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SIZE DISTRIBUTION AND POPULATION FLUX OF THE FLAT TREE OYSTER, *ISOGNOMON ALATUS*, IN TWO INLAND LAKES ON SAN SALVADOR ISLAND, THE BAHAMAS

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ABSTRACT

The flat tree oyster (*Isognomon alatus*) is often found in mangrove marshes growing on or around the intricate aerial root network of red mangrove trees. Work with *I. alatus* is limited and literature provides little information about their response to different environmental conditions. The purpose of this study was to examine the size distribution of *I. alatus* in two inland waterbodies, Oyster Pond and Osprey Lake on San Salvador Island, Bahamas. While these systems are spatially close and similar in size, they vary in terms of ocean connectivity, salinity, and dominant vegetation. During March of 2015 and 2018, samples of at least 100 oysters were collected randomly from each body of water. The hinge lengths of individuals were recorded in the field and size distribution was compared between years. Surprisingly, no live oysters were found in Osprey Lake in 2018; however, the lake bottom was covered in *I. alatus* shell remains, which were used to assess population size in 2018. Both Oyster Pond and Osprey Lake had a significant change in average hinge length from 2015 to 2018; Oyster Pond had a significantly smaller-sized population in 2018, while collections from Osprey Lake suggested a larger-sized population. We believe that a combination of hurricane activity and differential conduit connectivity to the ocean account for the differences seen between the ponds. Specifically, we think that hurricane activity damaged the red mangroves in Osprey Lake that provide habitat for *I. alatus*, thereby impacting *I. alatus* recruitment; additionally, lack of connectivity to the ocean and associated tidal activity may have resulted in a rapid and longer-term, detrimental drop in salinity. A shorter-term salinity drop in conduit-regulated Oyster Pond, on the other hand, may have triggered a mass spawning event resulting in high recruitment. Additional ecological information for *I. altatus* is necessary in order to draw further conclusions on the population fluctuations found in San Salvador's inland lakes.

INTRODUCTION

The flat tree oyster (*Isognomon alatus* Gmelin 1791) is widely distributed throughout the Caribbean region and is often found in mangrove marshes, growing on or around the intricate aerial root network of mangrove trees. *I. alatus* can spawn throughout the year, and mass spawning events are particularly common following significant rain fall, which cause water salinity to decrease. Prodissoconch larva are then released into the water column, where they grow and eventually attach to red mangrove roots via byssus threads. The oysters become reproductively mature after approximately one year; however, the general lifespan is unknown (Siung 1980).

On San Salvador, *I. alatus* can be found in several interior lakes and ponds. These inland waterbodies are unique, anchialine habitats as their salinity levels vary from brackish to hypersaline, depending on the level of subterranean connectivity to the ocean and impact of recent rainfall events (Edwards 2001). Those ponds that exhibit predictably marine conditions are often heavily influenced by conduits and associated tidal influence, while hypersaline ponds have more limited connectivity and are influenced by evaporative processes (Mylroie and Carew 1995). *Isognomon alatus* is known for its ability to tolerate a range of salinities (Siung 1980), more so than many of its invertebrate counterparts (Goodbody 1961); this is confirmed by the species' presence in a range of anchialine habitats on San Salvador Island.

The aerial root system of red mangroves (*Rhizomorpha mangle*) provides excellent habitat for *I. alatus* as well as a host of other invertebrate species (sponges, cnidarians, bivalves, gastropods, annelids, ascidians, etc.). Their root system dips into the water looking for substrate, allowing for further stabilization of the main stem. This rhizomatous tree can tolerate salinity levels up to 60 ppt; however, once this salinity level is surpassed, the trees experience stress (Liang *et al*. 2008). Red mangroves also tend to be intolerant to heavy wind and wave action caused by hurricanes, particularly as compared to the black mangrove (*Avicennia germinans*); furthermore, mangrove forests as a whole are less resistant to hurricanes as compared to semi-deciduous dry forests and rainforests (Imbert 2018). Considering the high dependency other marine organisms have on red mangroves, tropical storms can be detrimental to multiple populations including *I. alatus*, which depends on the roots system for support (Siung 1980).

Here, we examine and compare the size distribution of *I. alatus* in two of San Salvador's anchialine ponds that differ in terms of ocean connectivity and thus also salinity, Oyster Pond and Osprey Lake. We also compare oyster populations from these water bodies collected in March 2015 to those in March 2018. Notably, these sampling events were separated by Hurricane Juaquin, a category 4 hurricane that made landfall on San Salvador Island on October 2, 2015.

FIELD-SITE DESCRIPTION

Oyster Pond and Osprey Lake are both located less than 1 km south of the Gerace Research Centre (Figure 1). These water bodies are similar in location and size; however, they differ chemically and physically. Oyster Pond is a dissolution, marine water body that is influenced by a connection to the ocean that causes a tidal flux in water depth and stabilizes salinity. Rothfus (2012) reported an average salinity of 37.1 ppt from monthly data collected over a 22-month period in Oyster Pond; salinity does, however, decrease temporarily with precipitation. The shoreline is dominated by red mangroves, which protect the pond from strong winds and erosion. In 2015 and 2018, the red mangrove population surrounding Oyster Pond appeared to be in good health with a dense canopy cover, thick aerial root system, and evidence of reproduction (visual observations). The sediment of Oyster Pond is a mix of flocculants and shell hash.

Osprey Lake, a dissolution lake classified as a hypersaline water body, is found just northwest of Oyster Pond; the ponds are separated by only ~50 m in some areas (Figure 1). This water body is influenced by conduits, although not as heavily as Oyster Pond (Edwards 2001, McGee *et al*. 2010). Osprey Lake's hypersaline state (52.1 ppt on average, as documented by Rothfus 2012) is strongly regulated by evaporation as well as seepage from a nearby hypersaline water body, Blue Pond, found at its southwestern edge (McGee *et al*. 2010); Edwards (2001) reported a salinity range of 38.0-61.0 ppt for Osprey Lake, with rainy years accounting for reduced salinity. The dominant shoreline vegetation is the black mangrove with several off-shore patches of red mangroves. In 2015, the red mangrove patches were visually healthy and supported invertebrate life, such as *I. alatus*. In 2018, the patches were visually suffering; bark was discolored, aerial roots were fragile and broke easily, and the canopy cover was sparse (Figure 2); similar observations were made in June, 2019 (Beebout and Anderson, personal observation). The main organism living on the red mangroves was fuzzy finger algae (*Batophora oerstedii*). The sediment of Osprey Lake is a mix of flocculants and shell hash.

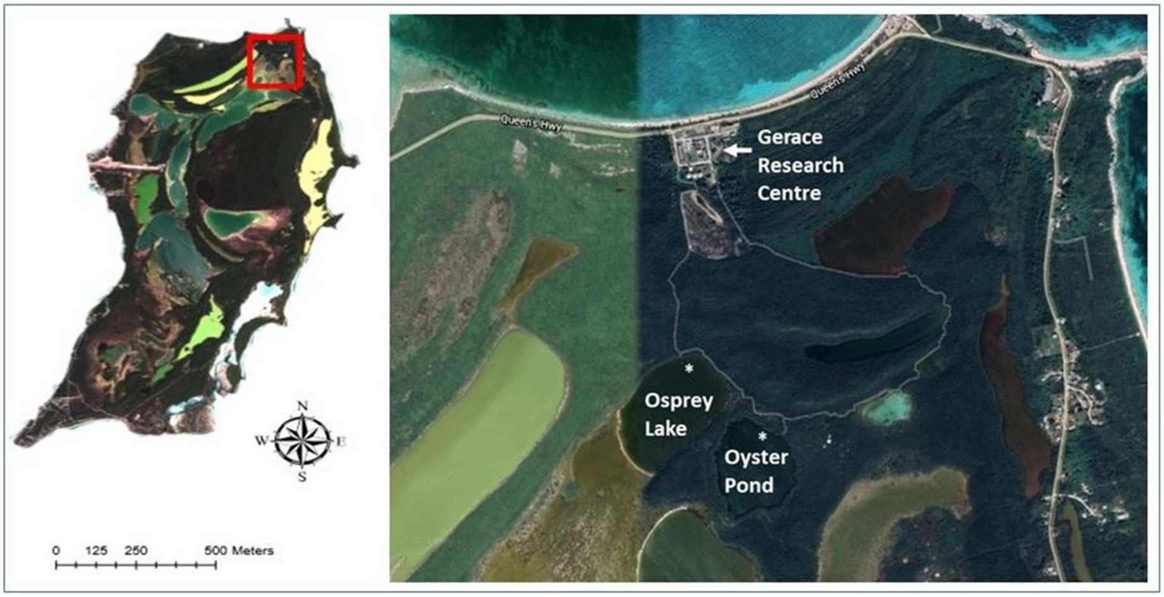

Figure 1: Location of Oyster Pond and Osprey Lake with respect to the Gerace Research Centre. Island map inset courtesy of the U.S. Geological Survey, Accessed 10-January 2019. Close-up image of ponds and Gerace Research Centre modified from Google Earth. Accessed 13-May 2020.

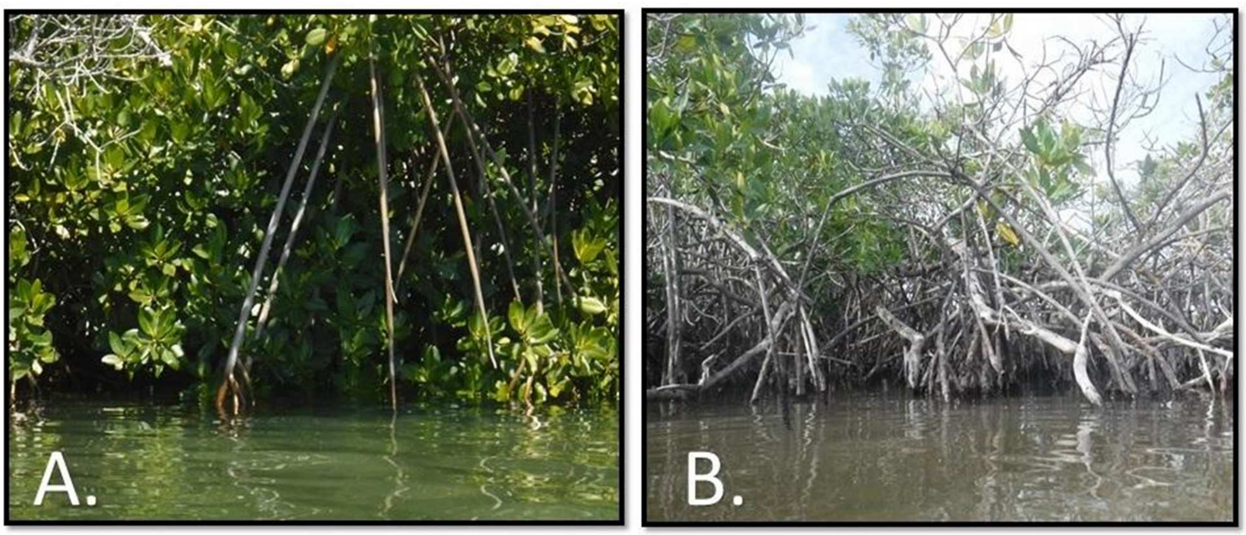

Figure 2. View of red mangroves in Osprey Lake in 2015 (A) and 2018 (B).

METHODS

At Oyster Pond and Osprey Lake, patches of *I. alatus* were identified and qualitatively assessed in March of 2015 and 2018. At both sites, collections of at least 100 individual oysters were taken and hinge length was measured with a hand-held caliper. All measurements occurred in the field and oysters were returned to their habitat following measurement. Considering the unique metazoan communities known to each pond, samples were collected from each system on different days so as not to introduce novel organisms. In Oyster Pond, *I. alatus* were collected from red mangrove prop roots along a ~100 m perimeter along the northern shoreline; up to five oysters were collected from each root. In 2015, Osprey Lake oysters were collected from prop roots of red mangrove stands located within 100 m of the lake's northern shoreline (Figure 1). In 2018, these mangroves were devoid of live oysters; however, the shell hash on the lake floor surrounding red mangrove stands included numerous flat tree oyster shells. We took measurements of shells found within this hash. Two-way analysis of variance (ANOVA) and Tukey Pairwise Comparisons were conducted to examine the effect of pond and year on hinge length.

RESULTS

Two-way ANOVA found significant interaction between the effects of pond and year on hinge length ($F_{1,506}$ = 232.9, p < 0.001). Significant main effects were also found for both pond and year (p < 0.001 for each factor). In Oyster Pond, we found a comparatively smaller-sized population in 2018, with an average hinge length of 17.0 mm in 2015 (n = 123) and 14.6 mm in 2018 (n = 103).

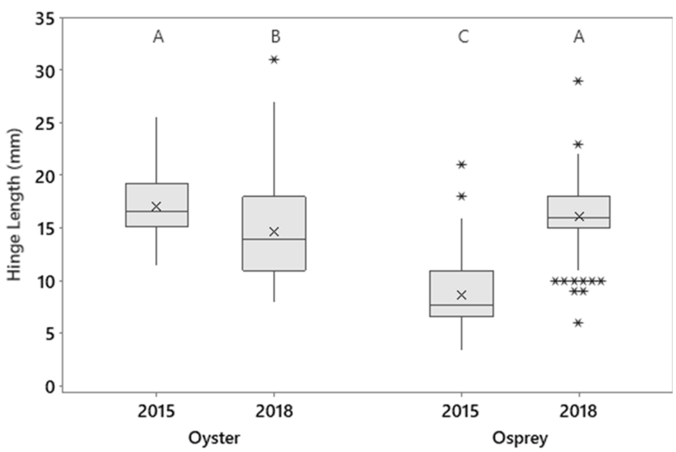

Figure 3. Box-plot of the hinge length distribution in I. alatus in Oyster Pond and Osprey Lake from samples collected in 2015 and 2018. Lower and upper box boundaries at 25th and 75th percentiles, respectively and whiskers extend to data points within 1.5 times box heights. Medians are represented by the horizontal line within the box, means are represented by an 'x' and outliers are shown with an "". Different letters indicate significant differences between groups, as indicated by Tukey Pairwise Comparison.*

In 2015, Osprey Lake had an abundance of living oysters growing on the red mangrove roots; however, live oysters were absent during the 2018 sampling event and also in June of 2019 (Beebout and Anderson, personal observation). The red mangrove patches within the lake also appeared stressed as compared to 2015 (Figure 2). Data from oyster shell hash suggested significantly larger hinge length in 2018 as compared to 2015; mean hinge lengths were 16.0 mm (n = 129) and 8.7 mm (n = 155) respectively (Figure 3).

Flat tree oysters also differed in size when comparing between ponds in a given year, with Oyster Pond having significantly larger oysters in 2015 as compared to Osprey Lake. The reverse was found in 2018 (Figure 3).

DISCUSSION

Our data led to two key findings: First, population size structure of *I. alatus*, as gauged by hinge length, differed between ponds and across years. Second, while Oyster Pond exhibited a thriving oyster population in both years, no live oysters were found in Osprey Lake in 2018. Considering that Oyster Pond's size distribution was lower in 2018 compared to 2015, we hypothesize that a younger population of *I. alatus* was present in 2018; this is likely because spawning does not occur at regular intervals but instead typically follows significant storm events, which are unpredictable. This would lead to different annual cohort size structure. Osprey Lake, however, had no live oysters in 2018. After measuring shells collected from the substrate, we found the reverse trend as compared to Oyster Pond; on average, the hinge length of flat tree oysters was 8.3 mm greater in 2018 as compared to 2015. This led us to believe that a younger population of *I. alatus* was originally sampled in 2015 and mass mortality followed hurricane activity, resulting in limited reproduction, recruitment, and establishment.

We recognize that comparing hinge lengths from samples of live oysters to those in the shell hash introduces confounding variables. Specifically, shells within the hash could have accumulated over a significant period of time, including the time-frame prior to this study; we attempted to account for this by randomly collecting shells and discarding shells that were not whole or were significantly degraded. There is also potential for smaller shells to break down faster or be overlooked more easily as compared to larger shells. We do not know the breakdown rate of *I. alatus*, nor did we assess whether smaller shells were comparatively more degraded than larger. These factors could have biased our results, and it is possible that the mean hinge length value for Osprey Lake reported in 2018 is artificially elevated. However, considering that no live specimens were present, there was little alternative. Additionally, the result of finding no live oysters in Osprey Lake in 2018 is certainly notable in itself.

Factors that may help explain our findings include variations in water chemistry, physical parameters, dominant vegetation, and significant storm events, such as Hurricane Joaquin. Oyster Pond and Osprey Lake are similar in size and location; however, the dominant vegetation and salinity influence varies greatly between these systems. The vegetation around the two water bodies demonstrates the effects of differential salinity. Red mangroves have limited tolerance of hypersaline conditions (Imbert 2018, Liang et al. 2008). In Oyster Pond, the tidal flux keeps salinity levels at near-marine conditions, making this system an ideal location for red mangroves to govern the shoreline. In Osprey Lake, black mangroves, which are more salt tolerant (Imbert 2018, Liang et al. 2008), dominate the shoreline with some patches of red mangroves just offshore; these patches are likely more prone to influence from environmental change and disturbance events.

Hurricane-caused disturbances are common throughout the Bahamas. After the initial sampling period in spring of 2015, Hurricane Joaquin hit San Salvador head on in October 2015. This hurricane caused major infrastructural damage throughout the island, with winds up to 110 knots (204 kph); while no official rainfall observations are available, estimates indicate the storm produced 12-25 cm of rain (Berg 2016). In 2018, when oyster sampling was repeated, damage to the red mangroves was apparent in Osprey Lake (Figure 2). Imbert (2018) describes the limited resistance that mangroves, especially red mangroves, have against hurricanes. Red mangroves depend on their aerial prop roots and rhizomous, underground root structure for support and stability. The strong winds brought with a hurricane can dislodge and destroy prop roots and whole trees, therefore damaging optimal habitat that *I. alatus* depends on for survival. The red mangroves that border the shoreline of Oyster Pond are more protected than the clustered populations found in Osprey Lake that are much more exposed to the elements. Damage to red mangroves can lead to cascading effects of less optimal habitats for mangrove-reliant invertebrates such as *I. alatus*, potentially contributing to mortality of the population that existed in 2015.

Along with damaging winds, hurricanes also bring in great amounts of precipitation. *I. alatus*, like many other marine bivalves, depends on these rain events to reduce the salinity levels of a water body and trigger mass spawning events (Siung 1980). However, Goodbody (1961) noted that too much rain in a limited time frame may cause mass mortality of sessile mangrove invertebrates. Considering the tidal activity in marine ponds such as Oyster Pond, it appears that storm events cause only a short-term drop in salinity that, in turn, could trigger mass spawning events for *I. alatus*. Conversely, Osprey Lake has little tidal influence, is hypersaline, and is influenced by evapotranspiration and seepage from Blue Pond (McGee *et al.* 2010). Precipitation events can cause rapid salinity drops in hypersaline ponds due to limited conduit regulation, and return to pre-storm salinity levels takes longer because of the evaporative-controlled conditions (Rothfus 2012). A prolonged drop in salinity also could have negatively impacted *I. alatus* populations in Osprey Lake.

Interestingly, Carlson *et al*. (2011) found similar, hurricane-driven results when examining populations of scaly pearl oysters (*Pinctada longisquamosa*) in ponds with varying salinity levels on San Salvador Island. Specifically, scaly pearl oysters in Oyster Pond exhibited a high level of resilience to hurricane events while adult oysters in Six Pack Pond, a hypersaline pond with limited conduit exchange that is much more susceptible to hurricanes, were nearly decimated following hurricane activity. Notably, the Six Pack Pond population rebounded within months, indicating that impending mortality of the adult population triggered a "suicide spawning" event. Further work on this system by Cole *et al*. (2016) concluded that storm-driven salinity and temperature drops induce mass spawning prior to adult decimation in ponds that are not buffered by conduit action.

The rainy season on San Salvador results in a salinity drop, thereby promoting spawning in *I. alatus* (Siung 1980). This stimulates the growth of new generations, and this appears to have been the case in Oyster Pond; however, in the case of hypersaline ponds, how much rain is too much? When there is a significant salinity drop, for example after a hurricane, and return to pre-storm salinity levels in hypersaline ponds is delayed because of the limitations imposed by the evaporative process, *I. alatus* is predicted to go into mass reproduction, similar to that seen by Carlson *et al*. (2011) in the scaly pearl oyster. However, unlike Carlson *et al*. (2011), we did not observe a rebound in *I. alatus;* if *I. alatus* populations in Osprey Lake followed a similar trajectory as scaly pearl oysters in Six Pack Pond, there should have been an ample number of adults by 2018. If the observed mortality was associated with Hurricane Joaquin, it is plausible that there *was* an associated mass spawning event, followed by adult mortality. However, perhaps juveniles were unable to re-establish due either to suboptimal salinity levels, limited available colonization habitat due to stress on the red mangrove patches, or a combination of these factors.

To summarize, we propose here that rainfall from hurricane activity in conduit-driven Oyster Pond lowered the salinity enough to trigger a successful spawning event; conversely, in hypersaline Osprey Lake, the lack of conduit-driven tidal regulation resulted in a more dramatic and extended salinity drop. This, paired with damage to red mangrove patches, created the 'perfect storm' that resulted in the demise of flat tree oysters in Osprey Lake.

While rainfall events that lower water salinity levels are necessary to trigger reproductive activity, our results reinforce the need to maintain a delicate balance. Too much fluctuation without the regulative activity driven by conduits may be detrimental, and past work has shown that major salinity drops can decrease *I. alatus* in the plankton (Siung 1980). None-the-less, there are still many unanswered questions related to the life history of *I. alatus*, thus drawing strong conclusions is difficult. The growth rate and age/size at maturity is still unexplored, and could vary depending on unique evolutionary trajectories within a certain habitat. There is also possibility that size differences seen here could be associated with differential growth rate in different years as opposed to differential age; changes in water quality parameters could lead to differential growth. Optimal water quality parameters are unknown as well. We know salinity is a factor in triggering spawning events, but what is the optimal threshold range? Longer-term water quality data for these inland waterbodies would also be beneficial. Also, it would be valuable to compare other sedentary invertebrates in Oyster Pond and Osprey Lake, especially after storm events, to further our understanding of the recovery time of each system. Finally, we recognize that the exact timing of mortality in Osprey Lake is unknown, so while we hypothesize that Hurricane Joaquin may have played a significant role, we recognize that we cannot draw firm conclusions.

While it is evident that flat tree oysters can tolerate a range of salinities, climate change may impact their survival either by enhancing evaporation rates, which will elevate already hypersaline conditions or by increasing frequency of severe storm events, which may result in rapid, dramatic drops in salinity. Either of these scenarios could exceed *I. alatus* tolerance limits, or impact the mangrove communities which they depend upon, thus hindering growth and reproduction. A continual study of these oysters, along with other members of the invertebrate community, is needed to further understand the stability of the unique inland ponds on San Salvador Island, the Bahamas.

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