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MORPHOLOGICAL CHARACTERISTICS OF EARLY LIFE HISTORY STAGES OF THE BLUE CRAB, *CALLINECTES SAPIDUS* RATHBUN, FROM THE NORTHERN GULF OF MEXICO WITH A COMPARISON OF STUDIES FROM THE ATLANTIC SEABOARD

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Abstract: Zoeae, megalopae, and early crab stages of *Callinectes sapidus* Rathbun, 1896 were described from the northern Gulf of Mexico (nGOM). Observations during this study were based on larvae reared in the laboratory through the early crab stages and on megalopae and early crab stages collected in the wild. Gulf of Mexico data are compared with similar information for the southeast Atlantic coast of the United States. Size and setation of *C. sapidus* larvae reared from nGOM stocks were different than those in published descriptions of larvae reared from Atlantic populations. Seasonal differences in size were noted in both reared and wild caught specimens. Zoeal stages I, II and III of larvae cultured in the spring were larger than corresponding larvae hatched in the summer/fall. Data sets on zoeal stages IV and V were incomplete; however, seasonal differences in measurements on all structures tended to be smaller in the summer/fall reared larvae. No seasonal differences were observed for the sixth and seventh zoeal stages, megalopal stage and first crabs. Spring reared larvae had higher survival rates when reared at optimal temperature (25°C) and required fewer zoeal stages (6) to reach the megalopal stage. Megalopae and first crabs collected from the plankton exhibited distinct seasonal variations and were larger in the spring than in fall.

Introduction

The blue crab, *Callinectes sapidus*, supports large commercial and recreational fisheries along the Atlantic coast and in the northern Gulf of Mexico (nGOM) (Guillory et al. 2001). The ability to reliably separate blue crab larvae from other portunids is beneficial over a broad range of ecological and fishery-related studies of coastal plankton. However, identification of *C. sapidus* larvae from plankton samples in the nGOM is complicated by the overlapping spawning periods among the large number of portunid species found in the region and the abundance and distribution of its sympatric congener, *Callinectes similis*. In addition, successful mass culture of blue crabs in Maryland and in Mississippi has generated interest in their culture for stock replenishment in the Chesapeake Bay and for expansion of the soft crab fishery in the nGOM (Zmora et al. 2005, Perry et al. 2005). Current aquaculture techniques require identification of specific larval stages to track development since feed size and type varies with zoeal stage.

Stuck and Perry (1982) provided characters useful in the identification of *C. sapidus* larvae and early crab stages, but these descriptions are not readily available in the general literature. The current study draws upon that early work and provides descriptions of developing blue crabs from the first zoeal stage through the second crab stage. Additionally, seasonal differences in morphology among larvae reared from nGOM populations are presented and the morphological differences in *C. sapidus* larvae reared from the nGOM are compared to existing data from the Atlantic coast. Data from this study will provide a means by which to track zoeal development in plankton collections and aquaculture operations in the nGOM.

Materials and Methods

Egg bearing females were collected from the Mississippi Sound in cold water temperature (April 1980; spring) and again during warm water temperature (late August 1980; summer/fall) and brought into the laboratory for spawning and collection of newly hatched larvae. Larvae hatched from 6 different females (3 spring, 3 summer/fall) were isolated and reared separately in mass and individual cultures. All larvae were reared in 30 ppt filtered artificial seawater with Penicillin (60 mg/l) and Streptomycin (50 mg/l) added. Larvae from each seasonal group were reared at both optimal (25.0°C, Sandoz and Rogers 1944, Costlow and Bookhout 1959, Sulkin and Epifanio 1975) and ambient temperatures. Ambient spring temperatures, initially l6.0°C, were slowly increased at a rate of about 1.0°C/week to correspond to naturally occurring conditions. Ambient summer/fall temperatures were initially 30.0°C and were gradually decreased at a rate of 1.0°C/week. Photoperiod was held constant at 12L:12D. Depending upon the experimental temperature, the culture period ranged from about 3 -13 weeks.

Larvae from each hatch were initially isolated in a series of three mass culture bowls, each with about 500 larvae in

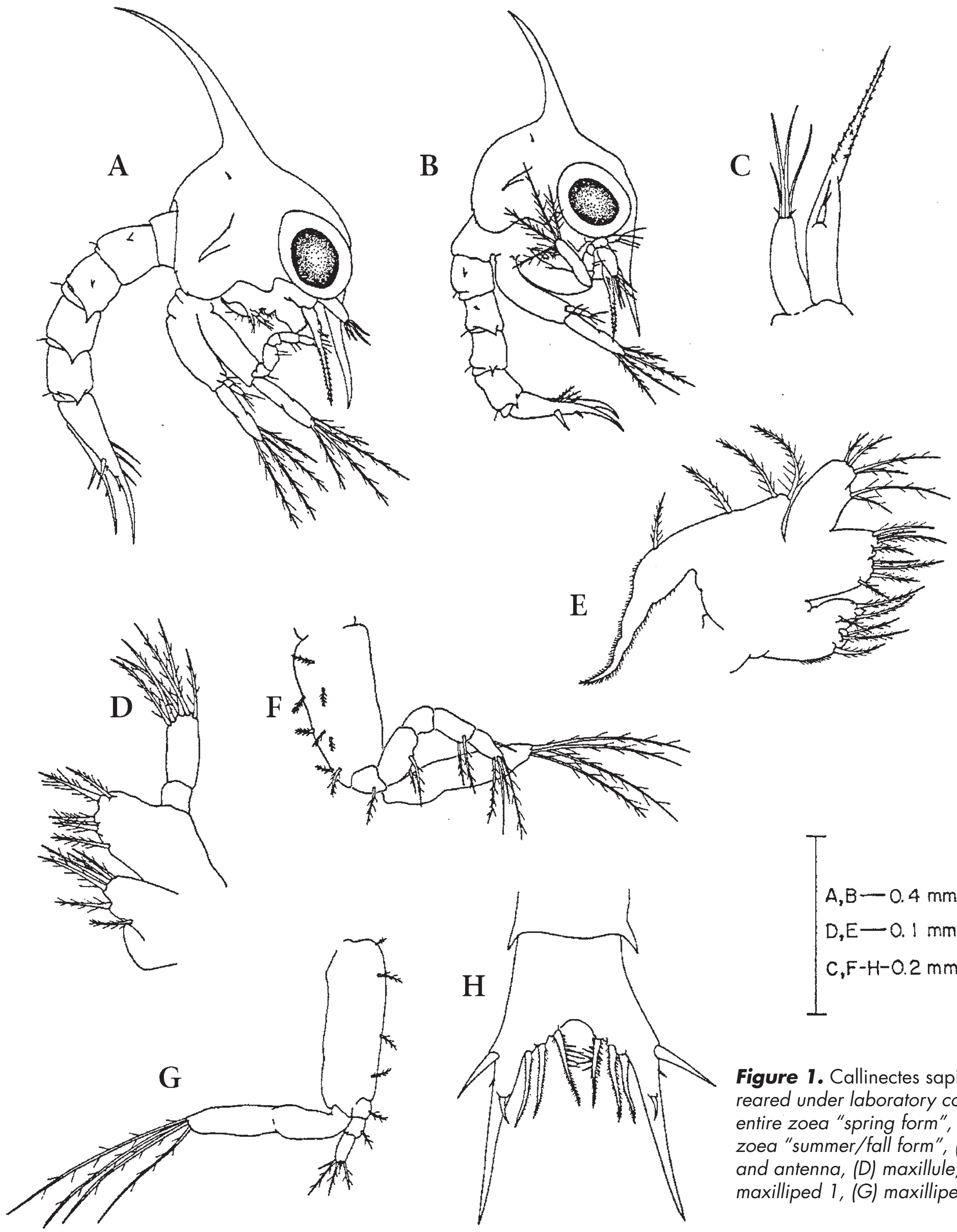

Figure 1. *Callinectes sapidus zoea I reared under laboratory conditions. (A) entire zoea "spring form", (B) entire zoea "summer/fall form", (C) antennule and antenna, (D) maxillule, (E) maxilla, (F) maxilliped 1, (G) maxilliped 2, (H) telson.*

1 L of seawater. Additional larvae (18) were placed in plastic boxes, one zoea per cubicle in 200 ml of seawater. Two identical sets of larvae were prepared from each parent, one reared at optimal and the other at ambient temperature for individual and mass culture. Zoeae were transferred to clean water daily and initially fed a diet of rotifers (first 14 d) and a combination of rotifers and brine shrimp after 2 weeks. Exuviae were removed and preserved in 5% formalin from both mass and individual cultures. Additional live zoeae from each developmental stage (about 20) were preserved in 10% formalin from mass cultures. Time required for larvae to become megalopae in mass cultures was determined by recovery of final stage zoeae exuviae from culture bowls. Percent survival to the megalopal stage was determined by daily observation of larvae in individual culture for each season and experimental temperature.

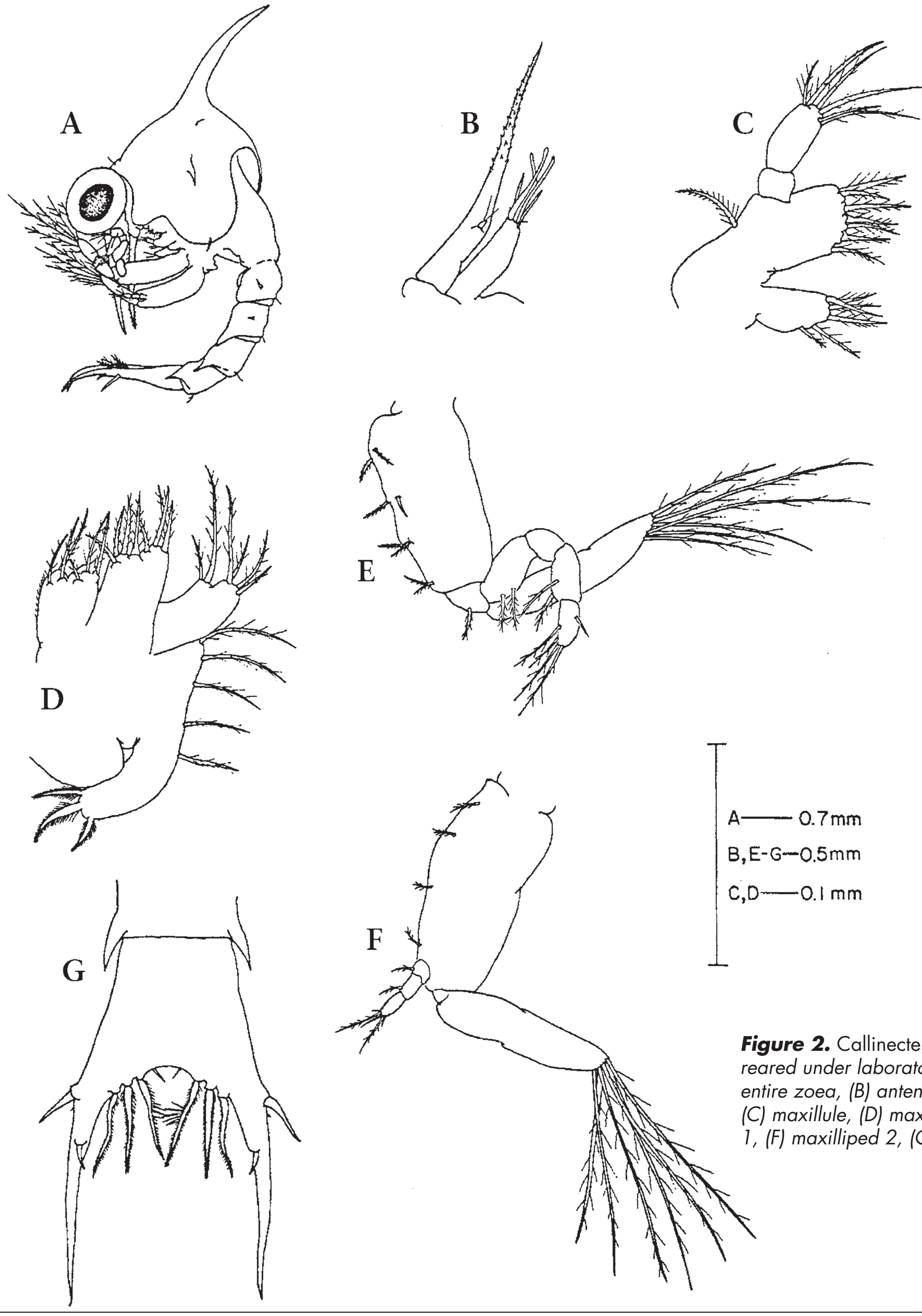

Figure 2. Callinectes sapidus *zoea II reared under laboratory conditions. (A) entire zoea, (B) antennule and antenna, (C) maxillule, (D) maxilla, (E) maxilliped 1, (F) maxilliped 2, (G) telson.*

Measurements (mm) were made on exuviae for a number of morphological characters of larvae obtained from each culture set for both spring and summer/fall broods. Measurements included total carapace length and width, dorsal and rostral spine length, and appendage setation for 10 larvae of each stage. Data were compiled as the mean and range for each character for each brood; raw data (individual measurements) were lost during Hurricane Katrina. All illustrations were made with a camera lucida.

Blue crab megalopae were collected in zooplankton samples taken from Dog Keys Pass, MS in May (spring) and October (fall) of 1980. These megalopae were cultured individually in the laboratory until they reached a size at which positive identification as C. *sapidus* could be made (crab stages 3-5). Measurements (mm) of total carapace length, rostral length, antennal length and carapace width for megalopae

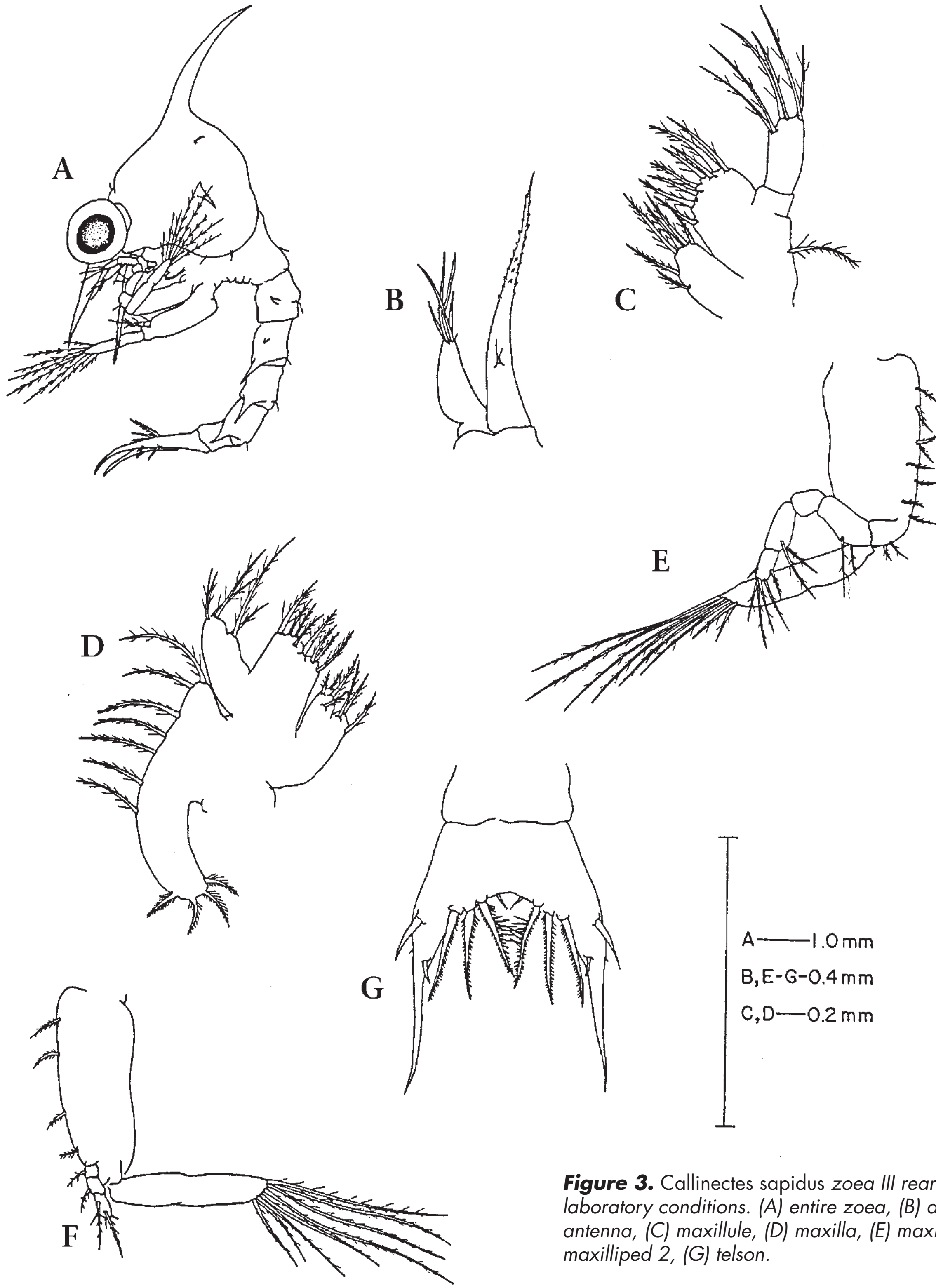

Figure 3. Callinectes sapidus *zoea III reared under laboratory conditions. (A) entire zoea, (B) antennule and antenna, (C) maxillule, (D) maxilla, (E) maxilliped 1, (F) maxilliped 2, (G) telson.*

and subsequent first crabs were made from the recovered exuviae.

Results

Survival, Rate, and Duration of Larval Development

The percent survival of individually held larvae reared through the megalopal stage varied with brood, temperature and season (Table 1). Larvae reared at 25.0°C in the spring showed the highest overall survival (44.5%), while larvae reared at 25.0°C in the summer/fall had the lowest survival (18.5%). Although quantitative survival estimates for larvae held in mass cultures were not made, trends were similar to those reported for larvae held in individual cultures.

Among larvae reared in individual culture, the number of zoeal stages required to reach the megalopal stage varied

TABLE 1. *Survival (%) of blue crab larvae reared from ovigerous females collected in spring and summer/fall and held in individual cultures. Survival is expressed as percent of larvae reaching the megalopal stage at each experimental temperature.*

	SPRING SPAWN		SUMMER/FALL SPAWN	
Temperature (°C)	**25.0**	**≥ 16.0**	**25.0**	**≤ 30.0**
Brood 1	38.9	27.8	22.2	44.4
Brood 2	38.9	16.7	27.8	61.1
Brood 3	55.6	66.7	5.5	11.1
Mean	44.5	37.1	18.5	38.9

from 6 to 9 (Table 2). Within the group of larvae reared in the spring, the majority reached the megalopal stage in 6 molts. In contrast, few of the larvae reared from summer/fall broods reached the megalopal stage in only 6 molts. Within a season there were no notable differences in the number of zoeal molts to the megalopal stage between optimal and ambient temperatures.

Time required for development of spring larvae cultured at ambient temperature (≥ 16.0°C) was about twice that of larvae reared at 25.0°C (Table 3). Spring larval groups held individually required a mean of 34.6 d to reach the megalopal stage when cultured at 25.0°C compared to 65.7 d when cultured at ambient temperatures. Additionally, the range of time for development was completely separate for the two temperatures (Table 3). Summer/fall larvae held individually at 25.0°C and ambient temperatures (≤ 30.0°C) required a mean of 44.3 and 46.6 d, respectively, to reach the megalopal stage, and the range in development times overlapped almost completely between temperatures. A minimum of 23 d was required to reach the megalopal stage for spring larvae (brood 3) held in mass culture at 25.0°C. Surviving spring larvae held in mass culture at ambient temperatures required a minimum of 52 d to become megalopae (brood 3). Minimum time required to reach the megalopal stage for summer/fall larvae held in mass cultures at 25.0°C and ambient temperatures was 37 and 32 d, respectively (brood 1).

Morphological Development and Description of Larvae

Seven zoeal and one megalopal stage were identified in the present study. While some larval series consisted of 6, 8 or 9 zoeal stages, the resulting "combined" or "additional" stages usually possessed a composite of morphological characters from the 7 types presented here. The pattern of the chromatophores was identical for all zoeal stages and similar to that described by Costlow and Bookhout (1959).

Zoea I. Total length 0.90-1.25 mm (Figure 1)

Carapace (Figure 1A, B): smooth with prominent dorsal, lateral and rostral spines, minute seta present on each side at base of dorsal spine, posterior ventral margin with 1 or 2 fine serrations. Rostral spine 0.20-0.30 mm, dorsal spine 0.30-0.48 mm, carapace spine width 0.45-0.67 mm (measured at base), carapace spine length 0.79-1.17 mm. Eyes unstalked.

Antennule and antenna (Figure 1C): antennule conical, bearing 3 aesthetascs, 1 or 2 slender setae and 1 or 2 minute "hair-like" setae (seen only under extreme magnification). Protopodite of antenna slender, bearing 2 rows of minute spines on distal half; exopodite small, terminating with 2 simple setae of unequal length.

Maxillule (Figure 1D): endopodite with 2 articles, distal article with 4 terminal and 2 slightly subterminal plumose setae; basal endite of protopodite bearing 5 plumose setae; coxal endite with 5 or 6 plumose setae.

Maxilla (Figure 1E): scaphognathite with 4 marginal setae on distal portion, proximal portion tapered; endopodite unarticulated, bearing 4 terminal and 2 subterminal setae; basal endite of protopodite with 7 or 8 plumose setae; coxal endite with 3 (rarely 2) plumose setae on each lobe.

Maxilliped 1 (Figure 1F): exopodite with 4 terminal plumose setae; basal article of endopodite with 8 (rarely 7 or 9) plumose setae, distal 5 articles usually with plumose setae arrangement of 1, 2, 0, 2, 5.

Maxilliped 2 (Figure 1G): exopodite with 4 terminal plumose setae; basal article of endopodite with 4 setae; distal 3 articles with plumose setae arrangement of 1, 1, 4 or 5 (2 long, 2 or 3 short).

Abdomen and telson (Figure 1A-B, H): abdomen consisting of 5 segments and a telson; second segment with a short knob-like process on each dorsal lateral surface, third seg-

TABLE 2. *Number of zoeal stages (indicated by Roman numerals) required to reach the megalopal stage listed by season, experimental culture temperature and brood. Numbers in parentheses indicate the actual number of complete larval series recovered from individual cultures and included in the analysis.*

	SPRING SPAWN		SUMMER/FALL SPAWN	
Temperature (°C)	**25.0**	**≥ 16.0**	**25.0**	**≤ 30.0**
Brood 1	VI (1) VII (6)	VI (2) VII (2) VIII (1)	VI (1) VII (4)	VI (1) VII (4) VIII (2) IX (1)
Brood 2	VI (3) VII (4)	VI (3)	VI (2) VII (2)	VI (1) VII (7) VIII (2)
Brood 3	VI (7) VII (3)	VI (8) VII (3)	VII (1)	VI (1) VII (1)
Overall	VI (24) VII (18) VIII (1)		VI (6) VII (19) VIII (4) IX (1)	

TABLE 3. *Time (in days) required for development of larvae through the megalopal stage in both individual (IC) and mass (MC) culture.*

SPRING SPAWN	Brood 1		Brood 2		Brood 3		Combined Data	
Temperature (°C)	**25.0**	**≥ 16.0**	**25.0**	**≥ 16.0**	**25.0**	**≥ 16.0**	**25.0**	**≥ 16.0**
Mean								
IC	37.6	66.4	34.3	66.0	31.9	64.6	34.6	65.7
MC	36.0	65.2	35.1	63.7	28.5	60.5	33.2	63.1
Range								
IC	33-49	62-72	26-41	62-72	26-42	56-75	26-49	56-75
MC	33-41	57-88	30-46	55-82	23-36	52-71	23-46	52-88
SUMMER/FALL SPAWN								
	Brood 1		**Brood 2**		**Brood 3**		**Combined Data**	
Temperature (°C)	**25.0**	**≤ 30.0**	**25.0**	**≤ 30.0**	**25.0**	**≤ 30.0**	**25.0**	**≤ 30.0**
Mean								
IC	38.0	39.0	49.0	43.3	46.0†	57.5	44.3	46.6
MC	48.0	40.3	46.1	47.3	49.5	48.0	47.9	45.2
Range								
IC	33-46	32-48	40-59	32-52	46.0†	56-60	33-59	32-60
MC	37-60*	32-50	40-60*	34-58	46-60*	37-56	37-60*	32-58

†Based on a single surviving larva.
*Terminated in final zoeal stage.

ment with a short hook on each side, segments 2 to 5 with pair of minute dorsal setae, segments 3 to 5 with prominent lateral spines; telson bifurcate ending in two acute spines, each furca with a single small dorsal seta and 1 large robust and 1 minute lateral seta, inner margin of each furca with 3 large, heavily armored robust setae.

Zoea II. Total length 0.94-1.45 mm (Figure 2)

Carapace (Figure 2A): similar to first zoea, but larger, bearing a single seta on anterior margin just above eyes and a single seta on posterior ventral margin, no serrations. Rostral spine 0.22-0.42 mm, dorsal spine 0.30-0.55 mm, carapace spine width 0.47-0.73 mm, carapace spine length 0.80-1.30 mm. Eyes stalked.

Antennule and antenna (Figure 2B): antennule with 3 aesthetascs and 1 to 2 setae. Antenna similar to first zoea.

Maxillule (Figure 2C): endopodite as in first zoea; most specimens with a large seta on inner margin of protopodite, basal endite with 7 plumose setae, coxal endite with 4 apical and 2 subterminal plumose setae.

Maxilla (Figure 2D): scaphognathite with 5 (rarely 4 or 6) distal marginal setae and 3 apical setae; endopodite similar to first zoea; basal endite of protopodite with 8 or 9 plumose setae, coxal endite with 3 plumose setae on each lobe, distal margin of inner lobe produced into a sharp seta.

Maxilliped 1 (Figure 2E): exopodite with 6 terminal plumose setae; endopodite similar to first zoea.

Maxilliped 2 (Figure 2F): exopodite with 6 terminal plumose setae; endopodite similar to first zoea.

Abdomen and telson (Figure 2A, G): abdomen similar to first zoea except lateral spines more developed. Telson similar to first zoea except for addition of a pair of slender setae to inner medial margin of furca.

Zoea III. Total length 1.12-1.80 mm (Figure 3)

Carapace (Figure 3A): similar to second zoea, but slightly larger, single seta added on rostrum between eye stalks, posterior ventral margin bearing 1 or 2 setae. Rostral spine 0.32-0.53 mm, dorsal spine 0.32-0.67 mm, carapace spine width 0.58-0.87 mm, carapace spine length 1.02-1.60 mm.

Antennule and antenna (Figure 3B): unchanged from second zoea.

Maxillule (Figure 3C): endopodite as in second zoea; all specimens with a large seta on inner margin of protopodite, basal endite with 8 or 9 plumose setae, coxal endite with 4 or 5 apical and two sub-terminal plumose setae.

Maxilla (Figure 3D): scaphognathite with 6 or 7 marginal plumose setae on distal portion, proximal margin with 4 (rarely 3) plumose setae; endopodite and protopodite similar to second zoea.

Maxilliped 1 (Figure 3E): exopodite with 8 terminal plumose setae; endopodite similar to second zoea except for the addition of a second subterminal seta on terminal article.

Maxilliped 2 (Figure 3F): exopodite with 8 terminal plumose setae; endopodite unchanged from second zoea.

Abdomen and telson (Figure 3A, G): abdomen consisting of 6 segments; pair of dorsal setae added to first 4 segments, sixth segment without lateral spine. Telson setation unchanged from second zoea.

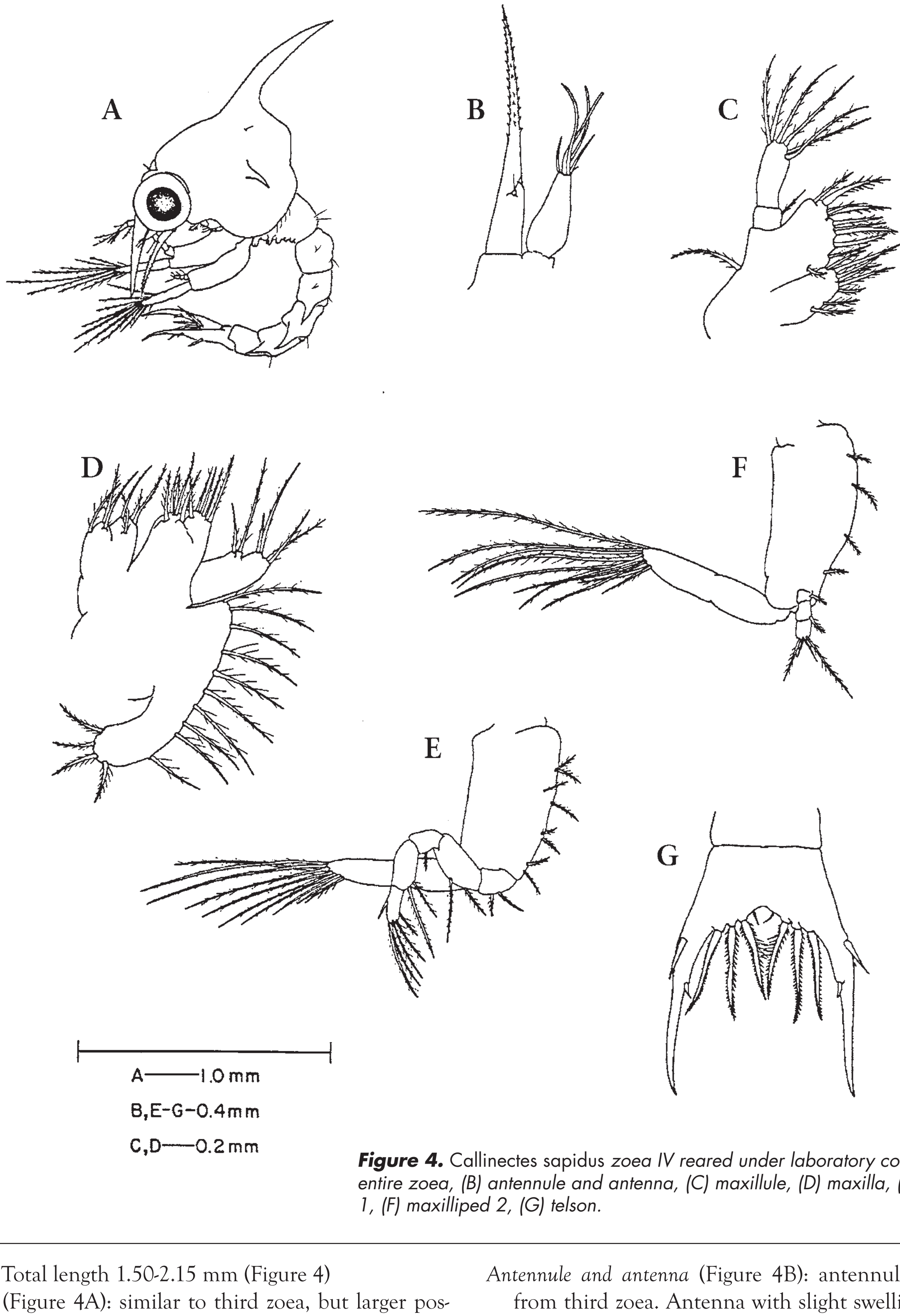

Figure 4. Callinectes sapidus *zoea IV reared under laboratory conditions. (A) entire zoea, (B) antennule and antenna, (C) maxillule, (D) maxilla, (E) maxilliped 1, (F) maxilliped 2, (G) telson.*

Zoea IV. Total length 1.50-2.15 mm (Figure 4)

Carapace (Figure 4A): similar to third zoea, but larger posterior ventral margin bearing 4 or 5 setae; buds of third maxilliped, chelae and pereiopods barely visible beneath carapace. Rostral spine 0.35-0.67 mm, dorsal spine 0.43-0.84 mm, carapace spine width 0.67-1.10 mm, carapace spine length 1.19-2.04 mm.

Antennule and antenna (Figure 4B): antennule unchanged from third zoea. Antenna with slight swelling just distal to insertion of exopodite marking development of endopodite bud.

Maxillule (Figure 4C): proximal article of endopodite armed with a single plumose seta, distal article as in third zoea; basal endite of protopodite with 9 terminal plumose se-

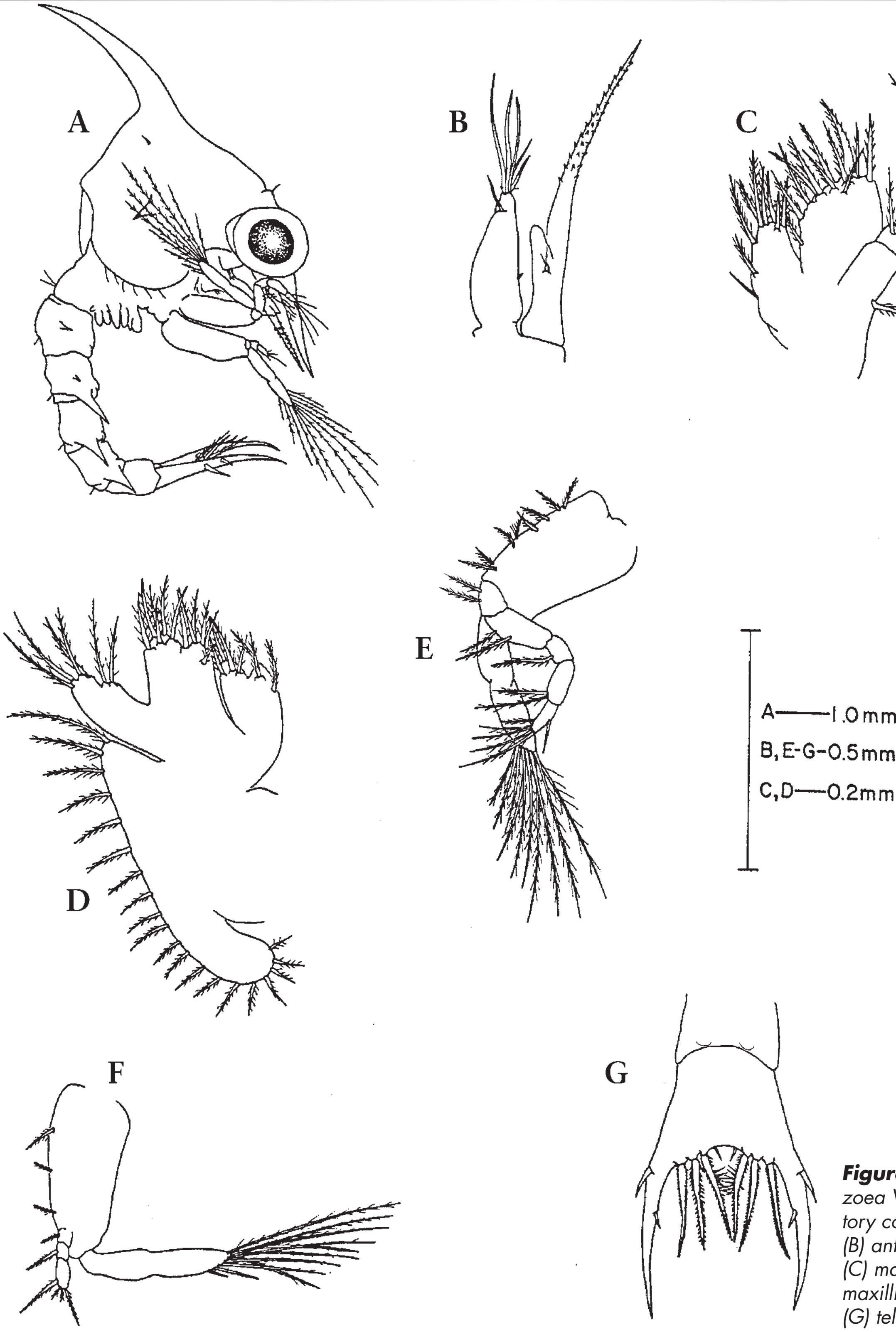

Figure 5. *Callinectes sapidus zoea V reared under laboratory conditions. (A) entire zoea, (B) antennule and antenna, (C) maxillule, (D) maxilla, (E) maxilliped 1, (F) maxilliped 2, (G) telson.*

tae and occasionally a single subterminal plumose seta, coxal endite with 5 or 6 terminal and 2 subterminal plumose setae.

Maxilla (Figure 4D): scaphognathite with 12 to 22 plumose setae along the entire length; endopodite unchanged from third zoea; basal endite with 9 to 10 plumose setae; inner lobe of coxal endite bearing 4 plumose setae, outer lobe with 3.

Maxilliped 1 (Figure 4E): exopodite with 9 or 10 (rarely 8) terminal plumose setae; endopodite with plumose setae arrangement of 2, 2, 1, 2, 6.

Maxilliped 2 (Figure 4F): exopodite with 10 (rarely 9) terminal plumose setae; endopodite unchanged from third zoea.

Abdomen and telson (Figure 4A, G): similar to third zoea.

Zoea V. Total length 1.70-2.40 mm (Figure 5)

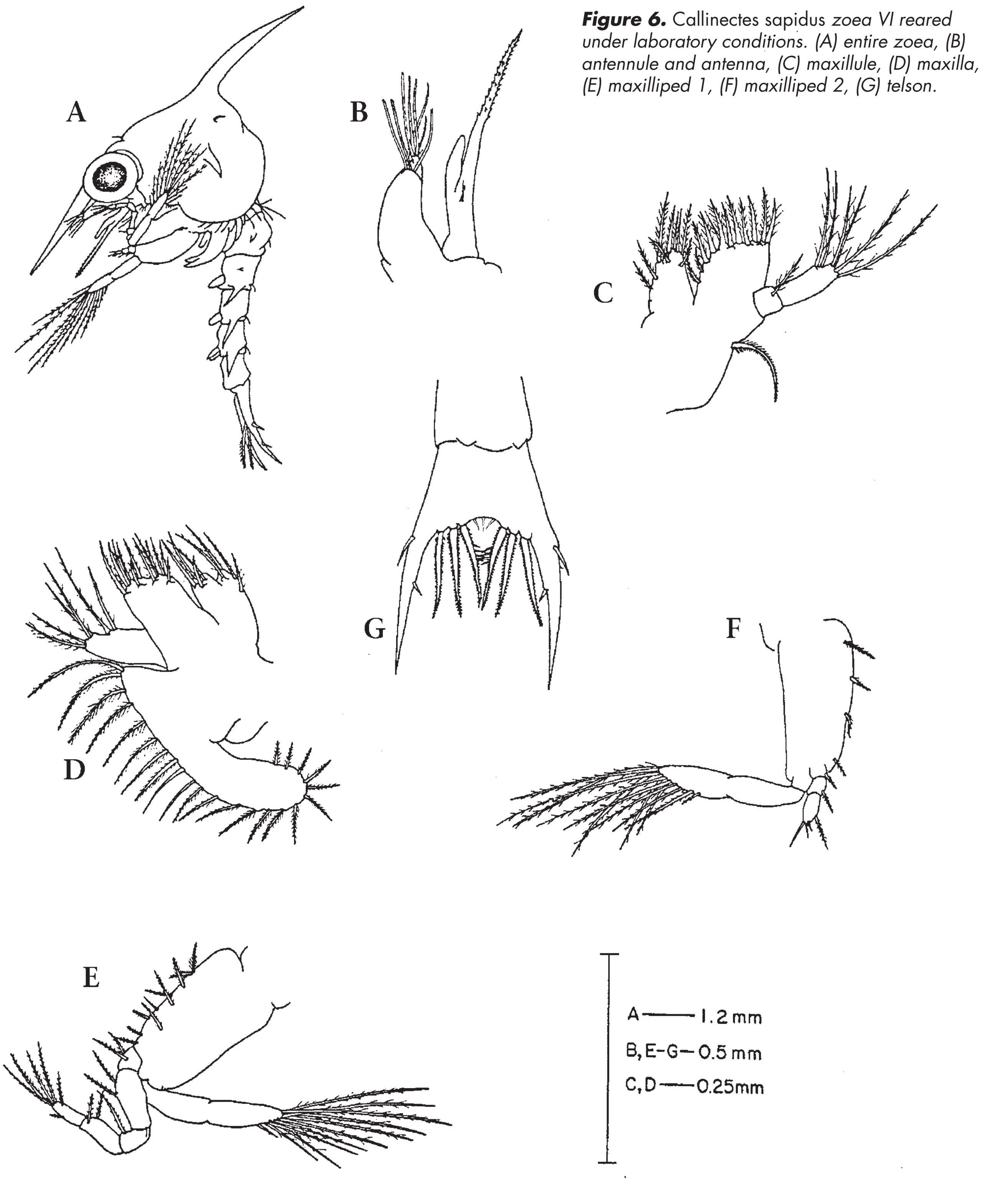

Figure 6. Callinectes sapidus *zoea VI reared under laboratory conditions. (A) entire zoea, (B) antennule and antenna, (C) maxillule, (D) maxilla, (E) maxilliped 1, (F) maxilliped 2, (G) telson.*

Carapace (Figure 5A): similar to fourth zoea but larger, posterior ventral margin bearing 6 (rarely 7) setae; buds of third maxilliped, chelae and pereiopods showing further development from fourth zoea. Rostral spine 0.42-0.78 mm, dorsal spine 0.58-0.97 mm, carapace spine width 0.85-1.17 mm, carapace spine length 1.60-2.30 mm.

Antennule and antenna (Figure 5B): antennule with 1 or 2 setae and 3 or 4 terminal aesthetascs plus 1 or 2 subterminal aesthetascs; antennal endopodite bud clearly visible, extending about one-sixth distance to tip of antenna.

Maxillule (Figure 5C): endopodite similar to fourth zoea; basal endite of protopodite with 11 or 12 total spines, coxal endite with 6 terminal and 2 or 3 subterminal spines.

Maxilla (Figure 5D): scaphognathite with 17 to 26 marginal

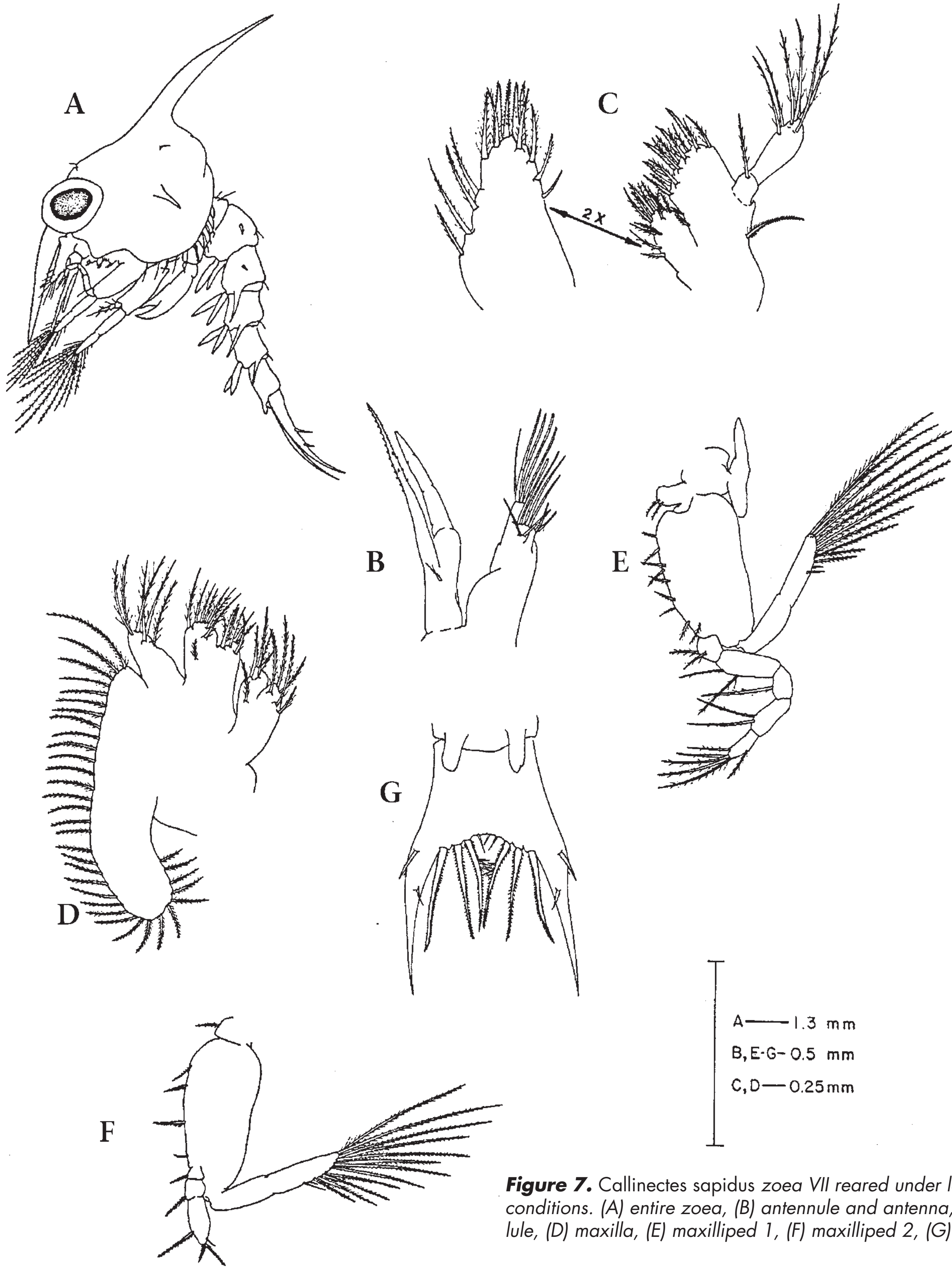

Figure 7. Callinectes sapidus *zoea VII reared under laboratory conditions. (A) entire zoea, (B) antennule and antenna, (C) maxillule, (D) maxilla, (E) maxilliped 1, (F) maxilliped 2, (G) telson.*

plumose setae; endopodite unchanged from fourth zoea; basal endite of protopodite with 12 total setae, coxal endite unchanged from fourth zoea.

Maxilliped 1 (Figure 5E): exopodite with 10 (rarely 9 or 11) terminal plumose setae; endopodite unchanged from fourth zoea.

Maxilliped 2 (Figure 5F): exopodite with 11 (occasionally 12) terminal plumose setae; endopodite unchanged from fourth zoea.

Abdomen and telson (Figure 5A, G): slight swellings on distal ventral margin of segments 2 to 5 indicating development of pleopods (visible on some specimens); 2 or 3 small setae present in telson furca; remainder of abdomen and telson similar to fourth zoea.

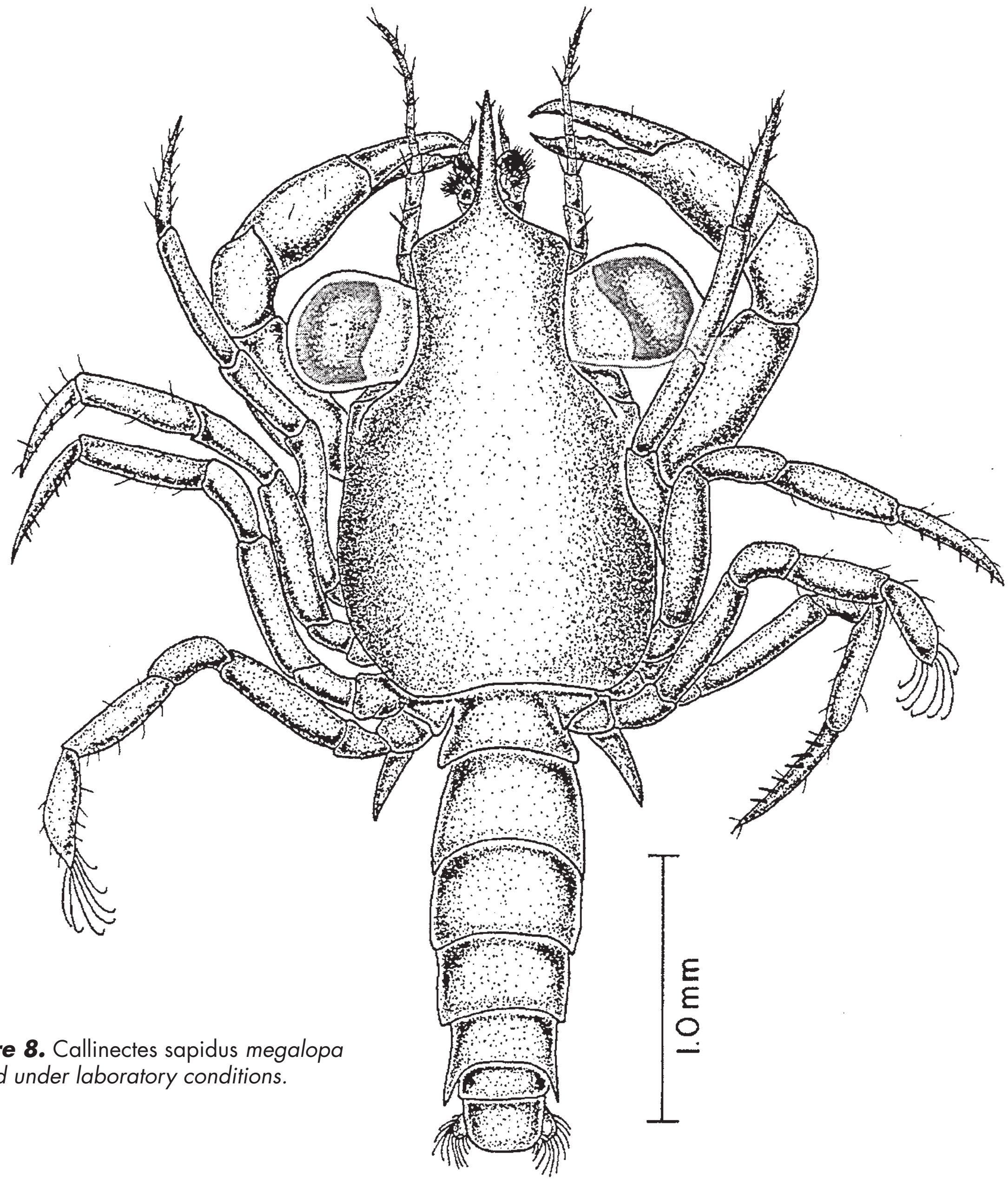

Figure 8. Callinectes sapidus *megalopa reared under laboratory conditions.*

Zoea VI. Total length 2.24-2.84 mm (Figure 6)

Carapace (Figure 6A): similar to fifth zoea but larger, posterior ventral margin bearing 9 setae; chela bud greatly lengthened with bifid distal tip, remaining appendage buds showing additional development from fifth zoea. Rostral spine 0.67-0.92 mm, dorsal spine 0.75-1.14 mm, carapace spine width 1.04-1.34 mm, carapace spine length 1.98-2.60 mm.

Antennule and antenna (Figure 6B): antennule with 1 or 2 setae and 3 or 4 terminal aesthetascs, second subterminal row of 2 or 3 aesthetascs added. Endopodite bud extending one-fourth to one-half distance to tip of antenna.

Maxillule (Figure 6C): endopodite similar to fifth zoea; basal endite of protopodite with 12 to 14 total plumose setae, coxal endite with 6 or 7 terminal and 2 or 3 subterminal plumose setae.

Maxilla (Figure 6D): scaphognathite with 22 to 30 marginal plumose setae; endopodite and basal endite of protopodite unchanged from fifth zoea; inner lobe of coxal endite with four plumose setae, outer lobe with 3 or 4 plumose setae.

Maxilliped 1 (Figure 6E): exopodite with 11 (rarely 10 or 12) terminal plumose setae; basal article of endopodite with 9 or 10 setae; endopodite unchanged from fifth zoea.

Maxilliped 2 (Figure 6F): exopodite with 12 (rarely 11 or 13) terminal plumose setae; endopodite unchanged from fifth zoea.

Abdomen and telson (Figure 6A, G): pleopods clearly visible on abdominal segments 2 to 5, barely visible on segment 6. Inner medial margin of telson furca with 3 (rarely 2) small setae, otherwise unchanged from fifth zoea.

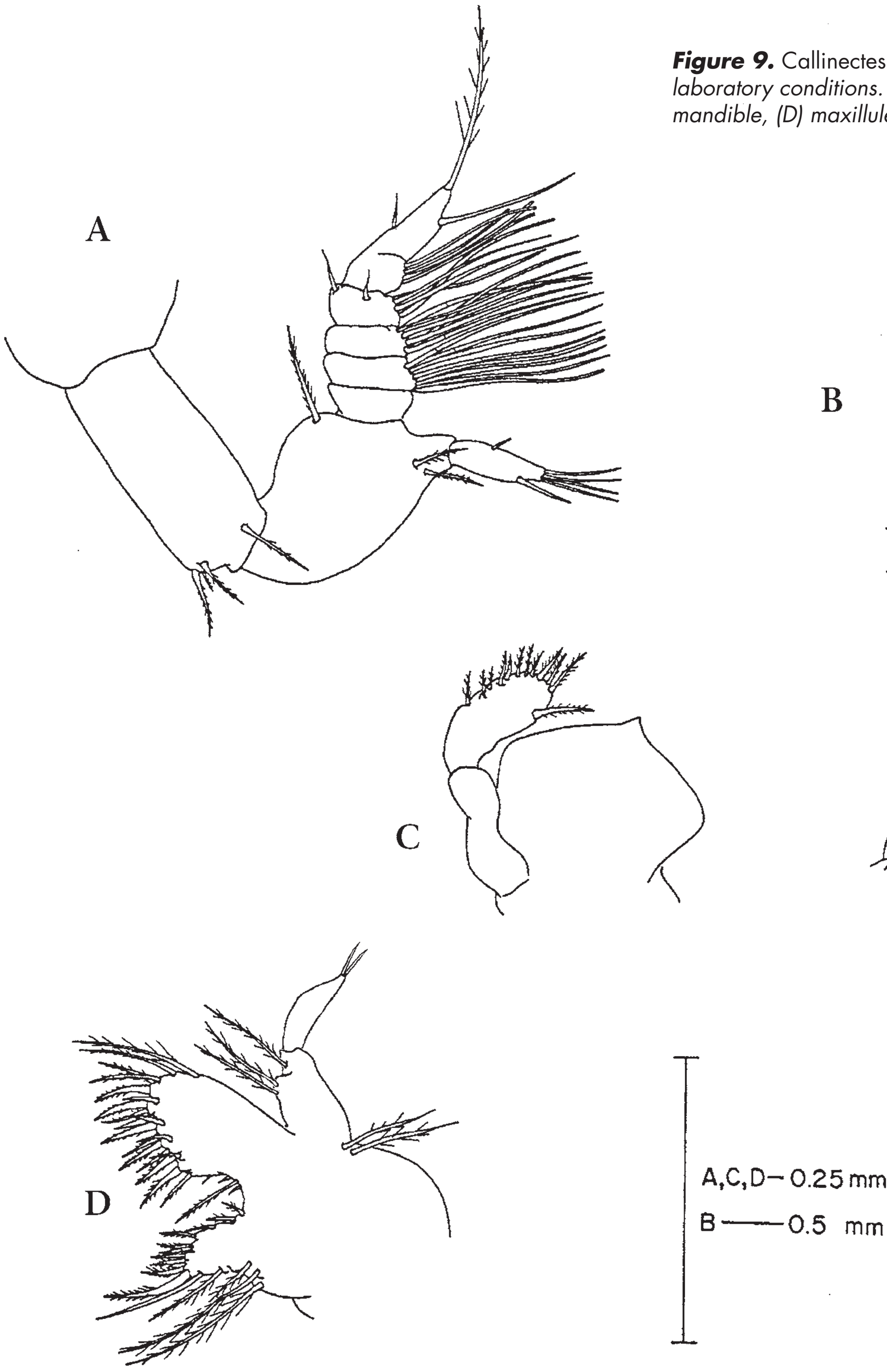

Figure 9. Callinectes sapidus *megalopa reared under laboratory conditions. (A) antennule, (B) antenna, (C) mandible, (D) maxillule.*

Zoea VII. Total length 2.62-3.34 mm (Figure 7)

Carapace (Figure 7A): similar to sixth zoea but larger, posterior ventral margin bearing 10-12 setae; chela bud well developed, "claw-like" with distinct articles, remaining appendage buds lengthened from sixth zoea. Rostral spine 0.77-1.14 mm, dorsal spine 0.75-1.50 mm, carapace spine width 1.22-1.67 mm, carapace spine length 2.33-3.24 mm.

Antennule and antenna (Figure 7B): antennule with large swelling at base, endopodite bud visible, aesthetascs arranged in 3 rows (4 plus 1 seta terminal, 4 to 6 subterminal and 4 to 5 basal). Endopodite bud of antenna equal to or slightly shorter in length to protopodite, swollen at base and showing evidence of articulation.

Maxillule (Figure 7C): endopodite unchanged from sixth zoea; basal endite of protopodite with 15 to 16 total plumose setae, coxal endite with 12 to 14 plumose setae.

Maxilla (Figure 7D): scaphognathite with 27 to 36 marginal plumose setae; endopodite unchanged from sixth zoea; basal endite of protopodite with 12 to15 total plumose setae, inner lobe of coxal endite with 5 plumose setae, outer lobe with 4 or 5 plumose setae.

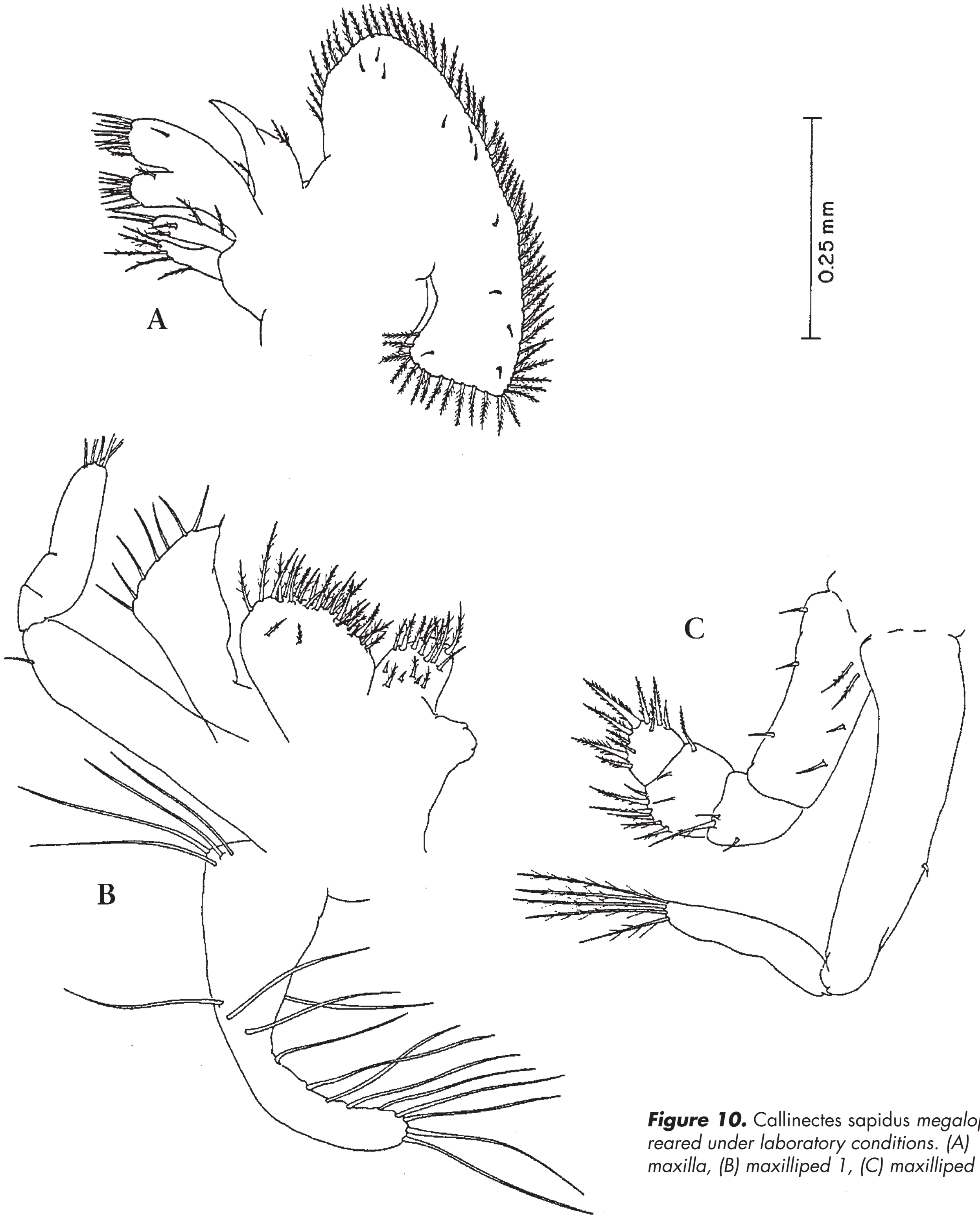

Figure 10. Callinectes sapidus *megalopa reared under laboratory conditions. (A) maxilla, (B) maxilliped 1, (C) maxilliped 2.*

Maxilliped 1 (Figure 7E): exopodite with 12 or 13 (rarely 11) terminal plumose setae; epipodite present as a T-shaped lobe bearing 2 setae on posterior margin; endopodite unchanged from sixth zoea.

Maxilliped 2 (Figure 7F): exopodite with 14 to 15 (rarely 13) terminal plumose setae; endopodite unchanged from sixth zoea.

Abdomen and telson (Figure 7A, G): pleopod buds lengthened from sixth zoea, clearly visible on segment 6. Inner medial margin of telson furca with 3 (rarely 4) small setae, remainder unchanged from sixth zoea.

Megalopa. Total length 2.62-3.80 mm (Figures 8-11)

Carapace and abdomen (Figure 8): carapace with pointed rostrum extending three-fourths length of antenna, rostral length 0.38-0.58 mm, carapace length 1.62-2.11 mm; pair of large spines project from the posterior ventral

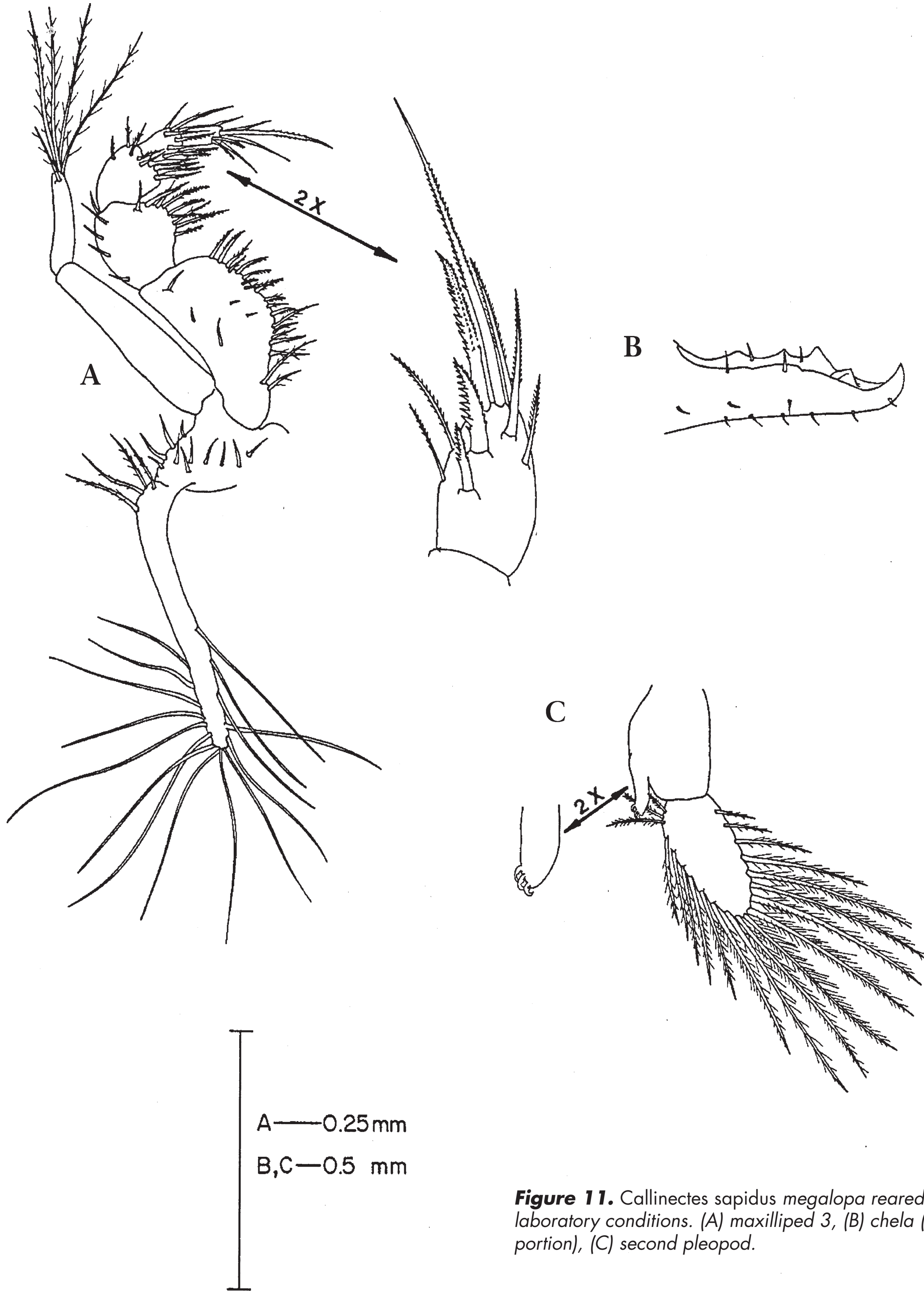

Figure 11. Callinectes sapidus *megalopa reared under laboratory conditions. (A) maxilliped 3, (B) chela (lower portion), (C) second pleopod.*

margin of cephalothorax; abdomen composed of 6 segments and telson, fifth segment with large lateral spines. Eyes stalked. Pigmentation pattern similar to that shown by Costlow and Bookhout (1959).

Antennule (Figure 9A): peduncle consisting of 3 articles, second article with 3 or 4 plumose setae on distal margin, third article with single medial seta and pair of distal setae; uniarticulate flagellum with 3 or 4 terminal setae and 2 subterminal; larger multiarticulated flagellum with 4 tiers of aesthetascs in arrangement of 8 or 9, 8 or 9, 8 or 9, 4; distal article with 1 terminal plumose seta and 2 subterminal setae.

Antenna (Figure 9B): consisting of 3 peduncle and 8 flagella articles, exact arrangement of setae variable, but often as shown.

Mandible (Figure 9C): palp with 2 articles, distal article with 11 to 12 spines, cutting edge smooth with medial "tooth".

Maxillule (Figure 9D): endopodite with proximal article bearing 3 or 4 plumose setae on outer distal half and 2 plumose setae at base near inner margin; terminal article bearing 1 or 2, usually 2, small, simple terminal setae; basal endite of protopodite with 20 to 23 plumose setae; coxal endite with 14 to 16 plumose setae of variable lengths.

Maxilla (Figure 10A): scaphognathite bearing 47 to 70 marginal plumose setae; endopodite lacking terminal setae; basal lobes of protopodite each with 8 to 9 terminal plumose setae and 1 subterminal seta; coxal lobes each with 5 to 6 total plumose setae.

Maxilliped 1 (Figure 10B): epipodite well developed with proximal cluster of 4 long simple setae and 13 to 14 distal simple setae; exopodite with 2 articles, bearing 5 long terminal setae (shown cut off) on distal article; endopodite with broad distal margin bearing 6 to 8 simple setae; basal lobe of protopodite with 23 to 25 marginal and 1 to 2 submarginal plumose setae, coxal lobe with 9 to 10 marginal and about 6 submarginal plumose setae.

Maxilliped 2 (Figure 10C): endopodite consisting of 4 articles, terminal article armed with 9 to 10 plumose setae, armature of remaining articles variable, but generally as shown; exopodite with 2 articles, terminal article with 5 to 6 plumose setae.

Maxilliped 3 (Figure 11A): endopodite consisting of 5 articles, setation variable but generally as shown, terminal article with several stout dentate setae; exopodite with 2 articles, distal article bearing 5 to 6 plumose setae, epipodite with cluster of 10 to 12 short setae and 4 long plumose setae on proximal portion, distal half with 15 to 17 long simple setae.

Chela (Figure 8A, 11B): well developed with prominent spine on basi-ishiopodite (not shown), distal process of propodus with four teeth in addition to terminal tooth.

Pleopods (Figure 11C): present on abdominal segments 2 to 6; endopodites developed on pleopods 1 to 4, bearing small curled setae on distal margin arranged as follows: first pleopod - 3 (rarely 4), second - 3, third - 3, fourth - 3; exopodites of pleopods 1 to 5 with long plumose setae arranged as follows: first pleopod - 20 to 22, second - 20 to 22, third - 20 to 22, fourth - 19 to 20, fifth - 10 to 11.

First Crab. (Figure 12A)

Carapace: carapace width 2.07-2.95 mm, two prominent lateral spines and 8 to 9 smaller spines (including outer margin of orbital socket), frontal margin slightly convex with small medial notch.

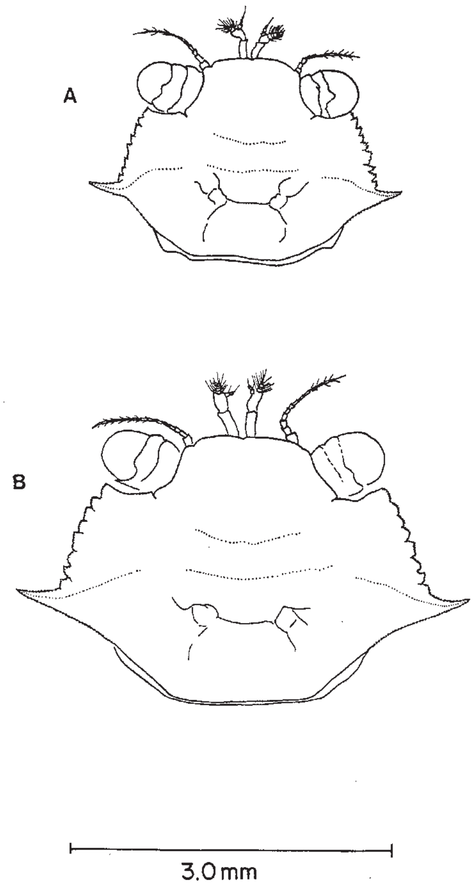

Figure 12. *Juvenile crabs of* Callinectes sapidus *reared under laboratory conditions. (A) first crab stage, (B) second crab stage.*

Second Crab (Figure 12B)

Carapace: carapace width 2.58-3.91 mm, similar to first crab except larger, medial notch less obvious.

Seasonal Variations in Laboratory Reared Larvae

Using developmental stages for which complete data sets were available (zoeal stages I-VII and the megalopal stage), the variation in total length, antennal length, dorsal spine, rostral spine, carapace spine length, and carapace spine width were summarized (range and mean) by season (Table 4). In all data sets examined, there were no notable differences observed between larvae obtained from different females within the same season or larvae at optimal and ambient temperatures within the same season. Differences between spring and summer/fall brood larvae were observed, but only in early stages (Table 4). The first, second and third zoeae from the spring brood were larger than corresponding summer/fall zoeae for all structures measured and ranges for spring and summer/fall did not overlap for first and second zoeae. Data sets on zoeal stages IV and V were incomplete; however, seasonal differences in measurements on all structures tended to be smaller in the summer/fall reared larvae although there was substantial overlap in the ranges. No seasonal differences were observed for the sixth and seventh zoeal stages and the megalopal stage. First

TABLE 4. *Comparison of spring and summer/fall reared blue crab zoeae, megalopae and first crabs. Measurements (mm) of range and means (in parentheses) on larval characters were calculated from combined data on all females and experimental temperatures. TL = Total length (carapace width for first crab); AL = Antennal length; DS = Dorsal spine; RS = Rostral spine (rostral length for megalopa); CSL = Carapace spine length (carapace length for megalopa); CSW = Carapace spine width.*

Stage	Season	TL	AL	DS	RS	CSL	CSW
1st zoea	Spring	1.10-1.25 (1.19)		0.43-0.48 (0.47)	0.25-0.30 (0.29)	1.00-1.17 (1.09)	0.58-0.67 (0.63)
	Summer/Fall	0.90-0.99 (0.94)		0.30-0.35 (0.33)	0.20-0.23 (0.21)	0.79-0.87 (0.83)	0.45-0.52 (0.49)
2nd zoea	Spring	1.22-1.45 (1.35)		0.43-0.55 (0.49)	0.32-0.42 (0.37)	1.14-1.30 (1.20)	0.62-0.73 (0.67)
	Summer/Fall	0.94-1.14 (1.07)		0.30-0.40 (0.35)	0.22-0.32 (0.29)	0.80-0.99 (0.91)	0.47-0.58 (0.52)
3rd zoea	Spring	1.32-1.80 (1.59)		0.45-0.67 (0.56)	0.32-0.53 (0.44)	1.17-1.60 (1.41)	0.68-0.87 (0.77)
	Summer/Fall	1.12-1.47 (1.27)		0.32-0.55 (0.43)	0.32-0.40 (0.35)	1.02-1.40 (1.10)	0.58-0.75 (0.62)
4th zoea	Spring	1.65-2.15 (1.92)		0.53-0.84 (0.68)	0.45-0.67 (0.56)	1.47-2.04 (1.72)	0.77-1.10 (0.90)
	Summer/Fall	1.50-1.98 (1.69)		0.43-0.58 (0.60)	0.35-0.58 (0.48)	1.19-1.84 (1.49)	0.67-1.00 (0.81)
5th zoea	Spring	1.70-2.40 (2.21)		0.58-0.95 (0.75)	0.42-0.78 (0.66)	1.70-2.30 (2.02)	0.89-1.17 (1.00)
	Summer/Fall	1.87-2.27 (2.11)		0.58-0.97 (0.77)	0.53-0.75 (0.63)	1.60-2.20 (1.92)	0.85-1.14 (1.00)
6th zoea	Spring	2.33-2.84 (2.50)		0.80-1.12 (0.95)	0.67-0.92 (0.80)	2.04-2.60 (2.31)	1.07-1.27 (1.18)
	Summer/Fall	2.24-2.66 (2.50)		0.75-1.14 (0.96)	0.67-0.89 (0.77)	1.98-2.50 (2.29)	1.04-1.34 (1.19)
7th zoea	Spring	2.62-3.28 (2.99)		0.75-1.44 (1.14)	0.87-1.10 (0.98)	2.33-3.18 (2.78)	1.23-1.50 (1.39)
	Summer/Fall	2.66-3.34 (3.06)		1.00-1.50 (1.19)	0.77-1.14 (0.95)	2.40-3.24 (2.81)	1.22-1.67 (1.40)
Megalopa	Spring	2.75-3.60 (3.27)	0.72-1.13 (0.99)		0.38-0.57 (0.49)	1.62-2.07 (1.89)	
	Summer/Fall	2.62-3.80 (3.34)	0.96-1.09 (1.01)		0.47-0.58 (0.50)	1.62-2.11 (1.94)	
First Crab	Spring	2.07-2.91 (2.67)					
	Summer/Fall	2.27-2.95 (2.63)					

***TABLE 5.** Characteristics of* C. sapidus *megalopae collected from the plankton and reared in the laboratory along with measurements of first crabs reared from these megalopae. Mean values (mm) in parentheses obtained from measurements on 10 megalopae and 20 crabs.*

Character	Total Carapace Length (mm)	Rostral Length (mm)	Antennal length (mm)	Carapace width (mm)
Megalopae				
Spring	2.06-2.24 (2.16)	—	1.14-1.20 (1.16)	
Fall	1.82-1.96 (1.89)	0.44-0.48 (0.47)	1.02-1.08 (1.04)	
First crabs				
Spring				3.0-3.2 (3.1)
Fall				2.4-2.7 (2.6)

crabs reared from spring and summer/fall larvae were also similar in size.

Seasonal Variations in Wild Stock Megalopae and First Crabs

Spring megalopae were always larger than fall megalopae with mean total carapace lengths of 2.16 mm and 1.89 mm, respectively (Table 5) and the seasonal ranges in size did not overlap. Similar differences were observed for mean measurements of antennal length (spring – 1.16 mm; fall – 1.04 mm). Spring megalopae also tended to have more setae on the scaphognathite of the maxilla and epipodite of the third maxilliped (Table 6). Few seasonal differences were observed in the number of plumose setae on the exopods of the pleopods; however, the number of hooked setae on the endopods was different between seasons. Spring megalopae normally had four (rarely three) hooked setae on pleopods 1 and 2 while pleopods 3 and 4 had three (rarely four) such setae. In contrast, fall megalopae had three (occasionally four) hooked setae on pleopods 1 and 2 and always three on pleopods 3 and 4. First crabs followed the same seasonal size trends observed for megalopae (spring, mean carapace width – 3.1 mm; fall, mean carapace width – 2.6 mm with no overlap in size ranges; Table 5).

Discussion

Morphological Development

Seven zoeal and one megalopal stage were identified; eighth and ninth zoeal stages were rarely found. Although larvae described here resemble those originally described by Costlow and Bookhout (1959) in most major features, a number of differences in overall size and setation of appendages were noted.

Throughout the entire larval series, measurements on a number of larval structures from individual stages were consistently larger than the corresponding measurements reported by Bookhout and Costlow (1977). Differences between larvae from the nGOM (present study) and the original description of those from the Atlantic coast (Costlow and Bookhout 1959, Bookhout and Costlow 1977) are summarized below.

Carapace: For all zoeal stages of nGOM larvae, a minute seta was observed just below and lateral to the base of the dorsal spine. A single seta was found on the anterior margin of the carapace just above the eyes on zoeal stages II to VII. These setae were not found by Costlow and Bookhout (1959).

Antennules: The numbers of terminal aesthetascs found from nGOM larvae were fairly consistent with Atlantic coast larvae. The addition of a third row of aesthetascs occurred in stage VII zoeae in the present study (Figure 7), whereas Bookhout and Costlow (1977) reported the third row only from stage VIII zoeae. Terminal "hooked setae" were not found in nGOM larvae. All terminal setae appeared relatively straight. One or two terminal "hair-like" setae were found on nGOM specimens, whereas, Bookhout and Costlow (1977) reported two to three "hair-like setae" from Atlantic specimens. For the megalopae, Bookhout and Costlow (1959) described and illustrated the terminal article of the flagellum with

***TABLE 6.** Characteristics of* C. sapidus *megalopae collected from the plankton and reared in the laboratory. Mean values in parentheses obtained from measurements on 10 megalopae.*

Character	Spring	Fall
Scaphognathite of maxilla		
Marginal setae	61-69 (65)	59-66 (62)
Submarginal setae	10-14 (11)	11-13 (12)
Epipodite of 3rd maxilliped		
Proximal setae	4-5 (4)	4
Distal setae	14-20 (17)	12-18 (16)
Plumose setae on exopods of pleopods		
Pleopod 1	22-24 (22)	22-24 (23)
Pleopod 2	21-23 (22)	21-23 (23)
Pleopod 3	20-23 (21)	20-23 (22)
Pleopod 4	19-21 (20)	18-21 (19)
Pleopod 5	11-12 (11)	11-12 (11)
Hooked spines on endopods of pleopods		
Pleopod 1	3-4 (4)	3-4 (3)
Pleopod 2	3-4 (4)	3-4 (3)
Pleopod 3	3-4 (3)	3
Pleopod 4	3-4 (3)	3

a simple terminal seta; however, for the nGOM specimens examined the terminal seta is plumose (Figure 9A), though the plumose condition may need confirmation at high magnification.

Mouthparts: Variability in mouthparts of larvae obtained in the present study complicates detailed comparison with Atlantic larval descriptions. In general, setation on the maxillule and maxilla of early stage zoeae as reported by Bookhout and Costlow (1977) was similar to nGOM larvae. In later stages, however, nGOM larvae tended to have a greater number of total spines and setae. This may be the result of fewer larval stages produced in the present study as compared to previous studies. One obvious difference between Atlantic and nGOM larvae is in the setation of the scaphognathite in early stage larvae. Costlow and Bookhout (1959) illustrated the distal margin of the scaphognathite of zoeal stages I and II as bearing 2 plumose setae. In the present study, all larvae examined had one and 3 such distal setae on zoeal stages I and II, respectively (Figures 1 and 2). For megalopae, Costlow and Bookhout (1959) describe the terminal article of the maxillule endopodite as bearing 4 long, plumose setae (two terminal, two subterminal), whereas, the nGOM specimens examined had only 2 terminal short, simple setae. Also, the 4 plumose terminal setae on the Atlantic specimens appear distinctly larger than the 2 simple terminal setae in the nGOM specimens.

Telson: A minute seta (visible only under high magnification) located just posterior to the insertion of a large lateral seta was observed in all zoeae examined in the present study (Figures 1-7). This minute seta was not reported in previous studies.

Seasonal Variations in Morphology

In the present study, early stage zoeae (I, II and III) reared from spring females were larger than summer/fall brood larvae. Differences in total size between spring and summer/fall larvae among intermediate and later stage zoeae were less apparent. Virtually no seasonal differences were observed in size of laboratory reared megalopae and first crabs. In contrast, seasonal differences were observed in megalopae and first crabs reared from the plankton. Wild stock megalopae and first crabs obtained in the spring were substantially larger than fall megalopae and first crabs.

The inability to reproduce seasonal variations in morphology through the entire larval series in the laboratory, as it occurs in the plankton, may be the result of factors influencing development other than temperature. Because of their large initial size, spring brood zoeae when reared at a static optimal temperature (25°C) and provided with excess food may have been able to feed more efficiently than larvae from other seasonal/temperature combinations and thus developed to megalopae in less time and with fewer total molts. Spring larvae initially reared at 16.0°C did not molt until culture temperature had increased to 19.0°C (18 d later). As the culture temperature continued to increase, at a rate of about 1.0°C/week, molting frequency also increased. Again, their large initial size and resulting increased feeding ability allowed most of these larvae to complete their development to megalopae in 6 molts. In contrast, summer/fall brood larvae reared at 25.0°C or 30.0°C molted more frequently than spring larvae; however, because of their smaller initial size and subsequent reduced ability to capture food, these larvae usually required 7 or more molts to complete their development. The tendency for greater number of larval stages and longer duration of development (at 25.0°C) may be the mechanism by which summer/fall larvae eventually equaled the size of spring larvae in laboratory culture. Assuming that larval growth is under the principal control of nutrition, all culture series would have the same growth potential. Other studies have found that the effects of quality and quantity of food on decapod larval development have been significant (Broad 1957, Chamberlain 1961, Welch and Sulkin 1974, Sulkin 1975, 1978, Terwilliger and Dumler 2001) and may be the principal factor controlling larval growth. Variation in size of megalopae and first crabs obtained from the plankton may also be related to seasonal trends in food availability rather than temperature. Investigations on trophic relationships of larvae in the plankton may provide further insights into seasonal variability of *C. sapidus* larvae.

Eco-phenotypic seasonal size differences have also been found to exist in other life stages of blue crab. Jacobs et al. (2003) found the eggs of *C. sapidus* were larger in the spring and similar results were found by Dennis (2008). Furthermore, Perry et al. (2007) found that spring females were larger than summer/fall females during a fishery-dependent survey of blue crab entering the trap fishery in Mississippi. Similar trends were noted in long-term monitoring data for adult females in Mississippi (GCRL, unpublished data[1]) and for legal-size crabs from Louisiana (LDWF, unpublished data[2]).

Although the number of zoeal stages required to reach the megalopal stage in this study varied from 6 to 9, in most cases (51%) 7 zoeal stages were observed. Larvae spawned in spring generally completed development to megalopae in fewer molts than did larvae spawned in summer/fall. In cases where development was completed in only 6 molts, zoeae with combined morphological characteristics from 2 stages were usually observed. This occurred most frequently in spring brood larvae between zoeal stages V and VII. Costlow (1965) reported that most (63%) of the

(1) GCRL. Unpublished data. Fisheries assessment and monitoring program, 1973-2005. The University of Southern Mississippi, Gulf Coast Research Laboratory, Ocean Springs, Mississippi.

(2) LDWF. Unpublished data. Fisheries independent long-term monitoring, 1967-2005. Louisiana Department of Wildlife & Fisheries, Baton Rouge, Louisiana.

larvae of C. sapidus reared at 25.0°C passed through 7 zoeal stages before reaching the megalopal stage; 21% had 6 zoeal stages and 16% passed through 8 zoeal stages. Morphological variability was observed in 40 to 63% of these larvae. Costlow (1965) also found that zoeal stages I to IV showed little morphological variability while stages V to VII commonly differed. The most frequently encountered variation was the occurrence of "combined stage" zoeae V/VI and VI/VII. Similar results were obtained in the present study.

In conclusion, the results of this study indicate that: (1) morphological differences in size and setation exist between *C. sapidus* larvae reared from the nGOM stocks and published descriptions of larvae reared from Atlantic stocks; (2) laboratory reared spring brood larvae were larger than summer/fall brood larvae among early zoeal stages (I, II and III); later stage zoeae, megalopae and first crabs were similar in size between seasons; (3) fewer larval stages occurred in the spring than in the summer/fall; and (4) megalopae and first crabs reared from the plankton were larger in the spring, which could not be reproduced in the rearing experiment.

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