JOURNAL OF CRUSTACEAN BIOLOGY, 16(3): 564–573, 1996

SYNALPHEUS REGALIS, NEW SPECIES, A SPONGE-DWELLING SHRIMP FROM THE BELIZE BARRIER REEF, WITH COMMENTS ON HOST SPECIFICITY IN *SYNALPHEUS*

J. Emmett Duffy

ABSTRACT

Synalpheus regalis (Decapoda: Alpheidae) is described from the demosponges *Xestospongia* cf. *subtriangularis* (Petrosiidae) and *Hyattella intestinalis* (Spongiidae) on the Belize Barrier Reef at Carrie Bow Cay. The new species is a member of Coutière's gambarelloides species-group, and more specifically is one of a complex of morphologically very similar species, including *S. rathbunae, S. filidigitus,* and at least one other undescribed species. Like most members of the gambarelloides group, *S. regalis* lives exclusively within the internal canals of living sponges, and at the type locality is found in only 2 of the 21 sponge species that harbor commensal shrimps. Such host specificity is typical of Caribbean species of *Synalpheus*. The pattern of shrimp distribution among sponge species, and among individual sponges, suggests that suitable habitat at this site is saturated and that competition for living space is intense. The resulting restriction of species of *Synalpheus* to those hosts in which they are competitively superior may thus be an important determinant of their characteristic host specificity.

Snapping shrimps in the genus *Synalpheus* form a prominent component of the diverse cryptofauna that abounds within the interstices of tropical reefs. With over 100 species worldwide (Chace, 1989), and 30 presently recognized from the Caribbean (Dardeau, 1984), *Synalpheus* is also among the most diverse genera of crustaceans. Many of its species regularly associate with sessile invertebrates, and the members of Coutière's (1909) gambarelloides (formerly laevimanus) species-group, in particular, are mostly obligate associates of living sponges (Dardeau, 1984; Duffy, 1992). A recent study (Duffy, in press a) showed that morphologically similar populations inhabiting different sponge hosts represent genetically distinct biological species, thus raising the possibility that these sponge-dwelling shrimp may be both considerably more diverse, and more ecologically specialized, than presently recognized. Here I describe one of these host-specific taxa as the new species *Synalpheus regalis*. The nearly complete lack of cohabitation between *S. regalis* and other shrimp species within individual sponges, and the total absence of unoccupied sponges at the type locality, suggest that competition for habitable space is intense, and that competitive exclusion may contribute to the narrow host range typical of sponge-dwelling species of *Synalpheus*.

MATERIALS AND METHODS

Live shrimp were obtained from the internal canals of sponges, collected using SCUBA. Sponges were taken from the outer reef ridge at Carrie Bow Cay, Belize (16°48′N, 88°05′W). Over 30 colonies of shrimp (i.e., samples from individual sponges) were removed from sponges, preserved in ~10% Formalin in sea water, and later transferred to 70% ethanol for storage. Carapace length (from base of rostrum to posteromedial margin of carapace) was measured using an ocular micrometer. For other measured structures, where a single value is reported, it is based on the male paratype (USNM 280093); where a range of values is reported, they are from the series of 35 specimens previously measured (i.e., *S.* "*rathbunae* C"; Duffy, in press a). Shrimps were dissected in 70% ethanol, and drawings were made with the aid of a camera lucida. Appendages were mounted temporarily in glycerin: 70% ethanol (1:1) on slides for examination and drawing under a compound microscope.

DESCRIPTION

Family Alpheidae Rafinesque, 1815
Genus *Synalpheus* Bate, 1888
Synalpheus regalis, new species
Figs. 1–5

Synalpheus "*rathbunae* C"—Duffy, in press a.

Material Examined.—All specimens were taken by divers from the demosponges *Xestospongia* cf. *subtriangularis* (Duchassaing) and *Hyattella intestinalis* (Lamarck) growing among the branches of the coral *Madracis mirabilis* (Duchaissaing and Michelotti) at depths of 15–20 m on the outer reef ridge at Carrie Bow Cay, Belize, between March 1993 and July 1995.

Types.—Holotype (USNM 280092): adult ♂, 2.39-mm carapace length. Paratypes: adult ♂ (USNM 280093, figured), 2.36-mm carapace length; ovigerous ♀

(USNM 280094, figured, in part), 3.40-mm carapace length, and 87 ♂♂ and juveniles (USNM 280095), all from a single specimen of the demosponge *Xestospongia* cf. *subtriangularis,* from 15-m depth, outer reef ridge at Carrie Bow Cay, Belize, 16°48′N, 88°05′W, 28 March 1993. The type series is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Description.—Small, smooth, compact alpheid, subcylindrical in body form. Rostrum (Figs. 1a, 2a) slender, approximately equal in length to ocular hoods, falling well short of distal margin of first segment of antennular peduncle, slightly upturned distally, ventral surface weakly convex but lacking orbitorostral process. Ocular hoods bluntly triangular, well separated from rostrum.

Pleuron of first abdominal somite of male (Fig. 1b) with acute, ventrally directed tooth at posteroventral corner; second pleuron with slightly concave ventral margin terminating in weakly to moderately protruding angle at posteroventral corner; third through fifth pleura each with ventral margin produced into blunt to obscure point; sixth with acute point between posteroventral angle and posterolateral angle. All pleura of female (Fig. 2b) with ventral margins broadly rounded. Telson (Fig. 1c) broadly triangular; anterior width about 3 times posterior width; lateral margins slightly concave in posterior third; dorsal surface bearing 2 pairs of stout spines, 1 pair situated slightly anterior, other posterior, to mid-length of segment; posterior margin armed with 2 pairs of spines, mesial pair averaging about 1.5 times longer than lateral pair; posterior margin between mesial spines bearing 2 pairs of dorsally directed simple setae and 2 posteriorly directed plumose setae.

Stylocerite (Figs. 1a, 2a) of antennular peduncle acutely triangular, overreaching rostrum and extending from 0.75 of length to nearly distal margin of first segment of antennular peduncle. Segments of antennular peduncle stout, first (visible portion) and second subequal in length and slightly longer than third.

Antennal scale (scaphocerite, Figs. 1a, 2a) slender, reaching to between proximal and distal margin of third segment of antennular peduncle, blade completely lacking. Basal antennal segment (basicerite) armed dorsally with stout spine, extending at least one-third length of lateral spine; lateral spine stout, extending to between proximal and distal margins of second segment of antennular peduncle, 0.5–0.75 of length of scaphocerite. Distal segment of peduncle (carpocerite) about 5 times as long as broad, slightly overreaching antennular peduncle.

Mouthparts as figured. Mandible (Fig. 3a) with 6 teeth on incisor process, molar process larger than incisor, palp 2-segmented. Palp of first maxilliped (Fig. 3d) consisting of 2 segments. Third maxilliped (Fig. 3f) overreaching antennal peduncle by about half length of distal segment, terminating in circlet of 7–9 spines, exopod reaching to or slightly beyond distal margin of antepenultimate segment.

Major first pereiopod (Figs. 4a, b, 2c, d) overreaching antennal peduncle by all but most proximal part of chela; chela subcylindrical, somewhat inflated proximally, 2.5–2.7 times as long as broad, 1–1.4 times carapace length in males, about 0.8 of carapace length in females; palm terminating dorsodistally in prominent, anteriorly directed, rounded tubercle bearing small secondary spine, often reduced to obscure bump, on its distoventral face; fingers about three-eighths as long as palm, dactyl overreaching fixed finger; carpus short and broad; merus more than half as long as palm, extensor margin lacking strongly produced distal tooth. Minor first pereiopod (Fig. 4c) overreaching antennal peduncle by most or all of length of chela; chela about 2.5 times as long as broad, palm cylindrical to slightly swollen centrally, fingers simple, their opposable margins developed as thin, obliquely curved blades; extensor surface of dactyl bearing numerous transverse rows of curved setae forming dense setal brush; carpus about half as long as chela; merus more than 3 times as long as wide.

Second pereiopod (Fig. 4d) overreaching antennal peduncle by length of chela, fingers more than 1.5 times as long as palm, slender and tapering to weakly hooked tips, fixed finger with slight constriction proximal to tip (Fig. 4e), both fingers bearing dense groups of setae. Carpus roughly 1.5 times as long as chela, composed of 4 articles with relative lengths about 4:1:1:2, proximal segment longest. Merus approxi-

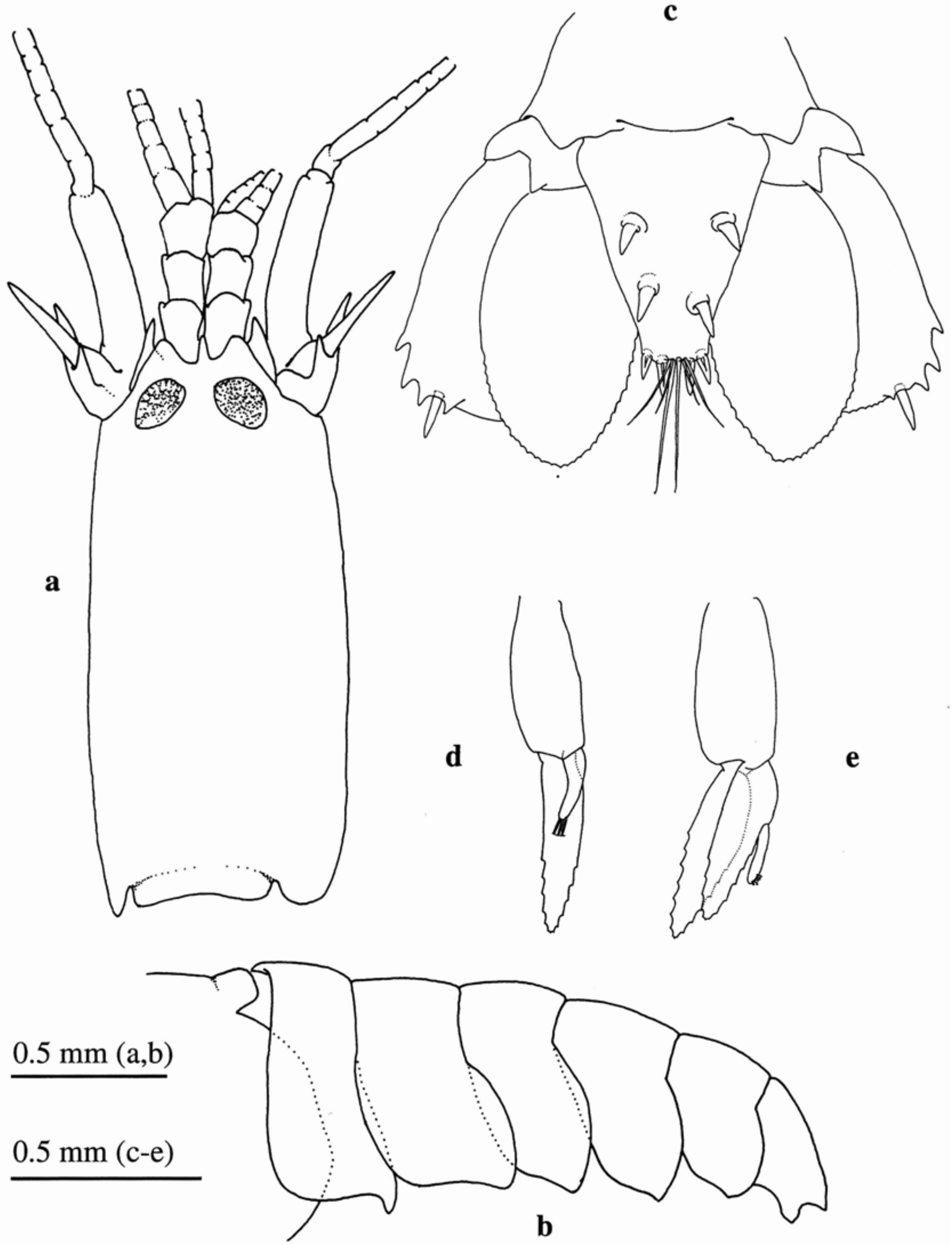

Fig. 1. *Synalpheus regalis,* new species, paratype male, carapace length 2.4 mm. a, anterior region in dorsal view; b, abdomen in lateral view; c, telson and uropods in dorsal view; d, left first pleopod; e, left second pleopod.

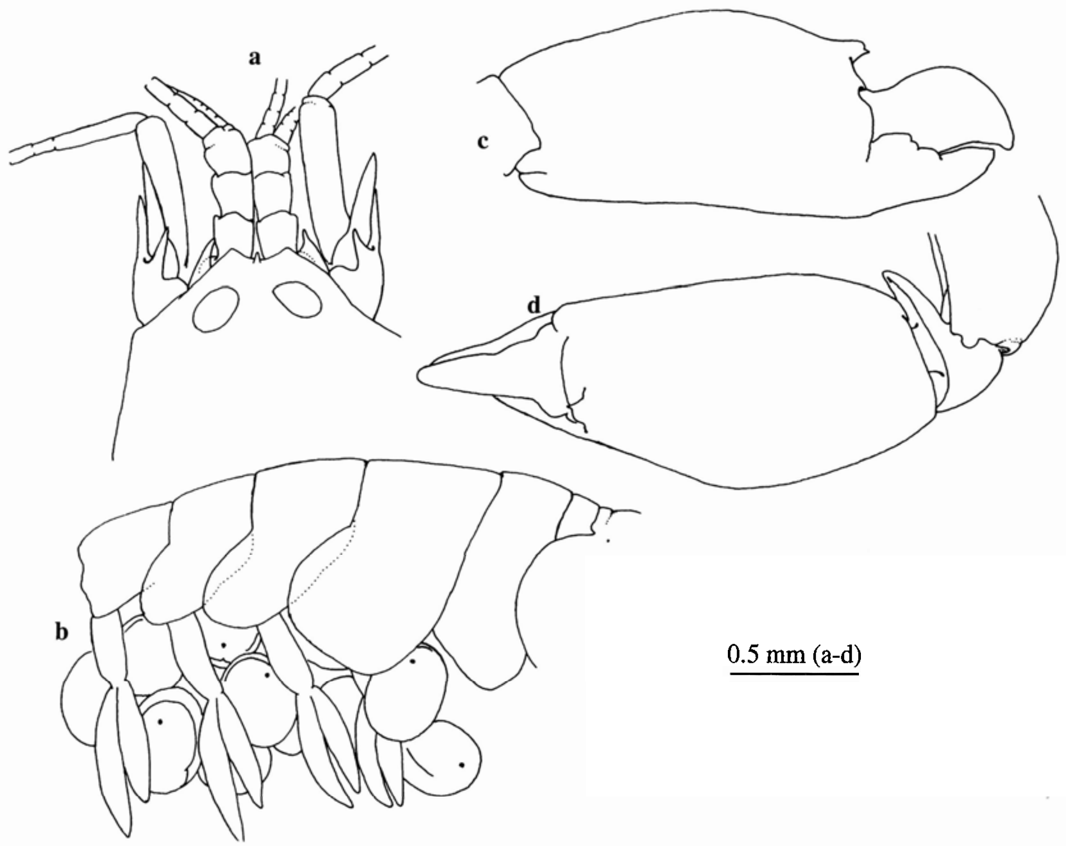

Fig. 2. *Synalpheus regalis,* new species, paratype female, carapace length 3.4 mm. a, anterior region in dorsal view; b, abdomen in lateral view; c, chela of major first pereiopod in lateral (medial) view; d, same, dorsal (extensor) view.

mately equal in length to carpus and about 1.5 times as long as ischium.

Third to fifth pereiopods (Fig. 5) similar in length and structure, relatively stout, biunguiculate; dactyl with tooth on flexor margin projecting at roughly right angle to axis of segment, slightly shorter and wider at base than terminal tooth. Third pereiopod (Fig. 5a, d) reaching approximately to distal margin of antennal peduncle; propodus more than 4 times as long as wide, flexor margin armed with 5 or 6 movable spines spaced evenly along its length as well as distal pair of movable spines, both flexor and extensor margins bearing several long, simple setae; carpus about 0.6 as long as propodus, extensor margin bearing well-developed distal lobe, flexor margin with movable spine at distal end; merus unarmed, about 1.5 times as long as propodus; coxa with tubercle bearing short, stout spine near distal end of flexor margin. Fourth pereiopod (Fig. 5b, e) similar to third but slightly shorter, extending to around midpoint of carpocerite. Fifth pereiopod (Fig. 5c, f) reaching approximately to anterolateral margin of carapace at antennal sinus; propodus somewhat less than 4 times as long as wide, flexor margin armed with pair of movable spines at distal margin, 3 movable spines along length of segment, and 4 transverse rows of stout serrulate setae in distal half of segment; extensor margin with several long simple setae; carpus unarmed, about three-fourths as long as propodus; coxa lacking spine on distal part of flexor margin.

Male first pleopod (Fig. 1d) with small endopod, about 0.4 of exopod length, bearing 3 simple setae distally. Male second pleopod (Fig. 1e) with endopod subequal in size to exopod; appendix masculina lacking; appendix interna arising at about 0.36 of endopod length, about 0.36 as long as

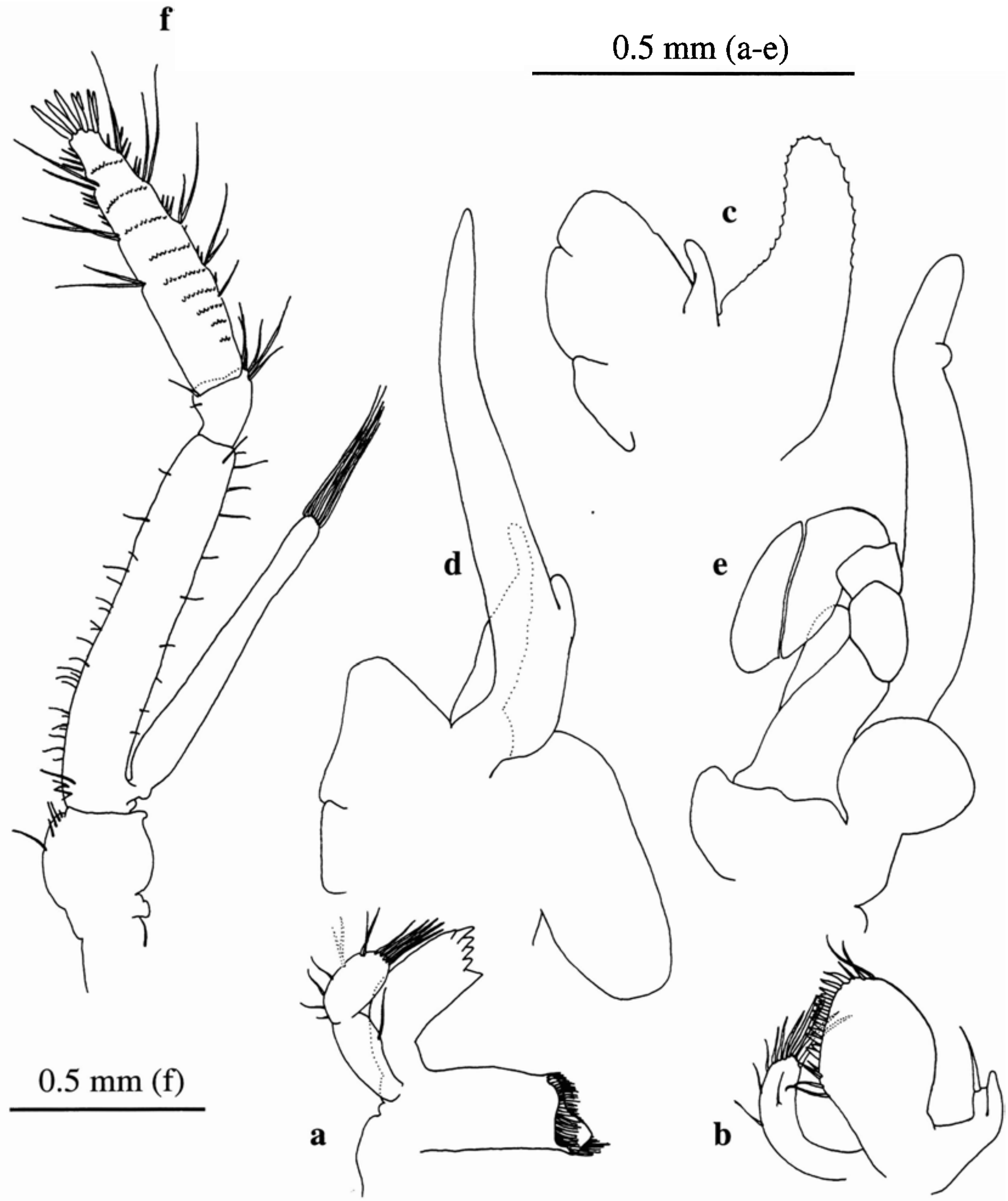

Fig. 3. *Synalpheus regalis,* new species, paratype male. a, left mandible; b, left first maxilla; c, left second maxilla; d, left first maxilliped; e, left second maxilliped; f, left third maxilliped.

endopod, with about 5 short curled setae (concinnuli).

Uropod lateral branch (Fig. 1c) with 2–4 (commonly 3) fixed teeth along margin proximal to movable spine, and single tooth distal to movable spine; lacking transverse articulation.

Eggs (Fig. 2b) rather large, 0.81–0.96 mm in length (mean = 0.87, N = 9).

Variation.—Species of *Synalpheus* are notorious for their morphological variability (Coutière, 1909; Chace, 1972; Banner and Banner, 1975; Christofferson, 1979; Dardeau, 1984) and *S. regalis* is no exception. For nearly every structure measured, a few individuals fell outside the range of values reported here. In the series of 35 specimens (5 or 6 from each of 6 sponges) measured

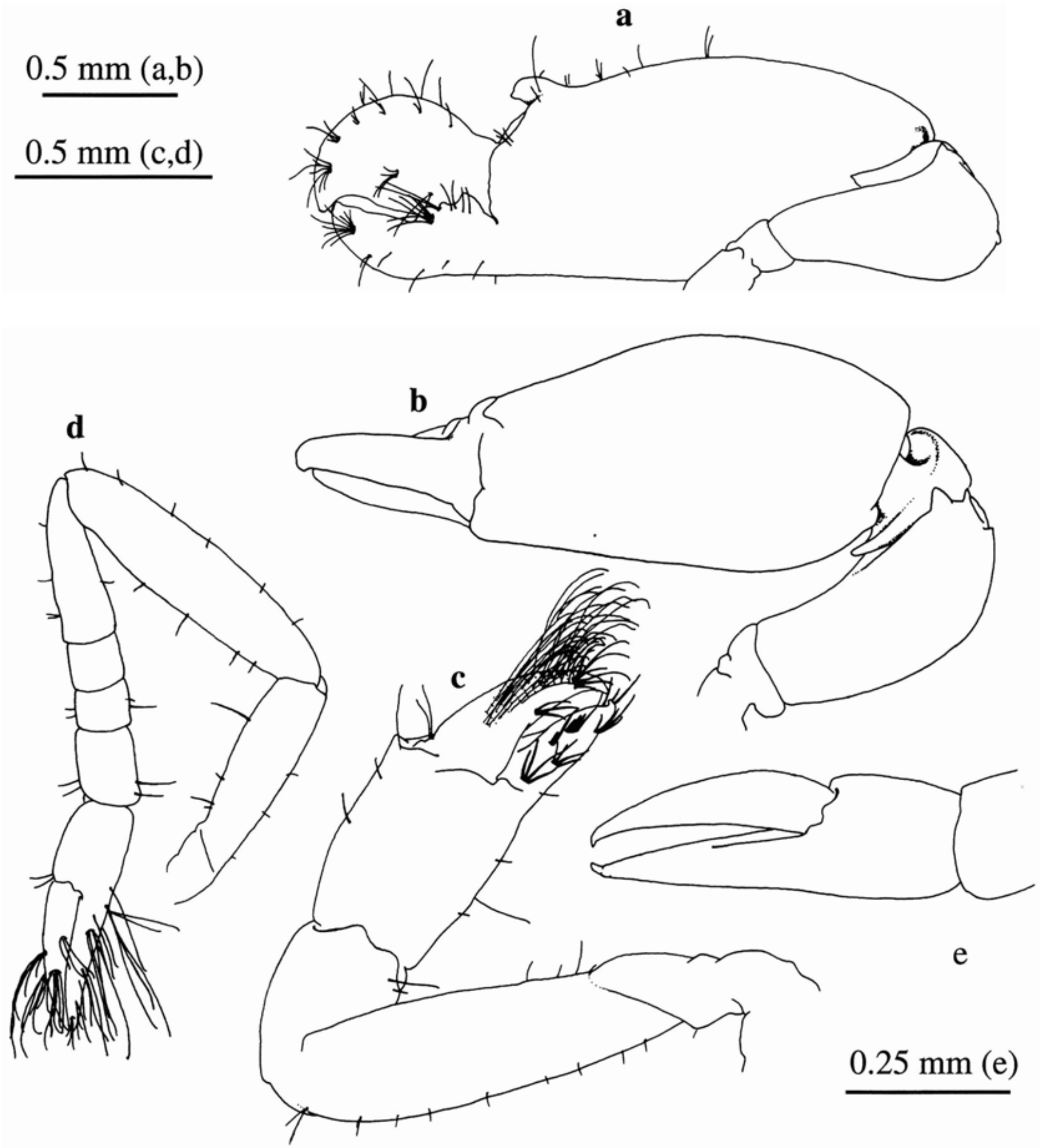

Fig. 4. *Synalpheus regalis,* new species, paratype male. a, major first pereiopod in lateral (medial) view; b, same, dorsal (extensor) view; c, minor first pereiopod; d, left second pereiopod; e, same, denuded chela.

(see also Duffy, in press a), for example, the ratio of carpus/chela length on the minor first pereiopod ranged from 0.41–0.54, with a mean of 0.48; the length of the merus of the minor first pereiopod divided by its width ranged from 2.76–3.95, with a mean of 3.32; the mean number of fixed teeth on the outer ramus of the uropods ranged from 2–4 with a mean of 3.0. Some of this variation was partitioned among local "colonies" inhabiting individual sponges (Duffy, in press a), but there was also considerable variation among individuals inhabiting the same sponge (as reported by Dardeau, 1984, for species of *Synalpheus* generally).

Color in Life.—Overall color of body faint translucent orange; sparse red chromatophores concentrated in facial region of carapace (between and lateral to eyes), and surrounding gut through abdomen; distal palm and fingers of major chela bright or-

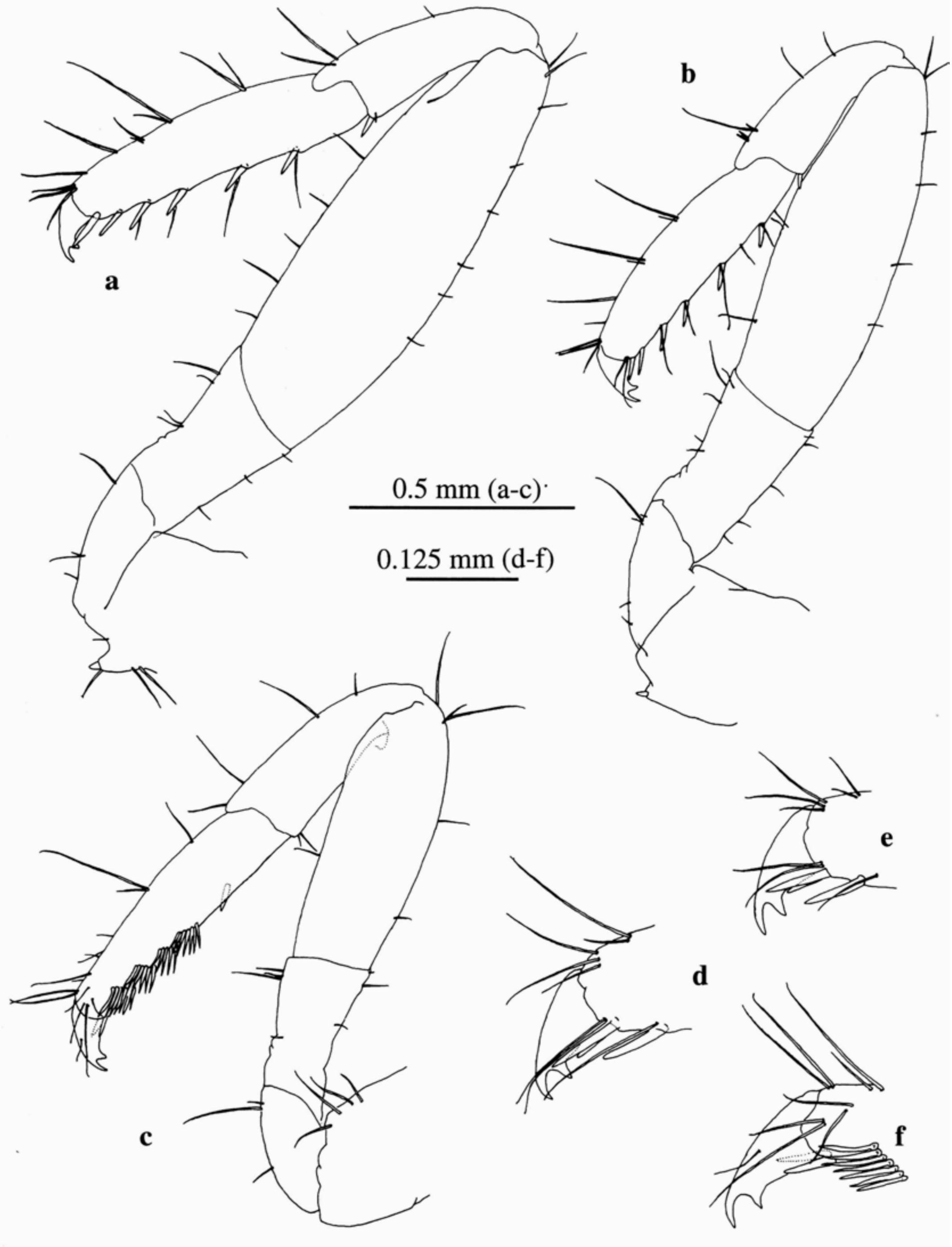

Fig. 5. *Synalpheus regalis,* new species, paratype male. a, left third pereiopod; b, left fourth pereiopod; c, left fifth pereiopod; d, left third pereiopod, dactyl; e, left fourth pereiopod, dactyl; f, left fifth pereiopod, dactyl.

ange to brown-orange due to concentration of pigment in thickened cuticle; ovaries and eggs pale green.

Size (carapace length in mm).—Ovigerous females 2.6–3.7; males and juveniles to 2.8 (males and juveniles are not clearly distinguished by any external morphological criteria).

Table 1. Distribution of *Synalpheus regalis* among specimens of its two known host sponges in field collections from Carrie Bow Cay, Belize.

	Xestospongia cf. *subtriangularis*	*Hyattella intestinalis*
Number of sponges sampled	34	30
% occupied exclusively by *S. regalis*	82	17
% occupied exclusively by other species of shrimps[1]	9	77
% occupied by both *S. regalis* and other species of shrimps[1]	9	7
% unoccupied	0	0

[1] Includes other species of *Synalpheus*, and species of *Periclimenaeus*, which were the only other shrimps found in these samples.

Habitat and Hosts.—Like most other gambarelloides species of *Synalpheus, S. regalis* lives exclusively in association with sponges. The type series was collected from within the internal canals of the demosponge *Xestospongia* cf. *subtriangularis* (Haplosclerida: Petrosiidae) growing at a depth of 15 m on the outer reef ridge at Carrie Bow Cay, Belize. *Synalpheus regalis* is common in this sponge at this locality, and also occurs less frequently in the demosponge *Hyattella intestinalis* (Keratosa: Spongiidae) at the same site (Table 1, see also Duffy, in press a). On the outer ridge at Carrie Bow Cay (Rützler and Macintyre, 1982), both of these sponges are found most commonly growing among the tightly packed, pencil-thin branches of the stony coral *Madracis mirabilis,* which is now among the most abundant corals there. At present *S. regalis* is known with certainty only from the type locality.

Etymology.—The species name comes from the Latin *regalis,* meaning royal, a reference to the structure of the colonies, in which only a single female (the "queen"), and possibly only a single male, breed (Duffy, in press b).

DISCUSSION

Synalpheus regalis is a member of Coutière's (1909) gambarelloides (formerly "laevimanus") group, characterized by a dense brush of setae on the dactyl of the minor first chela. More specifically, *S. regalis* is one of a group of morphologically very similar species, including *S. rathbunae* Coutière, 1909, *S. filidigitus* Armstrong, 1949, and at least one other undescribed species (*S.* "*rathbunae* A", Duffy, in press a), collectively characterized by a dorsally spinous first antennal segment (basicerite), 4-segmented carpus of the second pereiopod, and minor first chela with simple fingers. *Synalpheus regalis* may be distinguished from *S. rathbunae* by the more acutely produced abdominal pleura, the lack of secondary armature on the palmar tubercle of the major chela, and fewer fixed teeth (usually 1 or 2) on the outer branch of the uropod in the latter species. Compared with *S. regalis, S. filidigitus* has a relatively longer scaphocerite, which clearly exceeds the antennular peduncle; a broadly rounded second abdominal pleuron in males; acutely produced, filiform fingers on the second pair of chelipeds; and a small number (1 or 2) of fixed uropod teeth. Despite the rather subtle morphological characters distinguishing these species, allozyme analyses show that they are quite distinct genetically, and clearly different biological species (Duffy, in press a).

Like virtually all members of the gambarelloides group for which sufficient data exist (Dardeau, 1984; Duffy, 1992; Duffy, in press a), *S. regalis* is found exclusively in association with living sponges. Furthermore, like most of its congeners, *S. regalis* uses only a fraction of the host species available in its habitat. Of at least 21 species of sponges found to harbor shrimps in the vicinity of Carrie Bow Cay (J. E. Duffy, unpublished data), *S. regalis* was found only in *Xestospongia* cf. *subtriangularis* and *Hyattella intestinalis,* and was common only in the first of these (Table 1). The reasons for such specificity remain enigmatic. Although the host sponge obviously provides habitat for its shrimp guests, the nature of the relationship, and particularly the trophic interaction, between the two species is otherwise obscure. Examination of stomach contents from five species of *Synalpheus* in Caribbean Panama (J. E. Duffy, unpublished observations) revealed that the majority of the contents in all species comprised a mixture of unidentifiable flocculent material (probably detritus) and diatom fragments, although sponge spicules were present in stomachs of most species, and common in some. Rützler (1976) and Erdman and Blake (1987) also reported finding sponge skeletal elements in the stomachs of symbiotic species of *Synalpheus,* although their quantitative importance was not estimated. Although these observations are too limited to draw general conclusions, it appears that many sponge-dwelling species of *Synalpheus* probably feed partly on host tissue, and partly by scavenging material, drawn in by the feeding currents of the sponge from the walls of the aquiferous canals in which they live. It thus remains uncertain whether the shrimps are closer to the parasitic or commensal end of the spectrum, and thus whether host nutritional quality is likely to explain their characteristically narrow host preference.

On the other hand, patterns of shrimp distribution and behavior implicate a significant role for interspecific competition in determining host range. First, the two sponge species used by *S. regalis* as hosts were invariably occupied in the field, either by *S. regalis* or other shrimp species or both (Table 1), suggesting that available habitat is saturated at this site. Second, despite the saturation of available sponges, there were few instances of cohabitation (≤9% of sampled sponges) between *S. regalis* and other shrimp species (Table 1). The frequency of cohabitation tends to overestimate the degree of overlap between shrimp species. In those few cases where *S. regalis* co-occurred with other shrimps (in two specimens of *H. intestinalis* and three specimens of *X.* cf. *subtriangularis*), the other species was represented by ≤4 individual shrimps. In contrast, specimens of these sponges that lacked *S. regalis* frequently supported several dozen shrimps of the other species. Such mutually exclusive distributions of shrimps among individual sponges are reminiscent of the similar partitioning of host species by closely related shrimp species (Duffy, 1992, in press a), and suggest that competition among shrimp for living space within sponges may be severe. The likely importance of interspecific competition in producing these patterns is further supported by behavioral experiments showing that sponge-dwelling *Synalpheus* are extremely aggressive toward heterospecific individuals, sometimes even battling to the death (Duffy, 1996, in press b). Since body sizes of sympatric shrimp species tend to match the canal widths of their host sponges (Duffy, 1992), the characteristically narrow range of hosts used by sponge-dwelling *Synalpheus* may be dictated in part by the size of sponge canals that shrimps are able to defend effectively. A definitive resolution of this issue will have to wait, however, for experimental tests of the relationships between body size, competitive ability, and host range.

ACKNOWLEDGEMENTS

I am grateful to Brian Kensley, Nancy Knowlton, and John Olney for discussion and for generously sharing facilities; Klaus Rützler and Mike Carpenter for facilitating work at Carrie Bow Cay; Cheryl Morrison and Monica Lara for field assistance; Fenner A. Chace, Jr., Brian Kensley, and Jeff Shields for comments on a previous version of this manuscript; and finally to Fenner Chace, whose example is largely responsible for encouraging me to begin to do my duty to taxonomy. For support of this research I also thank the National Science Foundation (DEB Postdoctoral Fellowship) and the Smithsonian Institution's Carribean Coral Reef Ecosystem Program, from which this is contribution number 474.

LITERATURE CITED

Banner, D. M., and A. H. Banner. 1975. The alpheid shrimp of Australia. Part 2: the genus *Synalpheus.*—Records of the Australian Museum 29: 267–389.

Chace, F. A., Jr. 1972. The shrimps of the Smithsonian-Bredin Caribbean expeditions with a summary of West Indian shallow-water species (Crustacea: Decapoda: Natantia).—Smithsonian Contributions to Zoology 98: 1–179.

———. 1989. The caridean shrimps (Crustacea: Decapoda) of the *Albatross* Phillipine expedition, 1907–1910, Part 5: Family Alpheidae.—Smithsonian Contributions to Zoology 466: 1–99.

Christofferson, M. L. 1979. Campagne de la Calypso au large des côtes Atlantiques de l'Amérique du sud (1961–1962). I. Decapoda Crustacea: Alpheoidea.—Résultats Scientifiques des Campagnes de la Calypso 11: 297–377.

Coutière, H. 1909. The American species of snapping shrimps of the genus *Synalpheus.*—Proceedings of the United States National Museum 36: 1–93.

Dardeau, M. R. 1984. *Synalpheus* shrimps (Crustacea: Decapoda: Alpheidae). I. The Gambarelloides group, with a description of a new species.—Memoirs of the Hourglass Cruises 7, Part 2: 1–125.

Duffy, J. E. 1992. Host use patterns and demography in a guild of tropical sponge-dwelling shrimps.—Marine Ecology Progress Series 90: 127–138.

———. 1996. Resource-associated population subdivision in a symbiotic coral-reef shrimp.—Evolution 50: 360–373.

———. (In press a.) Species boundaries, specialization, and the radiation of sponge-dwelling alpheid shrimp.—Biological Journal of the Linnean Society.

———. (In press b.) Eusociality in a coral-reef shrimp.—Nature.

Erdman, R. B., and N. J. Blake. 1987. Population dynamics of the sponge-dwelling alpheid *Synalpheus longicarpus,* with observations on *S. brooksi* and *S. pectiniger,* in shallow-water assemblages of the eastern Gulf of Mexico.—Journal of Crustacean Biology 7: 328–337.

Rützler, K. 1976. Ecology of Tunisian commercial sponges.—Tethys 7: 249–264.

———, and I. G. Macintyre. 1982. The habitat distribution and community structure of the barrier reef complex at Carrie Bow Cay, Belize.—*In:* K. Rützler, and I. G. Macintyre, eds., The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize. I. Structure and communities. Pp. 9–45. Smithsonian Contributions to the Marine Sciences 12: 1–539.

RECEIVED: 13 January 1996.
ACCEPTED: 5 March 1996.

Address: School of Marine Science and Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062, U.S.A. (e-mail: jeduffy@vims.edu)