more than about 15 minutes, by which time the eruption apparently ceased and the ash flow dissipated. Our reconstruction of the deposit-forming flow is presented in Fig. 2d–f. These show, among other things, that the extended runout of the flow beyond about 40 km was due to the presence of fine particles in the parent suspension.

The total flux and near-vent solids concentration inferred for the Taupo event represent values which resulted form the collapse of the eruption column combined with continued discharge of new material at the vent. These values accordingly impose an upper limit on the rate of magma eruption of $5 \times 10^7 \, \text{m}^3 \, \text{s}^{-1}$. Given our assumptions regarding temperature and relative vapour content, this suggests that ejecta in the eruption column were at approximately 700 °C and that the fraction of water vapour was about 5% by weight. This result is consistent with independent estimates of water content in the eruption column[24]. Such conditions correspond to a scenario in which material erupted at vertical speeds in excess of $300 \, \text{m} \, \text{s}^{-1}$ from a vent with a radius of almost 1 km into a collapsing, fountain-like column[25]. The extensive dilution of vented material in the column, and thus its mobility in the resulting turbulent pyroclastic current, reflect the extreme explosivity of the eruption. Preliminary results of detailed calculations indicate that subtle changes in the inferred initial properties of the parent flow do not alter the basic picture presented here.

We are confident that additional details of the Taupo deposit can be reconciled with more sophisticated models for turbulent-flow emplacement. Some near-vent features of the ignimbrite, for instance, may be the result of inhomogeneities in particle concentration in the parent eruption column[26]. Abrupt changes in fines and lithic contents in the ponded deposits at distances of 50–60 km from the vent, on the other hand, may reflect changes in the degree of stratification of the transporting flow[15,22] or interaction of the flow with regional topography which, on average at these distances, comprises ridge-like obstacles that are 500–1,000 m above vent level. These details are qualitatively consistent with our approach but are not explicitly accommodated.

The ease with which our quantitative model can predict regional patterns in deposit characteristics at Taupo argues strongly for the reconsideration of other ignimbrites with similar geometry and sorting trends previously interpreted solely in terms of the prevailing model of emplacement by a highly concentrated flow. Broad consistency of field data with a turbulent-flow model alone does not, of course, exclude other mechanisms of emplacement. In our view, an important challenge is to determine additional deposit properties which can be used to differentiate emplacement mechanisms and relate these to eruption history and associated volcanic hazards. A potentially powerful tool in this regard is the measurement of anisotropy of magnetic susceptibility[27] which reveals the fabric of iron-bearing, elongate grains in a deposit which, in turn, is related to the mechanism of emplacement. Given the current developments in both theory and observation, we suggest that the term 'low-aspect-ratio ignimbrite' be applied only to the physical characteristics of a deposit, and be stripped of connotations regarding the mechanism of emplacement. □

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Eusociality in a coral-reef shrimp

J. Emmett Duffy

School of Marine Science and Virginia Institute of Marine Science,
The College of William and Mary, Gloucester Point, Virginia 23062, USA

THE apex of animal social organization is eusociality, which has three characteristics: overlapping generations, reproductive division of labour, and cooperative care of young[1,2]. So far, eusociality has been recognized only among social insects and the African mole-rats[3–5]. Here I report the first case of eusociality in a marine animal. The sponge-dwelling shrimp Synalpheus regalis lives in colonies that may have >300 individuals, but that contain only one reproductive female. Direct-developing juveniles remain in the natal sponge, and allozyme data suggest that most colony members are full sibs. In laboratory experiments, larger colony members, most of whom apparently never breed, defended the colony against heterospecific intruders. Ecological similarities among mole-rats, termites and these sponge-dwelling shrimp, all of which are diploid animals, strengthen arguments that eusociality is favoured by gradual metamorphosis, parental care, and occupation of protected, expansible niches[6].

The mobile cryptofauna of coral reefs is frequently dominated by snapping shrimps (Synalpheus)[7–9], many of which live within the internal canals of sponges. S. regalis is an abundant cryptofaunal species at Carrie Bow Cay, Belize, and inhibits the sponges Xestospongia cf. subtriangularis and Hyattella intestinalis[9,10]. Each of over 30 dissected sponges contained a colony of S. regalis consisting of 3–313 individuals ($\bar{x} = 149$, from 17 complete colonies examined). As tropical Synalpheus species apparently breed continuously (J.E.D., personal observation), reproductive females are easily identified by ripe ovaries or brooded eggs, yet each colony invariably contained only a single reproductive female. The remaining juveniles and mature males are difficult to distinguish morphologically, probably reflecting a socially mediated sex-determination system, as is known in another alpheid[11]. By having just one female, these colonies clearly meet the first criterion of reproductive division of labour.

Eusociality also requires that generations overlap[2], bringing individuals into contact with close kin such that altruistic behaviours can be favoured by kin selection[12]. Three lines of evidence indicate that S. regalis colonies consist primarily of sibling offspring of the lone female (the 'queen'). First, S. regalis eggs hatch into crawling juveniles; successive cohorts of small juveniles are clearly recognizable in many colonies, suggesting that they nor-

mally remain in the natal sponge. Second, larger (presumably older) queens have accumulated larger colonies than have smaller ones; queen body size explains 65%, and fecundity 75%, of the variation in colony size (Fig. 1). Finally genotype frequencies at three polymorphic allozyme loci yield an average value for r (relatedness[13]) of 0.57 (Table 1), close to the value of 0.50 expected for full sibs. This suggests that most colony members (there may be >300) are offspring of the queen, and possibly of a single male. If indeed a single 'king' fathers most offspring (the possibility of inbreeding complicates this conclusion), he is not obviously distinguished by morphology.

The distinctive feature of eusociality is the altruistic behaviour of non-breeders, particularly cooperative feeding and defence of young. Sponge-dwelling shrimps apparently obtain food from the host's feeding current and/or tissues[10,14,15], such that food within the sponge is probably not limiting. Instead, the biggest challenge facing shrimp colonies in the coral-rubble habitat, where unoccupied habitable sponges are virtually non-existent[8,10], is probably invasion of the nest by competitors. Responses of colonies to conspecific intruders have not yet been tested, but the role of non-breeders in defending the colony against interspecific competitors was demonstrated by exposing colonies in the laboratory to heterospecific intruders and to previously isolated colony-mates ('natives') (Fig. 2). The results were dramatic: contact between a resident and a 'foreign' intruder (an undescribed species near *Synalpheus bousfieldi*) generally resulted in an intense battle, with both individuals repeatedly snapping at one another with their powerful major chelae (claws). This continued sporadically until the intruder was killed. In two of ten experimental runs, two residents together gripped the vanquished intruder's carcass and dragged it out of the chamber. In stark contrast, contacts between residents and 'natives' were quite peaceful. Importantly, larger residents were most active and aggressive, contacting foreign

intruders more than twice as often as did smaller residents, and engaging intruders in combat (snapping) ten times more often than did juveniles (Fig. 2). Because larger individuals, most of whom are unlikely ever to reproduce, perform most of the colony defence, and thereby benefit juveniles, this nest defence amounts to cooperative brood care, fulfilling the third criterion of eusociality.

The finding of eusociality in a diploid marine shrimp is especially intriguing as *S. regalis* exhibits precisely those characteristics hypothesized to have fostered eusociality in termites and mole-rats, the two previously known diploid, eusocial taxa, namely 'gradual metamorphis, subsociality (extensive parental care), and life in long-lasting, expansible niches (nests or microhabitats) safe from predation and rich with food that does not require exiting the safety of the niche to obtain it' (ref. 6, p. 42). The advantage of cooperation in defending such nests is widely believed to be a primary selective pressure for advanced social life[2,5,6,16–20], and cavity nesting is indeed characteristic of nearly all eusocial taxa, including most ants[21], all termites[2], mole-rats[5], ambrosia beetles[22], and gall-dwelling aphids[23] and thrips[24]. Similarly, living within sponge canals appears to have been an important preaptation for eusociality in *S. regalis*, as many of its
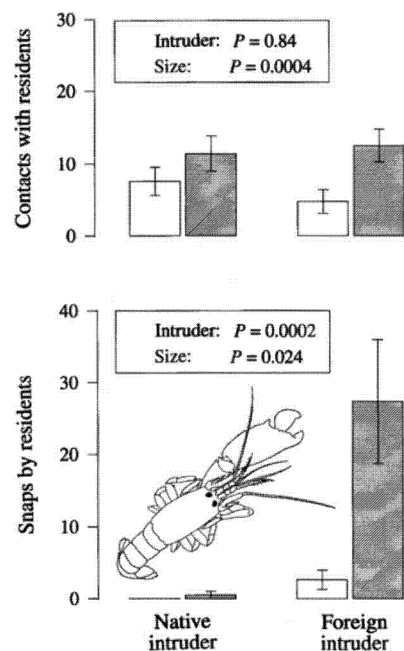
FIG. 2 Responses of laboratory colonies of *Synalpheus regalis* to intrusion by a heterospecific competitor, versus intrusion by their own colony-mates. Experiments were conducted in viewing chambers consisting of a system of canals cut in neoprene and pressed between transparent plastic plates. After submerging the assembly in a flow-through aquarium, part of a colony of shrimp (the female, 8 large males, and 8 juveniles) was introduced and allowed to acclimate overnight. In the morning, two experimental trials were conducted sequentially: (1) a member of the resident colony ('native') that had been isolated overnight was introduced to the chamber; and (2) a 'foreign' intruder of an undescribed species near *S. bousfieldi* was introduced. The order of introduction was alternated in successive trials ($n = 8$ trials). The colony was observed for 30 min, during which all contacts and snaps between residents and intruder were recorded, along with the size (small, white bars; large, shaded bars) of the resident involved in these interactions. Foreign intruders that remained alive at the end of 30 min were invariably killed by residents within a few hours. P-values were obtained by randomly reassigning the observed counts among the four treatment cells within a 'block' (that is, the replicates introducing foreigner and native to the same colony of residents) 10,000 times and calculating the proportion of these randomizations in which differences as great as or greater than the observed values were found. The P-value for Intruder is for the difference between responses to native versus foreign intruders, irrespective of size class; similarly, the P-value for Size is for the difference between small and large residents, irrespective of intruder type. Bars show $\bar{x} \pm 1$ s.e.m.
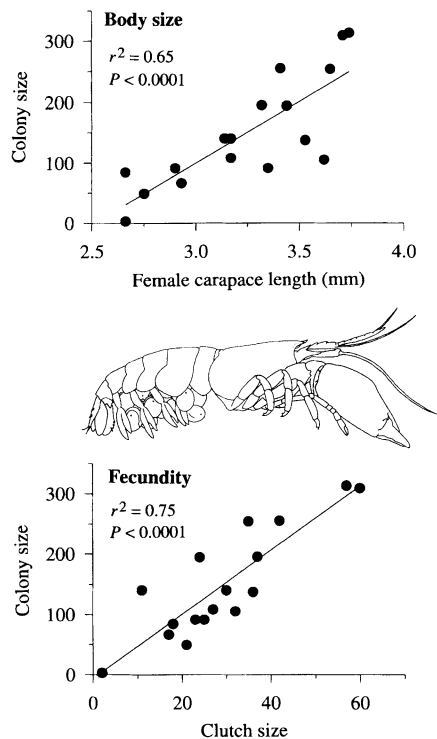

FIG. 1 Positive relationship between the body size and fecundity of the queen, and total colony size in *S. regalis*. Complete shrimp colonies were dissected from 17 sponges, *Xestospongia* cf. *subtriangularis* and *Hyattella intestinalis*, from the outer reef ridge (15–20 m depth) at Carrie Bow Cay, Belize; all individuals were counted, the carapace length (an index of body size) measured, and the number of embryos carried by the female in each colony counted.

TABLE 1	Estimates of average genetic relatedness among colony members in *Synalpheus regalis*		
Locus		*n*	Average *r*
Pgi		208	0.50 (0.14)
Tpi		201	0.66 (0.13)
Pep		194	0.56 (0.15)
Mean		208	0.57 (0.04)

Genotypes were scored, using standard methods[9], at three polymorphic allozyme loci in 17–22 individuals from each of 10 colonies (*n* is the total number of individuals used in a calculation) collected along a ~200-m transect on the outer reef ridge at Carrie Bow Cay, Belize. Relatedness (*r*) was estimated according to the expression given in ref. 13, with s.e. (in parentheses) estimated by jack-knifing over colonies; the estimates were obtained using the program Relatedness 4.2 (K. F. Goodnight). The mean value of within-colony relatedness, 0.57, is quite close to that (0.50) expected for full sibs, and suggests that colony members are offspring of a single breeding pair.

sponge-dwelling congeners live in groups of tens to hundreds per sponge[8,14,15,25], and direct development is common among such species[26,27] (J.E.D., unpublished observation). In contrast, most other alpheids produce planktonic larvae, live in heterosexual pairs, and are aggressive towards other conspecifics[11,26–29]. Eusociality in *Synalpheus* may also have been fostered by possession of a powerful weapon, the major chela, as argued for the sting of Hymenoptera and perhaps the conspicuous weapons of other eusocial taxa[2,20,23,24]. Interestingly, the likelihood of eusociality among crustaceans has been predicted[30], based in part on the direct development and cavity-dwelling habits of many crustaceans. Indeed, I have collected two other monogynous, probably eusocial, species of *Synalpheus* in Belize. This discovery supports conclusions that eusociality in disparate animal taxa was favoured by kin selection interacting with strong natural selection imposed by enemies. □

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CORRESPONDENCE and requests for materials should be addressed to the author (e-mail: jeduffy@vims.edu).

Embryology of vestimentiferan tube worms from deep-sea methane/sulphide seeps

Craig M. Young*, Elsa Vázquez*, Anna Metaxas* & Paul A. Tyler†

* Department of Larval Ecology, Harbor Branch Oceanographic Institution, 5600 U.S. Highway 1 North, Fort Pierce, Florida 34946, USA
† Department of Oceanography, University of Southampton, Southampton SO9 5NH, UK

THE Vestimentifera are gutless worms that live around deep-sea hydrothermal vents and cold seeps, obtaining energy from hydrogen sulphide with the aid of endosymbiotic chemosynthetic bacteria[1–3]. Their phylogenetic relationships have been debated ever since they were first discovered[4,5]. Moreover, hydrothermal vents are ephemeral and spatially patchy, raising questions about how vestimentiferan populations are established and maintained[6–9], and how symbionts are transmitted[10]. Although post-settling juveniles have been described[11,12], embryos and larvae have been neither collected nor cultured. Here we describe the early development of vestimentiferans from cold seeps in the Gulf of Mexico[13], and discuss the implications of our findings for dispersal potential and phylogeny.

Lamellibrachia sp. and *Escarpia* sp. (Fig. 1) were collected by manned submersible and dissected immediately. Details of the culture methods are given in the figure legends; developmental descriptions apply to both species unless stated. Eggs are optically dense and positively buoyant, those of *Escarpia* sp. being slightly