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Influence of sociality on allometric growth and morphological differentiation in sponge-dwelling alpheid shrimp

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Eusocial societies are defined by a reproductive division of labour between breeders and nonbreeders that is often accompanied by morphological differentiation. Some eusocial taxa are further characterized by a subdivision of tasks among nonbreeders, often resulting in morphological differentiation among different groups (subcastes) that specialize on different sets of tasks. We investigated the possibility of morphological castes in eusocial shrimp colonies (*Zuzalpheus*, formerly part of *Synalpheus*) by comparing growth allometry and body proportions of three eusocial shrimp species with three pair-forming species (species where reproductive females and males occur in equal sex ratios). Allometry of eusocial species differed in several respects from that of pair-forming species in both lineages. First, allometry of fighting claw size among individuals other than female breeders was steeper in eusocial than in pair-forming species. Second, breeding females in eusocial colonies had proportionally smaller weapons (fighting claws) than females in pair-forming species. Finally, claw allometry changed with increasing colony size in eusocial species; large colonies showed a diphasic allometry of fighting claw and finger size, indicating a distinctive group of large individuals possessing relatively larger weapons than other colony members. Shrimp are thus similar to other eusocial animals in the morphological differentiation between breeders and nonbreeders, and in the indication that some larger nonbreeders might contribute more to defence than others. © 2008 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2008, 94, 527–540.

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INTRODUCTION

Reproductive division of labour (i.e. the presence of both breeding and nonbreeding adult individuals) is one of the defining characteristics of eusocial animal societies (Wilson, 1971; Michener, 1974; Sherman, Jarvis & Alexander, 1991). This specialization is distinguished in some societies not only by differences in behaviour, but also by distinctive morphological differentiation, with female breeders (also called reproductive females or queens) usually having a larger abdomen than nonbreeders (often called workers or

helpers) to accommodate high reproductive output (Wilson, 1971; Michener, 1974; Oster & Wilson, 1978; Noirot, 1985; Choe & Crespi, 1997; O’Riain *et al.*, 2000). These differences in size and proportion result from differential growth of body parts (Huxley, 1931) and, when morphological variants within a social colony are so distinct that no or only a few intermediates are present, the discrete morphs are referred to as full castes (Wilson, 1971). Not only insects (Wilson, 1971; Aoki, 2003), but also social vertebrates, such as naked mole rats and meerkats (O’Riain *et al.*, 2000; Russel *et al.*, 2004), show clear morphological differentiation between breeders and nonbreeders, suggesting that evolutionary pressures associated with social life have produced similar changes in a range of vertebrate and invertebrate societies.

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In eusocial societies, not only do breeders and helpers differ in their roles, but also tasks are usually also divided among the helpers themselves, with the functionally different subgroups of helpers frequently referred to as castes or subcastes (= worker polymorphism; Wilson, 1971; Michener, 1974). This task specialization can be simply behavioural, in which monomorphic individuals specialize and pass through tasks as they age, but it can also involve morphological differentiation, such that individuals are morphologically better equipped to perform the tasks on which they specialize (Wilson, 1971; Bartz, 1979; Aoki, 1987; Crespi, 1992). *Sensu* Huxley (1931), Wilson (1953, 1971) classified such morphological differentiation as a function of the changing allometric relationships between body parts with size. He defined polymorphism as the 'occurrence of non-isometric relative growth occurring over a sufficient range in size variation within a mature colony to produce individuals of distinctly different proportions at the extremes of the size ranges'. The rationale is that non-isometric growth produces different body shapes at different body sizes, potentially allowing individuals in the colony to perform different roles more efficiently. Wilson showed that, in some social insect species, this morphological differentiation is even more marked, with the slope of the allometric relationship changing abruptly to yield segments of different slope (e.g. 'diphasic' allometry, where there are two segments), which correspond to even more distinct morphological castes. He suggested that the primary function of such diphasic allometry is to allow 'stabilization of the body form' in the smaller caste at the same time as allowing specialization of a larger, more robust caste to differentiate.

The evolution of worker polymorphism in a particular taxon can depend on factors such as life history constraints and colony size. First, developmental flexibility appears to be important. Worker polymorphism has not evolved in those hymenopteran species where workers develop in uniform-sized cells, such as honeybees and wasps (Wilson, 1971; Michener, 1974), whereas physical castes are more prevalent in ants, termites, thrips, and aphids that do not rear their progeny in cells, such that development is more flexible (Noirot, 1985; Wheeler, 1991; Choe & Crespi, 1997). In naked mole rats, which have continuous growth rather than metamorphosis, tasks are divided among subsets of behaviourally distinct colony members, and size correlations are more subtle (Lacey & Sherman, 1991; O'Riain *et al.*, 2000). Second, the distinction among worker subcastes is more apparent in larger colonies than in small ones, both within species (Wood & Tschinkel, 1981; Noirot, 1985; Okot-Kotber, 1985; Passera, 1985; Tschinkel, 1998; Nowbahari, Feneron & Malherbe, 2000) and

among species (Oster & Wilson, 1978; Bourke, 1999; Anderson & MacShea, 2001). In large, well-developed eusocial colonies, the easiest subcaste to distinguish is that of the soldiers, which are often larger-bodied and/or have proportionally larger weapons (Wilson, 1971; Aoki, 1987; Passera *et al.*, 1996), and are thus more effective in attacking and repelling enemies than other colony members (Bartz, 1979; Hölldobler & Wilson, 1990; Lacey & Sherman, 1991; Choe & Crespi, 1997; Shingleton & Foster, 2001). It is hypothesized that some societies that have soldiers (e.g. thrips, aphids, termites) evolved to be eusocial because this allowed them to defend their valuable nest more efficiently (Queller & Strassmann, 1998).

The consequences of social life for morphological evolution have been studied mainly in insects. The present study investigates whether polymorphism has evolved with social life in an unrelated and ecologically distinct taxon, shrimp of the genus *Zuzalpheus* (formerly the *Gambarelloides* species group within *Synalpheus*, Ríos & Duffy, 2007), which live obligately within the canals of tropical sponges and are the only known eusocial animals from marine environments. Most snapping shrimp (Alpheidae) are very territorial, have an asymmetrical first pair of claws (chela), and use their enlarged major chela primarily for fighting (Schein, 1977). This fighting chela houses powerful muscles, and its larger size renders it stronger than a smaller one (Kaiser, Hughes & Reid, 1990). Quick closure of the open fingers of the claw creates a rapid water jet (Herberholz & Schmitz, 2001) that irritates the opponent (Bauer, 2004). The fingers can also be used to injure the enemy (Knowlton & Keller, 1982; E.T. & J.E.D., pers. observ.), with longer fingers presumably opening wider to facilitate grabbing. Among snapping shrimp in the genus *Alpheus*, body size appears to be correlated with chela size and thus fighting ability (Schein, 1975, 1977; Hughes, 1996). Most species of *Alpheus*, *Synalpheus*, and *Zuzalpheus* live in heterosexual pairs (Knowlton, 1980; Dardeau, 1984; Bauer, 2004) but a few species of sponge-dwelling *Zuzalpheus* are eusocial (Duffy, 2007). Pair-living alpheid species typically are sexually dimorphic (Dawes, 1934; Nolan & Salmon, 1970; Schein, 1975; Knowlton, 1980), with females having larger bodies and proportionally smaller major chelae than males: this trend has also been described quantitatively in one pair-living *Synalpheus* species (Au & Banks, 1998). In eusocial shrimp species, breeding females (queens) also appear to be larger than other, nonbreeding colony members (Duffy, 2003). Although sexing of *Zuzalpheus* is very difficult and is often done by default for the pair-living species (i.e. breeding females carry embryos and have developed ovaries, whereas males do not; Banner & Banner, 1975;

Felder, 1982; Dardeau, 1984), it has recently been established via a scanning electron microscopy examination of the gonopores that helpers in eusocial species consist of both sexes in similar ratios (Tóth & Bauer, 2007). Usually, the few to a few hundred individuals in a shrimp colony belong to several generations spanning a range in body size (Duffy & Macdonald, 1999; E.T., pers. observ.). Embryos transform directly into benthic juveniles that are morphologically similar to adults and grow through many successive molts. Eusocial shrimp live in relatively simple societies in which juveniles appear self-sufficient from birth, neither the queen, nor the young appear to be tended, and the host sponge provides food (Duffy, 2003). Shrimp colonies thus apparently do not need to perform specialized foraging or tending tasks. However, because most sponge hosts are occupied and nest invasion is likely to be a frequent danger (Duffy, 2003), nest defence is likely at a premium (Tóth & Duffy, 2005), and a soldier-like caste efficient in fighting might enhance the fitness of eusocial shrimp colonies.

To date, only one study has reported on morphological variation among individuals within eusocial shrimp colonies; Duffy & Macdonald (1999) showed that in *Zuzalpheus filidigitus*, queens generally differ from other colony members in having no major chela. In that species, as well as in the eusocial *Zuzalpheus regalis* (Duffy, 1996), female carapace length (a widely used index of body size in decapod crustaceans) was positively correlated with colony size. No study, however, has systematically addressed the possibility of morphological caste differentiation in eusocial shrimp by measuring multiple morphological characters in entire colonies (queens and others), nor by comparing eusocial with pair-forming species. In the present study, we searched for evidence of morphological differentiation associated with eusocial life in shrimp by focusing on several morphological characters indicative of competitive or aggressive ability. Since a principal advantage of eusocial life in shrimp might be enhanced defence of the nest (Duffy, Morrison & Macdonald, 2002; Duffy, 2003; Tóth & Duffy, 2005), as is true of many other eusocial animals (Alexander, Noonan & Crespi, 1991; Choe & Crespi, 1997), we were particularly interested in the size and allometry of the primary aggressive weapon, the major chela (fighting claw). To evaluate the possibility of castes in eusocial shrimp, we compared allometric growth of three eusocial shrimp species with three less social species. In the latter, several individuals can be found in a sponge, but large individuals are found in equal sex ratios, and often as female–male pairs (hereafter referred to as pair-living species). The present study involves three main components. First, we ask whether allometry of individuals other than

breeding females (i.e. males, juveniles, and nonbreeding adult females, if present) differs consistently between eusocial and pair-forming species. Second, we compare allometric growth curves of breeding females with those of other individuals to test whether morphological differentiation of queens in eusocial species exceeds normal sexual dimorphism in pair-forming species. Finally, we compare allometry of eusocial species across a range in colony sizes to explore possible evidence for a defender subcaste among helpers.

MATERIAL AND METHODS

STUDY ANIMALS

We studied three eusocial and three pair-living species of *Zuzalpheus*, collected between 1995 and 2003 from tropical reef environments in Belize (around Carrie Bow Cay, 16°48'N, 88°05'W) and Bocas del Toro (9°23'N, 82°18'W) and the San Blas Islands (9°34'N, 78°58'W) of Caribbean Panamá. All species are obligate inhabitants of living sponges that provide both food and shelter. Specimens were collected from a number of sites at various times of year; we have noticed no obvious seasonal variation in reproductive activity or morphology. Of the eusocial species, *Z. regalis*, *Zuzalpheus chacei* and *Z. filidigitus*, usually one female breeder and many nonbreeders occur in one sponge (Duffy, 1996, 1998; Duffy & Macdonald, 1999; Duffy, 2003). In the studied pair-living species, *Zuzalpheus idios* (*S. 'brooksi* D' in Morrison *et al.*, 2004), *Zuzalpheus dardeau* (*S. 'pandionis giant'* in Morrison *et al.*, 2004) and *Zuzalpheus paranepentunus*, several pairs can be found in the same sponge. Of the eusocial species, *Z. chacei* shows an independent origin of eusociality from that of *Z. regalis* and *Z. filidigitus* (Morrison *et al.*, 2004). *Zuzalpheus idios* is closely related to the eusocial species *Z. chacei*. The relationships of *Z. dardeau* and *Z. paranepentunus* to the other species studied are poorly resolved. Evidence suggests that most of these species diverged in a rapid radiation several million years ago (Morrison *et al.*, 2004).

From the eusocial species, we measured ten entire colonies of *Z. regalis* (a colony is the population of shrimp within a single sponge) totaling 1321 individuals; five colonies (450 individuals) of *Z. filidigitus*; and five colonies (350 individuals) of *Z. chacei*. From the pair-forming species, we measured 23 females and 37 others (presumably males and juveniles) of *Z. dardeau*; 13 females and 41 males and juveniles of *Z. idios*; and 48 females and 83 males and juveniles of *Z. paranepentunus*. All the individuals of *Z. idios* came from one sponge, whereas we collected *Z. paranepentunus* from nine sponges and *Z. dardeau* from

ten sponges. Because shrimp are able to move within the sponge, during collection and sample processing, we generally could not be certain which individual animals were associated with one another in pairs.

MEASUREMENTS

Morphometric data were obtained using a dissecting microscope and digital camera connected to a computer, and measurements were obtained using the program IMAGE PRO PLUS, version 4.1 for windows (Media Cybernetics LP). Magnified images of animals were projected on the computer screen at $\times 15$ magnification, allowing us to draw straight lines between two points as well as to follow curvature of the body to measure distances to the nearest 0.001 mm. We separated the major chela of each individual shrimp and placed the shrimp on its left side for measurements.

As an index of body size, we determined total body length (measured from the rostrum to the tip of the telson as the body curved). We also recorded the commonly used metric of body size in crustaceans, carapace length (from rostrum to the posterior margin of the carapace as a straight line (Fig. 1)), to confirm that it grows proportionally with body size in all species. As potential indices of fighting ability, we measured three characteristics of the major chela or fighting claw. We chose chela length (from the tip of the fixed, immovable, finger to the most proximal part of the chela as a straight line), and chela width (measured at the broadest part of the chela) as indicators of the power of the chela. We chose fixed finger length (hereafter referred to as finger length, from the

tip of the fixed finger to the curving point at the base of the dactyl as a straight line) as an indicator of grabbing ability (Fig. 1).

For individuals that were damaged during collection, malformed, or missing some body parts, we excluded those parts from our measurements. *Zuzalpheus filidigitus* queens from larger colonies lacked a major chela and instead bore two small chelae, as is typical of this species (Duffy & Macdonald, 1999). Major chela measurements in these queens were made on the larger of the two chelae. Approximately 2–5% of individuals in the eusocial species were parasitized by abdominal bopyrid isopods, which appeared to stimulate abdomen growth and reduce chela growth. We excluded these individuals from analysis. Because small colonies tended to consist of smaller animals, and small colonies might not have had time to develop the size differentiation typical of a species (Wilson, 1971), our comparison of pair-forming versus eusocial species only included large, mature eusocial colonies ranging from 64 to 335 animals depending on the species.

MORPHOMETRIC ANALYSIS

We used allometric growth curves to detect differences among species in growth patterns. Although, for practical reasons, we could not measure individuals alive as they grew, knowing that all shrimp hatch very small, we assumed that the differences in size of the many animals that we measured were obtained by growth. The growth of morphological features is usually a close approximation of a straight line expressed logarithmically by the equation: $\log y = \log b + a \log x$ (Huxley, 1931) with the slope $\log b$ defining the type of allometric growth. Departure of $\log b$ from 1 (isometric growth) indicates either positive or negative allometry (Hartnoll, 1982). We generated scatter-plots of the relationships between morphological features on a log–log scale and performed regression analyses. To determine allometric relationships among structures we tested the slope of each regression against isometry using Student's *t*-test (Zar, 1999). For each pair-forming species, analysis of covariance was used to assess if allometry of breeding (i.e. egg-bearing, or ovigerous) females differed from that of others (males, young females, and juveniles, which are difficult to distinguish from one another based on external morphology). For among-species comparisons of body length, chela length, and sexual dimorphism, we used dimensions of the five largest reproductive females and five largest non-ovigerous individuals (presumably mature males) from the pair-forming species, and the queen and the five largest helpers in our sample from each colony for the eusocial species. Dimorphism was

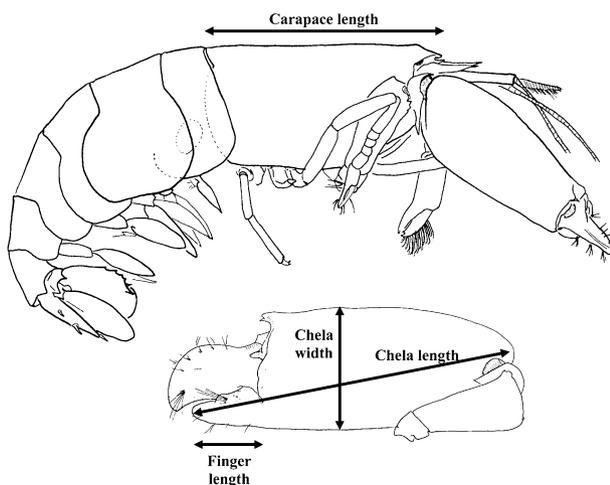


Figure 1. Lateral view of a *Zuzalpheus* shrimp (above) and of the major chela (below), showing structures measured in this study.

calculated as $[100 \times (\text{female value} - \text{other value})/\text{other value}]$; thus, a positive score indicates that males had larger values than females, and negative scores indicate the opposite.

We compared eusocial and pair-forming species in two different ways to test whether body dimensions and allometric relationships of the six species were related to level of social organization. First, because Caribbean *Zuzalpheus* underwent a relatively rapid radiation (Morrison *et al.*, 2004), phylogenetic relationships might have had little influence on morphological evolution so, in the first comparison, we entered all species as independent points in the analysis. Second, we computed phylogenetically independent contrasts (PICs), implemented with COMPARE, version 4.6b (Martins, 2004) to compare eusocial and pair-forming species. Phylogenetic relationships were taken from Morrison *et al.* (2004) and entered into the analyses as a pruned cladogram (i.e. with equal branch lengths) containing only the six species studied. To account for uncertainty in the phylogeny, we computed PICs using three of the phylogenetic hypotheses found by Morrison *et al.* (2004): (1) the most parsimonious tree based on combined molecular and morphological data; (2) trees based only on molecular characters using maximum likelihood (ML); and (3) molecular trees using the Bayesian methods.

We then computed separate linear regressions of selected morphometric variables against the eusociality index (E) of Keller & Perrin (1995):

$$E = \left(\sum_{i=1}^N |f_i - g_i| \right) / 2$$

where f_i and g_i represent an individual's proportional contributions of energy (work) and genes, respectively, to the next generation, and N is the number of individuals in the colony (i.e. within a given individual sponge). The calculation, assumptions, and rationale for using this index are described in detail by Duffy *et al.* (2000). Briefly, the E index accounts for both reproductive skew and colony size, both of which vary considerably among *Zuzalpheus* species, and the index can be calculated from data collected over short time spans, such as the point estimates available from our collections. In the absence of detailed behavioural data, we made the parsimonious assumption that all individuals in the colony contributed equally to colony work (f), and that all breeders contributed equally to production of offspring (g). Although some of these assumptions are simplistic, we believe that, if anything, they are likely to render our conclusions conservative in that division of labour would result in even higher values of E for the social species we studied. Data for calculating the E index and phylo-

genetic relationships came from Duffy *et al.* (2000) and from Macdonald, Ríos & Duffy (2006). We performed analyses for both raw data and phylogenetically independent contrasts.

RESULTS

Pair-forming *Zuzalpheus* species grew larger on average than eusocial species. Maximum body size in the pair-forming species varied over the range 12–21 mm whereas, in the eusocial species it reached only 7–10 mm (Fig. 2). As a rule, reproductive females grew larger than other individuals in both the pair-forming species and in eusocial species (Fig. 2).

BODY AND CLAW ALLOMETRY

In all species, and within individual colonies of eusocial species, there were strong correlations between body length and carapace length, and between chela length and chela width, and breeding females did not differ from others (Table 1). Body length and carapace length showed negative allometry in all species, i.e. the carapace was relatively shorter, and abdomen relatively longer, in larger individuals.

Length of the major chela and its finger showed positive allometry with body size in the eusocial species (Table 1), indicating that the chela and the fingers became relatively larger with increasing body size whereas, in the pair-living species, these relationships showed mostly a negative allometry. Phylogenetically independent contrasts based on the molecular phylogeny suggested that finger size tended to increase more steeply with body size in eusocial species than in pair-forming species, although these trends were not quite significant ($P = 0.099$ and 0.051 for the ML and Bayesian trees, respectively; Table 2).

SEXUAL DIMORPHISM AND CASTE DIFFERENTIATION

In pair-forming species, chela length of females overlapped with that of other large individuals (presumably mostly mature males) and followed approximately the same allometric relationship to body size (Fig. 3). By contrast, in all three eusocial species, breeding females (queens) differed markedly in allometry from the rest of the colony members, having a larger body and proportionally smaller chela (the extreme being *Z. filidigitus*, in which queens bore two small chelae; Fig. 3). Given these apparent differences, none of our analyses found that sexual dimorphism in body length differed in pair-forming compared with eusocial species ($P = 0.23$ – 0.69 for PICs using the three trees; Table 2, Figs 2, 3). Instead, eusocial species showed stronger sexual dimorphism in chela size compared

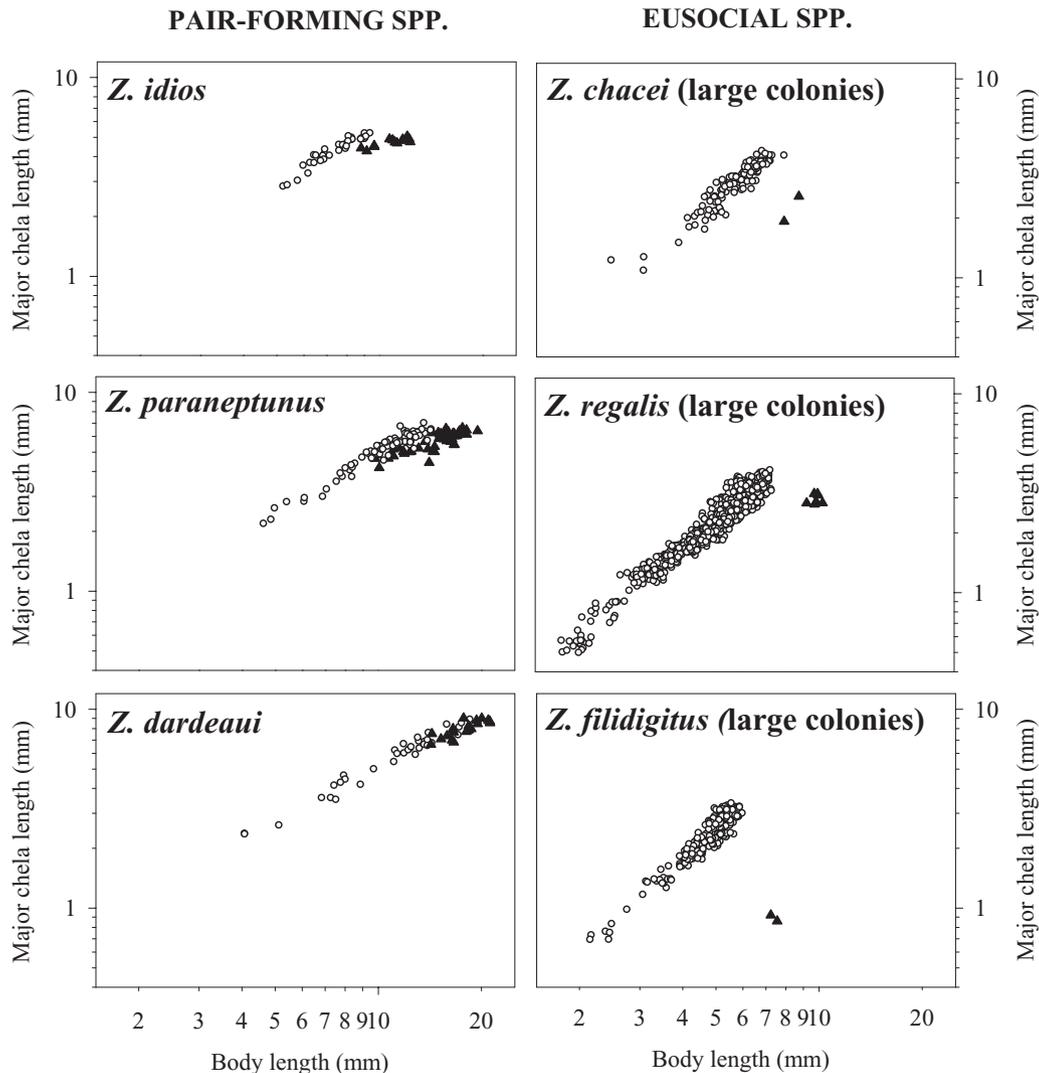


Figure 2. Logarithmic relationships between body length and major chela length in three eusocial (right column) and three pair-forming (left column) species of *Zuzalpheus*. Reproductive females are represented by black triangles, all other individuals are indicated by open circles.

with pair-forming species ($P = 0.006\text{--}0.11$ for the three trees; Figs 2, 4, Table 2). Moreover, among individuals other than breeding females ('helpers'), regressions of chela length on body length showed steeper slopes in eusocial than in pair-forming species ($P = 0.029\text{--}0.070$; Fig. 2, Table 2).

The fixed finger of the fighting chela grew proportionally with chela length in *Z. idios*, *Z. paraneptunus* and *Z. chacei*, whereas in *Z. dardeauui*, *Z. regalis* and *Z. filidigitus*, the relationship appeared to show a diphasic allometry, with the largest individuals developing major chelae with disproportionately long fingers (Fig. 5). The slopes of the allometric curves of finger length on chela length did not differ between eusocial and pair-forming species ($P = 0.33\text{--}0.71$ for PICs using the three trees, Table 2).

ALLOMETRY AND COLONY SIZE

In mature colonies of the eusocial species, allometries of both chela on body length (Fig. 2), and especially fixed finger on chela length (Fig. 5), tended to become steeper in larger individuals. To illustrate how these allometries change with colony size, we focus here on finger lengths (Fig. 6). Allometry of finger length showed similar patterns with colony size in the three eusocial species. First, in all three eusocial species, queens in small colonies were morphologically similar to other colony members whereas, in large colonies, queens diverged to have both larger body and relatively smaller finger (and chela) than other individuals (Fig. 5). Second, in *Z. chacei* and *Z. regalis*, individuals in small colonies had a larger chela/body

Table 1. Regression analyses of allometric relationships between log-transformed data for body length (BL), carapace length (CL), chela length (ChL) and chela width (ChW), and fixed finger length (FFL) in six *Zuzalpheus* species

	Intercept	Slope	R^2 (adj)	F	P	Allometry	P	t	N_{ind}	N_{col}
CL/BL										
<i>Zuzalpheus idios</i>	-0.231	0.85	0.931	717	0.0001	-	0.0001	26.81	52	
<i>Zuzalpheus paraneptunus</i>	-0.28	0.89	0.949	2 432	0.0001	-	0.0001	16.27	132	
<i>Zuzalpheus dardeauui</i>	-0.342	0.94	0.985	3 818	0.0001	-	0.0001	10.83	59	
<i>Zuzalpheus chacei</i>	-0.272	0.77	0.952	2 949	0.0001	-	0.0001	30.86	218	5
<i>Zuzalpheus regalis</i>	-0.191	0.79	0.947	22 033	0.0001	-	0.0001	34.99	1202	10
<i>Zuzalpheus filidigitus</i>	-0.186	0.74	0.931	4 202	0.0001	-	0.0001	52.21	314	7
ChW/ChL										
<i>Zuzalpheus idios</i>	-0.476	1.12	0.937	794	0.0001	+	0.0001	22.03	52	
<i>Zuzalpheus paraneptunus</i>	-0.422	1.05	0.926	1 619	0.0001	+	0.0001	6.87	131	
<i>Zuzalpheus dardeauui</i>	-0.446	1.04	0.963	1 440	0.0001	+	0.0001	4.64	56	
<i>Zuzalpheus chacei</i>	-0.454	1.06	0.960	2 665	0.0001	+	0.005	3.17	220	5
<i>Zuzalpheus regalis</i>	-0.531	1.21	0.971	37 903	0.0001	+	0.0001	21.98	1115	10
<i>Zuzalpheus filidigitus</i>	-0.485	1.16	0.976	12 819	0.0001	+	0.0001	20.02	311	7
ChL/BL										
<i>Zuzalpheus idios_f</i>	-0.290	0.37	0.685	24	0.0001	-	0.0001	9.26	13	
<i>Zuzalpheus paraneptunus_f</i>	-0.126	0.54	0.671	96	0.0001	-	0.001	3.56	48	
<i>Zuzalpheus dardeauui_f</i>	0.110	0.63	0.353	35	0.0001	-	0.0001	63.35	20	
<i>Zuzalpheus idios_o</i>	-0.236	1.00	0.914	404	0.0001	ns	0.5	0.43	39	
<i>Zuzalpheus paraneptunus_o</i>	-0.267	0.96	0.936	1 207	0.0001	-	0.0001	5.47	83	
<i>Zuzalpheus dardeauui_o</i>	-0.182	0.90	0.967	1 022	0.0001	-	0.0001	14.18	36	
<i>Zuzalpheus chacei_o</i>	-0.475	1.27	0.851	614	0.0001	+	0.0001	21.43	108	2
<i>Zuzalpheus regalis_o</i>	-0.624	1.39	0.931	14 933	0.0001	+	0.0001	33.41	1102	7
<i>Zuzalpheus filidigitus_o</i>	-0.711	1.59	0.898	1 826	0.0001	+	0.0001	47.42	208	2
FFL/BL										
<i>Zuzalpheus idios_f</i>	-0.203	0.35	0.131	2	0.163				9	
<i>Zuzalpheus paraneptunus_f</i>	-0.305	0.38	0.317	21	0.0001	-	0.0001	54.6	46	
<i>Zuzalpheus dardeauui_f</i>	-0.995	1.06	0.537	26	0.0001	+	0.001	4.50	23	
<i>Zuzalpheus idios_o</i>	-0.658	0.89	0.704	91	0.0001	-	0.0001	10.21	39	
<i>Zuzalpheus paraneptunus_o</i>	-0.804	0.90	0.796	289	0.0001	-	0.0001	7.91	75	
<i>Zuzalpheus dardeauui_o</i>	-0.635	0.78	0.886	361	0.0001	-	0.0001	6.74	37	
<i>Zuzalpheus chacei_o</i>	-1.02	1.32	0.883	374	0.0001	+	0.0001	40.59	104	2
<i>Zuzalpheus regalis_o</i>	-1.07	1.26	0.801	4 365	0.0001	+	0.0001	13.38	1102	7
<i>Zuzalpheus filidigitus_o</i>	-1.23	1.46	0.785	753	0.0001	+	0.0001	26.26	207	2
FFL/ChL										
<i>Zuzalpheus idios</i>	-0.432	0.87	0.727	137	0.0001	-	0.0001	44.33	52	
<i>Zuzalpheus paraneptunus</i>	-0.559	0.94	0.936	650	0.0001	-	0.0001	36.39	121	
<i>Zuzalpheus dardeauui</i>	-0.520	0.95	0.922	635	0.0001	-	0.0001	24.54	56	
<i>Zuzalpheus chacei</i>	-0.535	1.05	0.946	1 840	0.0001	+	0.0001	21.13	110	2
<i>Zuzalpheus regalis</i>	-0.519	0.93	0.928	11 303	0.0001	-	0.0001	25.67	1102	7
<i>Zuzalpheus filidigitus</i>	-0.557	0.89	0.864	1 330	0.0001	-	0.0001	27.98	210	2

The left-hand series of statistics tests whether the slope differed from zero, and the right-hand series tests deviation from isometry (i.e. whether slopes differed from 1). - and +, negative and positive allometry, respectively. *f*, reproductive female; *o*, others (juveniles, adult males, and nonreproductive adult females, if any). N_{ind} and N_{col} , numbers of individual shrimp and of colonies measured, respectively.

Table 2. Results of phylogenetically independent contrasts computed between the eusociality index (Keller & Perrin, 1995) and each of the metrics listed, using each of three trees (Morrison *et al.*, 2004)

Response metric	Combined data		Molecular (ML)		Molecular (Bayesian)	
	R^2 (adj)	P	R^2 (adj)	P	R^2 (adj)	P
Body length	0.170	0.270	0.285	0.206	0.148	0.284
Chela length	0.065	0.341	0.181	0.264	0.056	0.347
Sexual dimorphism in body length	-0.254	0.692	-0.144	0.532	0.240	0.230
Sexual dimorphism in chela length	0.503	0.110	0.901	0.009*	0.927	0.006*
Carapace/body length	0.446	0.132	0.311	0.193	0.453	0.130
Chela/body length (helpers)	0.622	0.070	0.765	0.033*	0.783	0.029*
Chela length/width	-0.309	0.829	-0.293	0.781	0.057	0.346
Fixed finger/body length (helpers)	0.391	0.156	0.535	0.099	0.693	0.051
Fixed finger/chela length (helpers)	-0.261	0.707	-0.199	0.603	0.075	0.333

The response metrics presented as ratios are slopes from regressions of log-transformed variables. * $P < 0.05$. ML, maximum likelihood.

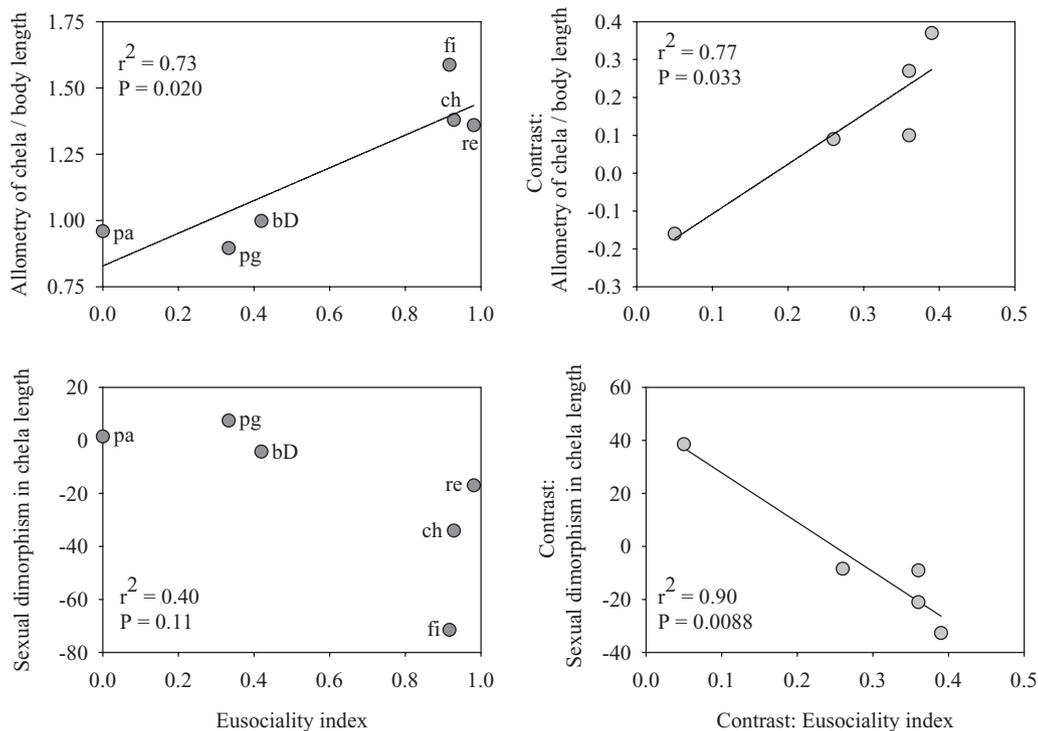


Figure 3. Cross-species relationships between level of social organization (the eusociality index; Keller & Perrin, 1995) and morphometric characteristics. Panels on the left are correlations using raw data, whereas panels on the right show phylogenetically independent contrasts computed with COMPARE, version 4.6b (Martins, 2004) using the tree derived from maximum-likelihood analysis of molecular characters (Morrison *et al.*, 2004). Symbols in left-hand panels correspond to species: ch, *chacei*; da, *dardeau*; fi, *filidigitus*; id, *idios*; pa, *paraneptunus*; re, *regalis*.

ratio than individuals in large colonies (Mann–Whitney test: *Z. chacei* $U_{14,108} = 525$, $P = 0.012$; *Z. regalis*: $U_{37,1102} = 9121$, $P < 0.0001$; *Z. filidigitus*: $U_{20,208} = 2062$, $P = 0.927$). The same trend was found for the finger/body ratio, in these two species (Mann–Whitney U -test: *Z. chacei* $U_{13,104} = 475$, $P =$

0.015; *Z. regalis*: $Z_{37,1102} = 8626$, $P < 0.0001$; *Z. filidigitus*: $U_{22,207} = 1914$, $P = 0.219$; Fig. 6). Finally, in large colonies, allometry of the finger relative to body length showed a change in slope (diphasic allometry) with the largest individuals having proportionately larger chelae and longer fingers than others (Fig. 6).

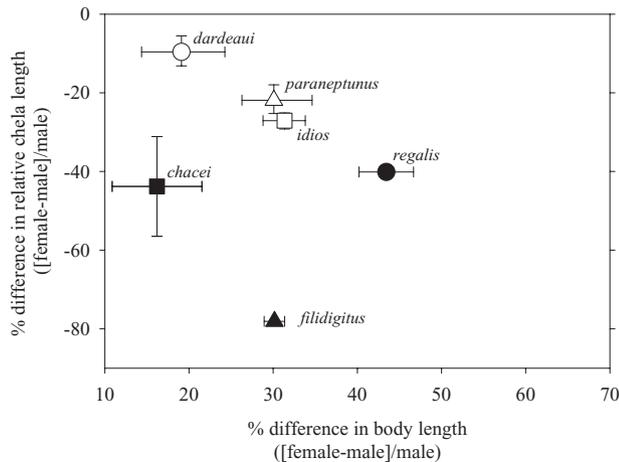


Figure 4. Sexual dimorphism of body and major chela length in three eusocial (filled symbols) and three pair-forming (open symbols) species of *Zuzalpheus*. For pair-forming species, symbols represent means (\pm bootstrapped 95% confidence interval) calculated from measurements of five females and five large males of each species pooled from several individual sponges. For eusocial species, colony means \pm standard error are given ($N_{\text{regalis}} = 7$, $N_{\text{chacei}} = 2$, $N_{\text{filidigitus}} = 2$). Relative chela length = chela length/body length.

DISCUSSION

Our comparisons of growth allometries in eusocial versus pair-forming shrimp species revealed that growth trajectories of several body features were closely correlated in both groups. However, several features of allometry differed consistently as a function of eusociality, including the steeper (log–log) slope of chela length on body length, and the stronger difference between breeding females and others in chela length, in eusocial species (Fig. 3). Moreover, comparisons of these characters among conspecific eusocial colonies differing in size (number of individuals) revealed further differences in growth allometry, particularly between helpers and queens, that may illuminate the ontogeny of caste differentiation as a colony grows. We consider several specific trends in allometry below.

In all species, breeding females had, on average, a larger body and a relatively smaller chela than other individuals did, generalizing results published on *Synalpheus paraneomeris* (Au & Banks, 1998) and several *Alpheus* species (Dawes, 1934; Nolan & Salmon, 1970; Schein, 1977; Knowlton, 1980). The larger body size of breeding females compared with others is easily understood in terms of their role as egg producers and embryo carriers. Interestingly, in contrast to eusocial societies of other animals, the degree of dimorphism in body size between breeding

females and others did not differ, on average, between eusocial and pair-forming shrimp species (Figs 2, 3). In both groups, breeding females carry embryos until they hatch, and elongate their bodies to be able to do so. Eusocial females do not carry as many embryos as pair-forming females do but, because their offspring are direct developers, they carry relatively larger embryos. Because most newly-hatched young in eusocial species do not disperse, but instead appear to stay in the sponge where they were born, their survival is probably enhanced by the effective colony defence of larger individuals. Reproductive fitness of breeding females in eusocial shrimp species may thus depend more on alloparental care, in the form of common colony defence. Also consistent with this hypothesis of alloparental care, the degree of sexual dimorphism in chela size in eusocial species was consistently and significantly stronger than that of pair-forming species; specifically, queens had smaller chela than males in eusocial species, whereas dimorphism was near zero in pair-formers. This implies that queens in eusocial colonies not only differ from paired species by producing fewer eggs, but also by a reduced share in defence. Reduced chela size is especially visible in *Z. filidigitus* (Duffy & Macdonald, 1999) in which the queen sheds the major chela and regenerates a second minor-form chela, providing strong indirect evidence that the queen in this eusocial species is insulated from any need for individual defence by protection of her colony. The similar, if less marked, trends in *Z. regalis* and the independently evolved *Z. chacei* (Morrison *et al.*, 2004) confirm that reduced chela size in queens might be a general phenomenon in eusocial shrimp. Our morphological results bolster previous findings of behavioural differentiation in *Z. regalis* between queens and others (Duffy *et al.*, 2002). In pair-forming alpheid species, successful defence of the territory depends on occupants of the pair (Schein, 1975; Mathews, 2002) and females in those species can be fairly aggressive (Knowlton & Keller, 1982; Hughes, 1996). Thus, this differentiation in chela dimorphism suggests a concomitant, functionally significant differentiation in defensive behaviour between eusocial and pair-forming species as well.

Our analyses of nonreproductive individuals in eusocial and pair-forming species revealed that the three eusocial shrimp we studied were not only smaller, but also tended to have proportionately larger and longer-fingered chelae than their less social congeners of similar size. Differences in weapon allometry may be related to effective territory defence. Oster & Wilson (1978) suggested that, all else being equal, reducing body size in eusocial colonies may provide an advantage because it permits a larger work force. Although small body size could be

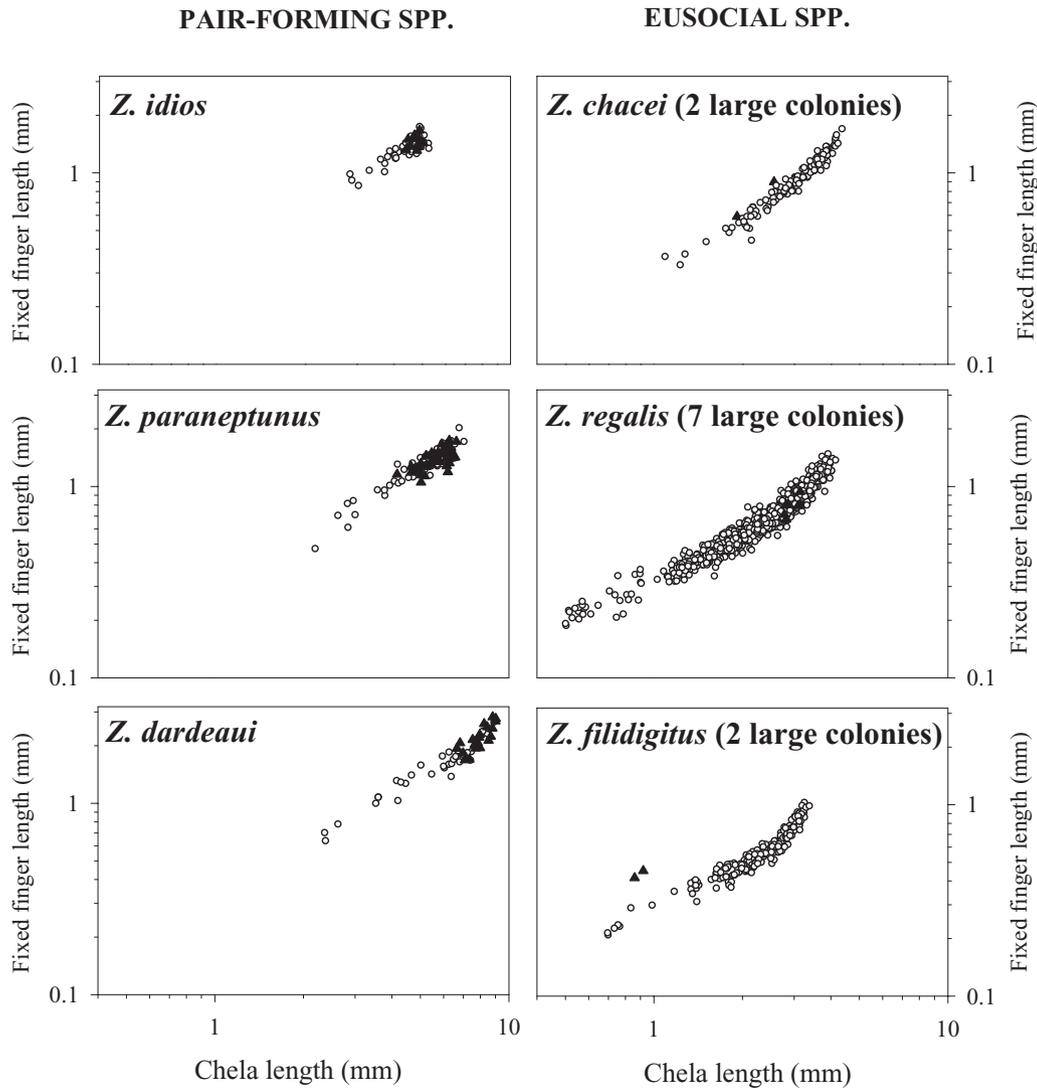


Figure 5. Logarithmic relationships between major chela length and fixed finger length in three eusocial (right column) and three pair-forming (left column) species of Zuzalpheus. Symbols and abbreviations are as indicated in Fig. 1.

advantageous in enabling colonies to produce more helpers for a given level of energy or resource availability, it has the disadvantage in territorial animals such as alpheid shrimp of reducing competitive ability in aggressive contests. This disadvantage of smaller body size in eusocial shrimp might be compensated if eusocial species live in narrow sponge canals that can be defended easily and that exclude larger animals that could invade them.

Our discussion so far has considered species-level patterns of differentiation that are visible when data are pooled across colonies and samples. Additional insights come from considering patterns of allometry among different sized colonies. Focusing on finger length of the fighting claw relative to body size (Fig. 5), the main result that emerges is that colonies

of all three eusocial species undergo a characteristic change in allometry with increasing colony size, and presumably age. Small, presumably young colonies are allometrically similar to those of pair-forming species in having an undifferentiated, approximately linear allometry with the reproductive female falling along the same line as helpers. As the colony grows in size (number of individuals), three things happen. First, the maximum size reached by non-queen individuals increases such that the largest colonies also have the largest individual shrimp. Second, the reproductive female diverges in size and proportion, growing distinctly larger than the largest non-queen, but with a much reduced major chela. Thus differentiation of the queen appears to be a gradual process, probably proceeding over many molts. Third, in the

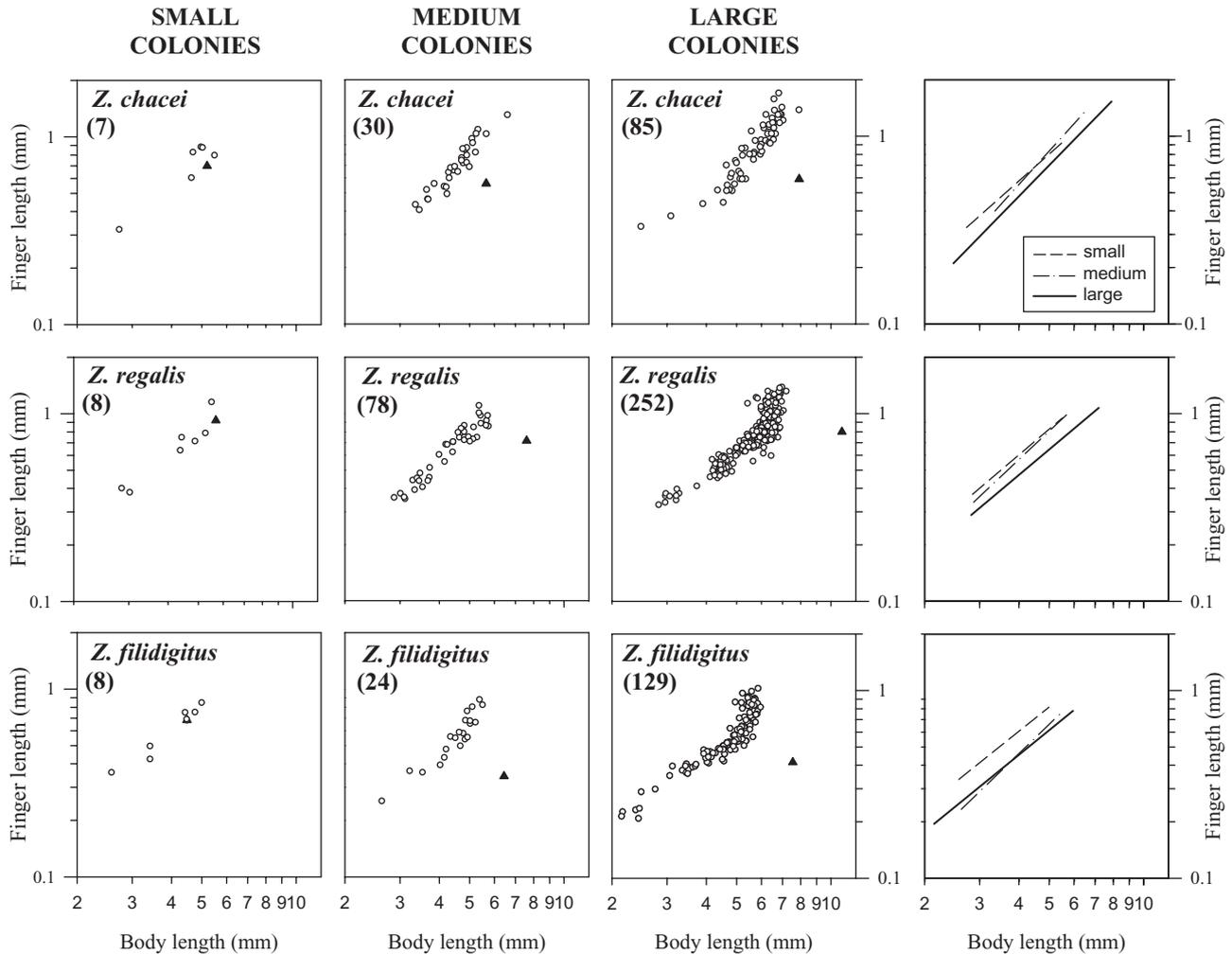


Figure 6. Logarithmic relationships between body length and fixed finger length in three eusocial species of *Zuzalpheus* in small (left), medium, and large (right) colonies. The column at far right shows the superimposed regression lines for colonies of the three sizes. Symbols and abbreviations are as indicated in Fig. 1.

largest colonies of all three species, there is a distinct change in the allometric relationship, with the largest animals reaching an asymptote in body length but continuing to grow in chela size.

Interestingly, there is a hint in the data for *Z. regalis* and *Z. chacei* that the largest animals in small colonies have larger chelae (and thus fingers) than animals of the same body size in mature colonies. Thus, the diphasic allometry in the largest colonies involves both decreased investment in chela growth at smaller body sizes, and increased investment in chela growth at larger body sizes, resulting in proportionately larger chela (and thus fingers) in large-bodied animals compared to the rest of the animals. One potential proximate explanation for this pattern is that, after reaching a certain size, investment in a larger body might not be favourable because individuals could outgrow their narrow sponge canals.

An ultimate explanation that does not exclude the previous hypothesis is that these larger, differentiated animals fulfil the function of soldiers, and their more frequent involvement in defence supports this (Duffy *et al.*, 2002; E. Tóth & J. E. Duffy, unpubl. data). Also consistent with this hypothesis that chela allometry responds to the changing defence needs of different-sized colonies is our finding that, in small colonies, individuals had relatively larger chelae. This makes sense in that defence of the resource by a smaller colony will be more difficult, and that all individuals need to participate in defence, requiring a higher average aggressive activity, than in a larger group (Oster & Wilson, 1978). Furthermore, as mentioned earlier, in small colonies, queens had chela proportions similar to those of other individuals, suggesting their more active role in defence as well.

The presence of diphasic allometry in large shrimp colonies is consistent with Wilson's interpretation of similar patterns in social insects, which he argued allow for production of a large, robust soldier caste. In eusocial shrimp, the larger individuals are more prone to fight (Duffy *et al.*, 2002; E. Tóth & J. E. Duffy, unpubl. data), consistent with their role as defenders analogous to the soldier caste of certain social insects. By contrast to some species of ants, social thrips and aphids (Wilson, 1971; Choe & Crespi, 1997), however, there is no discrete morphological separation in eusocial shrimp between soldier-like individuals and others; instead, the allometric curves show a more gradual transition in slope. Because shrimp molt many times, their growth is more gradual, and thus shrimp in this sense are similar to mole rats (Sherman *et al.*, 1991). Shrimp can thus gradually invest more in chela growth, and change is less constrained to be abrupt. As in mole rats, large individuals in *Z. regalis* are more involved in colony defence (Duffy *et al.*, 2002; Tóth & Duffy, unpublished data), although this defensive role does not seem to exclude smaller individuals, nor does it apparently involve all larger individuals in either mole rats (Lacey & Sherman, 1991) or in shrimp (E. Tóth & J. E. Duffy, unpubl. data).

In summary, our results demonstrate a clear morphological differentiation of reproductive females (queens) from other colony members in mature eusocial shrimp colonies, indicating that they belong to a separate breeder caste with proportionally smaller fighting claw and a tendency toward large body size. Body allometry in eusocial shrimp is flexible and changes during the course of colony growth, but differs consistently from that of pair-forming species. Small, young colonies of eusocial species have generalized morphology with no clear morphological differentiation among nonreproductive individuals (apart from that between the reproductive queen and the remaining individuals), whereas large colonies show both behavioural and morphological differentiation into queen, putative soldiers, and others. These results show that eusocial shrimp share several features of colony organization and caste differentiation with social insects and vertebrates, and suggest that selection pressures favouring eusociality have produced parallel results in these disparate taxa.

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