Morphological and Developmental Differences in Three Species of the Snapping Shrimp Genus *Alpheus* (Crustacea, Decapoda)

Heather R. Spence[1] and Robert E. Knowlton[2,*]

Abstract - Living, freshly collected individuals of three species of snapping shrimps were studied to determine any differing morphological, developmental, and ecological features: *Alpheus heterochaelis*, collected from Beaufort, NC; *A. angulosus*, found mainly in Jacksonville, FL, but also at one site in Beaufort; and *A. estuariensis*, collected at another Jacksonville site. Structural characteristics of these superficially similar species are summarized, with particular attention to coloration. Adult *A. angulosus* individuals have blue-green 2nd antennal flagella (vs. tan in the other two species) that are significantly shorter than those of *A. heterochaelis*. *Alpheus angulosus* and *A. estuariensis* bear smaller eggs (<1 mm, regardless of embryonic stage) than *A. heterochaelis* (>1 mm), and the former species displays the zoea larval form typical of alpheids (vs. abbreviated larval development in *A. heterochaelis*).

Introduction

Perhaps the most persistent and widespread noise in shallow-water tropical and subtropical seas is that produced by "snapping shrimps," decapod crustaceans belonging to the family Alpheidae. In most alpheids, the chelate first pereiopods ("claws") are asymmetrical, one member of the pair (the major chela) being much larger and more heavily calcified than the other (Fig. 1). The noise is produced by vast numbers of individuals, each one rapidly closing the dactylus, or movable finger, of its major claw onto the pollex, or immovable finger, of the propodus, in the manner of a pistol hammer (hence the alternative name "pistol shrimp") (Knowlton and Moulton 1963, Versluis et al. 2000).

Many alpheid species are morphologically very similar and consequently "difficult to recognize using traditional systematic methods" (Knowlton 1986). Preserved specimens have been relied upon in the process of defining species, but some distinguishing characteristics, such as color, cannot be considered as they are lost in the process of preservation (Knowlton 1986). Alternative methods are required to discern some species.

A number of morphologically similar species from the so-called *Alpheus edwardsii* group are found along coastlines of the southeastern United States. *Alpheus heterochaelis* Say (big-claw snapping shrimp) was first described in 1818, but since then new species have been delineated among specimens originally thought to be *A. heterochaelis*. One of these

[1]Department of Biology, University of Massachusetts, North Dartmouth, MA 02747-2300. [2]Department of Biological Sciences, George Washington University, Washington, DC 20052. [*]Corresponding author - knowlton@gwu.edu.

is *Alpheus estuariensis* Christoffersen (1984); another is *Alpheus angulosus* McClure (2002), initially named *Alpheus angulatus* (McClure 1995). Although the *A. heterochaelis* neotype is from northern Florida (Amelia Island), *A. angulosus* is actually the most common species collected in Florida locations, and *A. heterochaelis* is more commonly found in North Carolina (McClure 1995).

The morphological differences recognized among these three species are very subtle, and verbal descriptions, especially color, can be vague. Field identification is important because the species are sympatric, yet some of the most significant morphological differences documented are not useful distinguishing features in identifying live shrimps. For example, the angular carapace characteristic of *A. angulosus* (McClure 1995) is obscured by the pereiopods.

Developmental differences between *A. heterochaelis*, *A. angulosus*, and *A. estuariensis* have not yet been established. Knowlton (1970) described the developmental pattern of *A. heterochaelis* from North Carolina and postulated that then-assumed *A. heterochaelis* from Florida (now known to be *A. angulosus*) was a different species based on observations of smaller eggs in the Florida shrimps.

Snapping shrimps are characterized by unique behaviors and interesting interactions with other species and abiotic aspects of the environment. Aspects of behavioral-ecological investigation have included mechanics of the snap (e.g., Versluis et al. 2000), sociality (Duffy et al. 2002), aggression (Knowlton and Keller 1982), chemical and visual signaling (Hughes 1996), and habitat selection (Corfield and Alexander 1995). Animals thought to be *A. heterochaelis* have been and continue to be used as subjects of many investigations, making it all the more important to facilitate correct identification of this and its "look-alike" species.

The purpose of our research project was to discern and describe developmental, ecological, and additional morphological differences between *Alpheus* populations from two geographically separated areas: southern North Carolina and northern Florida. These lines of investigation, centered around the examination of live specimens, together can provide a further and clearer basis for distinguishing the three species.

Figure 1. Dorsal view of male *A. heterochaelis*, showing "balaeniceps-type" minor chela.

Field-site Descriptions

Shrimp were collected at two sites in each state. Both North Carolina sites were located at the mouth of the Newport River (estuary), Beaufort, approximately 0.4 km apart and on nearly opposite sides of Beaufort Inlet. The primary collection location was near the Duke University Marine Laboratory (DUML), on the western side ("Research Cove") of Pivers Island Road. The other North Carolina site was "Duncan's Green" (DG), at the west end of Front Street in Beaufort. The collection locations in Florida, about 10 km apart, were Fort George Inlet (FGI), and Round Marsh (RM), both along the shore of the St. Johns River (estuary), Jacksonville. The FGI collection site was near the mouth of the river, in Huguenot Memorial Park, near the south side of the bridge (FL Route A1A) linking Fort George and Little Talbot Islands. The RM site was near a salt marsh in the backwaters of the St. Johns River, near an observation platform in the Fort Caroline portion of the Timucuan Preserve.

Substrata at the collection sites consisted of a mixture of sand and mud in different proportions (of sand/silt/clay), and always included, to various degrees, *Crassostrea virginica* (Gmelin) (oyster) shells and some live oysters. At DUML, shell clumps were sitting on a muddier substrate, sloping toward the water, than the other locations. The FGI site was very flat, with a sandier substrate supporting rocks (mainly concrete slabs and other rubble from reconstruction of the bridge) encrusted with oysters. At RM, the oyster shells were comparatively more plentiful but generally looser (i.e., not in clumps). The salinity at RM was lower (25 ppt) than at the other sites (35 ppt).

Methods

Collection and maintenance

Shrimp were collected manually during low tide, at DUML, FGI, and RM, during two different seasons: July 1–5, 2004 (hereinafter designated "summer"), and November 15–17 and December 4–5, 2004 ("fall"); on March 14, 2005, a brief collection was made at DG. Animals were mostly found either by turning over shell clumps or rocks located around the mean low-water mark or pushing a hand-held dip net through loose shells. On site, each collected shrimp was placed into a plastic bag half-filled with seawater from the site, along with 1–2 oyster shells to provide a shelter for the shrimp. Multiple animals found under the same rock were usually two in number and of opposite sex, presumed to be a mating pair, thus kept in the same bag.

The bags and their contents were transported by plane to the laboratory at George Washington University, where they were catalogued (organized based on location, each animal assigned a number) and placed in 20-cm-diameter glass bowls individually (except for summer-collected paired animals; these were placed together in plastic 20-cm x 12-cm aquaria). Collection water was replaced with a solution of artificial sea salt mix made to the salinity of the water in which the shrimp were collected. Oyster shells

that were free of macroscopic encrusting organisms (to reduce the risk of bacterial infiltration) were positioned in each tank. Each animal was sized (carapace length measured) and characterized in terms of sex, "handedness" (side bearing the major chela), and any unusual features.

Temperature, salinity, and pH were kept within normal ranges while the animals were maintained in the laboratory. Water was aerated with pumps and air stones, supplemented with potassium iodide to facilitate molting, and changed approximately every 3 days. Laboratory lights were turned on and off in concert with the natural photoperiod to the extent possible. Shrimp were fed TetraMin tropical fish flakes or shrimp pellets every few days, generally preceding water changes to minimize fouling of the tank water. Shrimp that died were fixed using 4% formalin and preserved in 70% ethyl alcohol for future reference and morphological study. Voucher specimens were deposited into the US National Museum of Natural History (USNM), Washington, DC, as follows: *A. angulosus*—two specimens (mating pair), USNM 1098194, Fort George Inlet of St. Johns River, Jacksonville, FL, coll. R.E. and M.K. Knowlton, 3 July 2004 (died in lab 12 July 2004); *A. estuariensis*—one specimen, USNM 1098195, Round Marsh of St. Johns River (Timucuan Preserve: Fort Caroline), Jacksonville, FL, coll. R.E. Knowlton, 2 July 2004 (died in lab 7 September 2004); *A. heterochaelis*—two specimens (mating pair), USNM 1098193, "Research Cove" near Duke University Marine Laboratory, Beaufort, NC, coll. H. Spence, 1 July 2004 (died in lab 20 July 2004).

Morphology

Morphological features of adult shrimp and developmental stages were determined through observation and photography of our collected living material, supplemented by examination of all available preserved specimens of the three species stored in the USNM.

Digital photographs, made using an MTI 3CCD camera and FlashPoint FPG 3.10 program through a Leica MZ12 microscope and analyzed with program ImageJ 1.20s, were taken as quickly as possible after collection to document natural coloration. We found that using a bowl of about the same diameter as the animal, combined with drawing off some of the sea water in the bowl to about the animal's height, was reasonably successful in immobilizing a shrimp long enough to photograph it without desiccating it. Ventral views could be obtained by inverting the animal contained within a covered Petri dish. Turning off or dimming the lights between taking photographs also helped the shrimp stay still, as did the use of backlighting.

Development

Reproductive activity, such as the presence of eggs on pleopods (swimmerets) of females, or ripe ovaries, was noted at time of collection. Embryos of *A. heterochaelis* and *A. angulosus* in various stages of development were examined and photographed (as above), referenced with preserved specimens in USNM collections and Knowlton's (1973) description of *A. heterochaelis* development. Egg characteristics, such as

approximate number, size, shape, color, stage of embryonic development (indicated by percentage of egg area occupied by yolk and appearance of compound eyes), were recorded upon arrival at the laboratory and tracked subsequently until hatching or loss. Early larval characteristics were noted for a single live specimen.

Results

Collections

Overall, 77 individuals were collected. The summer collection yielded a total of 51 shrimps: 24 from Florida (19 *A. angulosus* from FGI, 5 *A. estuariensis* from RM) and 27 *A. heterochaelis* from North Carolina (DUML). Included among them were 12 ovigerous females: 5 *A. angulosus* and 7 *A. heterochaelis*. The fall collection yielded a total of 22 specimens: 15 from Florida (11 *A. angulosus* from FGI, 4 *A. estuariensis* from RM) and 7 *A. heterochaelis* from North Carolina (DUML); of these, 5 *A. angulosus* females bore eggs. In March, 4 shrimps were found from DG, the only site where both species were collected: 3 individuals of *A. angulosus* (including a mating pair) and one large female *A. heterochaelis*. The latter was found closer to the water and deeper into the mud than the former, which were, as in Florida (FGI), under more shallowly situated rocks.

Morphology

All alpheids collected from DUML clearly matched species descriptions for *A. heterochaelis* (e.g., McClure 1995, Williams 1984), while those from FGI and RM generally matched the species descriptions for *A. angulosus* and *A. estuariensis*, respectively (e.g., McClure 1995, 2002). Individuals of *A. heterochaelis* (in summer collection) were generally larger (mean carapace length ± standard deviation = 10.1 ± 2.5 mm; number of individuals = 24) than *A. angulosus* (8.2 ± 1.1 mm, n = 19), although there was some overlap; those of *A. estuariensis* were consistently smaller (7.1 ± 0.5 mm, n = 4). The difference in means between *A. heterochaelis* and each of the other two species was significant (vs. *A. angulosus*: $t = 3.06$, $df = 41$, $P < .01$; vs. *A. estuariensis*: $t = 2.33$, $df = 26$, $P < .05$), but between *A. angulosus* and *A. estuariensis*, it was not ($t = 1.85$, $df = 21$, $P > .05$).

At DG, where *A. heterochaelis* or *A. angulosus* were sympatric, an overall color difference between these species was discernable. While some *A. angulosus* individuals (collected at FG) and *A. estuariensis* (from RM) were seen to have diffuse blue pigment on their uropods (Fig. 2a), bright blue spots, with orange on anterior margins, were found to be a major distinguishing feature of *A. heterochaelis* (from DUML) (Fig. 2b). Also, there is a flattened triangular area of the carapace at the base of the *A. angulosus* rostrum (Fig. 3a), but not in the other two species (Fig. 3b). The minor chela of *A. angulosus* is visibly broader than that of *A. heterochaelis* (Figs. 4a, b), and it does not bear the row of long setae ("balaeniceps-type" claw) characteristic of *A. heterochaelis* males (Fig. 1; also noted and illustrated in McClure 1995, McClure and

Wicksten 1997). The long and slender minor chela of *A. estuariensis* (Christoffersen 1984, McClure 1995) is distinguishable (Fig. 4c). Another important feature of *A. estuariensis* is its diffusely banded color pattern (Christoffersen 1984); on the dorsal side of each abdominal segment, the anterior margin is lighter than the posterior one (Fig. 5).

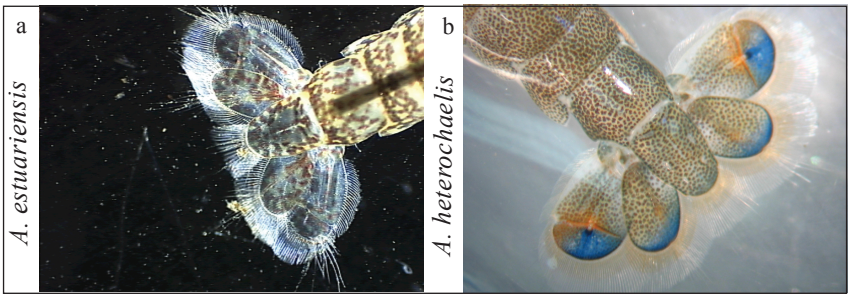

Figure 2. a. Tan to pale blue tail fan of *A. estuariensis* (also characteristic of *A. angulosus*). b. Tail fan of *A. heterochaelis*, with characteristic bright blue spots on uropods.

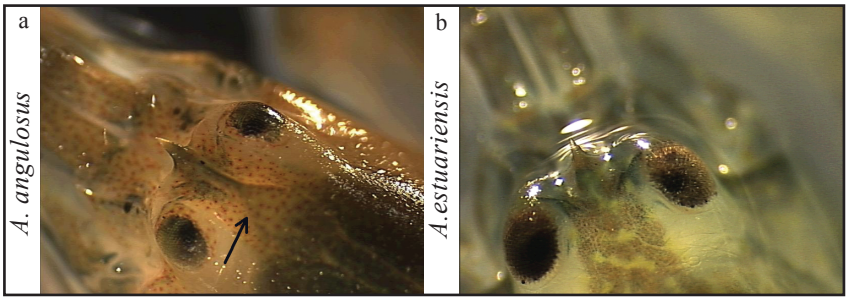

Figure 3. a. Rostrum of *A. angulosus*, exhibiting triangular base (indicated by arrow) and flanked by eyes. b. Rostrum of *A. estuariensis*, which lacks triangular base (as does the rostrum of *A. heterochaelis*).

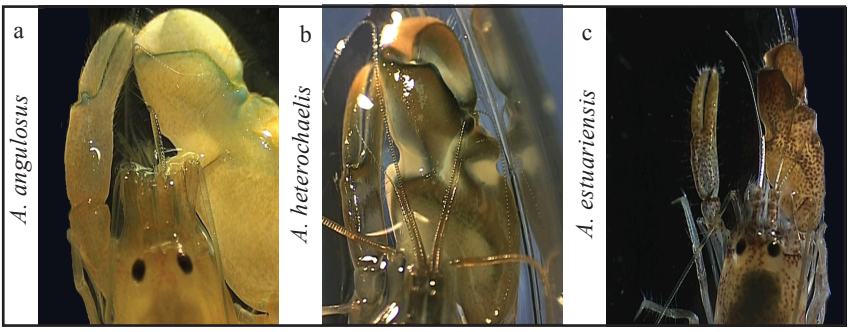

Figure 4. a. Anterior region of *A. angulosus* exhibiting relatively wide minor chela and paler coloration after being kept in the laboratory. b. Anterior region of female *A. heterochaelis*, showing thinner (vs. *A. angulosus*) minor chela and tan antennal flagella. c. Anterior region of *A. estuariensis*, exhibiting characteristic slender minor chela, tan antennae, and angular dactylus of major chela.

Figure 5. Dorsal view of *A. estuariensis* abdominal segments, showing characteristic banding pattern.

Figure 6. Dorsolateral view of *A. angulosus* head, showing blue antennal flagella (one indicated by arrow).

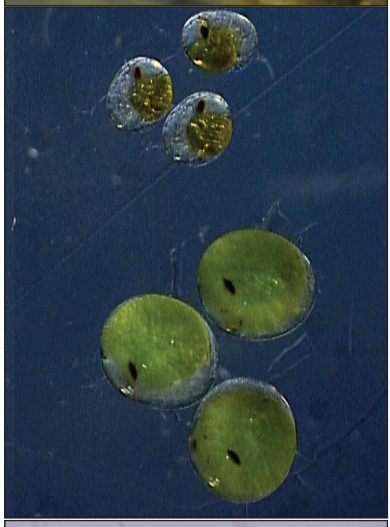

Figure 7. Eggs of *A. angulosus* (top) and *A. heterochaelis* (bottom) about halfway through embryonic development. Egg size: top, 0.71 x 0.60 mm; bottom, 1.12 x 1.03 mm.

Figure 8. Stage II zoea larva of *A. angulosus*. Total length = 2.56 mm.

The most significant and consistent new characteristics separating *A. angulosus* from the other two species are color of both pairs of antennal flagella and length of the 2nd pair: blue-green and short, respectively, in *A. angulosus* (Fig. 6); tan (red-brown) and long, respectively, in *A. heterochaelis* and *A. estuariensis* (Figs. 4b and 5). The proportion of antennal flagellum length to carapace length was found to differ significantly between *A. heterochaelis* and *A. angulosus* with means of 4.2 ± 0.7 and 3.2 ± 0.8, respectively ($t = 3.04$, $df = 18$, $P < .05$). *Alpheus estuariensis* (3.4 ± 0.9, n = 3) was not included in the length analysis due to low sample size.

In general, shrimps kept in the laboratory gradually lost the overall dark coloration present at collection, becoming pale tan to virtually translucent (Fig. 4a). This "blanching" phenomenon was markedly greater in *A. heterochaelis* and *A. angulosus* than in *A. estuariensis*. However, even after extended periods in the lab, the antennae of all *A. angulosus* individuals retained their blue-green color, and those of *A. heterochaelis* and *A. estuariensis* their tan color.

Development

In the fall collection of *A. angulosus*, the pleopods of females were observed to bear viable but numerically few eggs in various stages of embryonic development; *A. heterochaelis* females were not gravid in the fall. There was no obvious difference in egg number per female between the summer *A. angulosus* (FL) and *A. heterochaelis* (NC) populations. The number of eggs found on a given ovigerous female ranged from a few to over 200. Eggs of *A. heterochaelis* in the earlier stages were about twice as big as similarly developed eggs of *A. angulosus* (Fig. 7); this relationship persisted throughout later stages (e.g., *A. heterochaelis*, 1.53 x 1.21 mm, vs. *A. angulosus*, 0.75 x 0.60 mm). The eggs of both species contained green yolk, but there was one instance of brown-colored yolk in *A. angulosus*. Based on measurements of eggs attached to pleopods of *A. estuariensis* females preserved in the USNM collection, sizes at comparable stages are about 0.5 mm (early) and 0.9 x 0.7 mm (close to hatching).

More often than not, the ovigerous females kept in the lab did not retain eggs on their pleopods, but a single live larva was found to have hatched from one of the *A. angulosus* eggs (fall collection). Although the larva was photographed (Fig. 8) and examined upon discovery, the first instar was presumed to be missed since, in alpheids with extended larval development, it typically is only a matter of hours before the molt to the second instar occurs (Knowlton 1973). The larva swam around for a few days after hatching, but did not survive past "Stage II." Compared to descriptions and figures of *A. heterochaelis* larvae (Knowlton 1973), the two species at "Stage II" exhibited the following similarities: antennal scales with terminal segments, stalked compound eyes, three pairs of maxilliped exopods, visible rudiments of other thoracic appendages, telson with 7 + 7 plumose setae, and a median notch. Larval features of *A. angulosus* that were different include smaller size, the lack of pleopod rudiments on the abdomen, presence of a large red chromatophore at the base of the telson, less residual yolk, and possibly a more strongly notched telson.

Discussion

Habitats

Our collection data, albeit limited to four sites, are consistent with McClure and Wicksten's (1997) observation that, between *Alpheus angulosus* and *A. heterochaelis*, one or the other species was generally much more common at each of their sampling localities. In previous field work (R.E. Knowlton, unpubl. data) at the Beaufort sites, *A. angulosus* was rarely found at DUML (one individual, compared to 19 *A. heterochaelis*), but was more abundant at DG (10 animals, vs. 30 *A. heterochaelis*), confined mainly to a small area of predominantly loose oyster shells over a rather sandy substratum; in contrast, *A. heterochaelis* was almost always under larger shell clumps partially embedded in mud (at both sites).

Morphology

In our study, *A. angulosus* was found to be more difficult to distinguish visually from *A. heterochaelis* than from *A. estuariensis*. *Alpheus angulosus* is described as distantly related to *A. heterochaelis* and *A. estuariensis*, being more closely related to *A. armillatus*, which has a conspicuous banded color pattern (Mathews et al. 2002). However, since several species are currently confused with *A. armillatus*, and some of them are present in Florida and elsewhere along the southeastern US coast (Mathews 2006), the affinities and actual distribution range presently remain undetermined.

The main new morphological finding of our study is the difference in antennal flagellum color and length between *A. angulosus* and the other two species. While freezing has been used to preserve coloration for description (McClure 1995), examination of live animals, preferably recently collected ones, reveals important taxonomic characters that are not likely to be distorted. Especially among *Alpheus* spp., differences in coloration have been shown to be of systematic importance (Knowlton and Mills 1992).

Previous morphological descriptions generally matched our findings (summarized in Table 1), but further clarification is desirable for functional use in identification. Antenna length and color, plus chela morphology, are probably the easiest means of identification of these three species. Chela morphology, which exhibits a certain degree of sexual dimorphism (McClure and Wicksten 1997), is especially useful if shrimp are found in mating pairs; thus, males and females of the same species can be compared to each other.

Development

The *A. angulosus* larva that hatched exhibited the "zoea" larval form typical of most species of *Alpheus* (Knowlton 1973), as well as caridean shrimp in general. Based on observations of larvae captured in plankton and/or reared in the laboratory, alpheid species have typically been shown to exhibit an extended period (circa 2–3 weeks) of larval development involving at least 4, and probably more (about 9), instars (Knowlton 1970). In contrast, *A. heterochaelis* hatches as a larger (>l mm, regardless of

stage), more advanced larva that passes through only 3 instars in 4–5 days (Knowlton 1973). The smaller eggs and larva of *A. angulosus* (Table 1), however, are consistent with extended post-embryonic development, being the result of a shorter period of embryonic growth and morphogenesis; based on egg size, *A. estuariensis* also appears to demonstrate this pattern. The fundamental differences found between *A. heterochaelis* and *A. angulosus* with regard to egg size and pattern of larval development indicate strong differences in reproductive biology. Interspecies habitation of the same burrow has been observed for other species of snapping shrimp, and linked to facultative symbiosis with interspecific communication (Boltaña and Thiel 2001), but was not observed between males and females of different species in the present study.

Conclusions

Traditional taxonomic practices, such as careful observation of preserved adult specimens, are certainly of value in discerning some differences among species. But with regard to morphologically similar *Alpheus* spp., such as those described above, it becomes all the more important to consider additional characters (e.g., color) based on living animals in different ontogenetic phases, and to investigate ecological-behavioral features (e.g., habitat preferences), some of which may be found to be unique enough to be helpful in locating and identifying particular species in the field. The variety of features described here also are interrelated with each other (e.g., morphogenesis) and

Table 1. Key morphological features differentiating the principal southeastern US *Alpheus* spp., based on this study and Christoffersen (1984), Knowlton (1973), McClure (1995), McClure and Wicksten (1997), and Williams (1984). Unless otherwise indicated, characters refer to adults.

Character	*A. angulosus*	*A. estuariensis*	*A. heterochaelis*
Antennal flagella: color, length (of 2nd ant.)	Blue, short (Fig. 6)	Tan, long (Figs. 4c, 5)	Tan, long (Fig. 4b)
Base of rostrum	Widens into flattened triangular area on carapace (Fig. 3a)	Triangular area lacking (Fig. 3b)	Triangular area lacking
Major chela: distoventral merus spine	Present	Absent	Absent
Minor chela: propodus and dactylus	Short, broad (Fig. 4a)	Long, very slender (Fig. 4c)	Long, "balaeniceps" in male (Figs. 1, 4b)
Uropods: color	Tan to pale blue	Tan to pale blue (Fig. 2a)	Bright blue spots bordered with orange (Fig. 2b)
Egg size (regardless of embryonic stage)	Less than 1 mm (Fig. 7)	Less than 1 mm	More than 1 mm (Fig. 7)
Larva (1-day old): total length, pleopod development	2.5–2.6 mm, pleopods absent (Fig. 8)	(Unknown)	4.6–4.8 mm, pleopods biramous but rudimentary

the ecological roles of the species, and are important considerations for research involving complexes of superficially similar alpheid species.

Acknowledgments

We wish to thank William Kirby-Smith at the Duke University Marine Laboratory and Craig Morris and Daniel Tardona of the National Park Service at Fort Caroline for invaluable collection guidance, as well as Diana Lipscomb for guidance in using the microscope digital camera. Marilyn Schotte facilitated the museum work. Henry Merchant, Melissa Hughes, Nancy Knowlton, Lauren Mathews, Martin Thiel, and Arthur Anker provided indispensable input. We would also like to thank SuMin Hong, Matthew Lowery, and Tara Scully for their help in maintaining the animals in the laboratory, and Tony Chan for providing some useful observations in an unpublished preliminary study. We dedicate this paper to the late Paul Spiegler, who encouraged and inspired us with his love of natural history. Financial support for this project was received from the Enosinian Scholars Program at George Washington University.

Literature Cited

Boltaña, S., and M. Thiel. 2001. Associations between two species of snapping shrimp, *Alpheus inca* and *Alpheopsis chilensis* (Decapoda: Caridea: Alpheidae). Journal of the Marine Biological Association of the United Kingdom 81: 633–638.

Christoffersen, M.L. 1984. The western Atlantic snapping shrimps related to *Alpheus heterochaelis* Say (Crustacea, Caridea), with the description of a new species. Papéis Avulsos de Zoologia, São Paulo 35:189–208.

Corfield, J.L., and C.G. Alexander. 1995. The distribution of two species of alpheid shrimp, *Alpheus edwardsii* and *A. lobidens*, on a tropical beach. Journal of the Marine Biological Association of the United Kingdom 75:675–687.

Duffy, J.E., C.L. Morrison, and K.S. MacDonald. 2002. Colony defense and behavioral differentation in the eusocial shrimp *Synalpheus regalis*. Behavioral Ecology and Sociobiology 51:488–495.

Hughes, M. 1996. The function of concurrent signals: Visual and chemical communication in snapping shrimp. Animal Behavior 52:247–257.

Knowlton, N. 1986. Cryptic and sibling species among the decapod Crustacea. Journal of Crustacean Biology 6:356–363.

Knowlton, N., and B.D. Keller. 1982. Symmetric fights as a measure of escalation potential in a symbiotic, territorial snapping shrimp. Behavioral Ecology and Sociobiology 10:289–292.

Knowlton, N., and D.K. Mills. 1992. The systematic importance of color and color pattern: Evidences for complexes of sibling species of snapping shrimp (Caridea: Alpheidae: *Alpheus*) from the Caribbean and Pacific coasts of Panama. Proceedings of the San Diego Society of Natural History 18:1–5.

Knowlton, R.E. 1970. Effects of environmental factors on the larval development of *Alpheus heterochaelis* Say and *Palaemonetes vulgaris* (Say) (Crustacea Decapoda Caridea), with ecological notes on larval and adult Alpheidae and Palaemonidae. Ph.D. Dissertation, University of North Carolina, Chapel Hill, NC. 544 pp.

Knowlton, R.E. 1973. Larval development of the snapping shrimp *Alpheus heterochaelis* Say, reared in the laboratory. Journal of Natural History 7:273–306.

Knowlton, R.E., and J.M. Moulton. 1963. Sound production in the snapping shrimps *Alpheus (Crangon)* and *Synalpheus*. Biological Bulletin 125:311–331.

Mathews, L.M. 2006. Cryptic biodiversity and phylogeographical patterns in a snapping shrimp species complex. Molecular Ecology 15:4049–4063.

Mathews, L.M., C.D. Schubart, J.E. Neigel, and D.L. Felder. 2002. Genetic, ecological, and behavioral divergence between two sibling shrimp species (Crustacea: Decapoda: *Alpheus*). Molecular Ecology 11:1427–1437.

McClure, M.R. 1995. *Alpheus angulatus*, a new species of snapping shrimp from the Gulf of Mexico and northwestern Atlantic, with a redescription of *A. heterochaelis* Say, 1818 (Decapoda: Caridea: Alpheidae). Proceedings of the Biological Society of Washington 108:84–97.

McClure, M.R. 2002. Revised nomenclature of *Alpheus angulatus* McClure, 1995 (Decapoda: Caridea: Alpheidae). Proceedings of the Biological Society of Washington 115:368–370.

McClure, M.R., and M.K. Wicksten. 1997. Morphological variation of species of the edwardsii group of *Alpheus* in the northern Gulf of Mexico and northwestern Atlantic (Decapoda: Caridea: Alpheidae). Journal of Crustacean Biology 17: 480–487.

Versluis, M., B. Schmitz, A. von der Heydt, and D. Lohse. 2000. How snapping shrimp snap: Through cavitating bubbles. Science 289:2114–2117.

Williams, A.B. 1984. Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, DC. 550 pp.