0
Basis ct	0 or 1	0-2	0 or 1	0
Endopod ct	(0-2), $(1  or  2)$ , $(3-5)$ , $(2-4)$	(0-2), $(1  or  2)$ , $(3-5)$ , $(2  or  3)$	0, (1 or 2), (3–5), (2 or 3)	0, 2, 5, 2
Exopod ct	6-8	7 or 8	5-7	9
Pereiopod 3				
Coxa ct	0	0	0	0
Basis ct	0	0	0	0
Endopod ct	(0 or 1), (1 or 2), (2–5), (1–3)	(0 or 1), 2, (2–5), 2	0, (0-2), (3 or 4), 2	0, 2, 5, 2
Exopod ct	Α	Α	4 or 5	8
Pereiopod 4				
Coxa ct	0	0	0	0
Basis ct	0	0	0	0
Endopod ct	(0 or 1), (1 or 2), (1–4), (2 or 3)	(0 or 1), 2, (1-4), 2	(0 or 1), (0-2), (2-4), 2	0, 2, 5, 3
Exopod ct	Α	Α	0-2	8
Pereiopod 5				
Coxa ct	0	0	0	0
Basis ct	0	0	0	0
Endopod ct	0, (1 or 2), (2–4), (2 or 3)	0, (1 or 2), (2–5), 2	0, 0, (4 or 5), 2	0, 1, 9, 2
Pleopods	on somites 3–5	on somites 3–5	on somites 2–5	on somites 2-5
Telson				
Processes ct	(20-22)+1+(20-22)	(21-25)+1+(21-25)	(12-15)+1+(13  or  14)	18+1+18
Process 2 as hair	P	Р	Р	Р
Process 4 as strong spine	Р	Р	Α	Α
Median process	Р	Р	Р	Р
Uropods				
Endopod	7–10	7–11	8-11	13
Exopod	1+(12–15)	1+(13–16)	1+(12–14)	1+17

Table 7. Comparison of morphological characters for decapodids of *Callichirus major* (Gulf of Mexico), *C. major* (Florida Atlantic), *C. islagrande* (Gulf of Mexico; Strasse and Felder, in press b), and *C. garthi* (Chile; Aste and Retamal, 1983). Symbols represent: presence (P); absence (A); aesthetascs (I); counts of setae and spines (ct); and n record in description or record obtained from illustration (?). Setal counts are listed from proximal to distal. Groups of setae on the same segment, or on different lobes of th same endite, are separated with a plus (+). Setal groups on successive segments are separated with a comma (,). A semicolon (;) is used to separate groups of setae on different segments in which the distinction between segments is sometimes obscure. Total length and carapace length are presented as mean (mm)  $\pm$  95% CI.

	Callichiru	is major		
	Gulf of Mexico	Florida Atlantic	C. islagrande	C. garthi
Carapace length	$1.31 \pm 0.04$	$1.60 \pm 0.10$	$1.33 \pm 0.02$	3.94
Total length	$4.29 \pm 0.16$	$5.07 \pm 0.11$	$3.78 \pm 0.11$	9.14
Antennule				
Peduncle	(16-20), (7-18), (16-28)	(16-27), (10-20), (19-28)	(17-24), (6-10), (10-17)	?
Endopod ct	(0-2), $(1  or  2)$ , $(2  or  3)$ ,	(0–2), (2 or 3),	(1-3), $(0  or  1)$ , $(1-4)$ , $(1-4)$ ,	?
-	(3 or 4), (2–5)	(2 or 3), (3–6)	(3-6), (3-6)	
Exopod ct	(2-4), (1-3), (3  or  4)+2I, (4-6I)	(0-4), (1-3), (1-5)+2I, (4-8I)	0, (0-4), (0-4), (1-4)+2I, (5-8I)	?
Antenna				
Flagellum	Р	Р	Р	Р
Exopod ct	0	0	0–5	?
Protopod ct	(0 or 1), (5–7)+1	(0 or 1), (5–8)+1	(0 or 1), (1–3)+1	?
Maxillule				
Coxal endite ct	(18–24)+(0 or 1)	(21-28) + (0  or  1)	(15-22) + (0  or  1)	?
Basal endite ct	(7-11) +(19-25)+(1 or 2)	(6-11), (21-27), (1 or 2)	(3-5)+(14-19) + (0-2)	16+8
Endopod ct	0-8	0-8	0-8	2
Protopod	0 or 1	0 or 1	0	?
Maxilla				
Coxal endite ct	(16-19)+(8-14)+(5-12)	(18-25)+(9-15)+(6-12)	(17-21)+(7-10)+(6-9)	(38-40)+12
Basal endite ct	(9-13)+(17-29)	(11-16)+(22-41)	(8-10)+(8-15)	(14-16)+(13-15)
Endopod ct	4-9	4–11	5-11	5+2
Scaphognathite ct	36-49	33-48	37-45	68
Maxilliped 1				
Coxa ct	8-15	11–20	8-12	?
Basis ct	50-100	50-100	27–39	?
Endopod ct	0-5	0-8	0–11	?
Exopod ct	9–24	0–22	6-14	?
Epipod	Р	Р	Р	Р
Maxilliped 2				
Coxa ct	2-6	2-6	1–4	?
Basis ct	5-10	4–14	3–5	?
Endopod ct	(23-39), (0 or 1), (8-16), (6-12)	(25-42), (0 or 1), (9-17), (9-15)	(16-23), (0 or 1), (6-11), (4-8)	?
Exopod ct	0–16	0–14	0-8	?
Epipod	Р	Р	Р	?

Table 7. Continued.

	Callichiri	us major		
	Gulf of Mexico	Florida Atlantic	C. islagrande	C. garthi
Maxilliped 3				
Coxa ct	2–5	2-6	0-3	?
Basis ct	2-6	2-7	1-4	?
Endopod ct	(17-35), (7-14), (11-24),	(21-36), (12-20), (19-25),	(11–19), (9–15), (7–11),	5 on dactyl
	(15-32), (6-10)	(18–32), (8–13)	(8–21), (5–11)	
Exopod ct	0-8	0-9	0-9	?
Epipod	Р	Р	Р	?
Pereiopod 1				
Coxa ct	1-4	1-4	0-6	?
Basis ct	1–3	1–3	2–5	?
Endopod ct	(0-4), (3-6), (7-18), (26, 41), (2, 27, 2), (17, 20)	(2-5), (3-7), (11-22),	(4-7)+(0-3), (5-8), (10-14),	?
Example at	(20-41)+(2  or  3), (17-30)	(31-40)+(2-4), (20-32)	(27-37), $(3  of  4)$ , $(21-33)$	9
Exopod Cl	0=7	0-8	0=7	1
Cana at	0.5	1 4	2.5	2
Coxa ct	0-5	1-4	2-5	<i>!</i>
Basis ct				?
Endopod ct	(2-10), (8-31), (9-19), (21-47)+(2-4), (20-27)	(5-10), (19-28), (10-16), (31-49)+(2  or  3), (20-30)	(4-10), (15-20), (8-12), (30-40)+(1-4), (21-30)	?
Exopod ct	0-7	0-8	0-7	?
Pereiopod 3				
Coxa ct	1–5	2 or 3	2–5	?
Basis ct	0-2	1 or 2	1–3	?
Endopod ct	(0-5), (2-7), (5-13), (28-79) + 1, (6-26)	(3-6), (4-8), (9-19), (42-87)+1, (17-35)	(5-8), (6-9), (7-11), (25-34)+1, (15-21)	?
Exopod ct	small nub	small nub	0-5	9
Pereiopod 4	Shiwi nuo	Sman mao	0.5	·
Coxa ct	1-6	2–5	2–7	?
Basis ct	0-3	1 or 2	1-4	?
Endopod ct	(1-7), (2-8), (2-7),	(3-6), (3-7), (4-8),	(3-8), (5-11), (4-9),	?
	(20-46)+1, (10-20)	(28-47)+1, (12-21)	(27-38)+1, (15-19)	
Exopod ct Pereiopod 5	small nub	small nub	0–2	?
Coxa ct	0-4	1-3	2-6	?
Basis ct	0 or 1	1 or 2	1 or 2	?
Endopod ct	(1-4), (2-7), (2-6),	(1-3), (3-5), (5-7),	(2-5), (5-9), (4-7),	?
	(12–24)+1, (5–9)	(13-33)+1, (8-13)	(22-30)+1, (6-10)	
Exopod	small nub	small nub	Α	?

I	ab	le	7.	Continued.	
-	_	_			-

*C. islagrande* has been slightly abbreviated or that development of *C. garthi* has been

	Callichiru	us major	C. islagrande	C. garthi
	Gulf of Mexico	Florida Atlantic		
Pleopods (2)	Α	Α	Р	Р
Basis ct			0-3	0
Endopod ct			(3-5)+(10-17)+(0-2)	0
Exopod ct			(21-27)+(0  or  1)	0
Pleopods (3-5)	Р	Р	P	Р
Coxa ct	0	0	0	?
Basis ct	4–9	6-10	3-6	?
Endopod ct	(4-10)+(14-21)+(0-3)	(5-11)+(12-28)+(0-2)	(3-6)+(10-18)+(0-3)	?
Exopod ct	(35-63)+(2-7)	(41-54)+(0-9)	(20-29)+(0  or  1)	?
Telson				
Process 2 as hair	Α	А	Α	?
Median process	Α	А	Α	Α
Uropods				
Endopod ct	16-23	20-27	19–25	?
Exopod ct	56-108	31–103	35–58	?

of C. major did not respond to stimuli in the study of settlement cues, most of the larvae gests that development of C. major and pleopods and chelate pereiopods at ZIII. ZV. In each of these cases, the molt to ZV Gulf population of C. major rarely molts to and the Florida Atlantic C. major, while the mate conditions in their natural habitat. and 35 ppt salinity, respectively, to approxivation). In the present study, the Gulf and when reared at 25 or 35% (personal obsersalinity molted to ZV (personal observation) from ZIV to D, while those reared at 35 ppt Strasser and Felder, in press b). closer to ZIV (Aste and Retamal, 1983 son, dorsal spines, and swimming behavior of to ZIV. These larvae often took on a decapowas usually morphologically closer to D than Florida Atlantic population of C. major, ZV same way (Strasser and Felder, 1998). In the to a ZV (Strasser and Felder, in press a). Calstage, while the absence of stimuli at ZIV led molted directly from ZIV to the decapodid tioned water) at ZIV during a comparative ural conditions. When ZIV larvae were of rearings, and may not be present under nat artifact of subtle differences in laboratory presence of ZV in this population could be an Acquisition of these characters at ZIII sug veloped until ZIV (Aste and Retamal, 1983) while in C. garthi these characters are not debeyond ZIV (Strasser and Felder, in press b). ZV is somewhat common in C. islagrande be more consistent in C. garthi. The molt to variable in C. major and C. islagrande, it may Florida Atlantic populations were reared at 25 C. major consistently molted from ZIV to D ity of animals reared at 25 ppt salinity molted Atlantic population of C. major, the majoring the number of zoeal stages. In the Florida jor, C. islagrande, and C. garthi, ZV was ZIV, while in the Gulf population of C. ma did body shape, but retained the rostrum, tel lichirus islagrande and the Gulf population fered selected stimuli (sand and adult-condi ing protocols were rigidly standardized, the lantic C. major. However, even though rear involves little morphological advancement In contrast, larvae of the Gulf population of Larvae of C. major and C. islagrande acquire Salinity may also be a factor in determin While presence of the fifth zoeal stage is

extended. Development in the estuarine species Callianassa kraussi Stebbing, C. kewalramanii Sankolli, C. tyrrhena (Petagna), Lepidophthalmus louisianensis (Schmitt), and L. sinuensis Lemaitre and Rodrigues has been reduced to only two brief zoeal stages (Forbes, 1973; Sankolli and Shenoy, 1975; Thessalou-Legaki, 1990; Nates et al., 1997).

While the two populations of C. major are very similar morphologically, differences in the length of the outer process on the telson, the length of the dorsal spine of the second abdominal somite, and the occurrence of ZV separate them. These distinctions support previous work that reported genetic differences between these populations (Staton and Felder, 1995) and differences in larval behavior (Strasser and Felder, in press a). Although the duration of development in C. major is long in comparison to that of Lepidophthalmus spp. (Nates et al., 1997), it may nonetheless be insufficient for successful export of larvae from this northern Gulf of Mexico population to the Atlantic.

#### **ACKNOWLEDGEMENTS**

We thank R. Bourgeois, K. Hill, J. MaKinster, S. Nates, and Kurt Strasser who assisted with field collections, and M. E. Rice, Director of the Smithsonian Marine Station, Link Port, Florida, who facilitated access to station facilities. We also thank R. Bauer, R. Jaeger, R. Lemaitre, and G. Watson for their comments on the manuscript, and thank Raymond B. Manning who facilitated funding and gave advice on collecting sites. Direct support for this study was provided to Karen Strasser by a doctoral fellowship from the University of Southwestern Louisiana, a graduate student research grant from the LUMCON (Louisiana Universities Marine Consortium) Foundation, and a summer research award from the Smithsonian Marine Station. Additional support for field and lab activities was provided to D. L. Felder under Louisiana Sea Grant College Program Grant R/CFB-21, U.S. Fish and Wildlife Service Cooperative Agreement 14-16-0009-89-96 (Task Order No. 6), U.S. Department of Energy grant DE-FG02-97ER12220, and several small project grants from the Smithsonian Marine Station. Views expressed herein are those of the authors, and do not necessarily reflect views of supporting government agencies or subagencies mentioned above. This is contribution No. 459 from the Smithsonian Marine Station and contribution No. 64 from the USL Laboratory for Crustacean Research. All experiments conducted in this study comply with current applicable state and federal laws.

#### LITERATURE CITED

Aste, A., and M. Retamal. 1983. Desarrollo larval de *Callianassa garthi* Retamal, 1975 bajo condiciones de laboratorio.—Ciencia y Tecnología del Mar, CONA 7: 5–26.

- —, and —, 1984. Desarrollo larval de *Callianassa uncinata* H. Milne Edwards, 1837 (Decapoda, Callianassidae) bajo condiciones de laboratorio.— Gayana Zoológica 48: 41–56.
- Felder, D. L. 1978. Osmotic and ionic regulation in several western Atlantic Callianassidae (Crustacea, Decapoda, Thalassinidea).—Biological Bulletin 154: 409-429.
- —, and R. B. Griffis. 1994. Dominant infaunal communities at risk in shoreline habitats: burrowing thalassinid Crustacea.—OCS Study Number MMS 94–0007. U.S. Dept. of the Interior, Minerals Management Service, Gulf of Mexico OCS Regional Office, New Orleans, Louisiana. Pp. 1–87.
- Forbes, A. T. 1973. An unusual abbreviated larval life history in the estuarine burrowing prawn *Callianassa kraussi* (Crustacea: Decapoda: Thalassinidea).—Marine Biology 22: 361–365.
- Gurney, R. 1942. Larvae of decapod Crustacea.—Ray Society. London, Great Britain. Pp. 1-305.
- Konishi, K. 1989. Larval development of the mud shrimp Upogebia (Upogebia) major (De Haan) (Crustacea: Thalassinidea: Upogebiidae) under laboratory conditions, with comments on larval characters of thalassinid families.—Bulletin of the National Research Institute of Aquaculture 15: 1–17.
- ——, R. Quintana, and Y. Fukuda. 1990. A complete description of larval stages of the ghost shrimp *Callianassa petalura* Stimpson (Crustacea: Thalassinidea: Callianassidae) under laboratory conditions.—Bulletin of the National Research Institute of Aquaculture 17: 27–49.
- Manning, R. B., and D. L. Felder. 1986. The status of the callianassid genus *Callichirus* Stimpson, 1866 (Crustacea: Decapoda: Thalassinidea).—Proceedings of the Biological Society of Washington 99: 437–443.
- Martin, J. W., D. L. Felder, and F. M. Truesdale. 1984. A comparative study of morphology and ontogeny in juvenile stages of four western Atlantic xanthoid crabs (Crustacea: Decapoda: Brachyura).—Philosophical Transactions of the Royal Society of London Ser. B 303: 537-604.
- Nates, S. F., D. L. Felder, and R. Lemaitre. 1997. Comparative larval development in two species of the burrowing ghost shrimp genus *Lepidophthalmus* (Decapoda: Callianassidae).—Journal of Crustacean Biology 17: 497–519.
- Reeb, C. A., and J. C. Avise. 1990. A genetic discontinuity in a continuously distributed species: mitochondrial DNA in the American oyster *Crassostrea vir*ginica.—Genetics 124: 397–406.
- Rodrigues, S. de A. 1976. Sobre a reprodução, embriologia e desenvolvimento larval de *Callichirus major* Say, 1818 (Crustacea, Decapoda, Thalssinidea).—Boletim de Zoologia, Universidade de São Paulo 1: 85–104.
- Sankolli, K. N., and S. Shenoy. 1975. Larval development of mud shrimp *Callianassa (Callichirus) kewalramanii* Sankolli, in the laboratory (Crustacea, Decapoda).—Bulletin of the Department of Marine Science, University of Cochin 4: 704–720.
- Staton, J. L., and D. L. Felder. 1995. Genetic variation in populations of the ghost shrimp genus *Callichirus* (Crustacea: Decapoda: Thalassinoidea) in the western Atlantic and Gulf of Mexico.—Bulletin of Marine Science 56: 523-536.
- Strasser, K. M., and D. L. Felder. 1998. Settlement cues in successive developmental stages of the ghost shrimp

Callichirus major and C. islagrande (Crustacea: Decapoda: Thalassinidea).—Marine Biology. 132: 599–610.

- ———, and ———. (In press a). Settlement cues in the Florida Atlantic population of the ghost shrimp *Callichirus major* (Crustacea: Decapoda: Thalassinidea).— Marine Ecology Progress Series.
- ——, and ——. (In press b.) Larval development of *Callichirus islagrande* (Decapoda: Callianassidae).—Journal of Crustacean Biology.
- Thessalou-Legaki, M. 1990. Advanced larval development of *Callianassa tyrrhena* (Decapoda: Thalassinidea) and the effect of environmental factors.— Journal of Crustacean Biology 10: 659–666.
- Williams, A. B. 1984. Shrimps, lobsters, and crabs of the Atlantic Coast.—Smithsonian Institution Press, Washington, D.C. Pp. 1–550.
- Williamson, D. I. 1982. Larval morphology and diversity.—In: D. E. Bliss, ed.-in-chief, The biology of Crustacea. Vol. 2, L. G. Abele, ed., Embryology, morphology, and genetics. Pp. 43–110. Academic Press, New York, New York.

RECEIVED: 12 August 1998.

ACCEPTED: 12 October 1998.

Address: Department of Biology, University of Southwestern Louisiana, Lafayette, Louisiana 70504, U.S.A. (e-mail: kms@usl.edu; dfelder@usl.edu)