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The Nature of the Symbiosis Between Cannonball Jellyfish and Spider Crabs in Georgia's Coastal Waters

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Abstract - *Stomolophus meleagris* (Cannonball Jellyfish) is a common Cnidarian species in the coastal waters of Georgia. *Libinia* spp. (spider crab) juveniles commonly inhabit the bell of the Cannonball Jellyfish, but there is uncertainty as to whether the crabs are parasitic on the Cannonball Jellyfish or are commensals. To assess the nature of this symbiosis, Cannonball Jellyfish were randomly sampled at multiple sites along the Georgia coast. For each Cannonball Jellyfish, the number of juvenile spider crabs inhabiting the bell was recorded along with multiple measurements of Cannonball Jellyfish and spider crabs. Our results suggest that the symbiosis between the Cannonball Jellyfish and juvenile spider crabs is an example of commensalism and not parasitism.

Introduction

Several species of brachyuran crustaceans have symbiotic relationships with scyphomedusae (see Sal Moyano et al. 2012, Towanda and Thuessen 2006 for reviews). Crabs benefit through transport, shelter, and food availability (Corrington 1927, Rountree 1983, Sal Moyano et al. 2012, Shanks and Graham 1988, Towanda and Thuesen 2006). Larval and juvenile crabs prey on medusa but do not affect medusa growth rates (Jachowski 1963, Phillips et al. 1969, Rountree 1983, Shanks and Graham 1988, Towanda and Thuesen 2006). There does not seem to be any benefit for the jellyfish in the symbiosis (Corrington 1927). It is unlikely that the relationship is obligate for the jellyfish or all life stages of the crabs, though evidence suggests it may be obligate for juvenile crabs until they reach a size of 15–20 mm (Jachowski 1963, Weymouth 1910).

One of the most well-known of these symbioses is between *Stomolophus meleagris* L. Agassiz (Cannonball Jellyfish) and *Libinia* spp. (spider crabs) (Corrington 1927, Gutsell 1928, Phillips et al. 1969, Rountree 1983, Shanks and Graham 1988, Tunberg and Reed 2004). It has been hypothesized that the symbiosis between Cannonball Jellyfish and spider crabs is a commensalism with the crabs receiving shelter and sustenance (either stealing food from the jellyfish or consuming jellyfish tissues) and Cannonball Jellyfish not being affected by the presence of the crabs

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(Corrington 1927, Phillips et al. 1969, Shanks and Graham 1988, Rountree 1983). Spider crab symbionts are most often larvae and juveniles, though adult symbionts have been observed (Corrington 1927, Gutsell 1928, Phillips et al. 1969, Rountree 1983, Tunberg and Reed 2004). Cannonball Jellyfish are known to prey on crab zoea, but zoea comprise less than 1% of their diet (Larson 1991).

Despite the symbiosis being well known to the scientific community and fishing industry, there are few empirical studies documenting the nature of this symbiosis. Previous studies suggest that the symbiosis is a commensalism (Rountree 1983, Tunberg and Reed 2004). Spider crabs have been observed feeding on medusa tissue, though this is not thought to harm medusa due to their regenerative abilities (Phillips et al. 1969, Rountree 1983, Shanks and Graham 1988, Tunberg and Reed 2004). Only Rountree (1983) has studied the symbiosis across multiple months (May–December 1982), with spider crab abundance within jellyfish peaking in July and then declining throughout the rest of the year. Our aim was to assess the nature of the symbiosis between Cannonball Jellyfish and spider crabs along the Georgia coast. We hypothesized that the symbiosis is indeed a commensalism with the spider crabs benefitting but the Cannonball Jellyfish not being impacted by the presence of spider crab symbionts.

Methods

We conducted random sampling of Cannonball Jellyfish on 1 April 2014 (31°23'24"N, 81°8'24"W) and 8 May 2014 (31°22'12"N, 81°11'23.99"W) off the coast of Darien, GA, and 18 February 2017 off the coast of Savannah, GA (31°41'59.99"N, 81°6'35.99"W) as well as inshore from the St. Simons Sound on 25 July 2014 (31°6'35.99"N, 81°54'0"W). We also attempted additional sampling sessions during the spring of 2015–2017 and the fall of 2015 and 2016, but Cannonball Jellyfish were not present. We conducted offshore sampling aboard a commercial fishing vessel and inshore sampling from a Georgia Department of Natural Resources (GADNR) research vessel. We measured a random sample of Cannonball Jellyfish from the trawl nets of the commercial vessel on each sampling date. Inshore, we used a 500-micron dip net to sample Cannonball Jellyfish from the surface of the ocean; the GADNR vessel was stopped over a school of Cannonball Jellyfish, and we randomly netted medusa for study.

For all sampling dates, we sampled a single jellyfish at a time and measured the relaxed bell width to the nearest mm. We recorded the number of spider crab symbionts for each Cannonball Jellyfish and the carapace width (mm) of each crab. In 2017, we recorded additional jellyfish metrics including weight (g), the bell width minus the wings (mm), and height (mm).

To test the prediction that the symbiosis was a commensalism, we compared the weights and relaxed bell widths of Cannonball Jellyfish with and without spider crab symbionts using Mann-Whitney U tests because data were unbalanced. Data were natural-log transformed prior to analysis. We predicted no difference in weight or relaxed bell width in jellyfish with and without crab symbionts. If the symbiosis was parasitic, we expected that jellyfish with symbionts would weigh less and would be smaller than those without symbionts. We used logistic regression to predict the presence of spider crabs symbionts using relaxed bell width as the sole predictor variable. We predicted that relaxed bell width would have no relationship with the presence of spider crab symbionts. If the relationship was parasitic, we would expect that spider crabs would be more frequently present in smaller jellyfish.

To further assess if relaxed bell width influenced the presence of crab symbionts, a test of independence was conducted to determine if the size class of jellyfish was related to the presence of a spider crab symbiont. Cannonball Jellyfish were broken into 4 size classes based on the relaxed bell width: 90–125 mm, 126–160 mm, 161–195 mm, and >195 mm to satisfy the requirement of a test of independence that all expected frequencies must be over 5 (Ott and Longnecker 2001). A Bonferroni inequality was used to determine differences among size classes. To reduce the probability of making a Type I error, we used a corrected alpha level of 0.00625 for these multiple comparisons (Gotelli and Ellison 2004). Finally, we conducted a Spearman correlation between relaxed bell width and crab carapace width (CW) to determine if Cannonball Jellyfish size is correlated to crab symbiont size. A Spearman correlation was conducted as data could not be normalized through multiple transformations. Analyses were conducted using SPSS (IBM Corp. 2017).

Results

A total of 179 Cannonball Jellyfish were sampled across the 4 sampling days: 23, 47, and 89 offshore on 1 April 2014, 8 May 2014, and 18 February 2017, respectively, and 20 inshore on 25 July 2014.

A total of 60 Cannonball Jellyfish had spider crab symbionts (33.5%). Presence of spider crabs was highly variable across sampling; e.g., 83% of Cannonball Jellyfish had a spider crab symbiont in April 2014, yet in May 2014 only 2% had crab symbionts. Most Cannonball Jellyfish that had crab symbionts hosted just a single spider crab (87% of those with symbionts); the greatest abundance of crabs we found in a single jellyfish was 10 symbionts.

Overall crab CW varied from 2 to 29 mm, and the mean CW was 12.70 ± 6.63 mm (SD). Carapace width was 10–20 mm in February 2017 (Mean = 12.72 ± 3.31 mm), 12–22 mm in April 2014 (Mean = 16.79 ± 2.51 mm), and 2–29 mm in July 2014 (9.48 ± 8.87 mm). A single Cannonball Jellyfish in July harbored 10 spider crab symbionts with each symbiont having a CW around 2 mm. If the 10 crabs from this 1 jellyfish were removed from the mean calculation, the mean and standard deviation for July 2014 were 13.42 ± 8.65 mm which was similar to the other sampling dates. A single crab with a CW of 27 mm was observed in May 2014.

Relaxed bell width for Cannonball Jellyfish with spider crab symbionts varied from 97 to 250 mm with a mean of 166.02 ± 34.98 mm (SD, n = 60). Relaxed bell width for Cannonball Jellyfish without spider crab symbionts varied from 94 to 240 mm with a mean of 160.45 ± 27.23 mm (SD, n = 119). The mean rank (MR) of the relaxed bell width of jellyfish with crabs did not differ from the mean rank of the relaxed bell width of jellyfish without crab symbionts (Z = -1.154, *P* = 0.249, $MR_{Withcrabs}$ = 96.29, $MR_{Without\ crabs}$ = 86.83; Fig. 1).

There was no relationship between relaxed bell width and the presence of spider crab symbionts (χ^2 = 0.749, df = 1, *P* = 0.387). However, when Cannonball Jellyfish were separated into size classes, the presence of a crab symbiont was not independent of relaxed bell width (χ^2 = 12.004, df = 3, *P* = 0.007). Observed counts of Cannonball Jellyfish with crabs were lower than expected in the 126–160 mm size class (χ^2 = 9.24, df = 1, *P* = 0.0024), and observed counts of Cannonball Jellyfish without crabs were higher than expected in the 126–160 mm size class (χ^2 = 9.24, df = 1, *P* = 0.0024). Other size classes did not differ from expected values (Table 1, Fig. 2). There was no correlation between relaxed bell width and crab CW (*r* = 0.273, *n* = 79).

The mean weight of jellyfish without crab symbionts was 495.56 ± 202.86 g (SD, *n* = 62) and the mean weight of jellyfish with crab symbionts was 610.19 ± 220.74 g (SD, *n* = 27) (Fig. 3). The mean rank (MR) of the weight of jellyfish with crabs was significantly greater than the MR of the weight of jellyfish without crab symbionts (Z = -2.34, *P* = 0.019, $MR_{With\ crabs}$ = 54.72, $MR_{Without\ crabs}$ = 40.77).

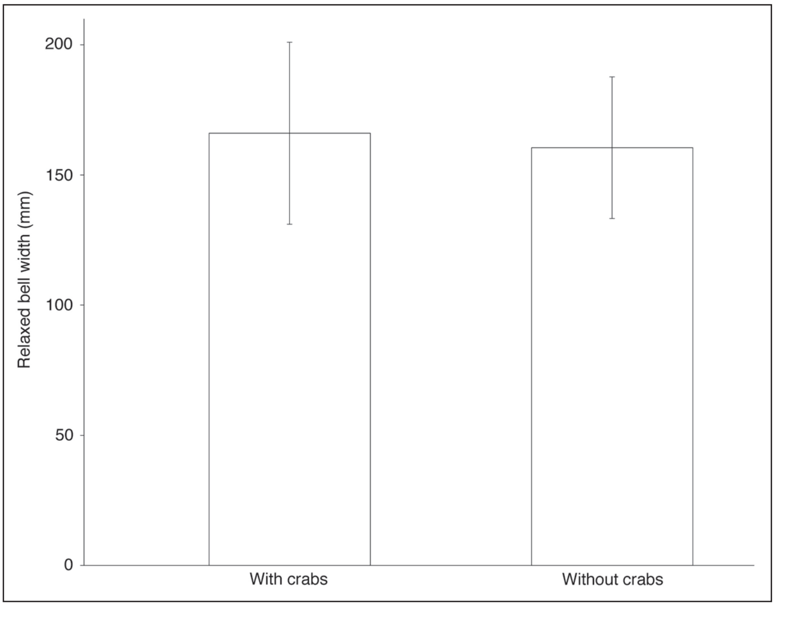

Figure 1. Mean relaxed bell width of Cannonball Jellyfish with and without spider crab symbionts. Error bars are ±1SD.

Table 1. Contingency table for test of independence of Cannonball Jellyfish relaxed bell width (mm) and whether a spider crab was present in the bell of the jellyfish. Numbers in parentheses are the expected values. A single Cannonball Jellyfish with a 250 mm relaxed bell width and a crab symbiont was included in the >195 mm bell-width category, and a single Cannonball Jellyfish with a 240-mm relaxed bell width without a crab symbiont was included in the >195 mm bell-width category. Observed values that differed significantly from expected values are indicated with an "*".

	90–125 mm	126–160 mm	161–195 mm	>195 mm
Without crab	8 (11.97)	60 (50.53)*	37 (38.56)	14 (17.95)
With crab	10 (6.03)	16 (25.47)*	21 (19.44)	13 (9.05)

Discussion

We observed crab CWs of 2–29 mm. Most of the spider crab larvae and juveniles found in association with Cannonball Jellyfish hav a carapace length or width less than 40 mm (Gutsell 1928, Phillips et al. 1969, Rountree 1983, Tunberg and Reed 2004). Corrington (1927) noted that adult spider crabs were found within the

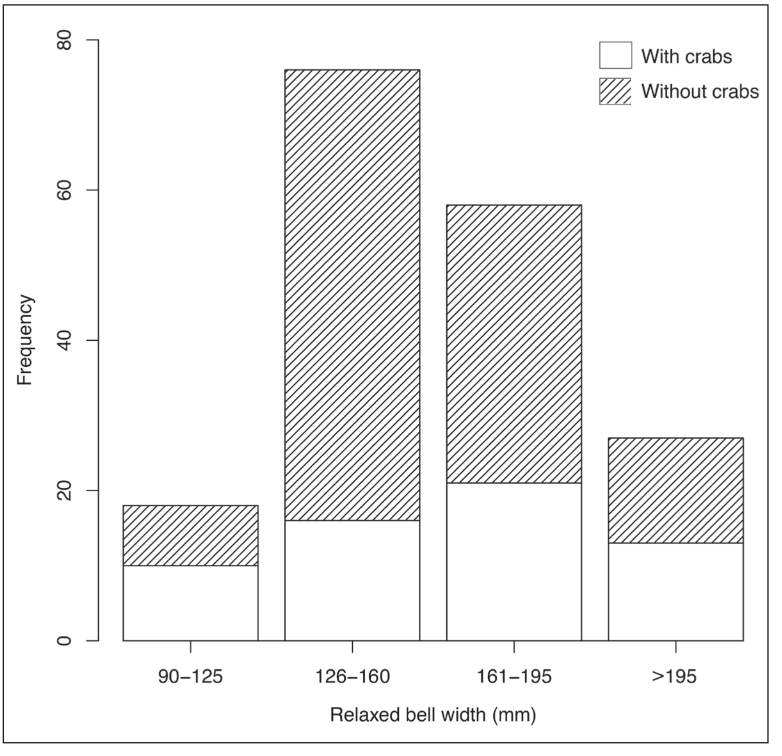

Figure 2. Relaxed bell width (mm) comparison for Cannonball Jellyfish that did (n = 60) and did not (n = 119) have a spider crab symbiont. The number of Cannonball Jellyfish with spider crab symbionts in the 126–160 mm size class was lower than predicted.

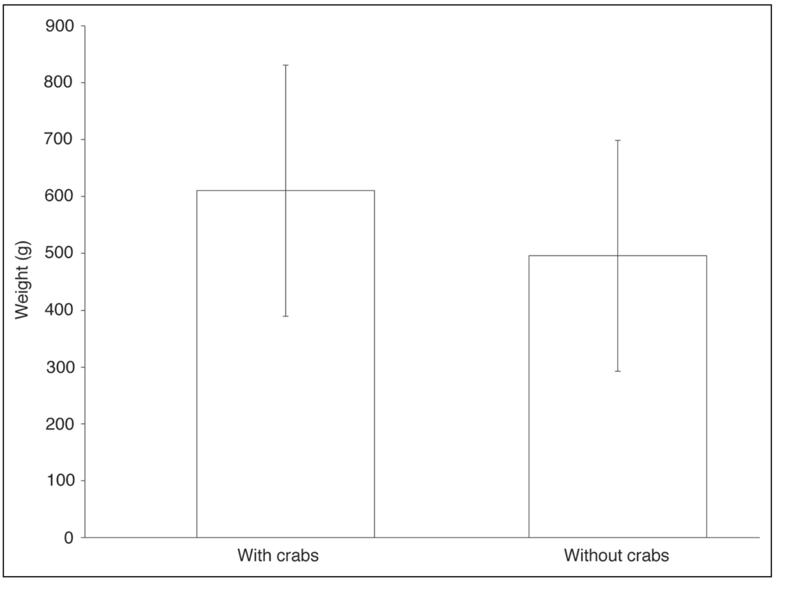

Figure 3. Mean weight of Cannonball Jellyfish with (n = 27) and without (n = 62) spider crab symbionts. Weights were only recorded from medusa sampled in February 2017. Error bars are ± 1SD.

subumbrellar space of the medusa, but no carapace measurements were provided. Adult spider crabs have a mean CW of 60 mm, but CWs can be as great as 88 mm (Corrington 1927, O'Brien et al. 1999).

In April, 83% of Cannonball Jellyfish had a spider crab symbiont, 65% had symbionts in July, and 30% had symbionts in February. Our high rates of symbionts in April and July coincide with increases in Cannonball Jellyfish and spider crab abundance. Large Cannonball Jellyfish appear off the Georgia coast during March, move inshore during May and June, and disappear in late fall (P. Geer, Georgia Depatment of Natural Resources, Brunswick, GA, unpubl. data; Kraeuter and Setzler 1975). Only a single Cannonball Jellyfish harbored a spider crab symbiont in May 2014 despite May traditionally being a month of high Cannonball Jellyfish and spider crab abundance (P. Geer, Georgia Dept. of Natural Resources, Brunswick, GA, unpubl. data, O'Brien et al. 1999). The spider crab *Libinia emarginata* (L.) is reproductively active from June through September (Hinsch 1968), and the duration of the larval stage of *Libinia dubia* H. Milne Edwards is only 9 days (Sandifer and Van Engel 1971). Spider crabs are most abundant during fall and spring with juvenile abundance peaking during the summer (DeGoursey and Auster 1992, O'Brien et al. 1999, Rountree 1983, Winget et al. 1974).

Cannonball Jellyfish with crab symbionts were heavier than those without symbionts. Therefore, Cannonball Jellyfish growth is likely not being negatively affected by the presence of the juvenile crabs. Crab symbionts are known to prey on medusa tissue, but it is unlikely that they impact medusa health due to the regenerative ability of medusa (Rountree 1983). Rountree (1983) noted that when offered Cannonball Jellyfish tissue or other food items, spider crabs would eat jellyfish tissue only when nothing else was available. Growth rates of the scyphozoan *Phacellophora camtschatica* Brandt were not affected by the crab symbiont *Cancer gracilis* Dana consuming *P. camtschatica* tissues (Towanda and Thuesen 2006). As growth rates of Cannonball Jellyfish are not being hindered, this supports our prediction that the symbiosis is not parasitism and more likely is commensalism. While the finding that jellyfish with symbionts were larger, significantly so in terms of weight, could conceivably suggest a mutualistic relationship, we are hesitant to draw such a conclusion because (1) we cannot propose a benefit the jellyfish might be getting from the crab symbionts or a mechanism by which the spider crabs are helping the jellyfish achieve a larger size, and (2) there are no other published studies that demonstrate a benefit for the jellyfish.

There was no relationship between relaxed bell width and the presence of a spider crab symbiont. There was also no difference in relaxed bell width between Cannonball Jellyfish that did and did not have a spider crab symbiont. When Cannonball Jellyfish were broken into size classes by relaxed bell width, the predicted number of Cannonball Jellyfish with spider crab symbionts in the 126–160 mm size class was lower than expected (Table 1). This is likely due to the fact we sampled more Cannonball Jellyfish in this size class in May 2014 compared to other sampling dates, but only a single medusa harbored a crab symbiont. No other size class had a difference between observed and expected values. Together, these results indicate that the presence of a spider crab symbiont does not negatively affect the growth of Cannonball Jellyfish and lends support to the classification of the symbiosis as a commensalism and not parasitism. We found no correlation between relaxed bell width and crab CW. Tunberg and Reed (2004) also reported no significant correlation between bell diameter and CW, which suggests that larger Cannonball Jellyfish do not harbor larger symbionts, though Sal Moyano et al. (2012) observed that larger specimens of the scyphozoan *Lychnorhiza lucerna* Haeckel were more likely to host the symbiont *Libinia spinosa* Milne-Edwards.

Our study is one of the few empirical studies to assess the nature of the symbiosis between Cannonball Jellyfish and spider crabs. To determine the exact nature of the symbiosis, Cannonball Jellyfish would need to be sampled at least once a month over the course of multiple years to track the growth and development of both spider crab juveniles and Cannonball Jellyfish. This approach could often be problematic as the location of Cannonball Jellyfish along the southeast coast is very unpredictable (P. Geer, , unpubl. data; H. Boone, Boone Seafood, Darien, GA, pers. comm.). Despite this limitation, multiple lines of evidence indicate that the symbiosis between Cannonball Jellyfish and spider crabs is a commensalism.

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