

REPORT

Perilous proximity: Does the Janzen–Connell hypothesis explain the distribution of giant barrel sponges on a Florida coral reef?

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Abstract One popular concept used to explain the high biodiversity of some ecosystems is the Janzen–Connell hypothesis, which states that the distribution of conspecifics is controlled by species-specific pathogens or predators that are attracted to adults or to their reproductive output. The distribution of the affected species would then display a distinct pattern, with survivorship increasing at greater distance from the conspecific adult (negative density dependence), leaving a vacant area around the adult where other species can survive. The giant barrel sponge, *Xestospongia muta*, is an abundant and long-lived sponge on Caribbean coral reefs that is actively grazed by sponge-eating fishes and is susceptible to disease. We tested the Janzen–Connell hypothesis on barrel sponges on Conch Reef, Florida, by examining their distribution as a function of size using spatial point pattern analyses. Clark and Evans tests and a series of Ripley's K function analyses revealed no consistent distribution pattern, with most analyses resulting in a random pattern of sponge distribution. While predation by sponge-eating fishes has recently been discovered to structure sponge communities on reefs across the Caribbean, these top-down effects do not translate to spatial distributions of *X. muta* that support Janzen–Connell predictions.

Keywords Spatial ecology · Coral reefs · Biodiversity · Predation · Pathogenesis

Introduction

The mechanisms that maintain high diversity in some ecosystems, like tropical forests or coral reefs, are often difficult to determine because of the complexity of abiotic factors and species interactions. One theory used to explain high biodiversity is the Janzen–Connell hypothesis, which states that the distribution of individuals is affected by the presence of species-specific pathogens or predators that are attracted to adults or to the high density reproductive output of adults (Janzen 1970; Connell 1971). The distribution of the affected species then displays a distinct pattern, with survivorship increasing at a greater distance from the conspecific adult (negative density dependence), leaving an unpopulated area around the adult. This maintains high biodiversity in an ecosystem, because the vacant space surrounding each adult is available for recruitment from other species.

Since its formulation, the Janzen–Connell hypothesis has been tested in both tropical and temperate forests and remains a popular explanation for the generation and maintenance of tree diversity (Augsburger 1983; Packer and Clay 2000; Bell et al. 2006; Johnson et al. 2012). Given the spatial representation of the hypothesis, ecologists frequently use spatial surveys to look for positive Janzen–Connell interactions in a community before identifying the specific pathogen or predator that is causing the spacing pattern (Augsburger 1983; Packer and Clay 2000). Although the hypothesis was specifically developed to explain tree distributions in tropical forests, it has recently been used to explain coral distribution on tropical reefs

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(Vermeij 2005; Vermeij and Sandin 2008; Marhaver et al. 2013).

While stony corals have historically dominated Caribbean reefs, these communities are becoming increasingly dominated by other benthic organisms (Norström et al. 2009; González-Rivero et al. 2011). On Caribbean coral reefs, sponges commonly surpass corals in dominance and occur at much higher levels of diversity (Diaz and Rutzler 2001; Loh and Pawlik 2014). Additionally, many sponges are long-lived and exhibit a variety of forms, providing structural complexity to coral reefs (Duffy 1992; Henkel and Pawlik 2005; McMurray et al. 2008). However, because of the difficulty associated with studying them (primarily taxonomic), sponges have historically been understudied, and the factors that influence their distributions remain largely unknown (Diaz and Rutzler 2001).

Like corals, sponges are susceptible to factors that may affect their distribution in accordance with the Janzen–Connell hypothesis (i.e., pathogenesis and predation). In addition to the many documented sponge diseases (Webster 2007), sponges have the ability to concentrate even rare waterborne pathogens from the water column by filter feeding (Hill 2004). Predation on sponges is also a common phenomenon. Sponges serve as a food source for vertebrate predators on the reef, including angelfish, parrotfish, and sea turtles (Meylan 1988; Dunlap and Pawlik 1996; Pawlik 2011; Pawlik et al. 2013), as well as some invertebrates (Pawlik 1983; Birenheide et al. 1993; Wulff 1995).

The giant barrel sponge *Xestospongia muta* is the second most common sponge on Caribbean reefs in terms of benthic cover (Loh and Pawlik 2014) and occupies over 9 % of the benthos in some locations (Zea 1993). Long-term monitoring of this species has resulted in a more comprehensive understanding of growth and demographics than for any other sponge species (McMurray et al. 2008, 2010). Sometimes referred to as the “redwood of the reef,” *X. muta* has been estimated to live for hundreds to thousands of years and can grow to over a meter in height and diameter (McMurray et al. 2008). Giant barrel sponges are broadcast spawners that release negatively buoyant eggs that cover the reef during reproductive events (Ritson-Williams et al. 2005). Because of their large size and morphology, barrel sponges do not reproduce by fragmentation and reattachment after dislodgement is very rare (McMurray and Pawlik 2009). *X. muta* is variably chemically defended (see Loh and Pawlik 2014), although it is primarily undefended in the Florida Keys reef tract, and most individuals exhibit fish-grazing scars (Chanas and Pawlik 1997; Dunlap and Pawlik 1998). Sponge orange band (SOB) syndrome was also described from the population of *X. muta* on Conch Reef (Coward et al. 2006). Therefore, both predation and pathogenesis affect

populations of *X. muta*, providing the conditions under which the Janzen–Connell hypothesis has been proposed to occur. Demographic studies of the Conch Reef population of *X. muta* have documented the highest levels of mortality among the youngest sponge recruits (~10 % within the first year, ~25 % for the smallest size class over a 3-yr interval between 2000 and 2006; McMurray et al. 2010). As with most study systems, there are no empirical data to specifically identify the sources of pre-recruitment mortality, but based on the sources of mortality acting on larger sponges, we can infer that some combination of predation and pathogenesis is partially involved.

In the present study, we examined the distribution of *X. muta* as a function of size through a series of point pattern analyses to test Janzen–Connell predictions on replicate survey plots at Conch Reef, Florida. Previous applications of this hypothesis to organisms in marine ecosystems have examined differential survival of reef-building corals using manipulative recruitment experiments (Marhaver et al. 2013), but unpredictable spawning (Ritson-Williams et al. 2005) and difficulty maintaining sponge larvae precluded this approach. Therefore, this study employed analyses of distribution maps from plots subjected to long-term monitoring to test for spatial patterns of sponge individuals ranging from ~1-cm new recruits to nearly 1-m diameter adults to determine whether their distributions reflect Janzen–Connell predictions of increasing sponge survival at increasing distances from adults.

Methods

This study was conducted on Conch Reef (24°56'59"N; 80°27'13"W) off Key Largo, Florida, where plots of *X. muta* have been monitored annually since 1997 for recruitment, mortality, disease, bleaching, and general sponge condition (McMurray et al. 2008, 2010). Every individual of *X. muta* was identified within six plots, three plots at each depth of 20 and 30 m. All plots are 16-m diameter circles with the exception of one of the deep plots, which has a 12 m diameter. In May 2012, the relative position of each *X. muta* was mapped within each plot using a basic triangulation technique, measuring from the center of the plot and from a directional stake on the circumference of the plot to each sponge. The long-term monitoring data confirmed that 2012 was not an anomalous year for sponge recruitment or mortality. The location of each individual sponge was converted into Cartesian coordinate points (x, y) representing the center of each sponge then plotted and analyzed. Additionally, at the time of mapping, all sponges were photographed from directly above and in profile as described in the previous studies (McMurray et al. 2008, 2010). All data were collected

using SCUBA, with the deepest sites sampled while saturation diving from the undersea research station *Aquarius*.

To determine whether sponges were randomly distributed within each plot, a Clark and Evans test (Clark and Evans 1954) was performed with a cumulative distribution function (CDF) border correction applied. The Clark and Evans test provides a crude test to determine patterns of distribution. Specifically, it produces a generalized distribution value (R) with a corresponding p value based on Monte Carlo simulations of a Poisson process (complete spatial randomness, or CSR). An R value <1 ($R < 1$) corresponds to a clustered point pattern, while an R value >1 ($R > 1$) corresponds to a regular or even point pattern.

To further examine the distribution of the sponges and gain more information about how the sponge distribution may deviate from random, a Ripley's K function was performed for each plot (Ripley 1977). The Ripley's K function represents a more informative method; it evaluates the distribution pattern of the sponges over a continuous distance, providing more data than a distribution value that has been averaged for the entire plot. The Ripley's K function compares the expected number of sponges within a distance (r) under the assumption of CSR to the observed density. If the observed pattern is CSR, the curve of the data will follow a known pattern. Deviations from this pattern can indicate clustering or regularity depending on the direction of the deviation from the pattern. In order to detect significant deviations from the expected curve under CSR, Monte Carlo simulations were used to generate an envelope around the expected curve. A total of 99 simulations were created. For this analysis, Ripley's isotropic border correction was applied (Ohser 1983; Ripley 1988).

The proximate analyses required placing the sponges into one of two size categories: adult or juvenile. Information regarding reproduction and size at sexual maturity for *X. muta* is limited (Ritson-Williams et al. 2005), and there have been no studies correlating sponge size with reproductive output. Therefore, size classes established by a previous demographic study of *X. muta* were used to categorize juveniles and adults (McMurray et al. 2010). Based on these classifications, sponges in the smallest size class were considered juveniles (≤ 143 cm³) and those in all larger size classes were considered adults (>143 cm³). The analysis was repeated reclassifying juveniles to include the two smallest size classes ($\leq 1,077$ cm³) to determine whether there was any variability in the relationship of the distribution patterns depending on the size ranges of the comparison. The size of each sponge was determined by measuring the osculum diameter using digital image analysis (UTHSCA Image Tool) and applying previously established osculum size/sponge volume ratios (McMurray et al. 2008, 2010).

Once the sponge life stage was categorized, the Ripley's K function was repeated for the adults alone to determine

whether a minimum distance was maintained. The final analysis compared the adult spatial point pattern to the juvenile spatial point pattern by using the Ripley's K Cross function (Ripley 1977). This analysis determines whether the distribution pattern of the juveniles is dependent on the pattern of the adults and it was conducted for each juvenile size classification. Data were analyzed in the statistical program *R* with the supplemental program *Spatstat* (Baddeley and Turner 2005).

Results

The three shallow (20 m) sites—S1, S2, and S3—contained 64, 73, and 63 individuals of *X. muta*, respectively, while the three deeper (30 m) sites—D1, D2, and D3—contained 63, 26, and 65 sponges (Table 1). The relatively low number of sponges in plot D2 was attributed to the slightly smaller size of the plot (12 vs. 16 m diameter), which was necessary to incorporate only areas of reef substrate and avoid sandy patches that are unusable habitat for sponges.

The Clark and Evans test was performed to assess the distribution of *X. muta* across the entire plot (Table 2). The R values for the Clark and Evans test of each plot were <1 , indicating clustering. The reported P values were based on Monte Carlo simulations (each simulation representing 1,000 trials). Significance (P value <0.05) in clustering was found in three of the six plots (S1, S3, and D1), with plots S2, D2, and D3 having P values slightly higher than significant (0.082, 0.058, and 0.094, respectively). The clustering indicated by the Clark and Evans test confirmed that, should Janzen–Connell interactions occur, the interactions would be at a smaller scale than the entire plot.

The Ripley's K function examines the distribution of sponges by analyzing their relative distances to each other, as opposed to comparing sponge distribution to the total available area, giving a more informative analysis of Janzen–Connell interactions. The Ripley's K function graphs

Table 1 Total number of sponges in each plot and the number of adult and juvenile sponges in each plot for both juvenile sponge classifications: Class I sponges ≤ 143 cm³ and Class III sponges $\leq 1,077$ cm³

	Adult	Juvenile ≤ 143 cm ³	Adult	Juvenile $\leq 1,077$ cm ³	Total
S1	48	16	31	33	64
S2	34	39	20	53	73
S3	40	23	31	32	63
D1	29	34	20	43	63
D2	–	–	–	–	26
D3	32	33	19	46	65

Table 2 Clark and Evans test (R values) with P values based on Monte Carlo simulations

Plot	R value	P value
S1	0.8169	0.020
S2	0.8707	0.082
S3	0.7976	0.010
D1	0.8363	0.050
D2	0.7259	0.058
D3	0.8680	0.094

showed no deviation from random for three of the six plots: S1, S2, and D3. The additional three sites (S3, D1, and D2) showed significant deviation toward clustering at near distances from each event, $r < 2$ (Fig. 1a; see also Electronic Supplementary Materials, ESM, Fig. A1a–5a). Clustering in the distribution patterns did not correlate with depth between the shallow and deep sites. The Ripley's K function analysis looked at all the sponges independent of size, but Janzen–Connell interactions could still be present if clustering was being driven by the juveniles while even spacing was maintained among adults. However, when the Ripley's K function was performed on adults alone, the distribution pattern was random in all plots (Fig. 1b; see also ESM Fig. A1b–5b), except in D2, where there were insufficient data points to yield significant results for adults alone.

The Ripley's K Cross function analysis was performed on juvenile and adults sponges. When juveniles were defined as less than or equal to 143 cm^3 , the analysis yielded no significant deviation from random in three of the six plots (S1, S2, and D3) and some areas of significant clustering in the remaining plots (S3 and D1; Fig. 2a; see also ESM Fig. A6a–9a). When the juvenile classification was regrouped to include the next size class (sponges less than or equal to $1,077 \text{ cm}^3$), only one of the plots deviated from random (S3; Fig. 2b). Plots S1, S2, D1, and D3 had

juvenile distributions that were completely random with respect to the adult distribution (ESM Fig. A6b–9b). Plot D2 was excluded from this analysis, because it did not have a sufficient number of data points to yield significant results. These results indicate that the clustering is primarily among juveniles, while the adults are randomly distributed.

Discussion

The relative distributions of adults and juveniles of *X. muta* did not reflect Janzen–Connell predictions, despite meeting all the requirements of the hypothesis, specifically that the sponge community on Caribbean reefs represents a diverse, dominant, and long-lived group of organisms with established pathogens and predators. No consistent distribution pattern was detected for *X. muta*, with most analyses demonstrating a random distribution. It could be argued that Janzen–Connell effects may result in a random distribution if, in the absence of those effects, the distribution is clumped, but such a low standard for the hypothesis would render it relatively meaningless in addressing the maintenance of biodiversity. While it may be possible that the presence of sponge pathogens or predators do have an influence on adjacent conspecifics, the interaction is not strong enough to result in a distinct spatial pattern that is distinguishable from other factors that are also likely influencing sponge distributions, such as habitat heterogeneity and allelopathic interactions. In the previous studies of tropical forest trees and Caribbean reef-building corals, spatial surveys were used to find evidence for Janzen–Connell interactions in the spacing pattern of a species, and then, the specific pathogen or predator that was responsible for causing the pattern was determined (Augsburger 1983; Packer and Clay 2000; Vermeij 2005; Marhaver et al.

Fig. 1 Ripley's K function of **a** all the sponges and **b** just the adults within plot S3. The dashed curve represents CSR [$K_{\text{theo}}(r)$]. Monte Carlo simulations were used to generate the shaded envelope around the expected curve [$K_{\text{rnd}}(r)$]. The solid line represents the Ripley's K function value at given distances [$K(r)$]

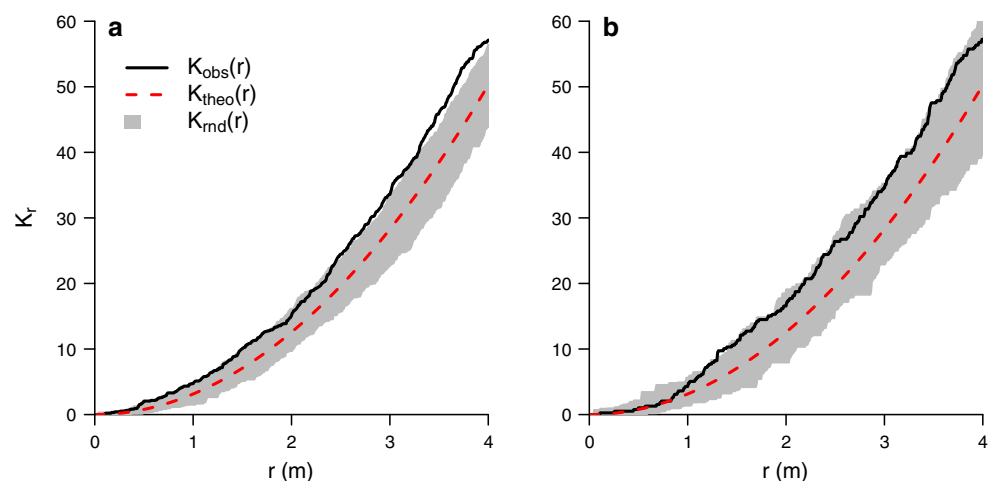
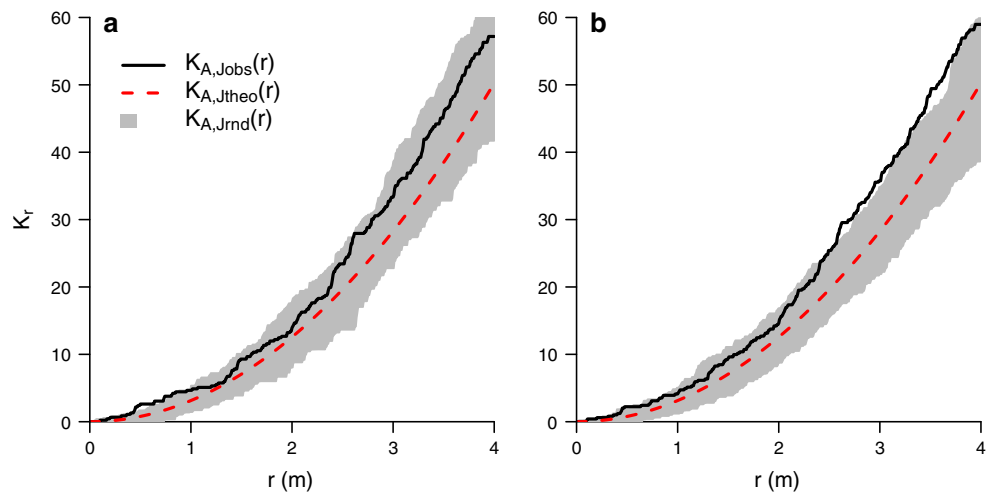


Fig. 2 Ripley's K Cross function comparing **a** juveniles $\leq 143 \text{ cm}^3$ to adults and **b** juveniles $\leq 1,077 \text{ cm}^3$ to adults for plot S3. The *dashed curve* represents CSR [$K_{\text{theo}}(r)$]. Monte Carlo simulations were used to generate the *shaded envelope* around the expected curve [$K_{\text{rnd}}(r)$]. The *solid line* represents the Ripley's K function value at given distances [$K(r)$]



2013). Given that the distribution pattern of *X. muta* did not reflect Janzen–Connell predictions, no additional investigations were conducted to determine the responsible pathogen or predator.

The primary objective of this study was to determine the spatial scale of possible Janzen–Connell interactions, which could vary depending on the specific factor (e.g., pathogen or predator) that might be acting on the sponge. However, an integrated interpretation of the results demonstrated that there was no spatial scale at which individual sponges were maintaining a minimum distance from each other. Throughout these analyses, each sponge was represented by a non-dimensional point, but these sponges take up area on the reef that scales with their size; therefore, any minimum distances maintained between individuals should appear larger in the analysis, as the distance between sponges includes both the distance from the center of each sponge to its edge and the distance between the edges of the two sponges. Sponges that are touching each other on the reef can appear spaced or separate in the point analysis. However, despite this spacing, many of the analyses showed clustering of the sponges. Juveniles could appear more clustered in the analysis when the actual distance between sponges was the same as between adult sponges. This conservative bias makes the evidence more compelling that Janzen–Connell interactions are not influencing sponge distributions, because despite this skewing of the data to appear more spaced, the sponges were primarily random in their distribution.

The results of this study contrast those observed for the Caribbean scleractinian corals *Siderastrea radians* and *Montastraea faveolata*, for which microbial pathogens caused decreased conspecific recruit survival around adult colonies (Vermeij 2005; Vermeij and Sandin 2008; Marhaver et al. 2013). Tropical coral reefs are not the only ecosystem to produce contradictory evidence of Janzen–

Connell interactions (Hubbell 1980; Hyatt et al. 2003). Community-wide studies of Janzen–Connell effects in tropical forests often reveal that Janzen–Connell interactions are species specific (Bagchi et al. 2011); density dependence, physical disturbances, seed dispersal method, niche differences, infrequent competition, and habitat availability are also cited as alternative factors affecting species distributions (Connell 1978; Clark and Clark 1984; Fragoso 1997; Wright 2002). These mechanisms are often not individually strong enough to control alpha diversity, but can work in conjunction with each other (Wright 2002).

Regardless of proximity to adult individuals, *X. muta* will not recruit to locations already inhabited by other organisms or otherwise unsuitable habitat, like sand patches. It is possible that, despite predation on eggs and larvae, post-recruitment survival of *X. muta* is dependent on the proportion of larvae settling on suitable, unoccupied habitat. Settlement selectivity of *X. muta* has not been examined, but the larvae of some sponge species respond to specific chemical and physical cues to enhance settlement in a given location (Whalan et al. 2008; Whalan et al. 2012), while other species are more non-specific (Maldozad 2006; Loh and Pawlik 2012). Additionally, many sponge species possess secondary metabolites in their tissues that have anti-overgrowth or allelopathic properties (Engel and Pawlik 2000; Pawlik et al. 2007). Allelopathy can reduce fouling and prevent overgrowth of the sponge by other species; however, allelopathic interactions around a sponge could also reduce heterospecific recruit survival, creating a “safe” space near an adult for conspecifics to grow. These allelopathic interactions could operate concurrently with, and in opposition to, Janzen–Connell interactions; therefore, the relative distribution of other species could also influence the survival of sponge recruits.

Our analyses do not support Janzen–Connell predictions for explaining the distribution of giant barrel sponges on

Conch Reef. While negative density dependence may contribute to recruit survival, other factors, such as allelopathic interactions and the availability of suitable habitat, may be more important in determining post-settlement sponge distributions.

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