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COMPARATIVE LARVAL DEVELOPMENT IN TWO SPECIES OF THE BURROWING GHOST SHRIMP GENUS *LEPIDOPHTHALMUS* (DECAPODA: CALLIANASSIDAE)

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ABSTRACT

The early life history is described and compared in the estuarine callianassid shrimp species *Lepidophthalmus sinuensis* from the Caribbean coast of Colombia and *L. louisianensis* from the northern Gulf of Mexico, on the basis of laboratory larval cultures and wild plankton collections. Both species have an abbreviated larval development of 2 zoeal stages usually transcended within 3–4 days, with that of *L. sinuensis* being the shorter and exhibiting greater advancement in the zoeal stages. Development in both species is markedly shorter and morphologically more advanced than in comparable callianassid species for which stages have been described, including most of those known to have only 2 zoeal stages. Larval duration in *Lepidophthalmus* is nearest that of the ecologically comparable *Callianassa* s.l. *kraussi* from southern Africa and suggests possible convergence in early developmental strategies. On the basis of presently known larval histories, genera allied to *Lepidophthalmus* within the Callichirinae appear to either have long larval histories of 5 zoeal stages, or, if of 2 stages, to bear a morphological resemblance as zoeae to comparable stages in some of the non-Callichirinae. The decapodid (first postlarval) stage is imaginal in form and exhibits burrowing behavior, though appendage development is far short of adult form. Successive early postlarval development and behavior beyond this stage remains unknown. Detailed illustrations of zoeal and decapodid stages are provided to support comparative discussions and for use in larval identifications.

Prior to recent systematic reevaluations of the ghost shrimp genus *Callianassa* Leach, 1814, the few known divergent patterns of larval development in these animals were difficult to correlate with subgeneric systematic groupings. Reported patterns of larval development in animals assigned to *Callianassa* ranged from a maximum of five to six planktonically dispersed zoeal stages (Aste and Retamal, 1984; Konishi *et al.*, 1990; Tamaki *et al.*, 1996) to no more than two zoeal stages which may remain in the parental burrow throughout metamorphosis (Forbes, 1973). While systematic revision has yet to treat all former congeners of *Callianassa* on a worldwide basis, the genus has now been defined on the basis of concise morphological characters which restrict its known members to certain European populations. The former American congeners have been partitioned into a number of genera defined on the basis of morphology and life history (Manning and Felder, 1991).

Among the western Atlantic genera now recognized, *Lepidophthalmus* Holmes, 1904, was resurrected to accommodate a group of tropical and warm-temperate intertidal and shallow subtidal species, many of which are highly adapted to oligohaline estuarine environments (Manning and Felder, 1991). This group, which includes a few similarly adapted, described and undescribed eastern Pacific forms, is composed of six known species in the western Atlantic, the sixth of which is currently in description (D. L. Felder and J. L. Staton, in preparation). The genus is assignable to the Callichirinae Manning and Felder, 1991, a subfamily of the Callianassidae Dana, 1852, which also encompasses familiar shallow-water forms now recognized as the genera *Callichirus* Stimpson, 1866, *Corallianassa* Manning, 1987, *Glypturus* Stimpson, 1866, *Neocallichirus* Sakai, 1988, and the more recently described *Sergio* Manning and Lemaitre, 1994. It may be readily distinguished from all of these relatives by a number of morphological characters, including its adult retention of an exopod on the third maxilliped. However, it also appears that members of the genus may share unique functional adaptations in osmoregulatory ability, tolerance of anoxia, lactate accumulation, burrowing behavior, and early life history, at least on the basis of general anecdotal descriptions of habitats and experimentation with one species to date (Felder, 1978, 1979; Felder *et al.*, 1986; Lemaitre and Rodrigues, 1991; Felder and Rodrigues,

1993; Felder and Griffis, 1994; Felder *et al.*, 1995; Felder and Manning, 1997).

In *Lepidophthalmus louisianensis* (Schmitt, 1935) development is known to be abbreviated; osmoregulatory capacity in reared zoeal stages of the species has been documented (Felder *et al.*, 1986), and putative larval stages of the species have been partially sketched from plankton samples (Shipp, 1977). However, to date there has been no published description of comparative ontogenetic morphology in this much-studied Gulf of Mexico endemic species or, for that matter, in any other member of the genus. Yet, abbreviated development in species of the genus is repeatedly alluded to in accounting for estuarine retention and accumulation of dense, ecologically dominant populations in this genus, a phenomenon which appears to be of benefit to benthic nutrient flux in natural habitats (Felder and Griffis, 1994; Nates *et al.*, 1994; Felder *et al.*, 1995). Interest in recognition and further understanding of early stages has been recently brought to prominence by the invasion of at least two species of *Lepidophthalmus* into commercial estuarine penaeid shrimp farms on the Caribbean and Pacific coasts of Central and South America, where exploding populations of these ghost shrimp have in some cases been linked to strikingly detrimental effects on maricultural penaeid shrimp production (Lemaitre and Rodrigues, 1991; Nates *et al.*, 1994; Felder *et al.*, 1995). Particularly on the Caribbean coast of Colombia, commercial farms are now experimenting with control strategies, both for reduction of adult populations in culture ponds and for prevention of reinvasion by larvae from surrounding estuaries.

The present work undertakes comparative description of zoeal and early postlarval life history in both the Gulf of Mexico species, *L. louisianensis*, and the southern Caribbean species, *L. sinuensis* Lemaitre and Rodrigues, 1991. It reports the time course for larval development and the number of stages involved, in addition to providing illustrations and utilitarian descriptions essential for accurate identification of these stages. These descriptions provide a basis for comparisons to developmental strategies and morphologies reported previously in other species of callianassids. For the purpose of those comparisons, we must herein refer to world-wide literature reports for a number of species which were originally reported as *Callianassa*, but which must be ultimately subjected to generic reassignment. To denote the unresolved generic status of those forms, we herein refer to them as *Callianassa* sensu lato.

Materials and Methods

Ovigerous females of *L. louisianensis* were collected, as described previously (Felder, 1978) during late spring and summer of 1982–1984, from the perimeter of a tidally influenced pond on Grand Terre Island, Louisiana, and in early September 1996, from the western shore of Bay St. Louis, Mississippi. Parental females were transported to the laboratory in individual perforated plastic vials immersed in water from the field site and were thereafter maintained individually in 20-cm diameter finger bowls of aerated 15-ppt salinity sea water until hatching of larvae. Upon hatching, larvae were usually mass-cultured in groups of 20–100 larvae transferred to each of several 11-cm diameter finger bowls containing 200 ml of 15 ppt salinity sea water. Both prior to hatching and throughout larval development, bowls were held in an incubator at a temperature of 26 ± 1°C and a 12:12 h photoperiod. A daily change of the sea water and bowl for each larval mass culture was followed by feeding with freshly hatched nauplii of *Artemia*. All cultures were monitored at least every 4–6 h for counting dead and molted individuals, with frequency of monitoring increased to every 2 h once evidence of stage transition was detected. Mean estimates of survivorship and stage duration were based upon results from our monitoring of 10 mass cultures of 25 larvae each.

Ovigerous females of *L. sinuensis* were collected with yabby pumps from margins of shrimp culture ponds and drainage canals of a commercial shrimp farm, Agrosoledad, S. A., and from a natural intertidal mudflat near the mouth of the Rio Sinú, both in Departamento de Córdoba, Colombia (9°17'N, 75°50'W) during late September 1991. Parental females were transported to a field laboratory at the farm and held much as described above prior to hatching. However, both parental females and larval cultures were maintained under ambient light and temperature and at a salinity of 10 ppt. Temperatures in culture bowls ranged from 25.5–27.5°C over the course of hatching and larval development. Upon hatching, larvae were mass-cultured in groups of 20, 50, or 200 individuals placed in plastic bowls containing 200 ml of 10 ppt salinity sea water. A daily change of sea water and container for each mass culture was followed by feeding with a combination of freshly hatched nauplii of *Artemia* and wild-caught planktonic copepods from a nearby estuary. All cultures were monitored every 2–4 h for counting dead and molted individuals. Mean estimates of survivorship and stage duration were based upon monitoring results from 4 mass cultures of 20 larvae each.

In the course of culturing both species, a few solitary zoeae were also isolated in separate compartments of plastic trays for greater ease of monitoring changes in behavior and signs of molting, as well as to facilitate collection of molted exuviae. Maintenance and feeding of these cultures were the same as for mass cultures of the respective species. In addition, wild larval populations of both species were sampled in periodic (~2-h interval), semiquantitative surface plankton tows taken over 24 h in heavily populated habitats of Bay St. Louis, Missis-

sippi, during July 1990, and in a densely infested pond on the Agrosoledad, S. A., shrimp farm in Colombia, during September 1991. In both of these habitats, mean water depths over sample transects ranged from about 0.7–1.2 m, and sampling with a number 0 (0.571-mm aperture) net was targeted to the upper 0.5 m of the water column. While samples from Bay St. Louis were archived in their entirety for later quantification, the archived samples from Agrosoledad, S. A., consisted of only nonquantitative aliquots useful in estimating relative percentages contributed by each developmental stage. These served to provide additional materials of larval stages for comparative studies and, together with field notes, indicated periodicity of larval presence in the plankton.

For morphological comparisons, larvae of each stage were fixed initially for a few hours in 5% buffered Formalin, rinsed briefly in distilled water, and then preserved in 70% ethanol. At least 8 specimens of each stage were transferred to a 50% glycerine solution prior to dissection. Selected specimens were cleared in 2% KOH and stained with methylene blue. The appendages were dissected free with insect pins and isolated on slides as temporary glycerine mounts. Line illustrations and measurements were made on a Nikon inverted microscope equipped with a camera lucida and calibrated ocular micrometer. Total length (TL) of each developmental stage was measured from the tip of the rostrum to the posterior margin of the telson, excluding all telsonal processes and setae. Length of the carapace (CL) was measured from the tip of the rostral spine to the posterolateral margin of the carapace. Measurements in descriptions and comparative tables are given as the mean ± the 95% confidence interval (CI) for all specimens examined. Setal arrangement was listed sequentially from proximal to distal position, in accord with Konishi (1989). The first postzoeal stage, herein termed the decapodid (see Felder *et al.*, 1985), is equivalent to the designations "megalopa" or "first postlarva" as applied by some authors. The abbreviations ZI and ZII are used for the first and second zoeal stages, respectively; where the abbreviation D is used, it refers to the decapodid stage.

Results

In parental females of *Lepidophthalmus sinuensis*, the mean number of eggs per female was 258 ± 80 (95% CI; $N = 10$), while in *L. louisianensis* it was 598 ± 212 (95% CI; $N = 4$). In both species, eggs changed from yellow orange to brown over several days prior to hatch. Over this same period, the eyespots in both species became much more strikingly developed, the beating heart became evident, and twitching became evident in the egg. Within two hours of hatching, the eggs were more strikingly elongate and translucent grey to light brown in color. Most hatched while the egg case remained attached to the female pleopod, though some eggs which dropped prior to hatch succeeded in hatching up to 24 h later, provided vigorous aeration was supplied. In two instances, parental females of *L. louisianensis* began consuming their own larvae when left in the same bowl after hatching had occurred.

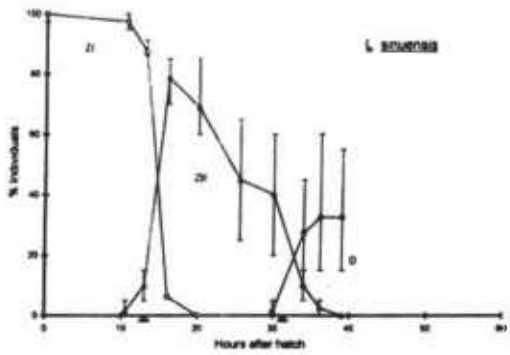


Fig. 1. Mean percent survival and range (vertical bar) at each stage for cultures over time course of early development in *Lepidophthalmus sinuensis* Lemaitre and Rodrigues. Means and ranges are derived from four mass cultures of 20 larvae each during September 1991. ZI indicates first zoea (open circles); ZII indicates second zoea (solid triangles); D indicates decapodid stage (solid circles). Arrows indicate mean durations for the first and second larval stages, respectively.

On the basis of four simultaneously reared mass cultures of 20 larvae each, all taken from the same parental female in September 1991, the larval development of *L. sinuensis* consists of two motile zoeal stages which are typically transcended within a mean of 31.8 ± 0.5 h (95% CI) after hatch (Fig. 1). This approximate overall duration of zoeal development (± 2 h) was also observed in our more densely stocked mass cultures from the same parental female (50 and 200 individuals in 200 ml sea water). A slightly longer overall mean period of near 44 h was observed in eight individually cultured larvae of *L. sinuensis* from another parental female which hatched larvae a few days earlier, perhaps because those initially hatched as prezoeae. The prezoeal stage, evident in some individuals immediately upon hatch and not herein monitored separately from the ZI stage, appears to be transcended simultaneously with shedding of the egg membrane or immediately after hatching in most healthy larvae. Failure to shed this prezoeal membrane after hatching appeared to contribute to a small but unmeasured fraction of the mortalities we observed in the ZI stage of the mass cultures. In a preliminary attempt to hatch larvae from an ovigerous female, a number of eggs that became detached from the pleopods prior to hatching subsequently hatched as prezoeae

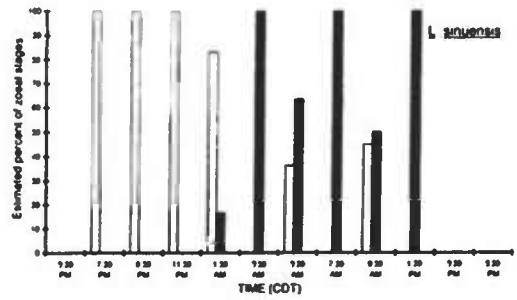


Fig. 2. Percentage of larvae by stage in aliquots of surface water (upper 0.5 m) plankton tows taken over 24 h in a pond densely infested with *Lepidophthalmus sinuensis* Lemaitre and Rodrigues on the Agrosoledad, S. A., shrimp farm in Colombia during 25–26 September 1991. Open bars indicate ZI stage; solid bars indicate ZII stage. Times shown are Central Daylight-Saving Time (CDT).

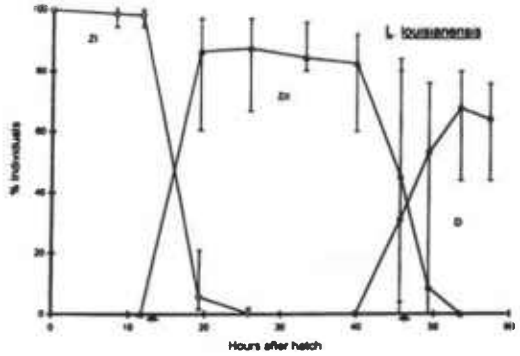


Fig. 3. Mean percentage survival and range (vertical bar) at each stage for cultures over time course of early development in *Lepidophthalmus louisianensis* (Schmitt). Means and ranges are derived from 10 mass cultures of 25 larvae each during September 1996. ZI indicates first zoea (open circles); ZII indicates second zoea (solid triangles); D indicates decapodid stage (solid circles). Arrows indicate mean durations for the first and second larval stages, respectively.

and died in that stage without further development.

Mean survivorship to the D stage at 40 h after hatching in our monitored mass cultures (Fig. 1) was 32% (range, R = 15–55%), with mortality higher in the molt from ZII to D than in that from ZI to ZII. Mean duration of each zoeal stage in *L. sinuensis*, estimated as the time required for 50% of the molt survivors to reach the successive stage, was 14.2 ± 0.3 h (95% CI) for the prezoeal plus ZI, and 17.6 ± 0.7 h (95% CI) for the ZII stage (Fig. 1). Feeding, monitored for individuals isolated in plastic trays, did not readily appear to influence success of the molt to the ZII stage. While unable to ingest whole nauplii of *Artemia* at this stage, the ZI larvae may have been able to ingest naupliar appendages or take in diatoms, rotifers, or parts of copepods from the natural food that was furnished. Throughout the ZI stage, larvae exhibited strong positive phototaxis and remained at or near the water surface in culture dishes. Upon molting to the ZII stage, they moved both at the surface and more readily throughout the water column, and all individuals fed and accumulated materials in the gut. Late in the ZII stage, larvae began to exhibit sustained, rapid directional movement more typical of the D stage. The decapodid D stage fed effectively and exhibited rapid and active sustained movement at all levels of water in the culture containers, but especially along the bottom perimeter. Several decapodids exposed to shallow sediment on the day following molt appeared to attempt burrowing.

During our observations over 24 h on 25–26 September 1991, plankton tows through the top 0.5 m of water in ponds on the Agrosoledad, S. A., farm produced larvae of *L. sinuensis* as early as 1930 (CDT), which was about dusk in the evening, and as late as 0930, but primarily between the hours of 2200 and 0330. Volumes of larvae from plankton tows over approximately equal distances during this period were at least twice those of the earlier evening or later morning samples. While samples during this period, observed as the height of settled larvae on the bottom of the preservation jar, were not quantified in terms of density per unit of area or water volume, archived aliquots taken during this period did allow estimation of relative percentages of the sample composed of ZI and ZII stages (Fig. 2). In accord with our field notes based upon microscopic examination of the whole samples shortly after each tow, these aliquots indicated an initial pulse of ZI larvae in the early to late evening hours, with a larger percentage of ZII stages occurring in the early morning hours, the latter of which was concomitant with an overall decrease in larval abundance which we observed in the surface plankton.

On the basis of 10 simultaneously reared mass cultures of 25 larvae each, all taken from the same parental female in September 1996, the larval development of *L. louisianensis* consists of two motile zoeal stages which are typically transcended within a

mean of 46.7 ± 1.7 h (95% CI) after hatch (Fig. 3). This approximate duration of larval development was very similar to that observed in three mass cultures of 25 larvae, each hatched from another parental female in May 1984, wherein duration of the zoeal life history ranged from 50–55 h, but water temperatures of cultures were 1–2°C lower than for the 1996 cultures. While evidence and duration of the prezoeal stage were difficult to monitor, at least some individuals hatched in a prezoeal stage, and, of these, some molted successfully to an active ZI stage.

Mean survivorship to the decapodid stage in *L. louisianensis* at 54 h after hatch in the 1996 cultures (Fig. 3) was 67.6% (R = 44–100%), with mortality during transition from ZI to ZII very similar to that in the successive molt from ZII to D. Duration of development to the D stage, estimated as for *L. sinuensis* above, could be determined with reasonable confidence for only the more closely monitored 1996 cultures, and was 15.9 ± 0.4 h (95% CI) for the prezoeal plus ZI stage and 30.8 ± 1.7 h (95% CI) for the ZII stage. Feeding did not appear critical to survivorship or duration of the ZI stage and was not evident in our observation of ZI stages for either the 1984 or 1996 cultures, both of which were fed an abundance of nauplii of *Artemia*. However, the ZI larvae did exhibit strong positive phototaxis and swam actively in a head-down to upside down position near the surface of the culture bowl, advancing the dorsal side first as they moved. With molt to the ZII stage, larvae began to move more frequently than before throughout the water column, to more often maintain an upright to horizontal orientation, and to have opaque material in the digestive tract. The decapodid D stages expended the majority of time at the bottom of the culture bowl, either feeding on *Artemia* or scavenging on dead siblings. On the day following the molt to D in 1996 cultures, several that were given access to shallow sediment immediately attempted to burrow.

During our 24-h monitoring of zooplankton in the upper water column along shores of western Bay St. Louis, Mississippi (Fig. 4), zoeae and decapodids of *L. louisianensis* occurred in samples from 2100 (CDT), which was just after dusk in the evening, until 0500, which was the immediate predawn. However, greatest densities occurred from 2100–2300

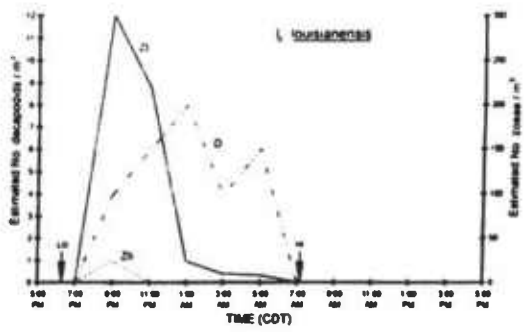


Fig. 4. Estimated number of larvae per m³ collected in semiquantitative surface water (upper 0.5 m) plankton tows taken over 24 h in a habitat heavily populated with *Lepidophthalmus louisianensis* (Schmitt) on the western shore of Bay St. Louis, Mississippi, during 16–17 July 1990. Solid lines indicate ZI stage; dotted lines indicate ZII stage; semidotted lines indicate decapodid (D) stage. Times shown are Central Daylight-Saving Time (CDT). LO indicates arrow marking time of −3-cm low tide; HI indicates arrow marking time of +52-cm high tide.

during slack to slightly rising tides, when ZI stages dominated the sample. Later collections from 0100–0500 during a nocturnal flood tide were dominated by the D stage. Occurrence of ZII stage larvae in the upper water column was limited to a sparse presence in only the 2100 sample.

Description of Zoeal and Decapodid Stages

The morphological account for developmental stages of both species follows. Prezoeal stages are presented only as figures of intact specimens.

Lepidophthalmus sinuensis

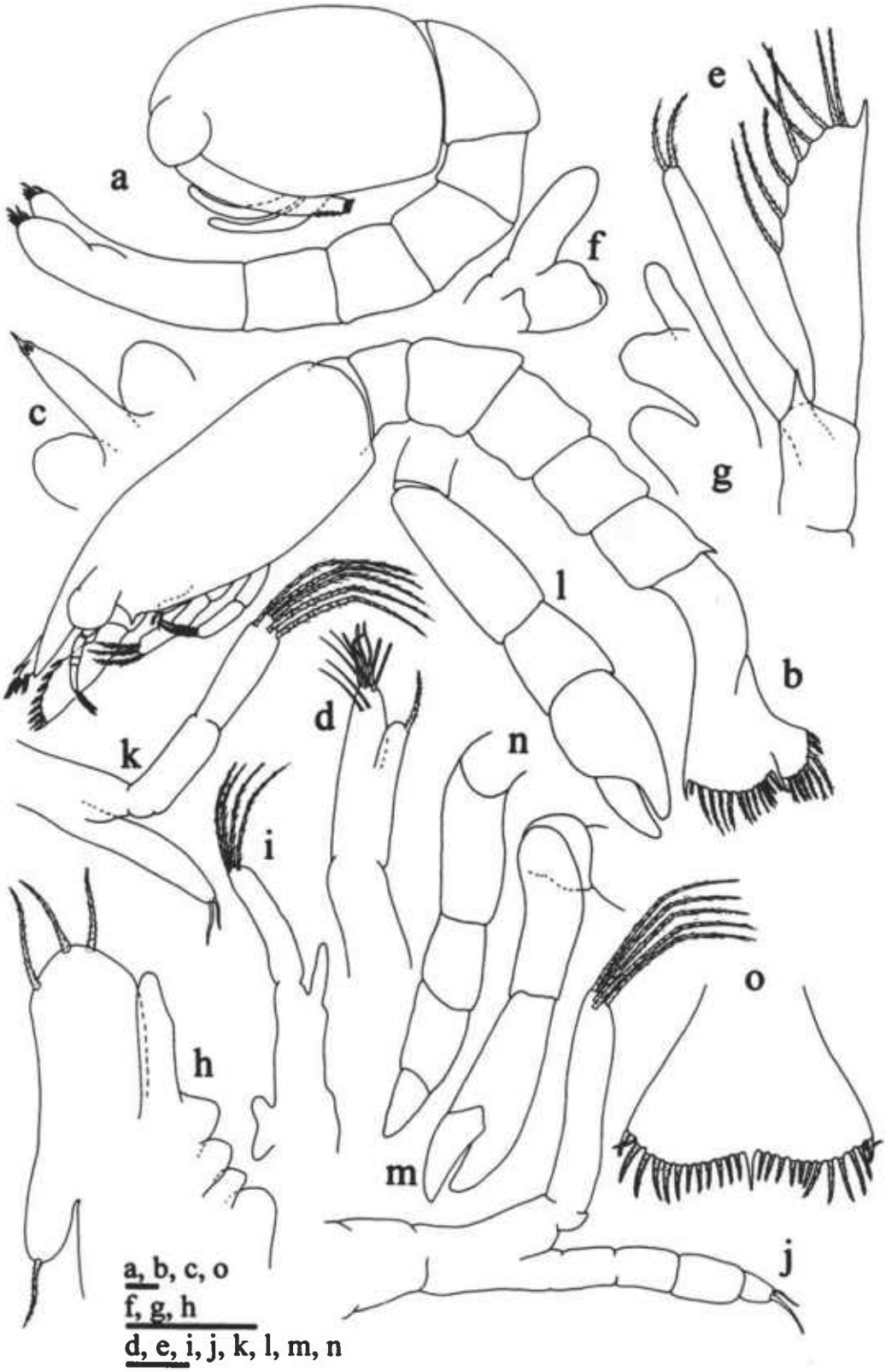
Prezoea
Fig. 5a

Zoea I
Fig. 5b–o

Size.—CL = 1.54 ± 0.06 mm, TL = 3.84 ± 0.07 mm.

Carapace (Fig. 5b).—Shorter than abdomen, anterolateral margin not markedly serrate, with pterygostomial spine; rostrum (Fig. 5c) longer than broad, with minute spines distally; eyes not free from carapace.

Abdomen (Fig. 5b).—Somites 1–5 evident, all without dorsolateral setae or spines; somite 2 lacking typical dorsal spine; somite 5 with short dorsal spine.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Antennule (Fig. 5d).—Biramous, coxa and basis partially fused; exopod with 6 thin aesthetascs of equal length, 2 subterminal and 2 terminal simple setae; endopod with single apical plumose seta, weak joint proximally.

Antenna (Fig. 5e).—Coxa and basis separated; endopod bearing 2 short apical plumose setae; exopod scaliform, with 8 or 9 inner plumose setae and 1 outer terminal spine; protopod with 1 spine at base of rami.

Mandible (Fig. 5f).—Symmetrical, processes not clearly defined, palp a large bud.

Maxillule (Fig. 5g).—Coxal and basal endite without spines; endopod unsegmented, without setation.

Maxilla (Fig. 5h).—Coxal and basal endite both bilobed, all lobes without setae; endopod unsegmented, without setation; scaphognathite with 3 anterior marginal setae, 1 or 2 posterior plumose setae.

Maxilliped 1 (Fig. 5i).—Coxa and basis fused, without setation; endopod unsegmented, without setation; exopod with 4 long jointed plumose setae; with small bilobed epipod; exopod much more than twice size of endopod.

Maxilliped 2 (Fig. 5j).—Coxa and basis partially fused, without setation; endopod 4-segmented, proximal joints weakly defined, with 2 terminal setae; exopod with 2 subterminal and 3 terminal jointed plumose setae; endopod almost as long as exopod.

Maxilliped 3 (Fig. 5k).—Coxa and basis fused, without setation; endopod unsegmented, with 2 terminal setae; exopod 2-segmented with 3 subterminal and 2 terminal long jointed plumose setae; exopod almost twice size of endopod.

Pereiopods (Fig. 5l–n).—1–3-segmented, uniramous, without setae; 1 and 2 chelate; 3 budlike, segmented; 4 and 5 not developed.

Pleopods.—Not developed.

Telson (Fig. 5o).—Triangular, with 13 or 14 processes as large spiniform setae on either side of fused median spine; first (lateral) process articulated, thick and short, second configured as the "anomuran hair," remaining processes larger and plumose; uropods not distinguishable beneath cuticle.

Zoea II
Fig. 6a–q

Size.—CL = 1.68 ± 0.09 mm, TL = 3.98 ± 0.15 mm.

Carapace (Fig. 6a).—Eyes weakly stalked, rostrum (Fig. 6b) denticulated on either side.

Abdomen (Fig. 6a).—Somites 1–5 evident; somite 2 with blunt dorsal spine; somite 5 with short dorsal spine.

Antennule (Fig. 6c).—Peduncle of 3 segments; proximal segment with 1 simple seta, penultimate segment with 2 simple setae and 1 plumose seta, distal segment bearing 3 long terminal plumose setae; exopod unsegmented, with 2 subterminal aesthetascs, 7 terminal aesthetascs, and 3 terminal simple setae; endopod of 2 segments, distal segment with single spinule.

Antenna (Fig. 6d).—Endopod 8-segmented with 1 short terminal seta; exopod scaliform, with 11 inner plumose setae and 1 outer terminal spinule; protopod with 2 spines at base of rami.

Mandible (Fig. 6e).—Molar and incisor processes not clearly defined; palp 3-segmented without spines or setae.

Maxillule (Fig. 6f).—No marked change from previous stage.

Maxilla (Fig. 6g).—Coxa, basis, and endopod unchanged; scaphognathite with 13 or 14 fringing plumose setae.

Maxilliped 1 (Fig. 6h).—Coxa and basis partially fused; basis with 2 setae; exopod 4-segmented with 1 short subterminal and 4 long terminal setae; endopod unsegmented; bilobed epipod present.

Maxilliped 2 (Fig. 6i).—Coxa, basis, and endopod unchanged; exopod partially 3-segmented with 2 subterminal and 3 terminal long jointed plumose setae; endopod almost as long as exopod.

Maxilliped 3 (Fig. 6j).—No marked change from previous stage.

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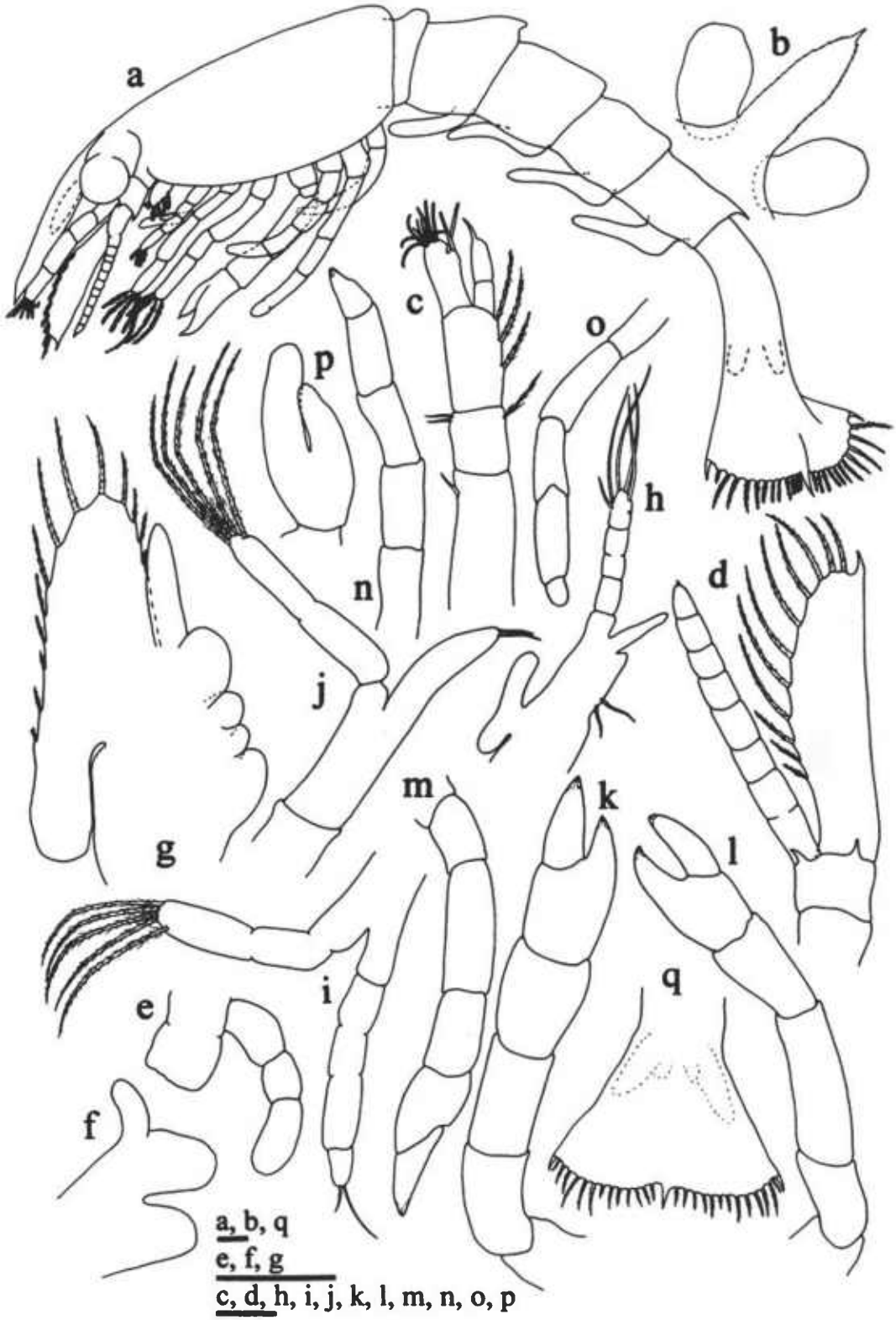
Fig. 5. *Lepidophthalmus sinuensis* Lemaitre and Rodrigues, prezoeal and ZI stages: a, lateral view of prezoeal stage; b, lateral view of ZI stage; c, rostrum; d, antennule; e, antenna; f, mandible; g, maxillule; h, maxilla; i, maxilliped 1; j, maxilliped 2; k, maxilliped 3; l–n, pereiopods 1–3; o, telson. Scale = 0.1 mm.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Pereiopods (Fig. 6k–o).—All 5 uniramous, segmented, without setae; 1 and 2 chelate, with terminal spines distinguishable under cuticle; 3–5 budlike, 3 and 4 with terminal spines distinguishable under cuticle.

Pleopods (Fig. 6a, p).—Biramous, budlike; present on somites 2–5, appendices internae not evident.

Telson (Fig. 6q).—Largely unchanged from previous stage; biramous uropods evident beneath cuticle.

Decapodid (first postlarva)
Fig. 7a–p

Size.—CL = 1.07 ± 0.05 mm, TL = 3.07 ± 0.09 mm.

Carapace (Fig. 7a).—Rostrum reduced, eyes stalked. Linea thalassinica not evident.

Abdomen (Fig. 7a).—Somites 1–6 evident, all without dorsal spines.

Antennule (Fig. 7b).—Peduncle 3-segmented; proximal segment without setation, statocyst evident beneath cuticle; penultimate segment with 2 setae; distal segment with 2 long setae; endopod partially 3-segmented, with 4 terminal aesthetascs; exopod 4-segmented, setation 0, 1, 1, 5.

Antenna (Fig. 7c).—Demarcation between peduncle and flagellum unclear; flagellum with 9 or 10 segments, proximal limit obscure; distal segment with 4 or 5 terminal setae, typical setation 0, 1, 0, 0, 3, 0, 3, 1, 2, 5; exopod limited to rudimentary bud.

Mandible (Fig. 7d).—Molar process evident; palp 3-segmented, setation 0, 0, 9; incisor process with restricted cutting edge bearing 3 or 4 teeth.

Maxillule (Fig. 7e).—Protopodal area without plumose setae; coxal endite with 4 spines and 7 setae; basal endite with 4 cuspidate spines and 5 setae; endopod rudimentary, unsegmented.

Maxilla (Fig. 7f).—Proximal and distal lobes of trilobate coxal endite with 7 or 8, 8, and 2 spines, respectively; basal endite with 3 spines on proximal lobe and 7 spines on distal lobe; endopod with 1 subterminal seta and 3 terminal setae; scaphognathite with 21 or 22 fringing plumose setae.

Maxilliped 1 (Fig. 7g).—Coxa with 4 setae; basis with 14 setae; endopod unsegmented, rudimentary; exopod with 1 subterminal seta; bilobed epipod without setation.

Maxilliped 2 (Fig. 7h).—Basis without setation; exopod 3-segmented, without setation; endopod 5-segmented, proximal joints obscure, setation 2, 5, 0, 2, 7.

Maxilliped 3 (Fig. 7i).—Exopod present as bud; endopod 5-segmented, setation 1, 7, 2, 3, 5.

Pereiopods (Fig. 7j–n).—All 5 uniramous; 1, chelate, numerous setae on chela, opposed margins of fingers without teeth, slightly corneous, ischium with small recurved hook (not visible in Fig. 7j); 2, chelate, more setose than 1, palm subequal in length to fixed finger, few short setae on opposable margin of fixed finger; 3, with propodus enlarged, similar to adult form; 4, with 7 segments and terminal spine, setation 0, 2, 1, 5, 8, 7, 2; 5, composed of 7 segments, without terminal spine, setation 2, 0, 0, 1, 3, 6, 6.

Pleopods (Fig. 7a, o).—Biramous, present on somites 2–5, that of somite 2 smaller than others; endopod of those on somites 3–5 with appendix interna bearing 4 or 5 hooked teeth and 8–10 plumose setae, exopod with 8–16 plumose setae.

Telson (Fig. 7p).—Subquadrate, with 16 processes to either side of median spine; uropodal exopod and endopod nearly equal in size, not reaching to posterior margin of telson; endopod with 8 or 9 plumose setae, exopod with 13 plumose setae.

Lepidophthalmus louisianensis

Prezoea
Fig. 8a

Zoea 1
Fig. 8b–n

Size.—CL = 1.68 ± 0.06 mm, TL = 4.22 ± 0.10 mm.

Carapace (Fig. 8b).—Carapace shorter than abdomen, anterolateral margin serrated to

←

Fig. 6. *Lepidophthalmus sinuensis* Lemaitre and Rodrigues, ZII stage: a, lateral view; b, rostrum; c, antennule; d, antenna; e, mandible; f, maxillule; g, maxilla; h, maxilliped 1; i, maxilliped 2; j, maxilliped 3; k–o, pereiopods 1–5; p, pleopod of second abdominal somite; q, telson. Scale = 0.1 mm.

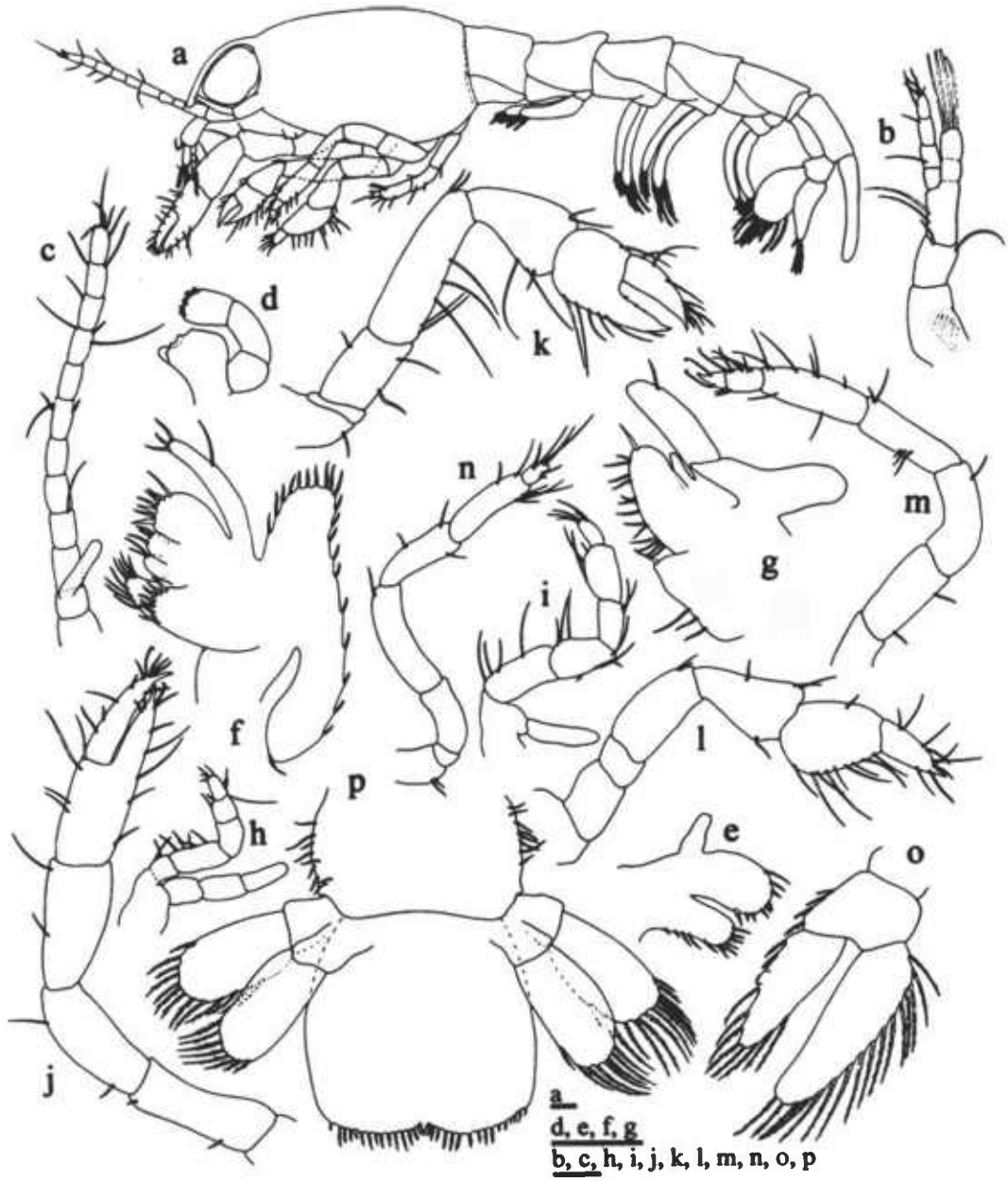

Fig. 7. *Lepidophthalmus sinuensis* Lemaitre and Rodrigues, decapodid (D) stage: a, lateral view; b, antennule; c, antenna; d, mandible; e, maxillule; f, maxilla; g, maxilliped 1; h, maxilliped 2; i, maxilliped 3; j–n, pereiopods 1–5; o, pleopod of second abdominal somite; p, telson. Scale = 0.1 mm.

form 3 or 4 minute spines, posterior to small ptergyostomial spine.

Rostrum (Fig. 8c).—Longer than broad, with minute spines distally. Eyes fused, not free from carapace.

Abdomen (Fig. 8b).—Somites 1–6 evident, all without dorsolateral setae or spines; somite 2 with typical long dorsal spine; somites 3–5 with short dorsal spines.

Antennule (Fig. 8d).—Not clearly biramous, coxa and basis fused; exopod with 1 aesthetasc, 5 terminal simple setae; endopod with single apical plumose seta.

Antenna (Fig. 8e).—Coxa and basis sepa-

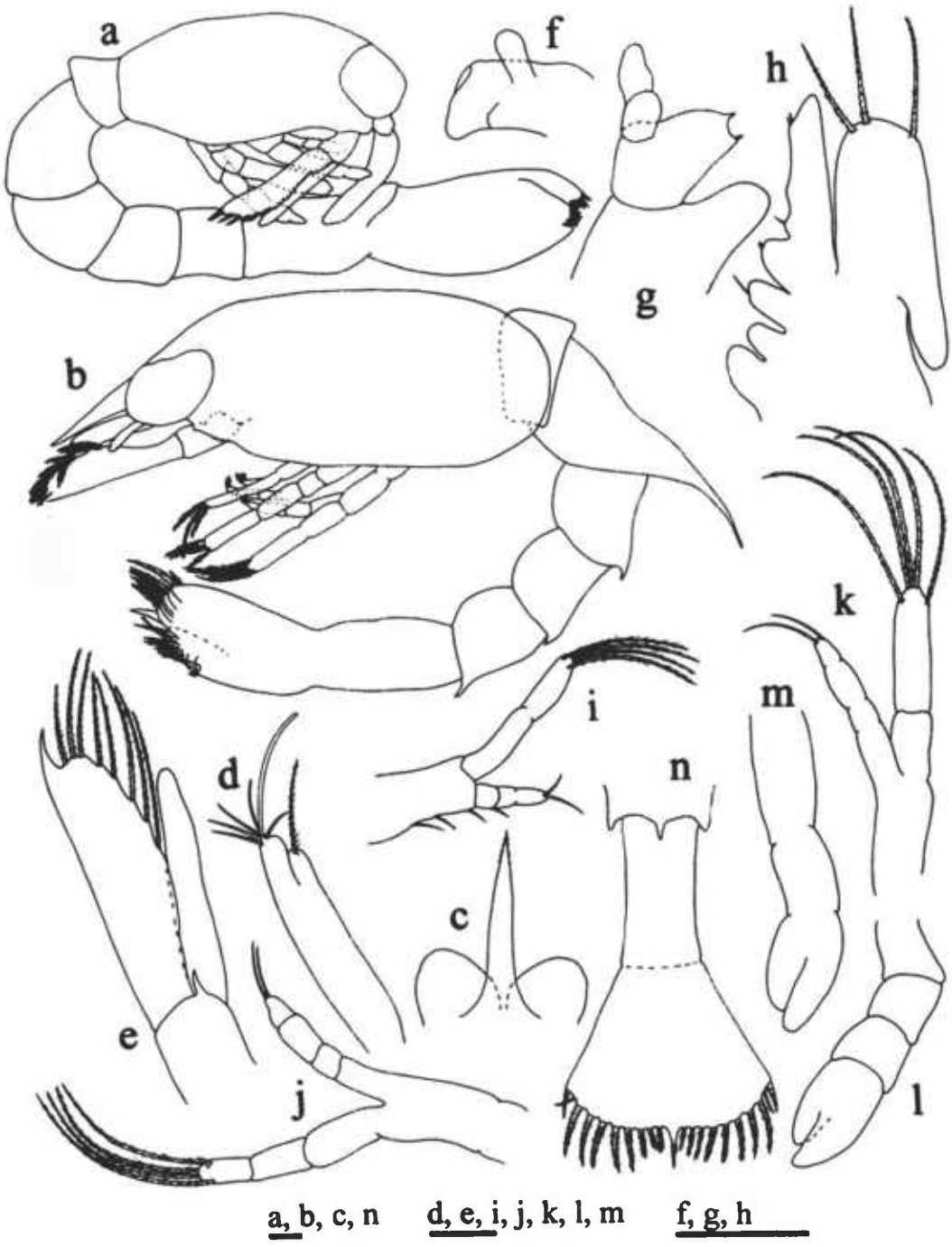

Fig. 8. *Lepidophthalmus louisianensis* (Schmitt), prezoeal and ZI stages: a, lateral view of prezoea; b, lateral view of ZI stage; c, rostrum; d, antennule; e, antenna; f, mandible; g, maxillule; h, maxilla; i, maxilliped 1; j, maxilliped 2; k, maxilliped 3; l, m, pereiopods 1 and 2; n, telson. Scale = 0.1 mm.

rated; endopod without setation; exopod scaliform, with 8 or 9 inner plumose setae and 1 outer terminal spinule; protopod with 1 spine near base of rami.

Mandible (Fig. 8f).—Symmetrical, processes not clearly defined, palp small bud.

Maxillule (Fig. 8g).—Coxal endite without

spines; basal endite with 2 spines; endopod 2-segmented, without setation.

Maxilla (Fig. 8h).—Coxal and basal endite both bilobed, basal lobes with 1+2 setae, respectively; endopod unsegmented, with 1 + 2 setae; scaphognathite with 3 anterior marginal setae, without posterior setation.

Maxilliped 1 (Fig. 8i).—Coxa and basis fused with 3 setae; endopod obscurely 3-segmented, setation 1, 0, 2; exopod with 2 subterminal and 2 terminal long jointed plumose setae; no epipod present; exopod about double size of endopod.

Maxilliped 2 (Fig. 8j).—Coxa and basis partially fused, without setae; endopod 4-segmented, proximal joint weakly defined, with 2 terminal setae; exopod with 2 subterminal and 2 terminal jointed plumose setae; endopod almost as large as exopod.

Maxilliped 3 (Fig. 8k).—Coxa and basis fused, without setation; endopod partially 4-segmented with 2 terminal setae; exopod 2-segmented, with 2 subterminal and 3 terminal long jointed plumose setae; endopod almost as large as exopod.

Pereiopods (Fig. 8l, m).—1–3 segmented, uniramous, without setae; 1 and 2 chelate; 3 budlike; 4 and 5 not developed.

Pleopods.—Not developed.

Telson (Fig. 8n).—Triangular, with 9 or 10 articulated processes as large spiniform setae on either side of fused median spine; first (lateral) process articulated, thick and short, second process configured as the "anomuran hair," remaining processes larger and plumose; uropods not distinguishable beneath cuticle.

Zoea II
Fig. 9a–q

Size.—CL = 1.69 ± 0.08 mm, TL = 4.32 ± 0.10 mm.

Carapace (Fig. 9a).—Eyes weakly stalked, rostrum (Fig. 9b) denticulated on either side.

Abdomen (Fig. 9a).—Somites 1–6 evident; somites 2, 3, and 4 with blunt dorsal spine; somite 5 lacking dorsal spine.

Antennule (Fig. 9c).—Peduncle of 3 segments, proximal without setae; penultimate with 4 simple setae, distal with 3 long plumose lateral setae and 4 short simple distal setae; exopod unsegmented, with 5 subterminal simple setae and 4 terminal aesthetascs; endopod unsegmented, with single seta.

Antenna (Fig. 9d).—Endopod 3-segmented with additional distal constrictions, without terminal setae; exopod scaliform, with 11 inner plumose setae and 1 or 2 outer terminal spines; protopod with 2 spines near base of rami.

Mandible (Fig. 9e).—Molar and incisor processes not clearly defined; palp 2-segmented without spines or setae.

Maxillule (Fig. 9f).—Coxal endite with 3 weak spines; basal endite with 2 spines; endopod weakly 2-segmented, without setation.

Maxilla (Fig. 9g).—Coxal and basal endite unchanged in shape, lobes of both without setation; endopod unsegmented, with 2 setae; scaphognathite with 7 or 8 fringing plumose setae, lacking posterior plumose seta.

Maxilliped 1 (Fig. 9h).—Coxa and basis partially fused; basis with 4 setae; exopod partially 2-segmented, with 5 long jointed plumose setae; endopod partially 3-segmented with 3 terminal setae; bilobed epipod present.

Maxilliped 2 (Fig. 9i).—Coxa and basis not fused, without setae; endopod weakly 4-segmented with 2 terminal setae; exopod with 2 subterminal and 3 terminal jointed plumose setae; endopod almost as large as exopod.

Maxilliped 3 (Fig. 9j).—Coxa and basis fused, without setae; endopod 4-segmented with 2 terminal setae; exopod partially 2-segmented, with 2 subterminal and 3 terminal long jointed plumose setae; exopod almost as large as endopod.

Pereiopods (Fig. 9k–o).—All 5 uniramous, segmented, without setation, without terminal spines distinguishable under cuticle; 1 and 2 chelate, 3–5 budlike.

Pleopods (Fig. 9a, p).—Biramous, budlike; present on somites 2–5, that of somite 2 smaller than others; endopod of those on somites 3–5 with appendix interna.

Telson (Fig. 9q).—Largely unchanged; uropods distinguishable beneath cuticle.

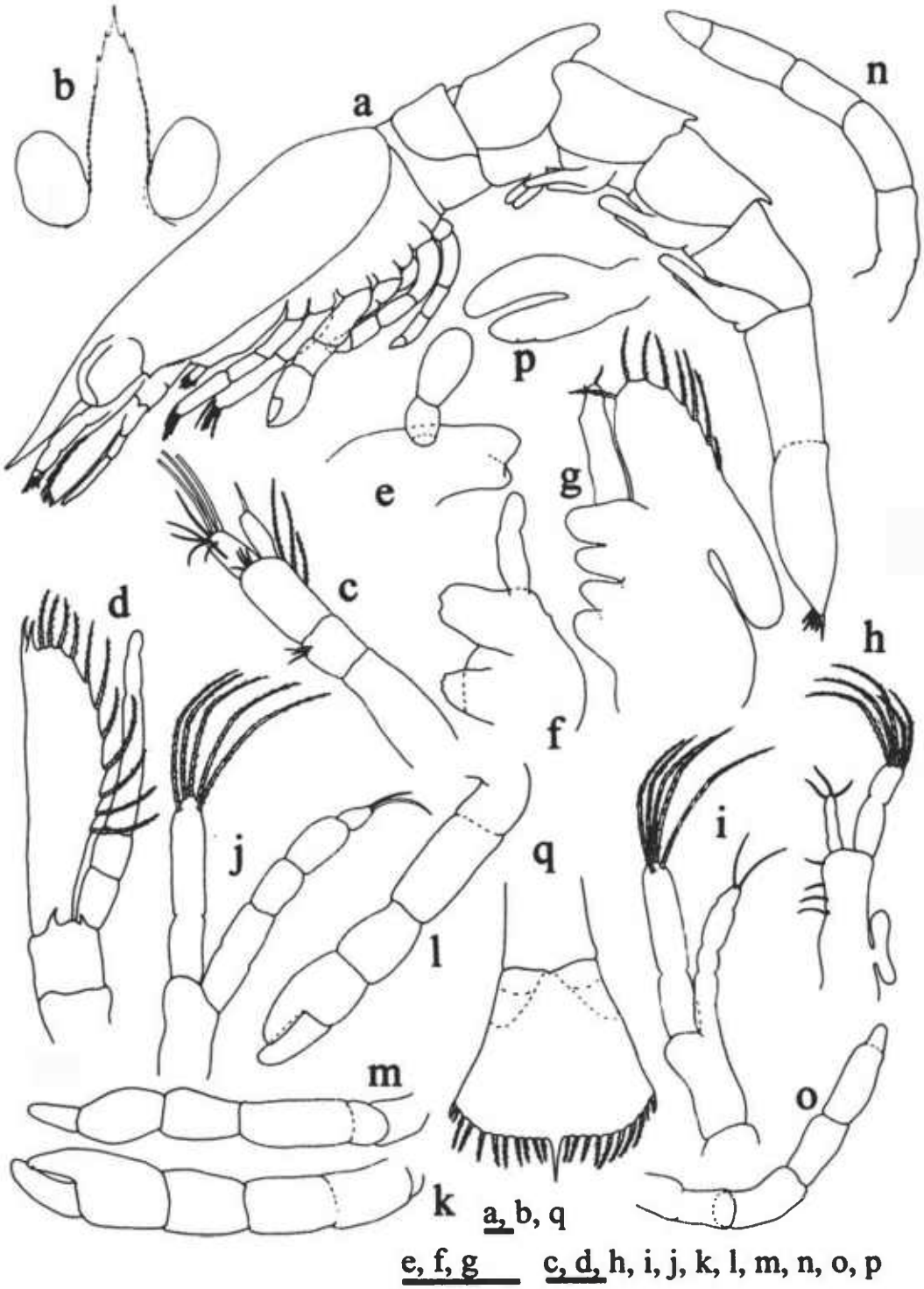

Fig. 9. *Lepidophthalmus louisianensis* (Schmitt), ZII stage: a, lateral view; b, rostrum; c, antennule; d, antenna; e, mandible; f, maxillule; g, maxilla; h, maxilliped 1; i, maxilliped 2; j, maxilliped 3; k–o, pereiopods 1–5; p, pleopod of second abdominal somite; q, telson. Scale = 0.1 mm.

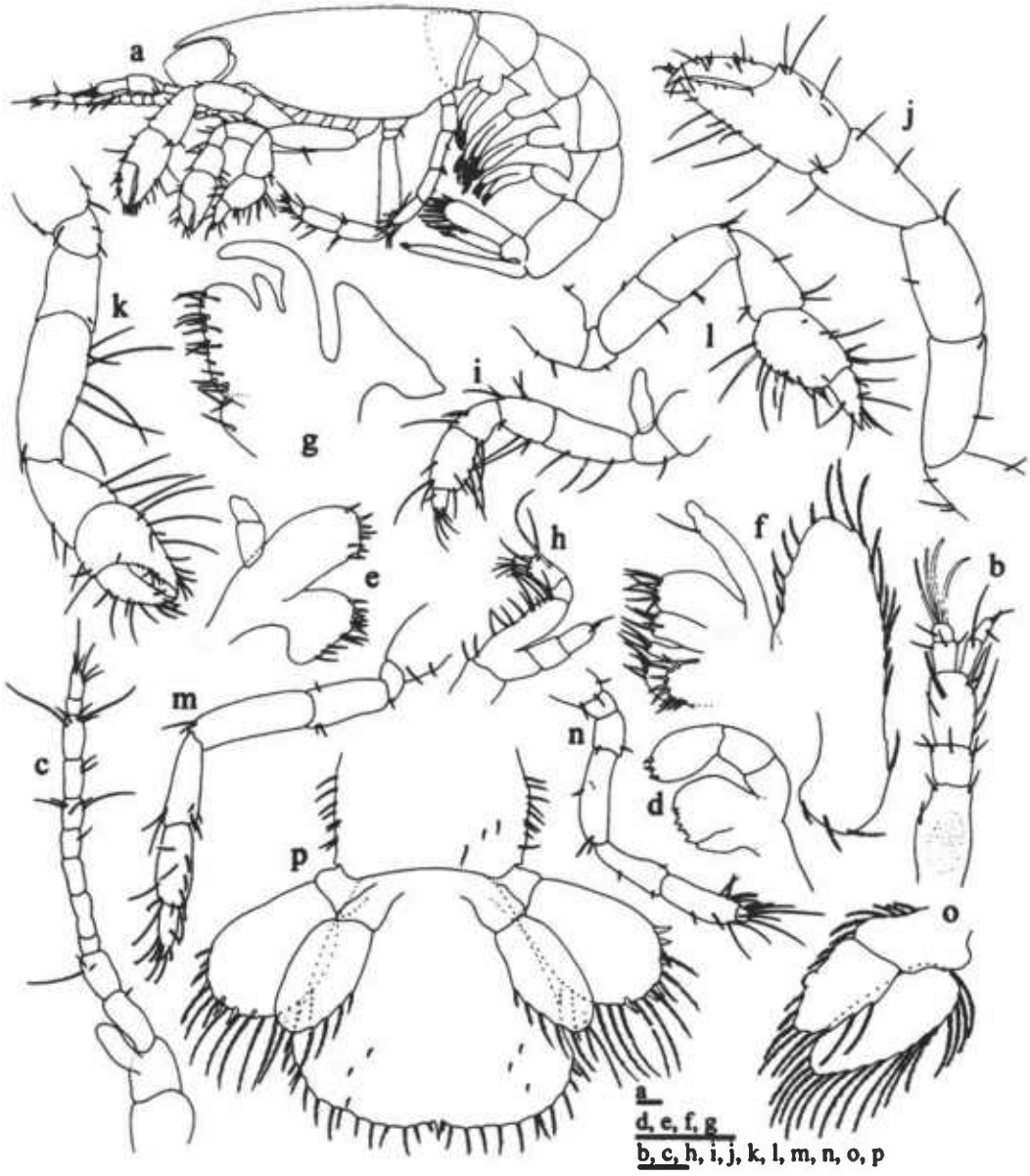

Fig. 10. *Lepidophthalmus louisianensis* (Schmitt), decapodid (D) stage: a, lateral view; b, antennule; c, antenna; d, mandible; e, maxillule; f, maxilla; g, maxilliped 1; h, maxilliped 2; i, maxilliped 3: j–n, pereiopods 1–5; o, pleopod of second abdominal somite; p, telson. Scale = 0.1 mm.

Decapodid (first postlarva)
Fig. 10a–p

Size.—CL = 1.18 ± 0.07 mm, TL = 3.27 ± 0.09 mm.

Carapace (Fig. 10a).—Rostral spine reduced, eyes stalked, free of carapace; linea thalassinica not evident.

Abdomen (Fig. 10a).—Somites 1–6 evident; somites 2–5 without dorsal spines.

Antennule (Fig. 10b).—Peduncle 3-segmented, proximal with 3 setae and statocyst evident beneath cuticle, penultimate with 5 setae, distal with 8 setae; endopod 2-segmented, setation 1, 3; exopod 2-segmented, proximal segment with 3 simple setae; distal

segment with 1 subterminal seta and 4 terminal aesthetascs.

Antenna (Fig. 10c).—Demarcation between peduncle and flagellum defined; flagellum with 9–11 segments; distal segment with 6 terminal setae, typical setation 1, 3, 0, 0, 0, 1, 5, 2, 5, 0, 6; exopod limited to rudimentary bud.

Mandible (Fig. 10d).—Molar process distinguishable; palp 3-segmented, setation 0, 0, 3; incisor process with cutting edge bearing 6 or 7 teeth.

Maxillule (Fig. 10e).—Protopod area without plumose setae; coxal endite with 7 spines and 5 setae; basal endite with 8 or 9 cuspidate spines and 1 seta; endopod partially 2-segmented.

Maxilla (Fig. 10f).—Proximal and distal lobes of trilobate coxal endite with 9, 5, and 3 spines, respectively; basal endite with 4 spines on proximal lobe and 7 spines on distal lobe; endopod with 1 subterminal seta; scaphognathite with 20 or 21 fringing plumose setae.

Maxilliped 1 (Fig. 10g).—Coxa with 2 setae; basal endite with 19 setae; endopod unsegmented, rudimentary; exopod without setae; bilobed epipod without setation.

Maxilliped 2 (Fig. 10h).—Basis with 1 seta; exopod 2-segmented with 2 terminal setae; endopod partially 5-segmented, setation 4, 7, 0, 5, 4.

Maxilliped 3 (Fig. 10i).—Exopod present as bud; endopod 7-segmented, setation 0, 1, 3, 8, 5, 8, 5.

Pereiopods (Fig. 10j–n).—All 5 uniramous; 1, chelate, with numerous setae on chela, ischium with recurved hook (not visible in Fig. 10j); 2, more setose than 1, palm subequal in length to fixed finger, opposable margin of fixed finger with 4 spinuliform teeth; 3, with propodus slightly enlarged, suggestive of adult form; 4, with 7 segments and terminal spine, setation 2, 1, 3, 2, 6, 10, 7; 5, composed of 7 segments, without terminal spine, setation 3, 0, 2, 3, 3, 9, 6.

Pleopods (Fig. 10o).—Biramous, present on somites 2–5, that on somite 2 smaller than others; endopod on somites 3–5 with appendix interna bearing 4 or 5 hooked setae and 4–10 plumose setae, exopod with 7–16 plumose setae.

Telson (Fig. 10p).—Subquadrate, with 12 processes to either side of median spine; uropods not reaching to posterior margin of telson; exopod larger than endopod; endopod with 6 or 7 setose setae, exopod with 12 plumose setae and 6 spines.

Discussion

Larval Duration and Settlement

Both *Lepidophthalmus sinuensis* and *L. louisianensis* have markedly abbreviated larval development composed of only two zoeal stages transcended within three days. These are among the shortest reported for any member of the Callianassidae (Tamaki *et al.*, 1996), but are probably typical of the genus (Manning and Felder, 1991). There is strong similarity in the duration of larval development, even though these two species represent two morphologically defined extremes of the genus; the Colombian species, *L. sinuensis*, is a member of the abdominally plated component of the genus (see Felder and Manning, 1997), while that from the Gulf of Mexico, *L. louisianensis*, is of the unplated form. A few individuals of a third (presently undescribed) abdominally plated member of the genus from the eastern Pacific have also been reared in our laboratory, and preliminary indication is that this species also exhibits remarkably attenuated development, perhaps to an even greater extreme than the two species herein treated (see below).

Of the two species herein reported upon, *L. sinuensis* appears to have the shorter duration of development, with molt to the postlarval decapodid typically occurring within about 50 h or roughly two days of hatch. While *L. louisianensis* has no more larval stages than *L. sinuensis*, molt to the decapodid in this more temperate form averages about 70 h or about three days. In both species, the decapodids exhibit burrowing ability within 12 h after molt from the ZII stage. This suggests that settlement is triggered quickly. Since both of these species are estuarine forms, we concur with previous proposals that this developmental strategy would serve to favor estuarine retention, especially since these early stages also appear to be physiologically adapted to the adult habitat (Felder *et al.*, 1986). The one-day differential in duration of

zoeal development may be of adaptive significance, perhaps reflecting specialization for retention in adult habitats that differ somewhat between the two species. In Colombian habitats of *L. sinuensis*, optimal settlement areas are confined to comparatively narrow coastal estuaries and river mouths, where preferred muddy substrates in low-salinity, oligohaline, upper estuaries give way over short distances to high-salinity tropical waters, mangrove-lined lagoons densely populated by small predatory fishes, and coarse calcareous substrates. Tidal cycling here may more rapidly flush planktonic forms from optimal settlement substrates than it would in the markedly more expansive euryhaline muddy habitats of *L. louisianensis* in the Gulf of Mexico, perhaps imparting some local advantage to species like *L. sinuensis* with reduced planktonic exposure over the course of larval development. By contrast, inhabitable muddy substrates and euryhaline water favored by adults of *L. louisianensis* can often extend offshore into coastal waters.

A more thorough linkage of habitat constraints and larval histories in the genus must await developmental studies of additional congeners. This will allow comparison of larval histories in more examples with varying degrees of adult habitat restriction. Of particular interest will be the ultimate inclusion of several eastern Pacific congeners in comparative studies, at least one of which, the earlier mentioned undescribed species, is an adult restricted to isolated narrow bands of intertidal clays no more than a few meters wide. The unusually restricted habitat of that species would suggest it to have an even more abbreviated larval development than that observed in *L. sinuensis* and *L. louisianensis*. This appears to have been borne out in our preliminary observations to date. However, we must defer characterization of early stages and duration of development until additional animals of that species can be reared under carefully controlled conditions.

Within sister genera of the subfamily Callichirinae, habitats are not usually restricted to estuaries as in *Lepidophthalmus*, though they are typically intertidal or shallow subtidal. Among the few species for which the complete larval development is known (Aste and Retamal, 1983; Rodrigues, 1984), early life history ranges from metamorphosis after five zoeal stages of 48 days total duration in *Callichirus garthi* (Retamal) to metamorphosis after two zoeal stages of 7–12 days total duration in *Sergio mirim* (Rodrigues). Early development is also known in part for another species of *Callichirus* from Brazil, for which the third zoeal stage was reached after 7 days, and a fourth zoeal stage was identified from plankton (Rodrigues, 1976), suggesting a sequence of stages near that reported for *C. garthi*. A comparatively long planktonic development in *Callichirus* may account for longshore dispersal of larvae which seed adult populations. These populations are distributed widely along intertidal and shallow subtidal shoreline margins, especially those composed in major part of siliceous sands along surf-washed beaches of open coastlines and large embayments. While adults of *S. mirim* may occur in similar environments, they are typically found in lower intertidal and subtidal sediments of southern Brazil and northern Argentina, sometimes within defined embayments (Ferrari, 1981; Rodrigues and Hödl, 1990). However, the genus *Sergio* as a whole is ecologically diverse, with some intertidal species associated with shoals, mud flats, or grass beds, often burrowed into sediments rich in calcareous materials, and other species that range into varied subtidal sediments. A diversity of developmental and dispersal strategies might be expected within that genus, once life histories are known for more of its member species.

Prolonged larval life histories, involving 5 or 6 zoeal stages transcended over periods ranging from 15–70 days, appear to be common among diverse species comprising various subfamilies of the Callianassidae, though evaluation must be limited to species for which the entire larval history has been documented from laboratory cultures or careful studies of wild plankton samples. At minimum, such full-scale developmental histories are, among non-Callichirinae, documentable in *Callianassa subterranea* Montagu, *Neotrypaea uncinata* (H. Milne Edwards), *N. californiensis* (Dana), *Trypaea australiensis* Dana, and other species of *Callianassa* s.l., such as *C.* s.l. *filholi* Milne Edwards, *C.* s.l. *petalura* Stimpson, and *C.* s.l. *japonica* (Ortmann) (Gurney, 1942; Hailstone and Stephenson, 1961; Devine, 1966; Johnson and Gonor, 1982; Aste and Retamal, 1984; Konishi *et al.*, 1990; Tamaki *et al.*, 1996). However, the non-Callichirinae include representatives with

highly abbreviated development, consisting of only two zoeal stages of short (minimally 3–5 days) duration, as exemplified in *C.* s.l. *kraussi* Stebbing, *C.* s.l. *kewalramanii* Sankolli, and *C.* s.l. *tyrrhena* (Petagna) (Forbes, 1973; Sankolli and Shenoy, 1975; Thessalou-Legaki, 1990). Provided present systematic separations of these taxa from *Lepidophthalmus* are well founded, this documents convergence in developmental strategies of distant groups, all of which appear to be adapted for retention of larvae in isolated or discrete adult habitats.

We cannot assume that numbers and mean durations of larval stages alone define recruitment strategies in callianassids, even though they may be valuable indicators. Behaviors, such as complete development of larvae within the adult burrow water in *C.* s.l. *kraussi* (see Forbes, 1973) and labile physiological responses, such as triggering of rapid metamorphosis by exposure to warm shoreline waters in *C.* s.l. *tyrrhena*, can also be of crucial importance in targeting of recruits to adult habitats. At least conceptually, the "benthic" development of larvae within parental burrows has also been proposed (Rowden and Jones, 1994) to account for a winter cohort of recruits in *Callianassa subterranea*. While that would be a remarkable facultative adaptation in a species which at other times of the year has five planktonic zoeal stages, it is certainly plausible in species of *Lepidophthalmus*, which have larval development abbreviated much as in *C.* s.l. *kraussi* and which have limited necessity to feed during the larval phase.

While we have no direct observations of such benthic development in either of the species we have studied, we have observed burrows of juveniles directly intersecting burrows of adults in burrow resin casts for both species, much as reported to occur in burrows of *C.* s.l. *japonica* by Tamaki *et al.* (1992). We cannot rule out benthic development and settlement within parental burrows as a facultative or alternative strategy under some conditions. However, in both species of *Lepidophthalmus*, at least some major component of wild larval populations exhibits nocturnal periodicities in surface plankton; these could also be of significance in transport toward settlement sites. The combination of vertical migration with flood tides is well documented as a means of shoreward dispersal preceding settlement in other estuarine decapods (Felder *et al.*, 1985) and may be of similar significance in confining settling decapodid stages of at least *L. louisianensis* to the preferred shallow subtidal and intertidal environments of adult populations. Of no less significance, decapodid stages were not found in our nocturnal sampling of nontidal, artificially circulating shrimp-culture ponds at Agrosoledad S. A. This suggests that, in the absence of tidal change, the massing of decapodids in surface waters for shoreward recruitment may not occur. This may contribute to remarkable accumulations of *L. sinuensis* in infested culture ponds. It is also noteworthy that distributions in the adults may not be defined solely by settlement in the decapodid stage. At least in Mobile Bay, Alabama, juvenile males of *L. louisianensis* have periodically been collected in abundance from midwater plankton tows (Felder and Rodrigues, 1993). This peculiar behavior could result in some secondary reassortment of adult populations well after initial postlarval settlement.

Morphological Comparisons

Morphological comparisons of developmental stages in *Lepidophthalmus* with those of other callianassids is greatly limited by lack of consistent and adequately detailed larval descriptions. Of particularly scant treatment are the prezoeal stages which are easily overlooked, rarely described, and often treated as artifactual products of laboratory rearings (Gore, 1985). They are probably common among thalassinids, have been noted to occur in a number of callianassid genera studied to date (Heegaard, 1963; Devine, 1966; Rodrigues, 1976; Aste and Retamal, 1983, 1984), and were recognized in the course of our rearing both species of *Lepidophthalmus*, but were persistent as nonmotile stages only in our less successful rearing trials. In our cultures, this stage usually either molted to the ZI stage shortly after hatch or persisted longer but died prior to molt. Significance of the callianassid prezoeal stage in natural populations remains undetermined.

As ZI larvae, the two species of *Lepidophthalmus* are remarkably similar in size, setal arrays, and general body configuration, especially when measured against stages of the only other two callianassid species for

Table 1. Comparison of ZI larval characters for *Lepidophthalmus sinuensis* Lemaitre and Rodrigues from the Caribbean coast of Colombia and *L. louisianensis* (Schmitt) from the northern Gulf of Mexico with two other members of the Callianassidae, *Sergio mirim* (Rodrigues) and *Callianassa* s.l. *kewalramanii* Sankolli, for which similar abbreviated development has been described. Serial listings are numbers of setae and spines arranged proximally to distally. Symbols represent: aesthetascs (I); presence (P); absence (A); not reported or not detectable from drawings (?); counts of setae or spines (ct). Setae and spines or groups of these processes on the same segment or on adjacent lobes of the same endite are separated by plus (+); such processes or groups of processes are separated by a comma (,) if on successive segments.

	L. sinuensis	*L. louisianensis*	*S. mirim**	*C. s.l. kewalramanii***
Total length (mm) ± 95% CI	3.84 ± 0.07	4.22 ± 0.10	5.5	3.5
Antennule				
Endopod ct	1	1	1	1
Exopod ct	2+2+6 I	5+1 I	6 or 7	3+3 I
Antenna				
Flagellum	A	A	A	A
Endopod ct	2	0	3	2
Exopod ct	8 or 9+1	8 or 9+1	12+1	14+1
Protopod ct	1	1	1	1
Maxillule				
Coxal endite ct	0	0	3+3+5	10
Basal endite ct	0	2	10	7 or 8+5 or 6
Endopod ct	0+0	0+0	1,2+4	2,4+2
Maxilla				
Coxal endite ct	0+0	0+0	10	11+3
Basal endite ct	0+0	1+2	4+3+4	3+1 or 2
Endopod ct	0+0	1+2	2,1,2,2+4	2+2+2+2+4
Scaphognathite ct	3+1 or 2	3	16+1	19 or 20+1
Maxilliped 1				
Coxa ct	0	0	7	8 or 9
Basis ct	0	3	15	13–15
Endopod ct	0	1,0,2	2,2,1,4	3+1,3,3,3+1
Exopod ct	2+2	2+2	4	6+2
Epipod	P	A	A	A
Maxilliped 2				
Coxa ct	0	0	0	1
Basis ct	0	0	2	6 or 7
Endopod ct	0,0,0,2	0,0,0,2	1,2,4,5	5+1,1,2,4+1
Exopod ct	0,2+3	0,0,2+2	5	8
Maxilliped 3				
Coxa ct	0	0	2	0?
Basis ct	0	0	6	1 or 2
Endopod ct	2	0,0,0,2	4,3,1,8	1,1+1,3,1+4
Exopod ct	0,2+3	0,2+3	5	6+4
Telson				
Processes ct	13 or 14	9 or 10	10 or 11	12 or 13
Process 2 as hair	P	P	P	P
Median process	P	P	P	P
Uropods	A	A	A	A
Endopod	A	A	A	A
Exopod	A	A	A	A

*From Rodrigues (1984).

**From Sankolli and Shenoy (1975).

which larval development of two stages has been described in adequate detail for comparison (Table 1). Differences between the ZI stages of the species of *Lepidophthalmus* are found only in the slightly larger size and stronger microspination of the carapacial margin and dorsal spination of the abdomen in *L. louisianensis*, larger number of telsonal processes and antennular exopodal setae in *L. sinuensis*, early appearance of a first maxillipedal epipod and a large mandibular palp in *L. sinuensis*, and generally fewer accessory setae on feeding appendages of *L. sinuensis*. Most of these morphological features suggest that, of the two congeners, *L. sinuensis* exhibits the more strongly abbreviated development because of its slightly more "advanced" (sensu Rabalais and Gore, 1985: 78) features at the ZI stage. Only in *Callianassa* s.l. *kraussi* does the abdomen show greater

reduction in dorsal spination (see Forbes, 1973). The ZI stages in *S. mirim* and *C.* s.l. *kewalramanii* are both much more setose than those of *Lepidophthalmus*, and neither shows strong evidence of advanced development. *Sergio mirim* more closely resembles its distant relative, *C.* s.l. *kewalramanii*, in most features of ZI stage setation than it does either of the species of *Lepidophthalmus*, its fellow members of the Callichirinae. While existing descriptions of the ZI stage in species of *Callichirus* (see Rodrigues, 1976; Aste and Retamal, 1983) are not presented in comparable detail to those of other Callichrinae discussed above, notable features, such as their strong, dorsal abdominal spines and setose feeding appendages, are much more similar to those of *Sergio* than to those of *Lepidophthalmus*. In this aspect, they also resemble early zoeal stages in other callianassids with long (5 or 6 stages) larval life histories (see Heegaard, 1963; Aste and Retamal, 1984; Konishi *et al.*, 1990).

In most respects, differences observed between *L. sinuensis* and *L. louisianensis* in the ZI stage persist into the ZII stage. In the ZII stage of only *L. louisianensis*, the anteroventral margin of the carapace continues to show microspination and there is distinct dorsal spination on the second through fourth abdominal somites. However, a strong, acuminate dorsal spine on the second abdominal somite in the ZI stage of *L. louisianensis* has become reduced and blunted in the ZII, while in the ZII stage of *L. sinuensis* there is for the first time rudimentary evidence of this spine. In terms of its smaller size, generally greater setation on the antennules and antennae, lesser setation on the feeding appendages, and larger number of telsonal processes, *L. sinuensis* varies from *L. louisianensis* much as it did in the ZI stage. Distinction also persists in the mandibular palp which is larger and more segmented in *L. sinuensis*. One stage later than in *L. sinuensis*, the ZII of *L. louisianensis* has a well-developed epipod, though marked differences between the species persist in segmentation and setation of this appendage. On the basis of the aforementioned characteristics, *L. sinuensis* continues in the ZII stage to exhibit the more advanced development, with at least one exception. While advanced development of budlike pleopods is evident in both species, only in pleopods of *L. louisianensis* could we detect clear evidence of the appendix interna at the ZII stage.

Since the ZII stage is the terminal zoeal stage for both species of *Lepidophthalmus* here treated, detailed comparisons to ZII stages of species with 5 or 6 larval stages result only in the expected array of morphological differences between early planktonic stages of other genera and immediately presettlement stages in *Lepidophthalmus*. In the ZII and sometimes later zoeal stages of forms lacking abbreviated development, including the *Callichirus* ZII stage (Rodrigues, 1976; Aste and Retamal, 1983), a well-developed dorsal spine typically persists on the second abdominal somite and the development of pleopods is postponed, while antennular and feeding setation remains well developed throughout most or all of zoeal development. For two genera other than *Lepidophthalmus* which have only two zoeal stages (Table 2), morphology of the ZII stage is in many respects nearer that of ZII stages in nonabbreviated forms than that in *Lepidophthalmus*. Despite the probable distant relationship between *S. mirim* and *Callianassa* s.l. *kewalramanii*, and the uniqueness of each in certain features of the ZII stage, both have biramous pereiopods, while the exopods of these appendages are lacking in *Lepidophthalmus*. Both also have pleopods only on abdominal somites 3–5, rather than on somites 2–5 as in *Lepidophthalmus*. Only in *C.* s.l. *kraussi* is it obvious that the advanced ZII stage also has four pairs of pleopods.

With transition to the decapodid stage, both species of *Lepidophthalmus* take on the imaginal form of adults. In the molt from the ZII to this stage, *L. louisianensis* retains a larger number of peduncular and exopodal setae on the antennae (Table 3), but exhibits more postlarval characteristics than does *L. sinuensis* in the number of endopodal setae on the third maxilliped and in the more densely armed incisor process on the mandible. The decapodid in *L. sinuensis* continues to be slightly smaller than the comparable stage of *L. louisianensis* and to have the larger number of telsonal processes. Both species have by this stage developed a distinctly 3-segmented mandibular palp characteristic of the adults (which is not 2-segmented in adults of *L. sinuensis*, contrary to the conclusions of Lemaitre and Rodrigues, 1991). Both also retain a small but distinct exopod on the third

Table 2. Comparison of ZII larval characters for *Lepidophthalmus sinuensis* Lemaitre and Rodrigues from the Caribbean coast of Colombia and *L. louisianensis* (Schmitt) from the northern Gulf of Mexico with two other members of the Callianassidae, *Sergio mirim* (Rodrigues) and *Callianassa* s.l. *kewalramanii* Sankolli, for which similar abbreviated development has been described. Serial listings are numbers of setae and spines arranged proximally to distally. Symbols represent: aesthetases (I); presence (P); absence (A); not reported or not detectable from drawings (?); counts of setae or spines (ct). Setae and spines or groups of these processes on the same segment or on adjacent lobes of the same endite are separated by plus (+); such processes or groups of processes are separated by a comma (,) if on successive segments.

	L. sinuensis	*L. louisianensis*	*S. mirim**	*C.* s.l. *kewalramanii***
Total length (mm ± 95% CI)	3.98 ± 0.15	4.32 ± 0.10	5.6	3.5–3.6
Antennule				
Peduncle ct	1,2+1,3	0,4,3+4	0,2+1+1,2+3	2 or 3,3,1
Endopod ct	0,1	1	0	1
Exopod ct	2+7 I+3	5+4 I	6	4+2 I+6
Antenna				
Flagellum	A	A	A	A
Endopod ct	I	0	I	I
Exopod ct	11+1	11+1 or 2	14+1+2	15–17+1
Maxillule				
Coxal endite ct	0	3	4+3+2	16
Basal endite ct	0	2	12	12–14+6+2
Endopod ct	0	0	2+2+4	2,6
Maxilla				
Coxal endite ct	0	3	8+1	15+4
Basal endite ct	0	0	4+4	6+7
Endopod ct	0	2	2+2+2+2+2	3+2+2+2+3
Scaphognathite ct	13 or 14	7 or 8	20+1	21–23+1
Maxilliped 1				
Coxa ct	0	0	6	0
Basis ct	2	4	14	6
Endopod ct	0	3	3,1,2,4	4,2,2,4
Exopod ct	0,0,0,1+4	0,5	5	10
Epipod	P	P	A	P
Maxilliped 2				
Coxa ct	0	0	2	1
Basis ct	0	0	5	6 or 7
Endopod ct	2	0,0,0,2	9,1,4,3	6,1,2,5
Exopod ct	0,0,2+3	0,2+3	5	11 or 12
Maxilliped 3				
Coxa ct	0	0	0	0
Basis ct	0	0	0	0
Endopod ct	2	0,0,0,2	5,2,6,4	2,2,3,4
Exopod ct	2+3	0,2+3	6	11 or 12
Telson				
Processes ct	13 or 14	9 or 10	10 or 11	13 or 14
Process 2 as hair	P	P	P	?
Median process	P	P	P	A
Uropods	P	P	A	P
Endopod	A	A	A	A
Exopod	A	A	A	A

*From Rodrigues (1984).

**From Sankolli and Shenoy (1975).

maxilliped, a feature evident also in the mature adult stages and valuable as a character of the genus (Manning and Felder, 1991).

It is of interest that the decapodids of both *S. mirim* and *C.* s.l. *kewalramanii* also retain the third maxillipedal exopod (Table 3), though it has not been noted to occur in the mature adults. In contrast to *S. mirim* and *C.* s.l. *kewalramanii* (Table 3), both species of *Lepidophthalmus* have distinctly less setation in the antennules, antennae, maxillules, first maxillipedal exopods, and uropodal exopods in the decapodid stage. As in the ZII stage, the decapodids of *Lepidophthalmus* are also distinct from those reported for *S. mirim* and *C.* s.l. *kewalramanii* (Table 3), but like those of *C.* s.l. *kraussi* (see Forbes, 1973), in that they retain a fourth set of well-developed pleopods, those being the slightly smaller set on abdominal somite 2. This difference may

Table 3. Comparison of decapodid (first postlarval) characters for *Lepidophthalmus sinuensis* Lemaitre and Rodrigues from the Caribbean coast of Colombia and *L. louisianensis* (Schmitt) from the northern Gulf of Mexico with two other members of the Callianassidae, *Sergio mirim* (Rodrigues) and *Callianassa* s.l. *kewalramanii* Sankolli, for which similar abbreviated development has been described. Serial listings are numbers of setae and spines arranged proximally to distally. Symbols represent: aesthetases (I); presence (P); absence (A); not reported or not detectable from drawings (?); counts of setae or spines (ct). Setae and spines or groups of these processes on the same segment or on adjacent lobes of the same endite are separated by plus (+); such processes or groups of processes are separated by a comma (,) if on successive segments.

	L. sinuensis	*L. louisianensis*	*S. mirim* *	*C.* s.l. *kewalramanii* **
Total length (mm ± 95% CI)	3.07 ± 0.09	3.27 ± 0.09	4.2	3.2–3.4
Antennule				
Peduncle ct	0,2,2	3,5,8	10	1,6,11+1
Endopod ct	0,0,4 I	1,3	0,2,0,2,4	2,1,3+1
Exopod ct	0,1,1,5	3,1+4 I	1,0,2+2 1,2 1+4	0,2+2 1,4+2 I
Antenna				
Flagellum segments	9 or 10	9 or 10	19	8
Endopod	A	A	A	A
Exopod	bud	bud	A	bud
Maxillule				
Coxal endite ct	4+7	5+7	≥18?	≥16?
Basal endite ct	4+5	8 or 9+1	≥20?	≥17?
Endopod segments	0	2	2	0
Protopod ct	0	0	1	0
Maxilla				
Coxal endite ct	7 or 8+8+2	9+5+3	8+1	≥16?
Basal endite ct	3+7	4+7	4+4	≥16?
Endopod ct	1+3	1	2+2+2+2+2	2+1+3
Scaphognathite ct	21 or 22	20 or 21	20+1	26
Maxilliped 1				
Coxal endite ct	4	2	≥5?	3
Basal endite ct	14	19	≥24?	≥16?
Endopod segments	0	0	0	0
Exopod ct	1	0	7+6	≥19?
Epipod ct	0	0	0	0
Maxilliped 2				
Coxal endite ct	0	0	0	0
Basal endite ct	0	1	2	3
Endopod ct	2,3,2,0,2,7	4,7,0,5,4	?	11,1,4,6
Exopod ct	0	0,2	5	18
Maxilliped 3				
Coxal endite ct	0	0	1	0
Basal endite ct	3	1	3	3
Endopod ct	1,7,2,3,5	3,8,5,8,5	14,12,8,15,7	21,2,8,4
Exopod	bud	bud	bud	bud
Telson				
Processes ct	16	12	16	13
Process 2 as hair	A	A	A	A
Median process	P	P	?	?
Uropods	P	P	P	P
Endopod ct	8 or 9	6 or 7	10–12	10
Exopod ct	13	18	>38	>34

*From Rodrigues (1984).

**From Sankolli and Shenoy (1975).

also reflect the more advanced development of adult features in *Lepidophthalmus*, since both *Sergio* and *Lepidophthalmus* will, in later postlarval and adult stages (Felder and Lovett, 1989; Manning and Felder, 1991), have uniramous pleopods on abdominal somite 1 and slender biramous appendages on abdominal somite 2.

Development of a full or nearly adult complement of feeding appendage setation in the species of *Lepidophthalmus* appears to ensue over a course of early postlarval stages following settlement of the decapodid. Given our unusually thorough insight into complexity in the adult forms of those appendages (Lemaitre and Rodrigues, 1991; Felder and Rodrigues, 1993), it is clear that the imaginal decapodid stage is capable of settling and

at least initiating its fossorial existence with far less than an adult appendage configuration and complement of setation. However, while we now know much about the growth, maturation, and reproduction of later stages (Felder and Lovett, 1989; S. F. Nates and D. L. Felder, in preparation), most aspects of early postlarval ontogeny and all facets of behavior in early postlarval stages remain important missing elements in understanding the life history of *Lepidophthalmus*, as well as other callianassid genera.

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