Will sponge introduction in bleached coral reef habitats slow the decline of eusocial behaviours in native shrimp populations?

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General overview: The disappearance of sea sponges has been correlated to decline and extinction of eusocial sponge-dwelling snapping shrimp (*Synalpheus regalis*). This study aims to assess whether the introduction of two different sponges into areas that have seen eusocial *S. regalis* decline would work as a conservation effort and consequently restore eusocial community structure.

Introduction

Background on eusocial *S.Regalis*: In 1996 the first instance of eusociality in tropical snapping shrimp (*S. regalis*) was reported, offering a unique insight into the evolution of sociality (Duffy, 1996). These sponge-dwelling shrimp live in large colonies (>300 individuals) containing only one reproductive female, similar to the eusocial behaviours and colony structures observed in social insects (Duffy, 1996; Ross & Keller1995). The maintenance of these eusocial species of shrimp is not only important in terms of maintaining diversity but will allow for further studies on the evolution of sociality. Eusociality requires that the following characteristics be met by a species: overlapping generations, reproductive division of labour, and cooperative care of young (Duffy, 1996). Not dissimilar to previously noted eusocial insects, eusocial *S. Regalis* are known to live in large multigenerational colonies, with one reproductive queen and cooperative brood care.

Sponge habitats for Eusocial Shrimp species: *S Regalis* only live inside these sponges, and this habitat is thought to be an important prerequisite for the eusocial behaviours seen in *S. Regalis* (Duffy, 2003). The sponge allows for the three eusocial characteristics to be met by the inhabitant species: The sponge allows for several generations to cohabit at any one time which in turn eases the reproductive division of labour, cooperative care of young and maintenance of large colonies. The eggs of eusocial sponge-dwelling shrimp hatch into non-swimming shrimp larvae that remain in the natal sponge (Duffy & Macdonald, 2010; Hultgren et al, 2017), which is in contrast to non-eusocial shrimp that release swimming larvae outside of the sponge habitat. Eusocial shrimp larvae remaining within the natal sponge facilitates the aforementioned 'natal philopatry'. All previous literature has suggested that *Synalpheus* species live their entire life in their colonies host sponge, which acts as a stable and predator free habitat (Duffy & Macdonald, 1999). Hence, the conservation of these sponge habitats is important to the maintenance of eusocial sponge-dwelling shrimp species.

Climate change and seas sponges: As global temperature rises, and the effects of climate change become ever-present, coral reefs around the world have seen mass events of bleaching and degrading due to ocean warming (Bell et al, 2013). Increased ocean temperatures can affect sea sponges in a number of ways. The sponge's reproductive capability and overall fitness can be negatively impacted, and at an extreme, ocean warming can kill sponges (Carbello & Bell, 2017). There is, however, evidence that some sponge species may not exhibit the same thermal sensitivities. For example, one 2002 study found that one particular sponge, in the Caribbean, *Chondrilla nucula,* survived a coral bleaching event caused by abnormally high ocean temperatures (Aronson et al. 2002). Additionally, deep-sea sponges such as *Euplectella aspergillum* are known to have an incredibly high melting points due to their silica composition(Sundar et al., 2003). Whilst a high melting point isn't necessary, this does suggest that these sponges would be unaffected by ocean warming events. Such sponge species offer hope and insight into possible solutions for maintaining eusocial shrimp colonies despite rising ocean temperatures.

Eusocial shrimp species decline: Eusocial shrimp that had previously dominated the Belize Barrier Reef were seen to decline in numbers (Duffy, 2013). In fact, three of the four dominant eusocial species had disappeared from the habitat. Prior to their disappearance strong declines were also observed in both average colony sizes and increases in the frequency of queenless colonies (Duffy, 2013). Simultaneously, several pair-forming, non-eusocial *Synalpheus* shrimp species increased in frequency. These non-eusocial species are not reliant on the sponges to the same extent as eusocial colonies. Duffy (2013) reported that the decline in eusocial shrimp species happened concurrently with the disappearance of two of the sponge species that usually act as shrimp habitats. The decline of eusocial shrimp and the increase in pair-living species happening simultaneously as the host sponge disappear from the habitat, suggesting that the changes in coral reef ecology affect eusocial species more negatively than their non-eusocial counterparts.

Study aims

Objective: To assess whether introduction of both *Chondrilla nucula* and *E.aspergillum* sponges into areas of the Belize Barrier Reef will slow the extinction rate of eusocial shrimp colonies, and increase observable eusocial behaviours.

Hypothesis and prediction: Declining native sponges causes decline in eusocial shrimp numbers, as well as observed eusocial behaviors in remaining inhabitant shrimp.In areas where new sponges are introduced compared to control areas, the following observations are expected: an increase in *S Regalis* eusocial shrimp abundance, increase in *S Regalis* colony size and increase in number of colonies with a queen.

Study population: The study site will be the Belize Barrier Reef. A decline and extinction event of eusocial sponge-dwelling shrimp was identified in this area by Duffy et al (2013). Specifically, I will study the shrimp populations in the same region of small reefs in the lagoon behind the Barrier Reef; in the vicinity of the Smithsonian Institution's field station at Carrie Bow Cay (16°48.155'N, 088°04.896'W).

Methods

Implementation of sponges: Maturing *C. nucula* and *E. aspergillum* sponges will be planted in the Belize Barrier Reef. This reef has experienced the recent extinction of several sponge species that were hosts to eusocial Synalpheus shrimp species (*Neopetrosia proxima, Neopetrosia subtriangularis,* and *Oceanapia sp*; Duffey et al, 2013). Whilst relocation of sponges is not a common conservation practice, both *C. nucula* and *E. aspergillum* have been shown to be robust to environmental change (Sundar et al., 2003 & Aronson et al. 2002). After planting, researchers will check the sponge's biweekly for 6 months to ensure they have survived.

Study areas & monitoring: Both the control and the experimental areas will be separated into 10 x 4m^2 quadrants that will be marked by red flags driven into the reef. This is a technique that worked well in a 2011 study by Duckworth and Wolff on reef sponge growth (Duckworth & Wolff, 2011). In order to assess the hypothesis, a control area will also be studied for the same period of time. This area will receive no new sponges and will act as a control. Each quadrant will be monitored every 4 months for 4 years.

Analysis of Shrimp populations: In order to characterise community structure observed in the reef and in the new sponge habitats, I will utilise Non-metric MultiDimensional Scaling (NMDS), which was previously used by Duffy et al (2013) for a similar purpose. In order to assess eusocial vs non-eusocial shrimp abundance, the NMDS analysis of shrimp communities will involve abundances of each in any given collected sample: % eusocial shrimp of total shrimp in sample. Identification of *S Regalis* species will be assessed via observations of their colour, body size, and social structure as observed by the researcher. These observations will be guided by the Zootaxa publication used for similar purposes by Duffy et al (2013), that can be found in the appendix (MacDonald et al., 2009). Notably, *S regalis* are distinguished from close relatives by their 'ventrally rounded abdominal pleura and their secondary spine on the major chela protuberance' (MacDonald et al, 2009). See figure 1 for more detail. These observations will be confirmed using microscopic examination of the shrimp morphology (Rios et al, 2007). Eusocial behaviours will also be assessed by the presence or absence of a queen in each colony, and overall size of each colony. As previously mentioned, both the presence of a queen and large colony sizes are characterized features of eusocial *S Regalis.*

Expected results: The control area will be compared to the experimental area that received the maturing sponges. If the hypothesis is correct, then the NMDS analysis will show that the areas where new sponges saw an increase in eusocial shrimp numbers and eusocial behaviours when compared to control areas. This will entail an increase in *S Regalis* eusocial shrimp abundance (%), increase in *S Regalis* colony size and increase in number of colonies with a queen.

Intellectual merit

By conducting this research, not only will we be contributing to coral reef conservation efforts, but we will maintain the eusocial *S.regalis* species so that the evolution of sociality can be further studied and understood. By maintaining these habitats, we are creating opportunities for further research into the specific traits and characteristics that allow for the evolution of eusociality. Future studies can utilise the habitats we create as a means to conduct comparative studies into the phylogenetic differences between the social and nonsocial shrimp species that cohabit these sponges.

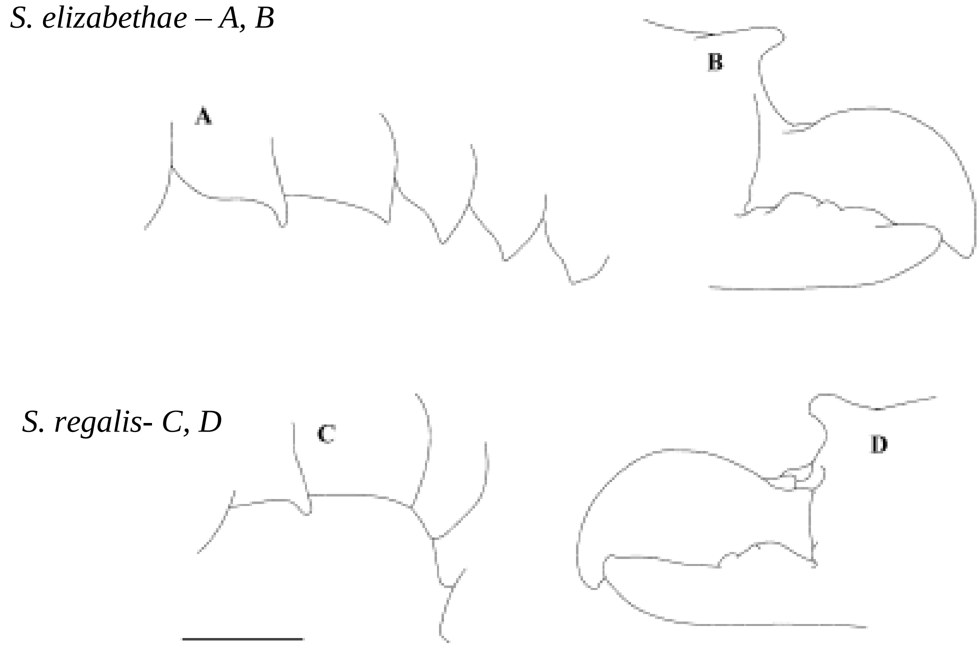

***Figure 1**. Comparison of S. regalis to close relative S. elizabethae. A&C represent the ventral region of the abdomen. B&D represent the chela of major first pereopod anterior region.* Drawn from Zootaxa: ‘The sponge-dwelling snapping shrimps (Crustacea, Decapoda, Alpheidae, Synalpheus) of Discovery Bay, Jamaica, with descriptions of four new species’ (MacDonald & Duffy 2009).

Appendix

From Zootaxa: 'The sponge-dwelling snapping shrimps (Crustacea, Decapoda, Alpheidae, Synalpheus) of Discovery Bay, Jamaica, with descriptions of four new species' (MacDonald & Duffy 2009).

***Synalpheus regalis* Duffy**
Figure 10, Color plate 5B

Material examined. Jamaica: 96 non-ovigerous individuals, 1 ovigerous female (VIMS 08JAM3303-05), fore-reef (near M1 channel marker), Discovery Bay, from canals of *Hyattella intestinalis*. 56 non-ovigerous individuals, 1 ovigerous female (VIMS 08JAM4201-03), fore-reef (near M1 channel marker), Discovery Bay, from canals of *H. intestinalis*. 59 non-ovigerous individuals, 1 ovigerous female (VIMS 08JAM4901-03), Columbus Park, Discovery Bay, from canals of *H. intestinalis*. 82 non-ovigerous individuals, 1 ovigerous female (VIMS 08JAM5101-03), Columbus Park, Discovery Bay, from canals of *H. intestinalis*. 7 non-ovigerous individuals (VIMS 08JAM5201), Columbus Park, Discovery Bay, from canals of *H. intestinalis*. 24 non-ovigerous individuals, 1 ovigerous female (VIMS 08JAM5401,02,04), Columbus Park, Discovery Bay, from canals of *H. intestinalis*. 59 non-ovigerous individuals, 1 ovigerous female (VIMS 08JAM6001-03), Columbus Park, Discovery Bay, from canals of *H. intestinalis*. 66 non-ovigerous individuals, 1 ovigerous female (VIMS 08JAM6201-03), Columbus Park, Discovery Bay, from canals of *H. intestinalis*. 265 non-ovigerous individuals, 1 ovigerous female (VIMS 08JAM6301-03), Columbus Park, Discovery Bay, from canals of *H. intestinalis*. 202 non-ovigerous individuals, 1 ovigerous female (VIMS 08JAM6401-03), Columbus Park, Discovery Bay, from canals of *H. intestinalis*. 6 non-ovigerous individuals (VIMS 08JAM7601), wall off Rio Bueno, from canals of *H. intestinalis*. 23 non-ovigerous individuals (VIMS 08JAM7901), wall off Rio Bueno, from canals of *H. intestinalis*. 25 non-ovigerous individuals, 1 ovigerous female (VIMS 08JAM8601-03), wall off Rio Bueno, from canals of *H. intestinalis*. 265 non-ovigerous individuals, 1 ovigerous female (VIMS 08JAM9101-03), Columbus Park, Discovery Bay, from canals of *H. intestinalis*. 29 non-ovigerous individuals (VIMS 08JAM9201,02), Columbus Park, Discovery Bay, from canals of *H. intestinalis*. 88 non-ovigerous individuals (VIMS 08JAM9301,02), Columbus Park, Discovery Bay, from canals of *H. intestinalis*. 31 non-ovigerous individuals, 1 ovigerous female (VIMS 08JAM9401,02), Columbus Park, Discovery Bay, from canals of *H. intestinalis*. 10 non-ovigerous individuals (VIMS 08JAM9501), Columbus Park, Discovery Bay, from canals of *H. intestinalis*. 18 non-ovigerous individuals (VIMS 08JAM9601,02), Columbus Park, Discovery Bay, from canals of *H. intestinalis*. MaxCL ovigerous female: 4.14 mm. MaxCL non-ovigerous individual: 3.17 mm.

Color. Translucent orange; distal portion of major chela brighter orange; embryos and ovaries pale green.

Hosts and ecology. In Jamaica, we have found *S. regalis* exclusively in *Hyattella intestinalis*, typically at depths exceeding 6 m. In Belize, the only other known locality of *S. regalis*, they are commonly found in *Xestospongia* spp. in addition to *H. intestinalis*.

Distribution. Belize (Duffy 1996a,d, Macdonald et al. 2006; Ríos and Duffy 2007); Jamaica (this study).

Remarks. *Synalpheus regalis* is distinguishable from its close relative, *S. elizabethae*, by the possession in non-ovigerous colony members of abdominal pleura (pleura 3–5) that are rounded ventrally versus the ventrally pointed pleura possessed by *S. elizabethae* (Fig. 10). Similarly to the *S. elizabethae* found here, *S. regalis* individuals in Jamaica lack a secondary spine on the major chela protuberance (Fig. 10).

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