

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).

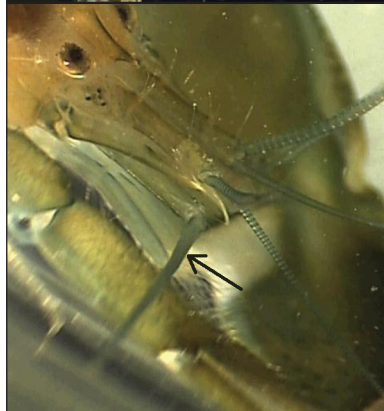


Figure 7. Eggs of *A. angulosus* (top) and *A. heterochaelis* (bottom) about halfway through embryonic development. Egg size: top, 0.71 x 0.60 mm; bottom, 1.12 x 1.03 mm.

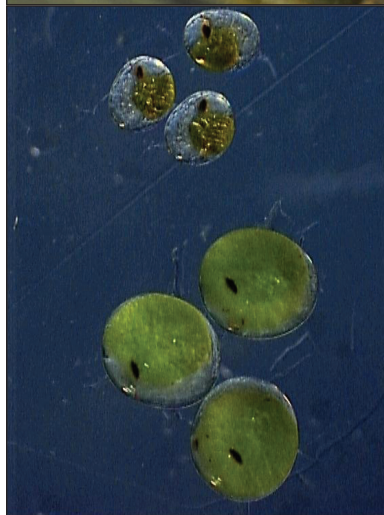


Figure 8. Stage II zoea larva of *A. angulosus*. Total length = 2.56 mm.



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*, 1.53×1.21 mm, vs. *A. angulosus*, 0.75×0.60 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 0.9×0.7 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 DURL (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 (>1 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	<i>A. angulosus</i>	<i>A. estuariensis</i>	<i>A. heterochaelis</i>
Antennal flagella: color, length (of 2 nd 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.

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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 differentiation 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.