COLONY STRUCTURE OF THE SOCIAL SNAPPING SHRIMP
SYNALPHEUS FILIDIGITUS IN BELIZE

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ABSTRACT

Several species of sponge-dwelling alpheid shrimps (*Synalpheus*) exhibit unusual colony organizations reminiscent of those found in social insects, but few of these shrimp species have been studied in detail. We sampled colonies of *S. filidigitus* from its two main hosts, the sponges *Oceanapia* sp. and *Xestospongia* spp., at Carrie Bow Cay, Belize. Colonies contained all size classes of shrimp, from recent hatchlings to mature, brooding females. The majority of colonies consisted of <30 individuals, although a few reached much greater numbers (maximum = 94 in *Oceanapia* and 121 in *Xestospongia*). In all but one of the colonies sampled containing mature female(s), only a single female (the "queen") was present. Distinct cohorts of juveniles, apparently produced by the resident female, were recognizable in several colonies, and the total number of individuals in the colony was strongly correlated with the resident female's size and fecundity. These observations suggest that, as previously shown for the eusocial *S. regalis,* the colony is a close-kin group consisting mainly of the queen's philopatric offspring. Comparison of females from a range in colony sizes revealed an apparent ontogenetic transformation in the queen's morphology. Although smaller (presumably younger) females were morphologically similar to males, queens from larger colonies were considerably larger than males, had proportionally longer and wider abdomens, and had the massive major chela of the first pereiopod replaced with a small chela identical to the normal minor first chela. Colonies of *S. filidigitus* are similar in organization to those of *S. regalis,* suggesting that *S. filidigitus* may be eusocial according to the traditional definition. This brings to 3 the number of species of *Synalpheus* reported to exhibit this paradoxical social organization.

The snapping shrimp genus *Synalpheus* comprises one of the largest genera of marine crustaceans, with over 100 species described (Chace, 1989). Most are commensal associates of sessile marine invertebrates, particularly sponges and crinoids, on tropical reefs (Banner and Banner, 1975; Bruce, 1976, 1978; Dardeau, 1984; Duffy, 1992), where they may comprise dominant components of the mobile cryptofauna (Felder and Chaney, 1979; Reed *et al.,* 1982; Snelgrove and Lewis, 1989). In the Caribbean, about two-thirds of the 32 described species belong to the gambarelloides species group, characterized by a distinctive setal brush on the minor first chela (Coutière, 1909; Dardeau, 1984) and the habit of living within the internal canals of sponges (Duffy, 1992, 1996b). Apart from their association with living hosts, however, the natural history and ecology of species of *Synalpheus* are poorly known, in large part because of their small size, cryptic habits, and the difficulty of identifying the many morphologically similar species in the genus.

Sponge-dwelling species of *Synalpheus* are commonly gregarious, being found in groups of 10s to 100s within a sponge (Pearse, 1932;

Chace, 1972; Banner and Banner, 1975; Dardeau, 1984). In several species, this sponge-dwelling habit is associated with puzzling features of population structure, such as skewed sex ratios and truncated size-frequency distributions, which have defied explanation for many decades (Coutière, 1909; Banner and Banner, 1975, 1981, 1983; Dardeau, 1984). Recently, however, these observations have been put into new perspective by the discovery in a new species of Caribbean *Synalpheus* of an unusual colonial organization reminiscent of that found in social insects (Duffy, 1996a). Colonies of *S. regalis* Duffy can number up to 350 individuals within a sponge, invariably with only a single female breeding. Of the remaining colony members, the larger individuals, presumably males [reliable secondary sexual characteristics are absent in *Synalpheus* (see Felder, 1982; Dardeau, 1984)], aggressively defended the colony against intruders in laboratory experiments. Moreover, genetic data indicate that colony members are closely related, probably constituting a nuclear family (Duffy, 1996a). According to the criteria traditionally employed by entomologists (Wilson, 1971), *S. regalis* is eusocial, marking the first find-

ing of such reproductively skewed, cooperative colonies among marine animals. Evidence suggests that similar colony structures occur in several other species of *Synalpheus* from around the world (Duffy, 1998).

In this paper, we analyze colony structure of one of these species, *Synalpheus filidigitus* Armstrong, from the Belize Barrier Reef and present evidence for multigenerational, monogynous colony structure similar to that reported (Duffy, 1996a) for *S. regalis* Duffy. *Synalpheus filidigitus* was described by Armstrong (1949) 50 years ago from cryptic reef sponges in the Dominican Republic and, to our knowledge, has been reported only once since (Duffy, 1996b). We have found this species to be a common inhabitant of two cryp-sponge genera in the vicinity of Carrie Bow Cay, Belize. Here we describe host use patterns and demographic structure of colonies in *S. filidigitus*. These data suggest, by analogy with the better known *S. regalis,* that *S. filidigitus* may be eusocial according to the traditional definition (Wilson, 1971), bringing to three the number of species of *Synalpheus* reported to exhibit this paradoxical social organization.

MATERIALS AND METHODS

We sampled *Synalpheus filidigitus* from living sponges collected by SCUBA from reefs in the vicinity of the field station of the Smithsonian Institution on Carrie Bow Cay, Belize (16°48'N, 88°05'W). Collections were made in March 1993, August 1994, June and July 1995, and June 1996. Sponges belonging to many common species, as well as associated coral rubble, were sampled initially to determine the diversity of hosts used (see Duffy, 1996b). Sponges were collected from the outer reef ridge at Carrie Bow Cay, enclosed in mesh bags, returned immediately to the laboratory, and dissected into small pieces in attempts to remove all associated animals that were present. All shrimps (which comprised the vast majority of animals in nearly all samples) were preserved in Formalin or ethanol, counted, and identified. *Synalpheus filidigitus* was recognized by the uniquely tapered, filiform fingers of the chelate second pereiopod (hence the species name; Armstrong, 1949). In addition, the relatively short dorsal spine of the basicerite (i.e., the lateral spine on the first article of the second antenna), and the more rounded abdominal pleura of males, serve to distinguish it from the closely related *S. rathbunae* Coutière, 1909. *Synalpheus filidigitus* was further distinguished from the closely related *S. regalis* by the generally larger body size and greater number of uropodal teeth in the latter species. For *S. filidigitus*, carapace length (CL) was measured, and number of eggs was counted for all females; CL was measured for all individuals in each of 12 colonies spanning a range in size. Because some individuals were missing chelae or were otherwise damaged, sample sizes for correlations between morphological and reproductive char-

acteristics differ slightly among comparisons for different variables.

RESULTS

Host Use Patterns

Synalpheus filidigitus is moderately host-specific at Carrie Bow Cay. During the five expeditions to this site, we sampled most of the common sponge species at least once, and found *S. filidigitus* in a total of 42 sponges of three species sampled (see also Duffy, 1996b); 20 of 62 samples (32%) of *Xestospongia* spp. (potentially including *X.* cf. *subtriangularis* (Duchassaing, 1850) and *X. proxima* (Duchassaing and Michelotti, 1864)); 20 of 22 samples (91%) of *Oceanapia* sp.; and two of 39 samples (5%) of *Hyattella intestinalis* (Lamarck, 1814). The last of these appears to be a somewhat incidental host, since we found only a single individual *S. filidigitus* in one of the samples, and a group of 21 individuals with no breeding female in the other sample. These sponges are typically small (<200 ml in volume) and cryptic, filling spaces among dead or live branches of finger coral, especially *Madracis mirabilis* (Duchassaing and Michelotti). *Synalpheus filidigitus* was rarely found outside a living sponge, and in cases where it was thus found one or a few individuals were found in sample buckets that contained or had previously contained a sponge harboring a colony of *S. filidigitus*. These individuals had almost certainly escaped from sponges during handling, and we thus conclude that this species, like most others in the gambarelloides group within *Synalpheus* (Dardeau, 1984; Duffy, 1992, 1996b), is an obligate sponge associate. In 39 of the 42 sponges (93%) in which *S. filidigitus* was found, it was the only species of shrimp present.

Colony Size and Composition

Colonies of *S. filidigitus* sampled (*N* = 42) spanned a wide range in size, from 1–121 individuals, and the frequency distribution of colony sizes was similar in the two most commonly occupied host genera (Fig. 1). In both hosts, the majority of colonies were relatively small, with a modal size of 20–30 individuals in *Oceanapia,* and <10 individuals in *Xestospongia*. Both distributions, however, were strongly skewed, with a few colonies reaching much larger sizes (maximum = 94 in *Oceanapia* and 121 in *Xestospongia*).
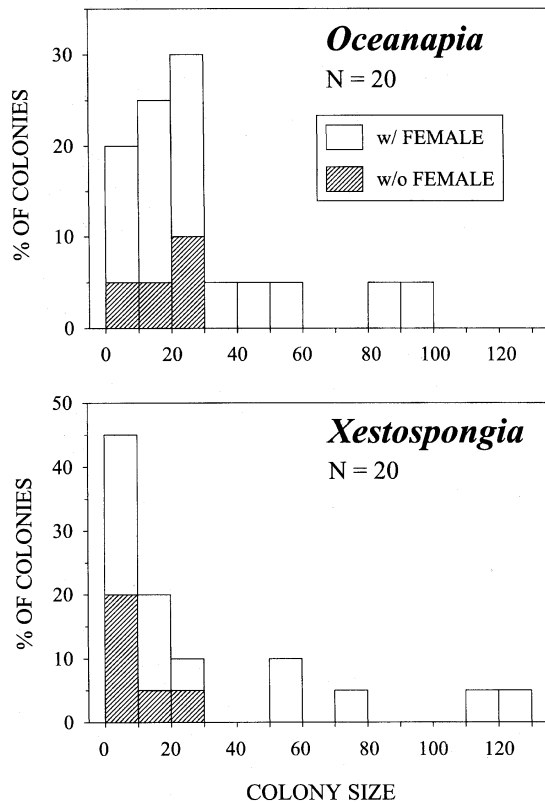
Fig. 1. Frequency distributions of colony sizes in the two host genera most frequently occupied by *Synalpheus filidigitus* at Carrie Bow Cay, Belize. Samples from *Xestospongia* include both *X*. cf. *subtriangularis* and *X*. cf. *proxima*.

Sponge-dwelling colonies contained all size classes of *S. filidigitus*, from small juveniles to mature, brooding females. Most colonies were skewed toward larger size classes, however (Fig. 2). In many colonies the smaller size classes exhibited two or more discrete modes in size, apparently corresponding to different cohorts of juveniles (Fig. 2). The size distributions differed noticeably among some colonies (Fig. 2), probably reflecting the size constraints of the available spaces within the host sponge.

As a rule, colonies of *S. filidigitus* contained a single breeding female. Specifically, of the 42 sponges sampled that harbored *S. filidigitus*, 31 (74%) contained a breeding female, recognizable by the presence of brooded embryos under the abdomen and/or developing oocytes visible through the dorsal body wall, and in all but one of these samples there was only a single female present (the "queen"). The exception was the largest

colony from *Oceanapia*, with 94 individuals of which two were females. In eight of the 12 colonies (67%) in which body sizes of all individuals were measured, the female was the largest individual present (in terms of CL; Fig. 2); in the colony with two females, one of these was the largest individual in the colony and the other female ranked sixth in size.

Biology of Breeding Females

Body size and fecundity of breeding females varied over a wide range, and were closely correlated with colony size (Fig. 3). All individuals in our samples that had rounded abdominal pleura characteristic of females also carried developing eggs. These females ranged from 1.76–3.13 mm CL, and the number of eggs carried ranged from 1–29 (median = 5, N = 22 females measured). Clutch size (i.e., number of eggs carried) increased with body size (Fig. 3), a relationship best described as a second order regression (number of eggs = 47.7–50.0 CL + 13.8 CL^2). The slope of this relationship was highly significant ($P <$ 0.0001), with female CL explaining 91% of the variance in clutch size. There was no apparent difference in size-specific fecundity between females from *Oceanapia* and *Xestospongia*. Interestingly, the number of individuals present in the colony was strongly correlated with the size (r^2 = 0.73, $P <$ 0.0001) and fecundity (r^2 = 0.88, $P <$ 0.0001, Fig. 3) of the breeding female.

A distinct morphological transition was evident with increasing body size of the female (Fig. 4). The smallest (presumably youngest) females were similar in overall appearance to males, typically having a short, narrow abdomen and a massive major chela on the first pereiopod. Larger "queens," in contrast, had proportionally longer and wider abdomens to accommodate a large clutch of eggs, and generally bore a minor-form chela on each of the first pereiopods, rather than the asymmetrical pair of one major and one minor chela typical of the genus (Fig. 4). The latter feature was rather striking: of the 29 females in our preserved samples, 18 had two minor-form chelae (recognizable because of their relatively small size, and the characteristic brush of setae on the dactyl), whereas only 4 had the normal pair of one major and one minor chela (Fig. 5). The remaining seven females were missing one or both chelae. In contrast only three (out of 180 carefully ex-

CARAPACE LENGTH (mm)
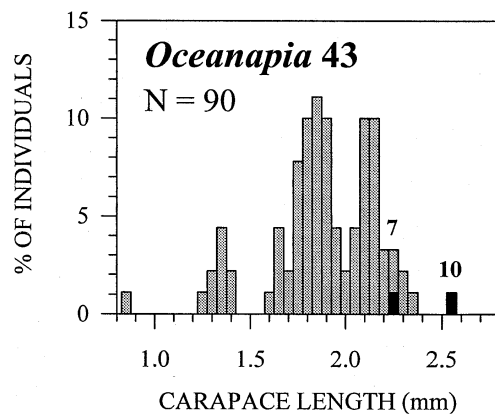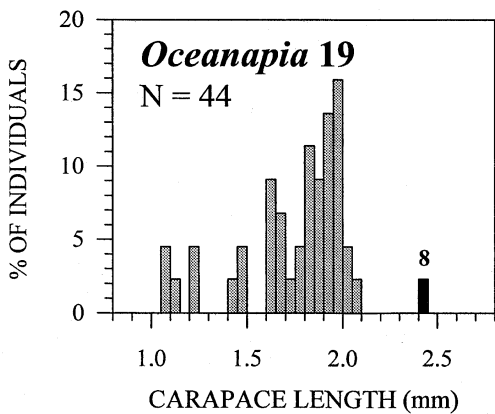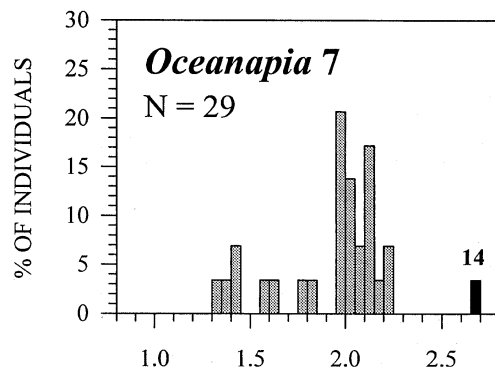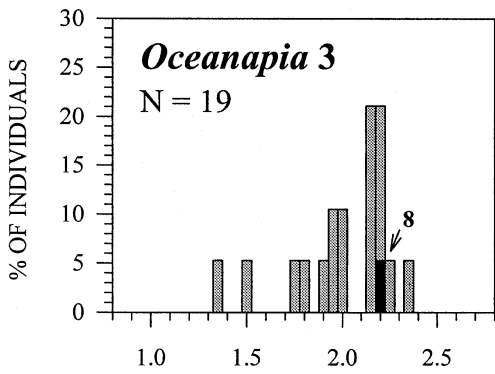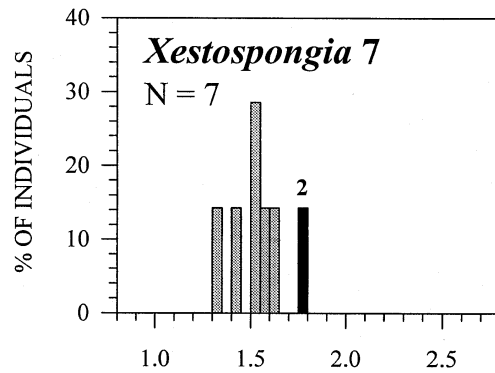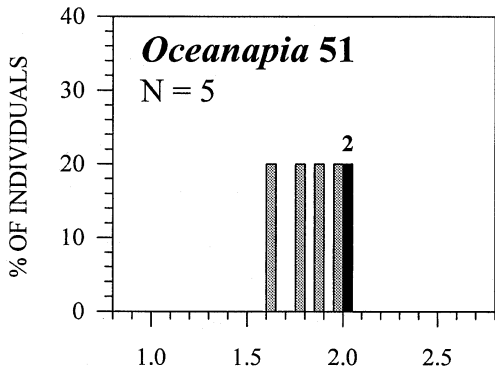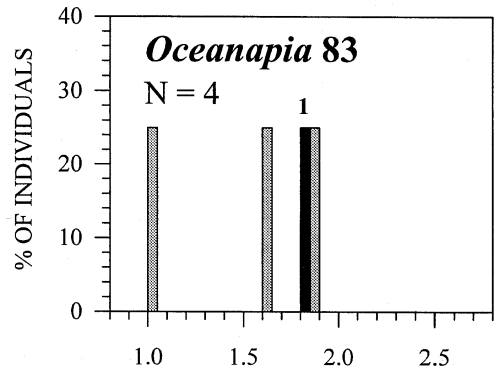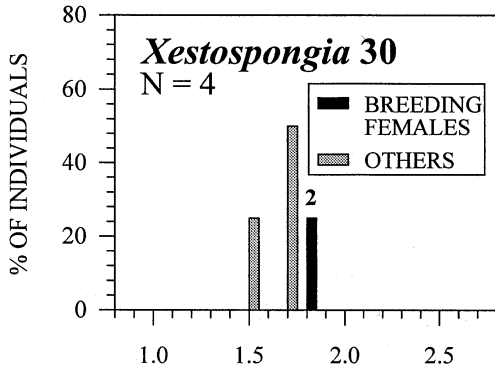
amined) of the males or juveniles had two minor chelae.

DISCUSSION

The sponge-dwelling alpheid shrimp *Synalpheus filidigitus* lives in large, multigenerational, monogynous colonies strikingly similar to those defined as eusocial in insects (Wilson, 1971) and in its social (Duffy, 1996a) congener *S. regalis*. Although we were unable to observe the ontogeny of individual colonies through time, we believe that the samples of colony structure we obtained support the hypothesis that colonies of *S. filidigitus* grow via accumulation of successive cohorts of philopatric juveniles, and, thus, that colonies represent matrilineal kin groups. Several lines of evidence support this conclusion. First, colonies of *S. filidigitus* contain individuals spanning the complete range in body size, from newly hatched juveniles to mature, brooding females (Fig. 2). Although we have not observed hatching of eggs in *S. filidigitus* in the laboratory, we have seen newly hatched juveniles in the closely related *S. rathbunae,* and in a morphologically similar undescribed species, *S. "rathbunae* A" (see Duffy, 1996b). Both of the latter species release crawling, benthic juveniles, as do several other species in the genus (Dobkin, 1965, 1969; J. E. Duffy, personal observation). Based on these observations of its relatives, and the very low fecundity of females (Fig. 2), we assume, first, that *S. filidigitus* also releases direct-developing benthic juveniles. Second, discrete cohorts of small juveniles are often recognizable in colonies of *S. filidigitus* (Fig. 2), suggesting that cohorts of hatchlings remain together in the sponge where they were hatched, rather than dispersing. Third, colony size is strongly correlated with the body size (and presumably age) of the breeding female (Fig. 3), as might be expected in an iteroparous animal in which cumulative reproductive output increases with age. Moreover, the size of juvenile cohorts tends to be larger in colonies where the breeding female is more fecund (e.g., *Oceanapia* 7, 19, and 43, Fig. 2), also
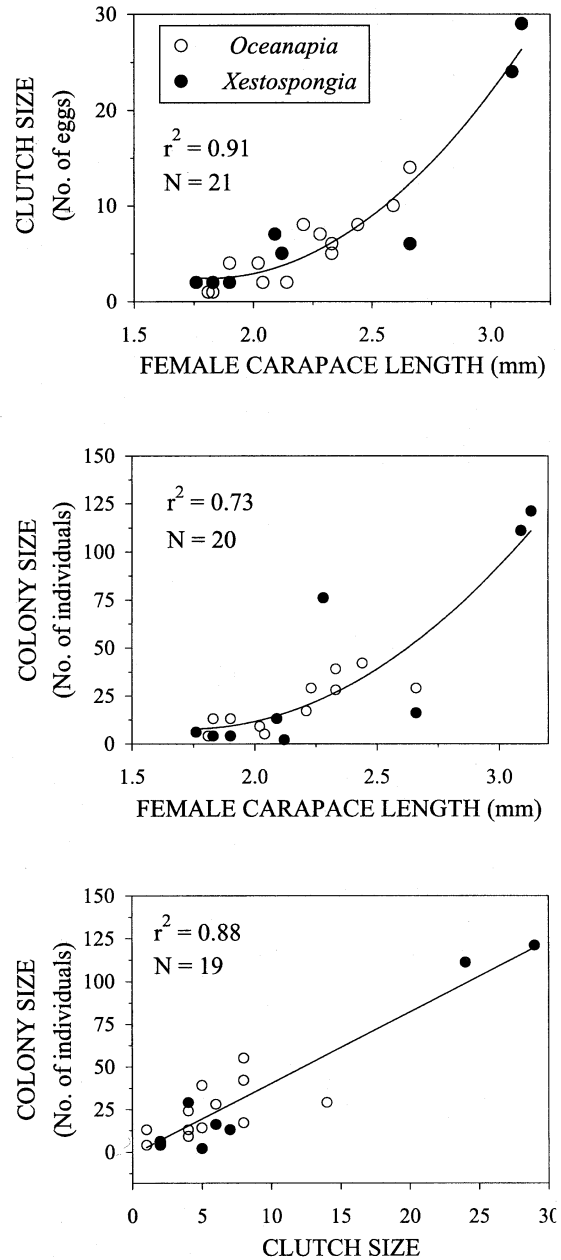

Fig. 3. Relationships between the body size of the breeding female (CL), fecundity, and the number of individuals in the colony in *Synalpheus filidigitus* from Carrie Bow Cay, Belize. Curves represent the best fit to the data using least-squares regression. All regressions are significant at *P* < 0.0001.

Fig. 2 Frequency distributions of body size (carapace length) in four small and four large colonies of *Synalpheus filidigitus* from Carrie Bow Cay, Belize (*N* = number of individuals in colony). The number of eggs carried by each female at the time of collection is represented by a number above her bar. Note the discrete groups of similar-sized juveniles, apparently representing cohorts, in several colonies.
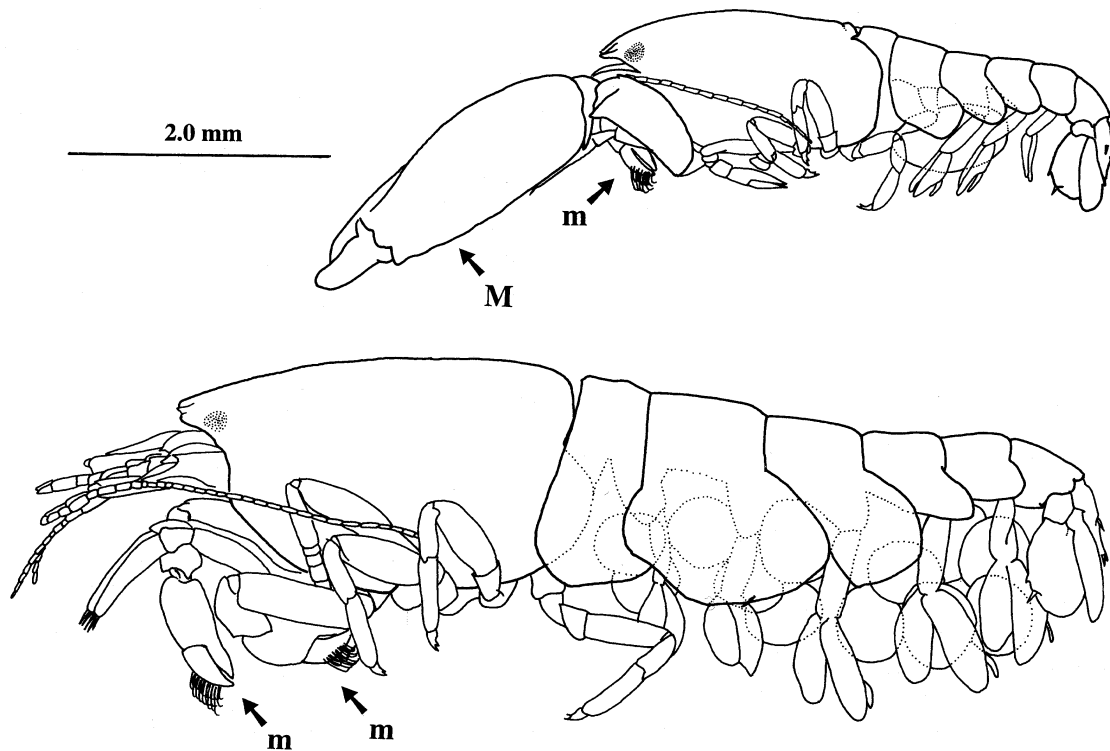
Fig. 4. Morphological differentiation of the queen. Top: a smaller female (CL = 1.81 mm) from a colony of 4 individuals; this specimen carried a single egg, and a normally developed major first chela (M). Bottom: the largest female found in our collection (CL = 3.13 mm), from a colony of 121 individuals. This specimen carried 29 eggs and bore two minor chelae (m). Note the enlarged abdomen, and replacement of the major chela by a second minor-type chela (m) in the larger queen. Both specimens drawn to same scale.

suggesting that she is the source of resident hatchlings. Finally, by comparison, high genetic relatedness within colonies of *S. regalis* confirms that colonies consist of close relatives in that species (Duffy, 1996a). Although we have no genetic confirmation for *S. filidigitus,* the similarity in colony structure and general ecology between this species and *S. regalis* suggest that colonies of *S. filidigitus* also comprise groups of close kin.

The most striking feature of a colony of *Synalpheus filidigitus* is its strong reproductive skew. In all but one of the colonies we examined, including those numbering >100 individuals, only a single breeding female was present (Fig. 2). This extreme reproductive skew is rare among animals generally, but is characteristic of a limited number of insect taxa including termites, ants, some wasps, some bees, and a few others (Wilson, 1971; Choe and Crespi, 1997); the naked mole-rat (Jarvis, 1981; Sherman *et al.,* 1991), and the recently described (Duffy, 1996a, c, 1998) snapping shrimps *Synalpheus regalis*

and *S. chacei* Duffy, 1998. All of these reproductively skewed taxa have been considered eusocial according to the classical criteria developed by entomologists (Wilson, 1971). The traditional definition of eusociality popularized by Wilson was based on the three criteria of overlapping generations, reproductive division of labor, and cooperative care of young. Our data on colony structure show that *S. filidigitus* meets the first two of these criteria. The third requires behavioral observations, which are not available for *S. filidigitus.* Nonetheless, the consistent occurrence of only a single breeding female in colonies as large as 121 individuals is almost unknown among animals outside the eusocial insects and mole-rats, and in virtually all other known cases, including that of *S. regalis,* such extreme reproductive skew is associated with high relatedness and cooperative behavior among colony members. This report thus brings to three the number of Caribbean species of *Synalpheus* known to display the multigenerational, monogynous
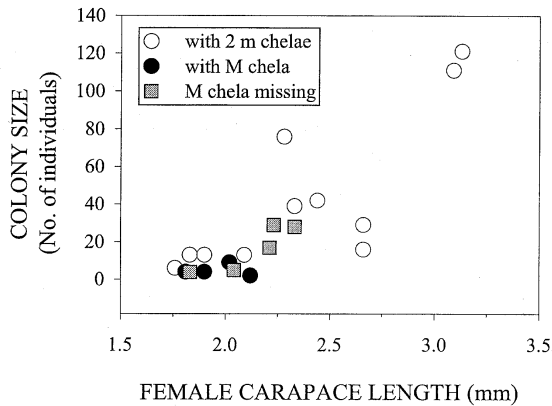
Fig. 5. The relationship between body size (CL) and colony size (number of individuals) for female *Synalpheus filidigitus* bearing two minor (m) chelae, versus the normal asymmetric pair of one major (M) and one minor chela. Data are not shown for seven females that had a damaged (unmeasurable) carapace and/or unrecorded colony size, nor for the two cohabiting females from colony 43 of *Oceanapia.*

colonies characteristic of eusociality among insects.

Whereas the paucity of mature females is clearly recognizable, identification of males in the genus *Synalpheus* is complicated by the absence of male secondary sexual characteristics (Coutière, 1909; Banner and Banner, 1975; Felder, 1982; Dardeau, 1984), a situation that may reflect protandrous sex change, as has been documented in several species of the alpheid genus *Athanas* (Suzuki, 1970; Nakashima, 1987; Gherardi and Calloni, 1993). Specifically, the appendix masculina borne by males in most caridean taxa is absent in *Synalpheus* (see Dardeau, 1984), and juveniles of both sexes in most species of *Synalpheus* have the hooklike first abdominal pleura characteristic of adult males, making it difficult to determine either the sex ratio or the number of adult shrimps. Thus, for colonies of social *Synalpheus,* including *S. filidigitus,* it is impossible without histological sectioning to count accurately the number of physiologically mature males or the number of potentially breeding females whose reproductive activity is suppressed. A rough estimate of the number of potentially mature individuals within a colony can be made indirectly by counting the number of individuals present that are larger than the minimum breeding female size observed (CL = 1.76 mm). In the colony from *Oceanapia* 43, for example, this approach results in an esti-

mate of 66 potentially mature individuals, only one of them breeding as a female. Regardless of the exact number of mature individuals, it seems safe to conclude that in such colonies a substantial number of physiologically mature individuals are not breeding.

Among the most perplexing questions concerning the social structure of the sponge-dwelling shrimps, and indeed of highly social animals generally, is how such strong reproductive skew is maintained (Wilson, 1975; Alexander *et al.,* 1991; Keller and Reeve, 1994). In highly social insects and vertebrates, there are two alternative mechanisms for the proximate control of reproduction within the colony (Fletcher and Ross, 1985; Keller and Reeve, 1994): aggression by the dominant reproductive individual(s), and pheromonal mediation of reproductive activity. The curiously high frequency of two minor chelae among females in our samples (Figs. 4, 5) may shed some light on the answer to this question for *S. filidigitus.* Since the major chela is the primary weapon for aggression and contests in alpheids (Hazlett and Winn, 1962; Schein, 1977; Knowlton, 1980; Knowlton and Keller, 1982; Hughes, 1996), an individual lacking a major chela would seem to be at a severe disadvantage in aggressive contests. Thus, the frequent absence of a major chela in the lone reproductive female *S. filidigitus* within a colony suggests that her monopoly on reproduction is unlikely to be maintained by aggressive behavioral dominance over her colony-mates. Although pheromone production by the queen might alternatively serve as the proximate control on sexual differentiation within the colony, suppression of "worker" breeding by such means is not evolutionarily stable unless backed up by the threat of effective enforcement (Keller and Nonacs, 1993). This leaves us with the possibility that reproductive activity is ultimately controlled by other members of the colony, as appears true in some ants (Keller and Nonacs, 1993) and termites (Zimmerman, 1983). Interestingly, the possession of two minor chelae by females has been noted in two other species of *Synalpheus.* A strikingly parallel situation to that of *S. filidigitus* was reported by Banner and Banner (1983) for *S. crosnieri* Banner and Banner from unidentified sponges in northwestern Madagascar: "Of the 147 specimens in the collections only 3 are female, 2 of which are ovigerous. . . .

Two of the females have both chelipeds, the third has one, but all of the chelipeds are of the form of the smaller cheliped of the male." Similarly, in samples of *S. rathbunae,* Chace (1972) reported that, "curiously enough, all of the large female specimens taken at Barbuda in 1956 (Sta. 85–56) have two minor first chelipeds, as if the major cheliped had been lost and regenerated to duplicate the opposite member of the pair." Interestingly, both *S. crosnieri* and *S. rathbunae* display the small body size, large colony size, and paucity of females characteristic of putatively eusocial *Synalpheus.* In contrast, the presence of two minor chelae appears to be very rare in non-eusocial species, as would be expected if the major chela is critical to aggressive and territorial interactions. Among several other species of *Synalpheus* which we have examined carefully, we found two minor chelae in only one female *S. chacei* Duffy (also a putatively eusocial species, Duffy, 1998), out of a total of 414 specimens from 22 species. The functional significance of the loss of the major chela in putatively eusocial species is obscure. It is tempting to speculate that, when the female is ensconced within the safety of her colony, the large and unwieldy major chela is no longer necessary for defense and becomes an energetic burden, either because of its sheer mass, or because it is useless or inefficient for feeding.

Although colonies of *S. filidigitus* appear to contain all life history stages, large colonies in this diminutive species are often dominated by individuals within a narrow range of adult size classes (Fig. 2). Such relative uniformity in body size, along with a paucity of breeding females, was also observed in several Indo-Pacific species of sponge-dwelling *Synalpheus* by Banner and Banner (1975, 1981, 1983). In the specific case of *S. neptunus* (Dana), sponge-dwelling colonies contained few or no breeding females, whereas larger sexually mature individuals of apparently the same species were collected outside sponges in the same habitats. Based on these observations, Banner and Banner (1975) developed the intriguing argument that the sponge-dwelling aggregations were juveniles, using certain sponge species as nursery-like habitats, from which maturing individuals emigrated into adult habitats. Our data appear instead to support an alternative explanation, that such colonies of small-bod-

ied sponge-dwellers represent multigenerational, reproductively skewed kin groups traditionally described as eusocial (Duffy, 1996a, 1998). The aggregations of "juveniles" in the Indo-Pacific species of *Synalpheus* discussed by Banner and Banner (1975) might be explained if those species were social in the same sense as *S. regalis* and *S. filidigitus* but the lone female in the colony had escaped collection. Our experience suggests that such a scenario is plausible given the physically complex and heterogeneous nature of the substratum in which these shrimps live. In fact, several of our colonies of *S. filidigitus* consisted of ~20 individuals but no female, which we attribute to our having missed the female during collection. It is also possible that the absence of breeding females in the collections of Banner and Banner (1975) was due to seasonal lulls in reproductive activity. However, most tropical *Synalpheus* appear to breed continuously after reaching maturity (Dardeau, 1984). As for the larger adults of *S. neptunus* found by Banner and Banner (1975) in adjacent habitats, we suggest that these may have been closely related sibling species, which are common in *Synalpheus* and other alpheid genera (Knowlton and Keller, 1983, 1985; Knowlton, 1992; Duffy, 1996b, 1998). Recent work on sibling species of *Synalpheus* indicates that they frequently differ markedly in microhabitat use, though they often live on the same reefs (Duffy, 1996b). If this explanation is correct, it raises the possibility that eusocial snapping shrimps occur outside the primarily Caribbean gambarelloides species group, which would almost certainly imply an independent origin of this paradoxical social organization among the Indo-Pacific species.

ACKNOWLEDGEMENTS

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