AN ABSTRACT OF THE THESIS OF

Kaliegh Schlender for the degree of Master of Science in Marine and Environmental Sciences presented November 17, 2020

Title: Beach Morphology and Anthropogenic Impacts on Ghost Crab Populations, St. Thomas, USVI

Abstract approved:

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Dr. Kristin Wilson Grimes

Globally, sandy beaches support local economies and are the most commonly-used type of coastline by people (Davis & FitzGerald, 2004; Schlacher et al., 2007), with beaches serving as popular attractions in the U.S. Virgin Islands (USVI) for visitors from around the world. However, high urbanization causes the degradation of coastal resources. Ghost crabs, *Ocypode*, display predicable responses to anthropogenic impacts, and are popular ecological indicator reflecting the level of ecological stress present in sandy beaches (Barros, 2001; Costa et al., 2019; Costa & Zalmon, 2019; Gül & Griffen, 2019; Peterson et al., 2000). Although St. Thomas, USVI is a popular tourist destination, there are no beach studies in the USVI identifying beach types or the impact of high urbanization from tourism through the use of ghost crabs, to-date. This study characterizes beach types using multiple indices (Beach Index, Beach Deposit Index, Log(1/Beach Slope), and Relative Tide Range) based on physical parameters (beach slope, grain size, and wave height) for eight beaches (Stumpy Bay, Santa Maria Bay, Caret Bay, Neltjeberg Bay, Lindberg Bay, Magens Bay, Coki Point Beach, and Sapphire Beach) on St. Thomas to establish a baseline for beach types on the island. Surveys were conducted during high tourist season from February 3 - March 19, 2020 and low- tourist season from May 18 - June 25, 2020 during early morning hours. Site values for Beach Index, Beach Deposit Index, and Log (1/Beach Slope) were compared using Kruskal-Wallis Rank Sum tests and Dunn Post Hoc tests, and results indicated that all beaches were wave dominated reflective, with slight variations detected best by Log (1/Beach Slope). Additionally, urbanization effects were assessed using a modified Urbanization Index using six different variables (buildings on sand, solid waste, visitor frequency, distance to urban center, beach cleaning, and vehicle traffic) to calculate specific urbanization levels across study sites. Overall urbanization was calculated and results were compared using Kruskal-Wallis Rank Sum test and a cluster dendrogram. Results indicated two groups of sites that were then classified as low- impact (Stumpy Bay, Santa Maria Bay, Caret Bay, and Neltjeberg Bay) and high- impact (Lindberg Bay, Magens Bay, Coki Point Beach, and Sapphire Beach). Ghost crab burrow surveys measured burrow abundance, width, and depth, and results were compared across sites using Kruskal-Wallis Rank Sum tests. To determine the drivers of burrow abundance, width, and depth, Generalized Linear Mixed Models were used with overall urbanization, log(1/beach slope), wave height, average grain size, and season. Results indicated overall urbanization was the primary driver of burrow abundance, width, and depth. Generalized Additive Models were used to determine if there was a primary variable within overall urbanization having the greatest impact on burrow abundance, width, and depth. Significant effects of urbanization variables were visitor frequency, distance to urban center, and beach cleaning on burrow abundance, visitor frequency on burrow depth, and distance to urban centers and vehicles on sand on burrow width. Further urbanization impacts of prolonged beach chair use were measured by establishing four experimental plots 1) fully shaded chair, 2) partially shaded chair, 3) chair frame with no shade, and 4) control with no chair, on the lowest urbanized site, Santa Maria Beach. The resetting method (Pombo & Turra, 2019) was used for six weeks measuring burrow abundance, width, depth, and distance to nearest chair leg within each plot. Nested ANOVA was used to examine burrow width, depth, and distance to nearest chair leg across experimental plot conditions, but no significant differences were found. Generalized Linear Mixed Model was used to compare burrow abundance across experimental plot conditions, but no significant differences were found. Temperature was recorded every 15 minutes, every week using HOBO Temperature loggers at the surface and at 33 cm in depth under each chair condition and in the corner of every plot. Temperature across sites was compared using a Repeated Measures ANOVA and Tukey Post Hoc test, and results indicated that there was a significant effect of beach chair condition on sediment temperature. Overall results from this study can inform future management actions based on beach morphology, megafauna populations, and urbanization data across popular St. Thomas Beaches to address local stressors and future climate change impacts.

Anthropogenic Impacts on Ghost Crab, *Ocypode quadrata*, Populations, St. Thomas, U.S. Virgin Islands

by
Kaliegh Schlender

A THESIS

submitted to the

University of the Virgin Islands

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented November 17, 2020
Commencement December 2020

ACKNOWLEDGEMENTS

Thank you to Sapphire Beach Resort for their donation of the beach chairs used in my beach chair experiment. Thank you for the funding provided by Lana Vento Trust, Virgin Islands EPSCoR, NSF INCLUDES, and Friends of Virgin Islands National Park. Additionally, thank you to the Department of Planning and Natural Resources for approving the permits for this project.

Thank you to Allie Durdall and Maggie Rios for the field assistance, support, flexibility, and encouragement during the course of these experiments that made data collection possible. Thank you to my committee members Dr. Kristin Wilson Grimes, Dr. Guilherme Corte, and Dr. Sennai Habtes for their feedback, flexibility, and patience during the delays and changes of this project due to COVID-19.

Special thanks to Dr. Maria Pombo who provided feedback and advice on implementing the burrow resetting method to the beach chair experiment.

Enormous thank you to Dr. Kristin Wilson Grimes for her guidance and prompt responses to incidents and COVID-19 that made this project continue regardless of the different curveballs that were encountered.

Finally, a big thank you to Andi Greene, Nicole Foster, Chellby Johnson, and Brynn Pecher from the Coastal and Estuarine Research Federation Conference who provided the support, feedback, and encouragement during this project’s ups and downs.

CONTRIBUTION OF AUTHORS

Kaliegh Schlender contributed to experimental design, data collection, statistical analysis, interpretation of results, writing, and editing this document. Dr. Kristin Wilson Grimes, Dr. Sennai Habtes, and Dr. Guilherme Corte contributed to the project conceptualization, experimental design, interpretation of results, and editing. Dr. Guilherme Corte and Dr. Sennai Habtes also provided statistical analysis guidance. Dr. Kristin Wilson Grimes also contributed to the data collection.

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DEDICATION

This master’s thesis is dedicated to my grandparents, Marlene and Victor Schlender, who always encouraged educational growth and instilled in me a sense of environmental stewardship. I want to also dedicate this thesis to my father, Kevin Schlender, who always believed I could accomplish anything I put my mind to and was a constant source of support.

Chapter 1: Introduction

There are a multitude of different types of coastlines around the world (e.g., sand dunes, lagoons/coastal inlets, tidal inlets, wetlands, estuaries, deltas, reef coasts, rocky coasts and glaciated coasts), each supporting its own biodiversity and ecosystem services. Sandy beaches specifically, compose the majority of open coastline, and globally, they are the most widely used coast type by humans (Davis & FitzGerald, 2004; Schlacher et al., 2007). Sandy beaches can vary dramatically in their physical features; which controls biodiversity within the sandy beach habitat and recreational potential, depending on the beach type and morphology.

Beaches around the world are physically characterized primarily by sand particle size, slope, wave period/height, and tidal patterns (Mclachlan et al., 2018; Pilkey et al., 2011). Initial categorization distinguishes sites as wave dominated (WD), tide modified (TM), or tide dominated (TD). WD beaches are shaped physically by waves, TM are shaped by both waves and tides, and TD beaches are shaped by tides. Within each beach type, different beach morphologies are distinguished as reflective, intermediate, and dissipative (Mclachlan et al., 2018). Seven distinct beach types can be identified using beach type and beach morphologies (1) WD reflective, (2) WD intermediate, (3) WD dissipative, (4) TM reflective, (5) TM intermediate, (6) TM ultradissipative, (7) TD flats with subtypes (Mclachlan et al., 2018). Beach morphologies vary on the reflective/dissipative continuum. Beaches that possess more dissipative characteristics have fine grained and homogeneous sand, flat and wide beach areas that disperse wave energy, and well-developed offshore bars that cause waves to break further from shore (Jaramillo, 1994; Pilkey et al., 2011). On the other end of the continuum, beaches with reflective characteristics are narrow, steep, have no offshore bars, and are composed of coarse, heterogeneous sediment (Jaramillo, 1994; Pilkey et al., 2011).

Defining the beach type and morphology, helps inform estimates of potential biodiversity and impacts of human use. Benthic organisms inhabiting sandy beaches are referred to as sandy beach infauna (i.e. living between sand grains) or epifauna (living on the surface of the sediment) and are divided into three categories based on size: microfauna (<0.04mm), meiofauna (0.04mm - 0.5mm), and macrofauna (>0.5 mm;

Giere, 2008; Pilkey et al., 2011; Warwick & Gee, 1984). A dissipative beach environment typically possesses larger amounts of macrofaunal biodiversity compared to reflective beaches, with specific variations depending on epifauna type (i.e. soft bodied, hard bodied, size; Jaramillo, 1994). Organisms are found within different zones across the beach, which can be defined in multiple ways. The upper beach, supralittoral zone, is above the drift line and can be found on all beaches. When not restricted by human construction, this zone is dominated by species such as Ocypodid crabs in warmer regions and Talitrid amphipods (commonly known as sand fleas) in more temperate regions (McLachlan, 2001). The midlittoral zone stretches from the drift line to the swash where the waves meet the beach, but this can also be separated into the littoral and sublittoral zones. The mid-shore area, also called the littoral zone, contains high populations of Cirolanid isopods as well as Spinonid and Opheliid polychaetes (McLachlan, 2001). Closest to the ocean is the sublittoral fringe and is home to Hippid crabs, Mysids, Haustoriids, Donacid clams, amphipods, and Nephtyid worms. The lower zone of the beach, the sublittoral fringe, containing the highest species richness of all zones, is not always present depending on beach characteristics and type (McLachlan, 2001).

Within sandy beach ecosystems, the total number of organisms has been found to decrease from temperate to tropical regions, with communities being shaped by temperature, wave power, grain size, and beach slope (Defeo et al., 2009; Dexter, 1992; Pilkey et al., 2011). Species richness was found to increase as temperature increased from temperate to tropical, and macrofaunal richness decreased as beach slope increased (Barboza & Defeo, 2015). Aside from trends in latitude, wave exposure has been found to significantly shape infauna community structure, globally. Across various beach sites, macrofaunal density was found to be higher on beaches with more protected shorelines and species diversity increased with more protection from waves (Dexter, 1992). Similar patterns can be found comparing Atlantic Ocean beaches versus Pacific Ocean beaches, with the highest biodiversity being found on tropical beaches with limited wave exposure compared to temperate beaches with high wave exposure (Defeo et al., 2009; Dexter, 1992). This indicates the importance of physical beach characteristics for macrofaunal species richness and diversity (Defeo et al., 2009). The most common organisms found across beaches were isopods, amphipods, polychaetes, and bivalves respectively, with tropical regions having higher diversity and species richness (Dexter, 1992). Researchers found that among ≥ 200 beaches globally, locations with high wave exposure tend to be dominated by crustaceans, with the relative abundance of macrofauna increasing as beaches become more dissipative (Defeo & McLachlan, 2005; McLachlan & Dorvlo, 2005; Dexter, 1992).

Despite their value, sandy beach ecosystems are facing increasing threats from habitat loss, pollution, recreational activities, beach nourishment projects, and climate change (Crain et al., 2009; Defeo et al., 2009; Peterson et al., 2000; Schlacher et al., 2007). These impacts have long lasting consequences for sandy beach biodiversity and ecosystem function (Cardinale et al., 2012; Cernansky, 2017; Huston, 1979). Global threats such as climate change have a significant effect on sandy beaches, however, local anthropogenic stress can exert a stronger influence (Schooler et al., 2017). For example, in a Californian study, over a period of three decades when local stressors were continuous, loss of species and ecosystem services persisted, whereas beaches where local stressors were relieved, slowly regained species and ecosystem services (Schooler et al., 2017). This indicates the importance of local conservation and management actions for sandy beaches, particularly those with high visitor frequency or tourism traffic.

Anthropogenic alterations on sandy beaches displace infauna, kill species, degrade available habitat, and/or destroy burrows within the sediment (Peterson et al., 2000). Human development along sandy beaches physically alters habitat and attracts additional visitor frequency (Defeo et al., 2009). Development can include the removal of physical characteristics such as sand dunes which combat erosion and provide habitat for macrofauna. These alterations offer little support to the beach structure and can lead to extensive erosion (Peterson et al., 2000). Beach cleaning is another alteration used to accommodate tourism and recreational use in general (Defeo et al., 2009; Peterson et al., 2000). Raking or sieving beach sand to remove litter, wrack, debris, or other materials from the ocean are commonly used to create more tourist-friendly beaches (Defeo et al., 2009). Cleaning effects on infauna vary, with some species populations remaining consistent between cleaned and uncleaned beaches, and others having lower populations on cleaned beaches (Malm et al., 2004). These variations are attributed to infauna body type (i.e. soft or hard bodied animals, small or large individuals); with more susceptible individuals being soft bodied, juveniles, or smaller infauna (microfauna & meiofauna; Malm et al., 2004). Beach cleaning also decreases organic matter within the sandy beach habitat, decreasing key resources for infauna and negatively impacting populations across beach zones (Gheskiere et al., 2005). Beach cleaning, especially using mechanical methods, in combination with high tourism results in lower organic matter, lower species density, and lower diversity leading to reduced sandy beach ecosystem function (Gheskiere et al., 2005).

Pollution, defined as contaminants introduced into an environment, is found in multiple forms such as gas, liquid, solid, or energy altering the habitat in which they are introduced (Crain et al., 2009). Human contaminants lead to a variety of negative impacts. Pollutants can alter the physiology of various species and influence beach infauna survival and reproduction (Crain et al., 2009; Defeo et al., 2009). Solid waste such as plastics can alter the health of organisms that ingest or are entangled within them and can often lead to the death of the organism. Bacteria, metal contaminants, and chemicals can also be introduced through terrestrial runoff, and can negatively impact the health of a population (Crain et al., 2009; Defeo et al., 2009). Additionally, pollutants can damage or reduce food and other resources available or required for populations to be maintained within an ecosystem causing populations to diminish (Crain et al., 2009; Defeo et al., 2009).

Human recreation poses a threat for sandy beach environments through destruction of the beach habitat from consistent trampling (Defeo et al., 2009). Various activities by tourists such as trampling and bonfires can destroy crab burrows, seabird nests, and sea turtle nests which pose a threat to their reproduction and survival (Defeo et al., 2009). Long-term urbanization decreases beach invertebrate populations, with research indicating significantly lower populations on beaches with urbanization compared to remote beaches. Researchers involved in that work attributed the change in population abundance to increased human impact, since physical characteristics of the beach remained constant over time (Bessa et al., 2014).

Ecosystem biodiversity helps maintain ecosystem resiliency, higher ecosystem function, and productivity among species within an ecosystem. Loss of this biodiversity can create adverse effects on the native epifauna and habitat degradation (Cardinale et al., 2012; Loreau et al., 2001). Significant disturbance to an ecosystem from urbanization can cause the loss of functional redundancy, the ability for multiple organisms to perform the same ecosystem services (Huijbers et al., 2015). Often reduced functional redundancy is associated with the loss or extinction of various keystone species, those who perform specific and important ecosystem services within their habitat. Often these individuals help maintain a balance between both plant and animal species within their habitat through their services and/or predatory behavior (Cardinale et al., 2012; Cardinale et al., 2006; Cernansky, 2017). The damage to an ecosystem can become irreversible when functional redundancy and keystone species are lost (Balvanera et al., 2006; Cardinale et al., 2012; Cardinale et al., 2006; Huijbers, 2015). Functional redundancy and high biodiversity with competition among species aids in building habitat resilience and stability, which allows an ecosystem to adapt and recover from disturbance (Cardinale et al., 2012; Huijbers et al., 2015; Huston, 1979; Loreau et al., 2001). Within a sandy beach ecosystem, loss of faunal biodiversity, such as filter feeders and scavengers, could result in impaired water quality from reduced or halted detritus break down (Balvanera et al., 2006; Cardinale et al., 2012; Cardinale et al., 2006; Huijbers, 2015).

Select species are used to measure the effects of anthropogenic impact and can be used as environmental indicators (reflecting changes in the local environment), ecological indicators (reflecting ecosystem stress), and biodiversity indicators (reflecting levels of taxonomic diversity; Gerlach et al., 2013). An extensively-used ecological indicator in sandy beach ecosystems are ghost crabs (sub-family Ocypodinae), omnivorous macrofauna found in the phylum Arthropoda, whose diets and populations vary according to anthropogenic impacts and available resources (Barros, 2001; Costa et al., 2019; Costa & Zalmon, 2019; Gül & Griffen, 2018; Gül & Griffen, 2019; Peterson et al., 2000). Ghost crab species of the genus *Ocypode,* are a popular choice of ecological indicator for sandy beach environments used by many researchers (Barros, 2001; Costa et al., 2019; Costa & Zalmon, 2019; Gül & Griffen, 2018; Gül & Griffen, 2019; Peterson et al., 2000). The burrows of this nocturnal species are distinct, easy to see, and can accurately reflect the species population abundance and age (Gül & Griffen, 2019). Ghost crabs also have predictable responses to sandy beach stressors, with populations negatively impacted by increased human activity (Gül & Griffen, 2019). Under the pressures of urbanization, population abundance of foraging crabs and burrow abundance has been found to significantly decrease, making this species an ideal indicator of urbanization stress on sandy beach environments (Barros, 2001; Costa et al., 2019; Costa & Zalmon, 2019). Additionally, ghost crabs are mostly scavengers, but they can display predatory behavior, making their diet accurately reflect the community structure of lower taxa (Wolcott, 1978). Food supply directly impacts population size, so when there is a large supply of smaller invertebrates, algae, or other food sources the crab population will be greater compared to locations that have a more limited food supply (Dittel et al., 2000; Doi et al., 2005; Wolcott, 1978).

Ghost crabs eat various carcasses on the beach such as birds, fish, insects, sea turtle hatchlings, and mammals, and in some locations deposit feed or use food waste from human visitors as a food source. This additional food source is a potential explanation for an increase in ghost crab populations in the presence of increased human activity in some environments (Strachan et al., 1999). Ghost crabs have also been observed by the water line at night, potentially feeding on marine invertebrates (Strachan et al., 1999). Ghost crabs create burrows with one or two openings in different patterns that can vary in size, depth and location for a variety of reasons. Common shapes are J-shaped, L-shaped, U-shaped, Y-shaped, and spiral, with the deepest point at least 1cm above the water table. Burrows are generally found between 1.5 m and 10 m from the water line, with those located closer to the swash tending to be shallower due to water table restrictions (Pombo & Turra, 2013; Strachan et al., 1999). Although burrows are shallower closer to the swash, almost all burrows less than 10 cm are generally uninhabited, and the occupation rate increases as burrows become deeper from 10 cm to 35 cm (Pombo & Turra, 2013). Burrow width corresponds to the carapace size and age of the occupant with burrows up to 20 mm in diameter associated with smaller juvenile crabs, medium adults between 20 and 33 mm, and large older crabs having burrows larger than 33 mm (Pombo & Turra, 2013; Strachan et al., 1999; Souza et al., 2017). Smaller juvenile crabs commonly burrow closer to the water line with more shallow burrows compared to larger adult crabs who burrow further up the beach (Pombo & Turra, 2013; Strachan et al., 1999). Burrow maintenance occurs at night and at sunrise;

during the day most adult crabs will remain within their burrows to shelter from high temperatures (Strachan et al., 1999). Ghost crabs will also seek shelter within their burrow in inclement weather and low temperatures (Pombo & Turra, 2013). Juveniles, however, can be seen out of their burrows during the day (Strachan et al., 1999). A study in São Paulo, Brazil reported a seasonal increase in juvenile ghost crabs during the summer (particularly August), suggesting that ghost crab recruitment occurs during the summer months (Negreiros-Fransozo et al., 2002).

Ghost crabs have been used as an indicator globally on various beach sites to measure the effects of anthropogenic impact, however, studies in the Caribbean are extremely limited. Within the U.S. Virgin Islands (USVI) there have been no studies to-date which characterize beaches and assess potential anthropogenic impacts on their biodiversity. This thesis will address this research gap by characterizing eight St. Thomas beaches and investigating the anthropogenic impacts on ghost crab populations by counting and measuring ghost crab burrows as a proxy for the population of crabs on the beach. Select sites will have urbanization, ghost crab populations, and environmental variables assessed to characterize the environmental state of populated and remote beaches around St. Thomas, USVI. Additional human impacts of beach chairs will also be measured to determine if beach chairs alter burrowing behavior and sediment temperature. Through comparing beach morphologies, urbanization impacts, and ghost crab populations and behavior, these data can inform site-specific management to address specific urbanization impacts. This study provides impact specific data so future management strategies can target urbanization impacts that pose the greatest threat to specific individual sites around St. Thomas. It is the first time such data have been collected for St. Thomas, USVI.

Chapter 2: Morphological Characterization of St. Thomas Sandy Beaches and Effects of Urbanization on Ghost Crab Populations

Of the many coastline types, sandy beaches make up one-third of the world's coastlines and support local economies, globally (Amaral et al. 2016; Luijendijk et al., 2018; Schlacher et al. 2007). Sandy beaches provide a multitude of ecosystem services ranging from economic to recreational benefits and are home to diverse and endemic biota that provide services such as organic material breakdown and the filter or capture of pollutants (Checon et al. 2018; Defeo et al. 2009; Nel et al. 2014). Despite their value, sandy beaches are threatened by urbanization and climate change, leading to the potential for half the world's beaches to disappear by the end of the century under current climate change projections (Vousdoukas et al. 2020).

To understand the changes sandy beaches are undergoing, it is vital to understand the relationship between modifications to environmental characteristics and resultant changes in biodiversity within sandy beach ecosystems, so that threats and impacts can be addressed (McLachlan et al. 2013). Unfortunately, in contrast to their large importance and geographic extent, sandy beaches are the least studied coastal ecosystem (Nel et al., 2014). According to Nel et al. (2014), the total number of sandy beach studies corresponds to only 26% of the total number of mangrove studies, 15% of the number of studies on reefs, and less than 10% of the total for estuaries.

Globally, little is known about sandy beach ecosystems, and in the Caribbean information is even more limited with studies primarily conducted in temperate and subtropical regions (Barboza and Defeo, 2015; Defeo and McLachlan, 2013; Sibaja-Cordero et al., 2019). Sandy beaches within the Caribbean serve as a popular attraction for visitors around the world. In 2017, St. Thomas welcomed 1,944,115 tourists (Bureau of Economic Research, 2017), many of whom likely visited popular beaches such as Magens Bay, Coki Point Beach, or Sapphire Beach. Although other research reveals that high urbanization can decrease sandy beach infauna populations and ecosystem services (Barros, 2001; Costa et al., 2019; Costa & Zalmon, 2019; Gül & Griffen, 2018; Gül & Griffen, 2019; Peterson et al., 2000), no studies have been conducted within the U.S. Virgin Islands or on St. Thomas, regarding the human impact oftourism and tourism infrastructure on sandy beaches, to-date.

To assess the ecosystem stress on sandy beach ecosystems from anthropogenic impacts, ghost crabs are a popular choice of ecological indicator species due to their predictable responses to human impact and widespread distribution from South to North America (Barros, 2001; Costa et al., 2019; Costa & Zalmon, 2019; Gül & Griffen, 2018; Gül & Griffen, 2019; Peterson et al., 2000). Additionally, crab burrows also serve as an accurate proxy to the ghost crab population, where burrows accurately reflect the size of the population and the individuals inhabiting them; thus, making this species low cost and easy to survey (Gül & Griffen, 2019).

In this study, I examined environmental and biotic characteristics of eight beaches on St. Thomas, U.S Virgin Islands, including 1) Stumpy Bay, 2) Santa Maria Bay, 3) Caret Bay, 4) Neltjeberg Bay, 5) Lindberg Bay, 6) Magens Bay, 7) Coki Point Beach, and 8) Sapphire Beach (Figure 1); all of which have different levels of human impact. I used the data collected to identify beach types based on environmental factors such as beach slope, grain size, and wave characteristics and described the environmental and biotic features at sites. I also investigated the effect of urbanization, tourism, and morphological beach characteristics on the abundance, width, and depth of the ghost crab, *Ocypode quadrata*, burrows. I hypothesized that burrow abundance would be lower on beaches with higher urbanization (Magens Bay, Lindberg Bay, Coki Point Beach, and Sapphire Beach), compared to beaches with lower urbanization (Neltjeberg Bay, Caret Bay, Stumpy Bay, and Santa Maria Bay), with the decrease driven by urbanization and anthropogenic stress. I also expected the fluctuations in tourism to shape the burrow width and depth, causing a difference between high- and low- tourist season (February 3-March 12 & May 18-June 25, 2020 respectively). Specifically, I hypothesized that burrows would be deeper and wider as adult ghost crabs attempted to create more protective burrows on beaches with higher human use during high tourist season and that smaller more vulnerable crabs, would be absent from or in reduced numbers, on those beaches. Results from this study will provide important information about the morphological characterizations of beaches around St. Thomas, and address key data gaps regarding the effects of urbanization on sandy beaches, including ghost crab populations. These results will inform research-based management plans and the conservation of St. Thomas beaches.

Methods

Site Selection

All study sites were located on the island of St. Thomas, USVI, located in the Caribbean (Figure 1). Eight beaches were selected *a priori* with two levels of predicted impact: four sites each for predicted high- and low- human impact (Figure 1). Predictions were based on the presence or absence of human structures such as bars on the beach, visible machinery or tool marks that could be associated with beach grooming, proximity to resorts, and pedestrian accessibility. Predicted low-impact beaches included Caret Bay, Neltjeberg Bay, Santa Maria Bay, and Stumpy Bay (Figures 1, 2), all located on the northwest side of St. Thomas. Beaches at low-impact sites lacked human structures, grooming marks, and were not easily accessible from the public road, and often required a short hike and/or four-wheel drive vehicle to access. Predicted high-impact beaches included Magens Bay, Coki Point Beach, Lindberg Bay, and Sapphire Beach (Figures 1, 2). High-impact beaches experienced beach grooming and all had access to human structures such as food trucks, concession stands, or restaurants and bars. Magens Bay and Coki Point Beach were considered popular tourist destinations, with taxis regularly taking visitors to these locations (pers. obs.); while Sapphire Beach and Lindberg Bay were associated with popular tourist resorts: Sapphire Beach Resort and Emerald Beach Resort, respectively. Predicted human impact levels were verified using a modified Urbanization Index (UI; Gonzalez et al., 2014).

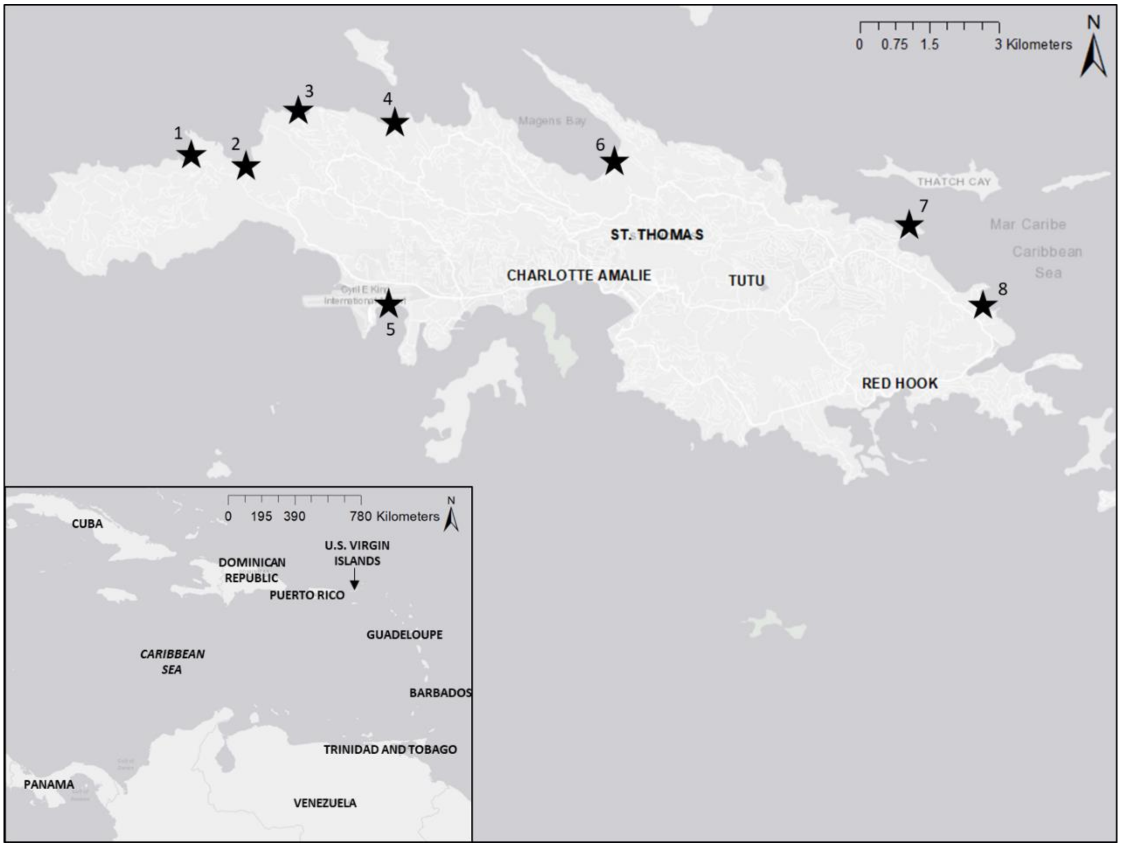


Figure 1: St. Thomas is located in the United States Virgin Islands within the Caribbean Basin. Low- human impact sites include (1) Stumpy Bay, (2) Santa Maria Bay, (3) Caret Bay, and (4) Neltjeberg Bay. High human impact sites include (5) Lindberg Bay, (6) Magens Bay, (7) Coki Point Beach, and (8) Sapphire Beach. Urban centers include Charlotte Amalie, Red Hook, and Tutu. Maps were created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Light Gray Canvas Maps 2020, copyright © Esri.

Figure 2: Aerial images of study sites from World Imagery Basemap (2009). Low-impact sites include (1) Stumpy Bay, (2) Santa Maria Bay, (3) Caret Bay, and (4) Neltjeberg Bay. High-impact sites include (5) Lindberg Bay, (6) Magens Bay, (7) Coki Point Beach, and (8) Sapphire Beach. Maps were created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri.

Sampling Period

To compare how seasonal changes in tourist abundance impacted characteristics of ghost crab populations (abundance, width, and burrow depth), I conducted ghost crab burrow surveys and urbanization assessments during two, 6-week sampling periods: high-tourist season (February 3-March 12, 2020), and low-tourist season (May 18-June 25, 2020). Ghost crab burrow surveys were conducted in the early morning three times each season, and urbanization variables: solid waste, vehicles on sand, buildings on sand, and beach cleaning were observed. Visitor frequency surveys at high impact sites (Lindberg Bay, Magens Bay, Coki Point Beach, and Sapphire Beach) were conducted three times each season between 12-2 pm. Low- season coincided with the outbreak of the novel coronavirus (COVID-19) in the United States and was characterized by no cruise ship activity (Center for Disease Control, 2020) and limited resort visitors within the USVI (U.S. Virgin Islands Office of the Governor, 2020).

Beach Characterization

Physical beach characteristics such as slope, sediment temperature, and grain size shape benthic population abundances and impact burrowing behavior for ghost crabs (Strachan et al., 1999; Pombo & Turra, 2013). Beach type and morphology were determined using multiple indices (Relative Tide Range (RTR), Beach Index (BI), Beach Deposit Index (BDI), and the logarithm log(1/slope) (McLachlan & Dorvlo, 2005) derived from the physical characteristics wave height, tide range, grain size, and beach slope. Indices or categorizations that detected the greatest differences between sites, were used in further models to assess drivers of burrow abundance, width, and depth.

Beach slope measurements were taken using the Emery Rod Method (Emery, 1959) along four, shore-perpendicular, transects at every site visit across all eight sites and during both seasons (n=192). The change in elevation was calculated for each two-meter segment along each transect, then these were used to create individual beach profiles. Total elevation change from the swash to the vegetation line was used to calculate the slope of each transect. The number of slope segments varied based on the width of the beach. The transition from the supralittoral zone to the midlittoral zone was noted on each transect and was estimated visually by scanning along the beach and noting where on the transect the texture and moisture of the sediment changed. Sites were sampled before 8 am most days.

Additional measurements needed for beach indices included maximum spring tide range (retrieved from tidesandcurrents.noaa.gov using the 9751540 Red Hook Bay Station) and mean grain size. To characterize mean sediment grain size, two 7.5 cm diameter and 20 cm long push cores were collected in the supralittoral and midlittoral zones along the first transect of the burrow surveys upon each site visit (n = 96). Cores were transported to the University of the Virgin Islands Environmental Assessment Laboratory for processing. Each core was homogenized using the quartering method twice before a subsample was split, as defined by the United States Environmental Protection Agency (EPA) methods (Simmons et al., 2014). During homogenization, I noted if gravel or cobbles were present in the sample, with gravel defined as any sediment granule larger than -2 phi. If gravel was present, a subsample of 250 g was taken for sieve shaker analysis. If no gravel was present a 75 g split was taken from the homogenized sample. The subsample sizes were determined using the United States Geological Survey (USGS) recommendations (Poppe et al., 2005). Subsamples were dried in a drying oven at 90°C for 12 hours or until a constant weight as achieved. When no weight difference was detected, subsamples were placed in individually labeled bags until sieving. Stacked sieves following the Wentworth grain sizes (1922) (2000, 1000, 500, 250, 125, and 63 µm) were used to analyze each sub sample. Samples were shaken in a sieve shaker for 10 minutes then each sieve was emptied, and contents weighed.

Initial observations and categorizations were made of beach type based on wave and tidal patterns using the RTR categorization defined by McLachlan, Defeo, and Short (2018). Beach types were defined as wave dominated (WD), tide modified (TM), and tide dominated (TD), and morphology as dissipative, intermediate, or reflective. Sites with RTR <3 were categorized as WD, RTR = 3-10 were categorized as TM, and RTR >10-50 were categorized as TD. Grain size and beach slope were then used to classify sites as WD reflective (medium/coarse grain size, slope >.05), WD intermediate (fine/medium grain size, slope 0.02-0.05), WD dissipative (fine grain size, slope<0.02), TM reflective (various grain size, steep with flat lower shore), TM intermediate (variable grain size, steep upper shore with low tide bars and troughs), TM ultradissipative (fine sand, flat beach slope), or TD flats with subtypes (variable grain size, flat beach slope, McLachlan, Defeo, & Short, 2018).

The BI equation (McLachlan and Dorvlo, 2005), used beach slope, grain size, and spring tide range to assign a quantitative number indicating the classification of beach type. Values from 0.11-1.3 correspond with reflective beaches, values around 2.17 correspond to intermediate beaches, and values around 3.6 correspond with dissipative beaches (McLachlan and Dorvlo, 2005). From previous observations, I expected BI values for the study sites to fall between 1 and 2.5. For areas with little tidal variation and sites within a small geographic area, log*(1/beach slope)* is used to detect differences between beach morphologies, with steeper slopes indicating more reflective characteristics, and gradual slopes indicating more dissipative characteristics. BDI uses fewer environmental variables compared to the BI, using beach slope and average grain size to distinguish beach types. Low BDI values indicate reflective beaches, while high BDI values correspond to dissipative characteristics. This index was selected to detect beach differences because it excludes tidal variations, making it a suitable index for my study sites, since beaches on St. Thomas are microtidal (range = +/- 0.14 m, from tidesandcurrents.noaa.gov using the 9751540 Red Hook Bay Station).

Urbanization Assessment

A modified Urbanization Index (UI), was used to independently confirm *a priori* human impact characterizations across sites (Table 1; after Gonzalez et al., 2014). The level of urbanization was estimated by calculating an index with indicators of human impact: 1) distance to urban centers, 2) buildings on the sand, 3) beach cleaning, 4) solid waste, 5) vehicle traffic on sand, and 6) visitor frequency. Each variable was assigned a value between 0 to 5 each visit, with “0” indicating absence of that variable, and “5” indicating a high level of the specified variable (Table 1). Most variables were estimated visually by direct observation in the field by one consistent observer. The urbanization variable “quality of night sky” was excluded due to safety concerns, and detailed definitions were added to the remaining variables to provide clearer and consistent value assignment. for this study. For buildings on the sand, I distinguished rankings by the size, type, and number of human structures on the site, resulting in sites with larger and more numerous human structures having high value assignments, and distinguishing sites that have a combination of small and large structures (Table 1). Beach cleaning on St. Thomas normally does not entail machine use on the sites included in this study, so other forms of cleaning such as raking incoming sargassum blooms were added to the index definition as a medium rank of beach cleaning differentiated by perceived frequency (occasional raking = 2, regular raking = 3, Table 1). Distance to urban centers was defined as the straight-line distance from the center of the beach to the center of the closest urban center using the Google Maps measure tool (Figure 1). Urban centers Charlotte Amalie, Red Hook, and Tutu on St. Thomas were chosen due to their high traffic and shopping areas. Original UI visitor frequency definitions fit low-impact sites; however high-impact sites could not be differentiated. To detect differences in visitor frequency across high-impact beaches, visitor traffic surveys were conducted between the time of 12-2 pm (estimated time of maximum visitor frequency) using three transects spread equidistantly across the beach for a total of five minutes. Visitors were counted as they passed a set transect line, then values were used to calculate the number of visitors passing the transect per minute. This method was repeated at high traffic sites twice per season (n=8).

Table 1: Modified Urbanization Index (after Gonzalez et al., 2014). Six index variables were modified and used to measure anthropogenic impact with the following categorizations. Variables* were modified to have more detail for better value assignment.

	Low (0-1)	**Medium (2-3)**	**High (4-5)**
Proximity to Urban Centers*	3-4 km = 1 >4 km = 0	2-3 km = 2 1-2 km = 3	0.5-1 km = 4 0-0.5 km =5
Buildings on the Sand*	No buildings/structure = 0 One small building = 1	2-3 small structures = 2 >3 small structures = 3	2 buildings/structures = 4 >3 buildings = 5
Beach Cleaning*	None = 0 Occasional trash pick up = 1	Occasional raking = 2 Regular raking = 3	Small machinery used = 4 Large machinery used = 5
Solid Waste on Sand*	None = 0 Minimal = 1	Some waste within $3m^2$ = 2 Some waste within $1m^2$ = 3	Multiple types/pieces of waste within Some waste within $3m^2$ = 4 A lot of small/large pieces of waste within Some waste within $3m^2$ = 5
Vehicle Traffic*	No access/traces = 0 Faint traces of potential traffic = 1	Weathered/scarce traces = 2 Scarce/clear tracks = 3	Frequent but limited traffic = 4 Frequent across full beach = 5
Visitor Frequency*	None = 0 Very few = 1	Several = 2 Many visitors; considered “popular” = 3	2-3 people/minute = 4 >3 people/minute = 5

Burrow Surveys

Crab burrows were surveyed as a proxy for crab abundance (Gül & Griffen, 2019) using four, 3 m wide, shore-perpendicular belt transects haphazardly placed across each beach from the vegetation line to the swash zone during each sampling event (n = 192; Figure 3). Each transect was separated from the next by at least 15 m. For each transect, burrow, depth, width, and distance from the vegetation line was documented. Starting at 1.5 m from the vegetation line and proceeding every 3 m and in the center of each belt, sediment temperatures at 1 cm and 14 cm were recorded, using a handheld thermometer (Harbor Digital Cooking Thermometer). Previous studies measuring burrow depth used a flexible steel cable (Pombo & Turra, 2013); however, I used a zip tie marked in one cm increments. Using a zip tie allowed for greater flexibility when measuring the burrow as it was able to curve when the burrow turned underground or to break through surficial plugs (Milne & Milne, 1946). Burrows depths ≤ 10 cm were excluded from data analysis (n=51), as these shallow burrows have been found to be uninhabited by ghost crabs (Pombo & Turra, 2013). A Vernier caliper was used to measure burrow width to the nearest millimeter. For each burrow, crab activity was noted as follows (after Pombo & Turra, 2013): none (N; no sign of occupation), subtle (Sb; faint tracks and/or excavated sand), moderate (M; obvious presence of sand movement or tracks), and strong (St; presence of more than one clear sign of occupation and/or a very prominent sign such as crab seen or felt tugging on zip tie) to ensure that burrows measured were active. These methods were modified from Marine Biodiversity Observation Network Pole to Pole of the Americas protocols (Gauisas et. al., 2018) ghost crab survey protocol. Burrow abundance, width, and depth were measured using the guidelines outlined in Gauisas et al., (2018), however sections regarding marine debris, detritus, or macrofauna identifications were not used.

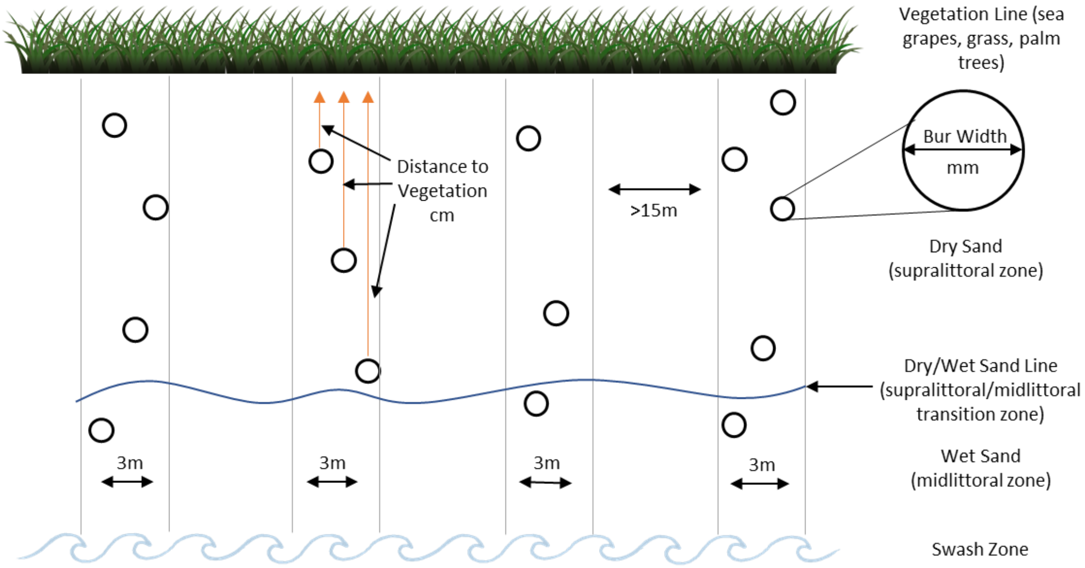


Figure 3: Experimental design of ghost crab burrow surveys. Figure modified from Gauisas et al., (2018).

Beach Characterization Data Analysis

To assess the seasonal changes in beaches across individual sites, the dataset was split, and Wilcoxon Rank Sum Tests were used to compare beach slope between high-and low-tourist season (n=24). A Kruskal Wallis Test was then used to compare the beach slope across all sites (n=192) and a Dunn's Multiple Comparison Post-Hoc Test was used to determined significant differences between individual sites. Individual transect measurements from each site were used to calculate the BI, BDI, and log(1/beach slope) for each visit.

Grain size was converted to phi from millimeters by using the transformation: -log (number, base 2), then cumulative percentages were calculated at 16%, 50%, and 84%. Phi grain sizes at 16%, 50%, and 84% were averaged to give the mean grain size per core (n=96). Wilcoxon Rank Sum Tests were used to compare the mean grain sizes across the supralittoral and midlittoral zones, then mean grain sizes per zone were averaged for an overall mean grain size per visit (n=48). Mean grain sizes of each visit were used in the BI and BDI to characterize beaches around St. Thomas, and in linear mixed models to determine the effects of grain size on ghost crab burrow abundance, width, and depth.

To determine the beach type, Relative Tide Range (RTR) was calculated using $RTR = TR/H_B$ where TR is mean tide range and H_B is mean breaker height. H_B was calculated from visual estimations during each site visit (n=48) and used to calculate an RTR for every site visit (n=48). RTR was then averaged to determine each individual sites' mean RTR (n=8). BI was calculated using $BI=log((Sand*Tide)/Slope)$ where *Sand* is mean grain size (phi) +1, *Tide* is the max spring tide range (meters), and *Slope* is the mean beach slope. BI calculations used individual transect slopes (n=192), and average grain sizes of each visit (n=48) to calculate a BI value for each transect (n=192). To distinguish differences in BI between beach sites, BI values were compared across sites using a Kruskal Wallis and Dunn Post-Hoc test. BDI was calculated using $BDI=(1/tan(Slope))*(a/Mz)$ where *Slope* is the mean beach slope, *a* is the constant 1.03125 (mm), and *Mz* is mean grain size (mm). BDI calculations used individual transect slopes (n=192) and average grain size for each visit (n=48), then a BDI value was calculated for each transect (n=192). To distinguish beach types using the BDI classification, a Kruskal Wallis Test was used to compare BDI values across sites, and a Dunn's Multiple Comparison Post-Hoc test was used to specify site differences. The final beach classification, *log(1/beach slope)*, was calculated with individual transect slopes, then compared using a Kruskal Wallis Test to compare the values across sites. Significant differences were tested using a Dunn Post-Hoc test.

Urbanization Data Analysis

After individual values for each UI variable (visitor frequency, solid waste, distance to urban center, buildings on sand, beach cleaning, and vehicles on sand) were assigned, values were normalized using $X' = ((X-X_{MIN})/(X_{MAX}-X_{MIN}))$ with X' equaling the final UI value for the individual variable and X = raw UI variable score, X_{MIN} = zero, and $X_{MAX} =$ 5 (because the individual scores can range from 0-5). Final values ranged from zero (no anthropogenic impacts) to 1 (high anthropogenic impact). All index variables were scored during each site visit and both sampling seasons, normalized, then averaged to create a modified overall UI for each site per visit (n = 48). Overall UI was then averaged by site per season resulting in two seasonal UI per site (n=16). Seasonal UI was compared between high- and low- tourist season using a Wilcoxon Rank Sum Test.

Using the overall UI calculated per site visit (n=48) a complete linkage Euclidian distance cluster dendrogram was used to confirm *a priori* classifications of low- and high-impact beaches. After *a priori* classifications were confirmed using a cluster dendrogram, a Wilcoxon Rank Sum Test was used to determine if there was a significant difference in overall UI between high- and low- impact sites. A Kruskal-Wallis Test and Dunn Post Hoc Test were used to compare overall UI (n=48) across all sites to detect further variations aside from predicted impact. When variations were observed across sites, a Principal Component Analysis (PCA) was used on individual UI variables (n=288) to test the effects of individual anthropogenic impacts. A second PCA was conducted on individual UI variables of high- impact sites (n=144) when variation was observed in the first PCA.

Ghost Crab Burrow Data Analysis

Burrow abundance was standardized by dividing the number of burrows per transect by the area of the transect. To compare site-specific differences in burrow abundance across study sites, a Shapiro-Wilkes test was used to test for normality, then a Kruskal-Wallis and Dunn Post Hoc test were used. These tests were repeated for both burrow width and burrow depth across study sites to determine population differences across sites. Site-specific differences in burrow abundance, width, and depth across seasons were assessed using Wilcoxon Rank Sum Tests. Ghost crab life stages were determined using size classifications by Souza et al. (2017). Burrow widths less than 20 mm were classified as juveniles, burrows ranging from 20-33 mm were classified as medium adult, and burrows greater than 33mm were classified as older adult. To assess the distribution of age classifications across the beach surface, abundances of burrows for each life stage were graphed in relation to the supralittoral/midlittoral transition line and compared using a Kruskal Wallis and Dunn Post Hoc analysis. Proportions of burrows were calculated for each life stage by dividing the number of crab burrows classified at each life stage by the total number of burrows per site survey. Proportions of burrows per life stage were compared across sites using Kruskal Wallis tests. Activity classification (strong, moderate, subtle, or none) proportions were calculated by dividing the number of burrows with a specific activity level by the total burrows per visit. Proportions were compared across sites using Kruskal Wallis tests.

To assess the drivers of ghost crab population variation, independent variables were first assessed for collinearity (overall urbanization, grain size, log(1/beach slope), beach slope, season, sand temperature at 14cm in depth, sand temperature at 1 cm in depth, and wave height). Variables with strong correlations were removed from further analysis, these included beach slope which was correlated to log(1/beach slope) and temperature at 1 cm in depth which was correlated to temperature at 14 cm depth. Remaining variables overall urbanization, log(1/beach slope), mean grain size, season, wave height, and mean temperature at 14 cm in depth (n= 6) were treated as independent fixed variables along with date as a random variable, season as an interaction with overall UI, and transect nested within each site in Generalized Linear Mixed Models (GLMM).

When overall urbanization was found to be a significant variable impacting burrow metrics (abundance, width, and depth), I performed a further analysis to investigate the individual effect of UI variables (visitor frequency, buildings on sand, proximity to urban centers, solid waste, vehicles on sand, and beach cleaning) on *Ocypode* populations. After excluding buildings on sand due to collinearity with distance to urban center and visitor frequency, a Generalized Additive Model (GAM) was used to determine which individual UI variables had the greatest impact on burrow metrics (abundance, width, and depth). GAMs were selected to detect any potential non-linear effects from UI variables.

Results

Environmental Variables

Results from a Kruskal-Wallis Test comparing the average slope across all eight study sites indicated a significant difference in mean slope ($\chi^2(7) = 97.62$, $p = 2.2e\text{-}16$). Dunn Post Hoc pairwise comparisons indicated further differences across sites (Table 2). Stumpy Bay was statistically different compared to all other sites and possessed the greatest slope (approximately 0.13 m), while Santa Maria possessed the lowest slope gradient (approximately 0.05 m) and was statistically different from all sites except Lindberg Bay (Table 2, Figure 4). Results of the Wilcoxon Rank Sum test comparing beach slope between by high- and low-impact sites indicated no significant difference (Z = 22,976, *p* = 0.372).

Table 2: *p*-values from Dunn Post Hoc pairwise comparisons of average slope across sites. Statistically significant differences are indicated*.

	Santa Maria Bay	Caret Bay	Neltjeberg Bay	Lindberg Bay	Magens Bay	Coki Point Beach	Sapphire Beach
Stumpy Bay	3.48e-14*	3.79e-2*	2.0e-5*	7.33e-12*	9.24e-6*	6.35e-7*	1.02e-2*
Santa Maria Bay		3.56e-8*	6.65e-4*	3.08e-1	1.2e-3*	7.0e-3*	6.85e-7*
Caret Bay			2.96e-2*	2.57e-6*	2.09e-2*	4.62e-3*	5.99e-1
Neltjeberg Bay				1.36e-2*	8.51e-1	4.96e-1	1.0e-1
Lindberg Bay					1.96e-2*	7.06e-2	3.08e-5*
Magens Bay						5.83e-1	7.24e-2
Coki Point Beach							2.20e-2*

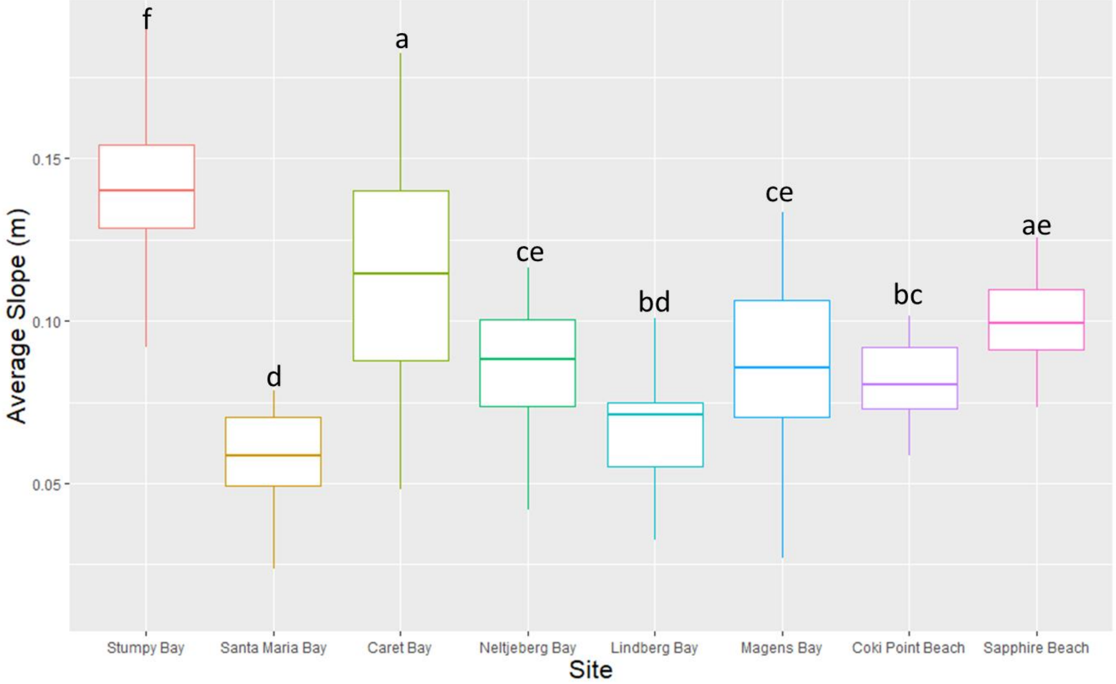


Figure 4 Average beach slope across all sites. Letters indicate Dunn Post Hoc significantly different average slopes.

Results of Wilcoxon Rank Sum Tests for individual sites indicated no significant difference in beach slope between high- and low- tourist season on Caret Bay (*p* = 0.93), Santa Maria Bay (*p* = 0.47), Neltjeberg Bay (*p* = 0.66), Lindberg Bay (*p* = 0.31), Magens Bay (*p* = 0.51), and Coki Point Beach (*p* = 0.64). Significant differences in beach slope between high- and low-tourist season were found on Stumpy Bay (*p* = 0.01) and Sapphire Beach (*p* = 0.01). Results indicated beach slope was steeper on Stumpy Bay during high-tourist season (low- 0.13, high- 0.14), and steeper on Sapphire Beach during low-tourist season (low- 0.11, high- 0.09; Figure 5).

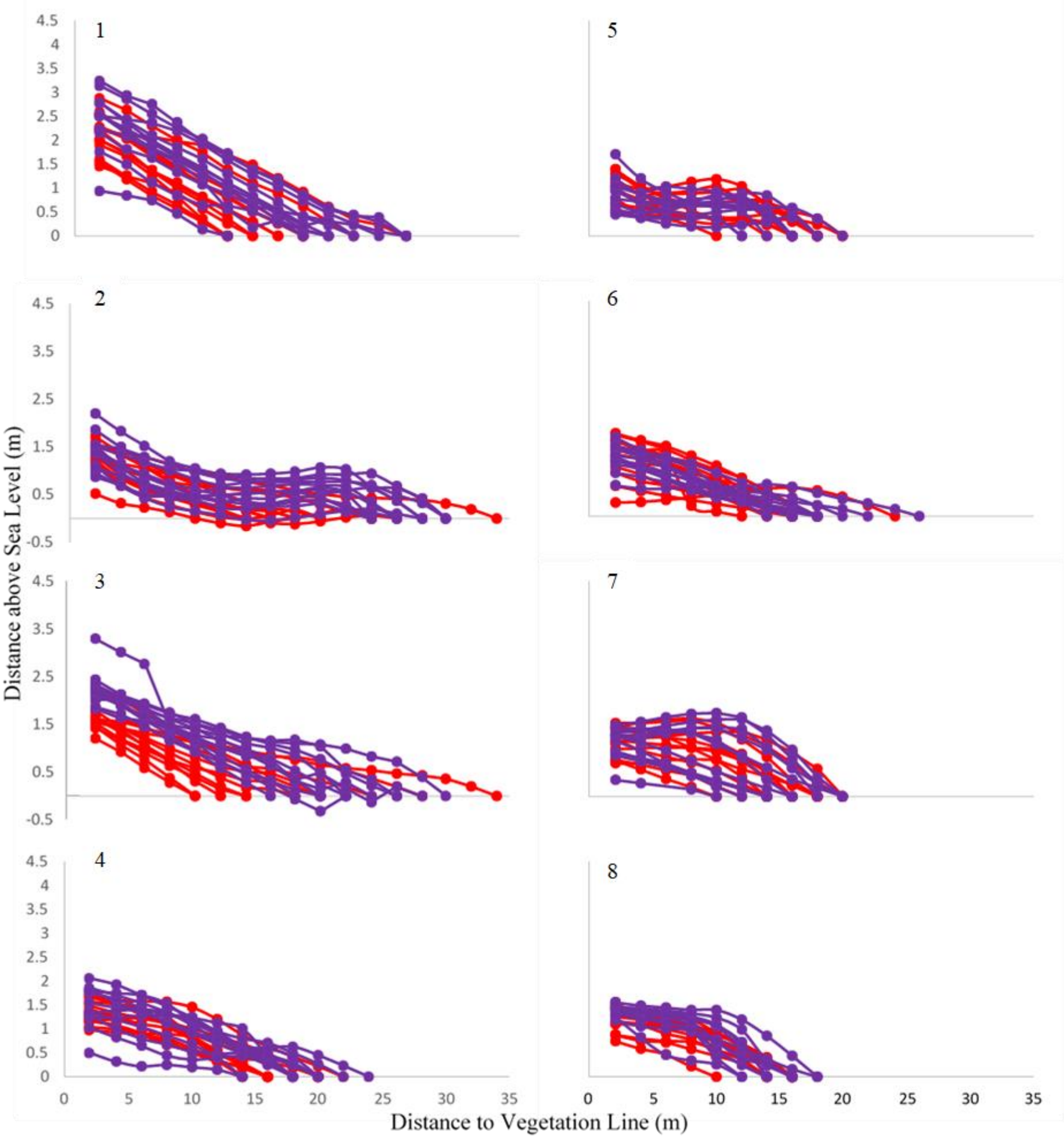


Figure 5: Beach slope profiles of all sites (1) Stumpy Bay, (2) Santa Maria Bay, (3) Caret Bay, (4) Neltjeberg Bay, (5) Lindberg Bay, (6) Magens Bay, (7) Coki Point Beach, and (8) Sapphire Beach. Slope profiles collected during peak tourist season (red, February 3-March 12, 2020, and slope profiles collected during low-tourist season (purple, May 18-June 25, 2020).

Average slope results indicate that Stumpy Bay and Caret Bay displayed more reflectiveness in their beach characteristics while Santa Maria Bay and Lindberg Bay displayed were less reflective (Table 4). Beach profiles also documented differences in beach widths with some sites such as Santa Maria Bay and Caret Bay being wider reaching a maximum width of approximately 35 m in some places and other sites being noticeably narrower such as Lindberg Bay, Coki Point Beach, and Sapphire beach reaching a maximum width of only 25 m (Figure 5). Results of a Kruskal Wallis test confirmed a significant difference in beach width across all sites ($\chi^2(7) = 59.69$, p = 1.74e-10), with Dunn Post-Hoc results indicating beach width differences across sites and that Santa Maria Bay was significantly different compared to all sites (Table 3). Post Hoc results accompanied with beach profiles resulted in Santa Maria possessing the widest average beach slope of all study sites. Distinct berms were also observed on Santa Maria Bay, Lindberg Bay, Sapphire Beach, and Coki Point Beach (Figure 5).

Table 3: *p*-values from Dunn Post Hoc pairwise comparisons of average beach width across sites. Statistically significant differences are indicated*.

	Santa Maria Bay	Caret Bay	Neltjeberg Bay	Lindberg Bay	Magens Bay	Coki Point Beach	Sapphire Beach
Stumpy Bay	5.47e-4*	5.2e-1	7.41e-1	1.34e-1	3.16e-1	9.08e-2	7.41e-3*
Santa Maria Bay		5.64e-3*	1.48e-4*	2.84e-7*	3.87e-6*	9.89e-.8*	4.19e-10*
Caret Bay			3.63e-1	2.88e-2*	1.04e-1	1.79e-2*	6.52e-4*
Neltjeberg Bay				2.5e-1	4.85e-1	1.58e-1	1.92e-2*
Lindberg Bay					6.21e-1	7.93e-1	3.02e-1
Magens Bay						4.8e-1	1.27e-1
Coki Point Beach							4.0e-1

Table 4: Environmental variables of all sites. Mean temperatures and grain sizes are reported for the supralittoral and midlittoral zone. Average wave height, wave period, and average slope are reported for each site. Average beach classification indices (RTR, BI, BDI, and log(1/slope) are reported by site.

Site	Zone	Mean Temp at 14cm (C)	Mean Grain Size (ϕ)	Mean Wave Height (m)	Mean Wave Period (wave/sec)	Average Slope (m)	Log(1/slope)	Relative Tide Range (RTR)	BI	BDI
Caret Bay				0.8 (n=6; SD=0.45; SE=0.18)	8 (n=6; SD=0.95; SE=0.39)	0.1 (n=24; SD=0.04; SE=0.01)	1.0	0.3	-0.1	6.4
	Infra	26.6 (n=69; SD=2.59; SE=0.31)	0.4 (n=6; SD=0.14; SE=0.06)							
	Supra	28.1 (n=97; SD=3.38; SE=0.34)	0.9 (n=6; SD=0.14; SE=0.06)							
Coki Point Beach				0.2 (n=6; SD=0.12; SE=0.05)	4.6 (n=6; SD=2.78; SE=1.13)	0.1 (n=24; SD=0.02; SE=0.003)	1.1	1.3	0.4	5.1
	Infra	26.5 (n=33; SD=1.34; SE=0.23)	1.4 (n=6; SD=0.02; SE=0.01)							
	Supra	27.7 (n=88; SD=2.41; SE=0.26)	1.3 (n=6; SD=0.02; SE=0.01)							
Lindberg Bay				0.2 (n=6; SD=0.10; SE=0.04)	4.5 (n=6; SD=1.59; SE=0.65)	0.1 (n=24; SD=0.02; SE=0.004)	1.2	0.9	0.6	4.6
	Infra	27 (n=30; SD=1.70; SE=0.31)	2.0 (n=6; SD=0.10; SE=0.04)							
	Supra	28.3 (n=96; SD=2.05; SE=0.21)	1.7 (n=6; SD=0.10; SE=0.04)							
Magens Bay				0.2 (n=6; SD=0.16; SE=0.06)	6.6 (n=6; SD=1.33; SE=0.54)	0.1 (n=24; SD=0.03; SE=0.01)	1.1	1.3	0.6	3.9
	Infra	26.8 (n=36; SD=1.28; SE=0.21)	2.2 (n=6; SD=0.05; SE=0.02)							
	Supra	27.3 (n=93; SD=2.01; SE=0.21)	2.0 (n=6; SD=0.05; SE=0.02)							
Neltjeberg Bay				0.6 (n=6; SD=0.51; SE=0.21)	4.6 (n=6; SD=1.15; SE=0.47)	0.1 (n=24; SD=0.02; SE=0.003)	1.1	0.9	0.5	3.4
	Infra	26 (n=76; SD=1.69; SE=0.19)	1.9 (n=6; SD=0.01; SE=0.002)							
	Supra	26.8 (n=144; SD=2.20; SE=0.18)	1.9 (n=6; SD=0.01; SE=0.003)							
Santa Maria Bay				0.7 (n=5; SD=0.63; SE=0.28)	6.4 (n=5; SD=2.04; SE=0.91)	0.1 (n=24; SD=0.01; SE=0.002)	1.2	0.6	0.7	5.0
	Infra	26.8 (n=96; SD=2.38; SE=0.24)	1.9 (n=6; SD=0.01; SE= 0.002)							
	Supra	28.8 (n=139; SD=3.30; SE=0.28)	2.0 (n=6; SD=0.01; SE=0.002)							
Sapphire Beach				0.2 (n=6; SD=0.09; SE=0.04)	4.5 (n=6; SD= 1.66; SE=0.68)	0.1 (n=24; SD=0.02; SE=0.003)	1.0	1.4	0.2	4.4
	Infra	27.3 (n=43; SD=1.28; SE=0.20)	1.2 (n=6; SD=0.05; SE=0.02)							
	Supra	27.3 (n=84; SD=1.68; SE=0.18)	1.2 (n=6; SD=0.06; SE=0.02)							
Stumpy Bay				0.4 (n=6; SD=0.33; SE=0.13)	5.9 (n=6; SD=2.10; SE=0.86)	0.1 (n=24; SD=0.02; SE=0.004)	0.9	1.0	-0.1	4.4
	Infra	27.6 (n=73; SD=2.55; SE=0.30)	0.4 (n=6; SD=0.01; SE=0.002)							
	Supra	28.0 (n=91; SD=2.97; SE=0.31)	1.2 (n=6; SD=0.01; SE=0.002)							

Environmental variables including RTR, BI, BDI, log(1/slope), average slope, average wave period, average wave height, and average temperature are reported in Table 4. All sites possessed RTR <3 and were classified as WD. Average wave height was <1 m for all sites and average beach slope was > 0.05 (Table 4) corresponding with the WD reflective morphological beach state. Additional characteristics that aligned with this classification included steep swash zones and the presence of a cusp or berm at some sites such as Sapphire Beach, Coki Point Beach, or Neltjeberg Bay. RTR results were the same across all sites. BI calculations resulted in a range of values from -0.1-0.7, and Kruskal Wallis results indicated a significant difference in BI values across sites (χ^2(7) = 141.4, *p* = 1.74e-10). Significant differences were compared between sites using a Dunn Post Hoc pairwise comparison (Table 5). Twenty out of twenty-eighty comparisons were statistically significant.

Table 5: *p*-values from Dunn Post Hoc pairwise comparisons of BI values across sites. Statistically significant differences are indicated*.

	Santa Maria Bay	Caret Bay	Neltjeberg Bay	Lindberg Bay	Magens Bay	Coki Point Beach	Sapphire Beach
Stumpy Bay	2.86e-16*	4.0e-1	5.35e-9*	1.32e-13*	2.15e-10*	3.95e-6*	1.14e-2*
Santa Maria Bay		1.34e-13*	9.31e-3*	2.43e-1	3.42e-2*	1.53e-4*	7.21e-9*
Caret Bay			5.56e-7*	6.04e-11*	3.26e-8*	1.78e-4*	9.28e-2
Neltjeberg Bay				1.31e-1	6.01e-1	2.32e-1	1.23e-3*
Lindberg Bay					3.0e-1	6.71e-3*	1.5e-6*
Magens Bay						9.02e-2	1.71e-4*
Coki Point Beach							4.74e-2*

BDI calculations resulted in a range of values from 6.1-14.4. Kruskal Wallis test results indicated a significant difference across sites in BDI values (χ^2(7) = 64.23, *p* = 2.15e-11). Dunn Post-Hoc results indicated fifteen of twenty-eight pairwise comparisons were significantly different (Table 6).

Table 6: *p*-values from Dunn Post Hoc pairwise comparisons of BDI across sites. Statistically significant differences are indicated*.

	Santa Maria Bay	Caret Bay	Neltjeberg Bay	Lindberg Bay	Magens Bay	Coki Point Beach	Sapphire Beach
Stumpy Bay	5.86e-1	8.0e-3*	3.58e-3*	9.32e-1	3.1e-3*	1.75e-1	9.75e-1
Santa Maria Bay		7.25e-2	8.26e-4*	6.85e-1	6.8e-4*	5.59e-1	5.88e-1
Caret Bay			1.77e-8*	1.26e-2*	1.91e-8*	2.75e-1	7.78e-3*
Neltjeberg Bay				2.69e-3*	9.56e-1	1.23e-5*	3.66e-3*
Lindberg Bay					2.14e-3*	2.31e-1	9.41e-1
Magens Bay						1.0e-5*	3.12e-3*
Coki Point Beach							1.74e-1

Finally, Kruskal Wallis results comparing log(1/beach slope) across sites indicated a significant difference in values across sites ($\chi^2(7) = 97.62$, $p = 2.2\text{e-}16$, Figure 6). Dunn Post Hoc pairwise results indicated twenty out of twenty-eight comparisons were significantly different (Table 7). Log (1/beach slope) and BI detected the same amount of significant differences in pairwise comparisons, however log(1/beach slope) has been identified as more appropriate for beaches in a close geographic range (McLachlan and Dorvlo, 2005). Log (1/beach slope) beach classifications were used in further modeling to represent differences in physical site characteristics. Beach morphology results indicated that beach types around St. Thomas are WD reflective beaches with slight variations in reflectiveness, with sites like Stumpy Bay being highly reflective and Santa Maria being less reflective. The greatest variation in physical characteristics across sites was characterized best by the beach slope of each site and not via grain sizes or wave heights.

Table 7: *p*-values from Dunn Post Hoc pairwise comparisons of Log(1/Beach Slope) across sites. Statistically significant differences are indicated*.

	Santa Maria Bay	Caret Bay	Neltjeberg Bay	Lindberg Bay	Magens Bay	Coki Point Beach	Sapphire Beach
Stumpy Bay	3.48e-14*	3.79e-2*	2.0e-5*	7.33e-12*	9.23e-6*	6.35e-7*	1.02e-2*
Santa Maria Bay		3.56e-8*	6.65e-4*	3.08e-1	1.2e-3*	7.0e-3*	6.85e-7*
Caret Bay			2.96e-2*	2.57e-6*	2.09e-2*	4.62e-3*	5.99e-1
Neltjeberg Bay				1.36e-2*	8.51e-1	4.96e-1	1.0e-1
Lindberg Bay					1.96e-2*	7.06e-2	3.08e-5*
Magens Bay						5.83e-1	7.24e-2
Coki Point Beach							2.02e-2*

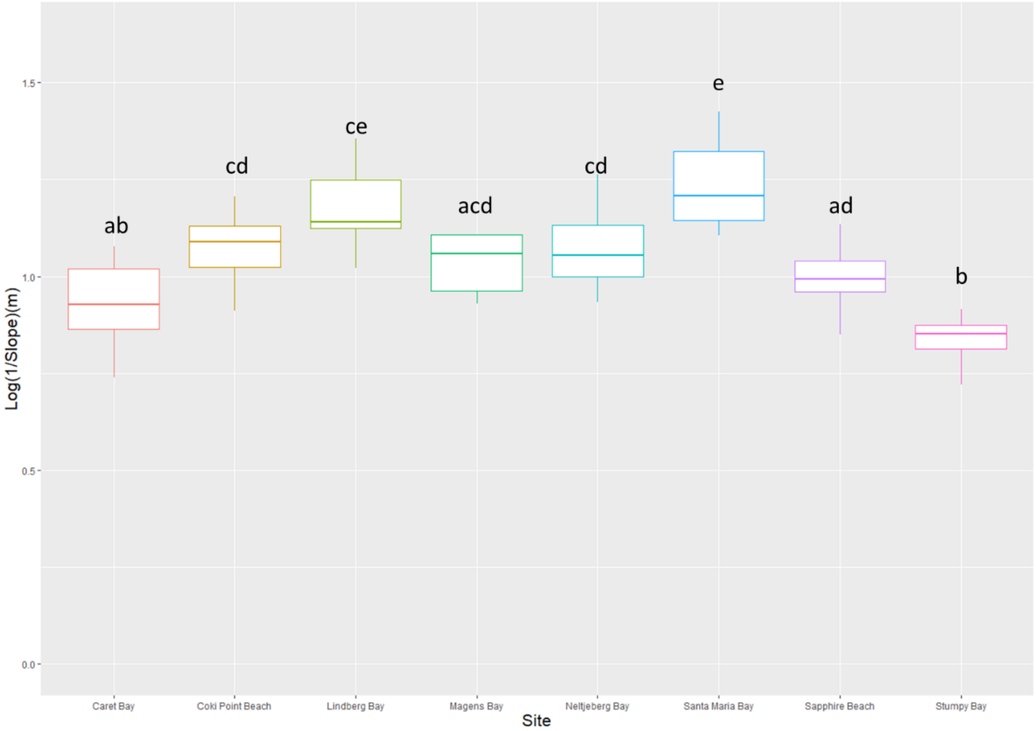
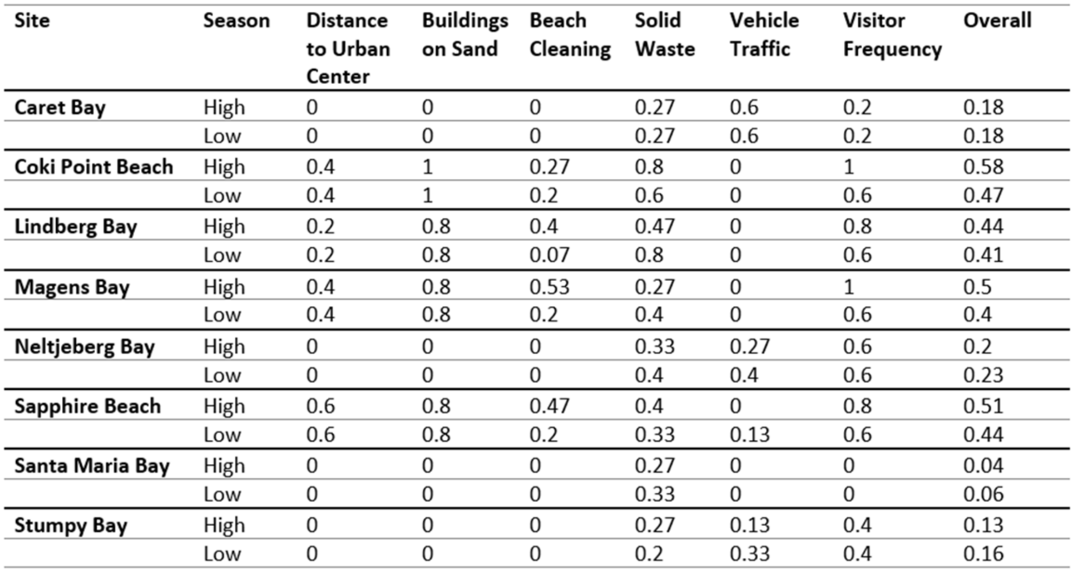


Figure 6: Log(1/Beach Slope) of all sites. Caret Bay, Coki Point Beach, Magens Bay, Neltjeberg Bay, and Sapphire Beach were not significantly different, and Lindberg Bay and Santa Maria Bay were not significantly different, and Stumpy Bay was physically significantly different from all sites.

Urbanization

Santa Maria Bay was the site with the lowest anthropogenic impact displaying an UI value of 0.04 during high- tourist season and 0.05 during low- tourist season due to an increase in solid waste (Table 8). Coki Point Beach had the highest anthropogenic impact with a value of 0.56 during peak tourist season and 0.45 during low- tourist season (Table 8). Overall UI ranged from 0.04 to 0.58 across all sites, with the highest overall UI at Coki Point Beach during high- tourist season (Table 8).

Table 8 Reported urbanization index values for all study sites. Urbanization index variables were calculated individually for each site, then averaged for the overall urbanization value. This was done during high- tourist season (February-March 2020) and low- tourist season (May-June,2020).



Site	Season	Distance to Urban Center	Buildings on Sand	Beach Cleaning	Solid Waste	Vehicle Traffic	Visitor Frequency	Overall
Caret Bay	High	0	0	0	0.27	0.6	0.2	0.18
	Low	0	0	0	0.27	0.6	0.2	0.18
Coki Point Beach	High	0.4	1	0.27	0.8	0	1	0.58
	Low	0.4	1	0.2	0.6	0	0.6	0.47
Lindberg Bay	High	0.2	0.8	0.4	0.47	0	0.8	0.44
	Low	0.2	0.8	0.07	0.8	0	0.6	0.41
Magens Bay	High	0.4	0.8	0.53	0.27	0	1	0.5
	Low	0.4	0.8	0.2	0.4	0	0.6	0.4
Neltjeberg Bay	High	0	0	0	0.33	0.27	0.6	0.2
	Low	0	0	0	0.4	0.4	0.6	0.23
Sapphire Beach	High	0.6	0.8	0.47	0.4	0	0.8	0.51
	Low	0.6	0.8	0.2	0.33	0.13	0.6	0.44
Santa Maria Bay	High	0	0	0	0.27	0	0	0.04
	Low	0	0	0	0.33	0	0	0.06
Stumpy Bay	High	0	0	0	0.27	0.13	0.4	0.13
	Low	0	0	0	0.2	0.33	0.4	0.16

A cluster dendrogram analysis confirmed *a priori* beach anthropogenic categorizations and that there were two primary groups of urbanization (1) Caret Bay, Neltjeberg Bay, Stumpy Bay, and Santa Maria Bay, and (2) Sapphire Beach, Magens Bay, Coki Point Beach, and Lindberg Bay (Figure 7). With dissimilarity represented by the height of the cluster dendrogram, results indicated that a cut off of one grouped the sites into distinct groups without overlapping overall UI values from one site across multiple groups. A cut off below one would result in some individual sites being assigned to more than one group. Results indicate the greatest amount of dissimilarity across the overall UI is approximately two, and two groups of sites are distinguishable at a dissimilarity of one (Figure 7).

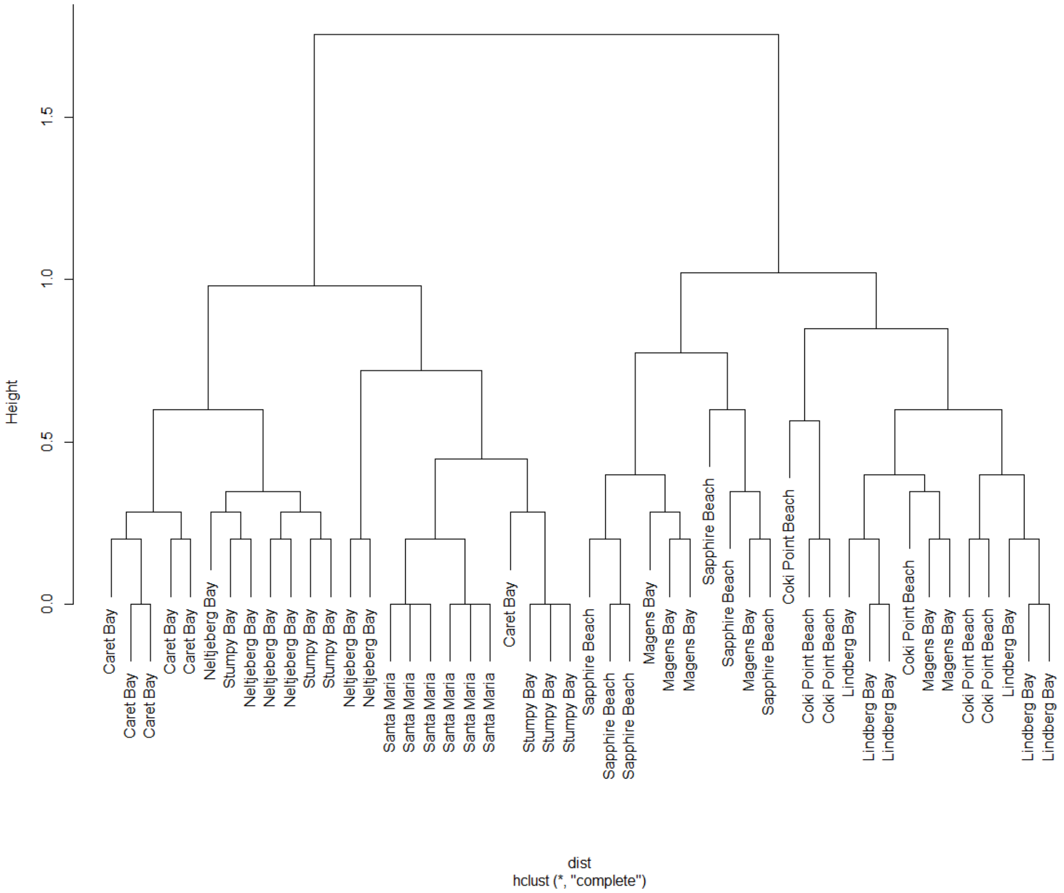


Figure 7: Complete connection Euclidean distance cluster diagram. Two groups of sites can be observed branching off around height = 1 and into the *a priori* predicted levels of human impact.

A non-parametric Kruskal-Wallis test revealed a significant difference in overall urbanization across sites ($\chi^2(7) = 41.291$, $p = 7.119e\text{-}7$; Figure 8). Dunn Post Hoc pairwise comparisons further distinguished differences between sites (Table 9). Results indicated significant differences between high- (Lindberg Bay, Magens Bay, Coki Point Beach, and Sapphire Beach) and low- impact beaches (Stumpy Bay, Santa Maria Bay, Caret Bay, and Neltjeberg Bay). Figure 8 depicts the comparison of mean overall UI across sites; Santa Maria Bay and Stumpy Bay had the lowest overall UI, while Sapphire Beach, Coki Beach, and Magens Bay had the greatest overall UI.

Table 9: *p*-values from Dunn Post Hoc pairwise comparisons of overall UI across sites. Statistically significant differences are indicated*.

	Santa Maria Bay	Caret Bay	Neltjeberg Bay	Lindberg Bay	Magens Bay	Coki Point Beach	Sapphire Beach
Stumpy Bay	6.52e-2	4.86e-1	8.53e-2	1.02e-6*	2.82e-8*	2.69e-13*	3.8e-10*
Santa Maria Bay		1.14e-2*	3.26e-4*	4.15e-11*	6.39e-13*	6.91e-19*	4.55e-15*
Caret Bay			3.0e-1	2.79e-5*	1.3e-6*	3.36e-11*	2.76e-8*
Neltjeberg Bay				1.99e-3*	1.81e-4*	2.74e8*	7.39e-6*
Lindberg Bay					5.09e-1	1.66e-2*	1.95e-1
Magens Bay						8.12e-2	4.91e-1
Coki Point Beach							3.02e-1

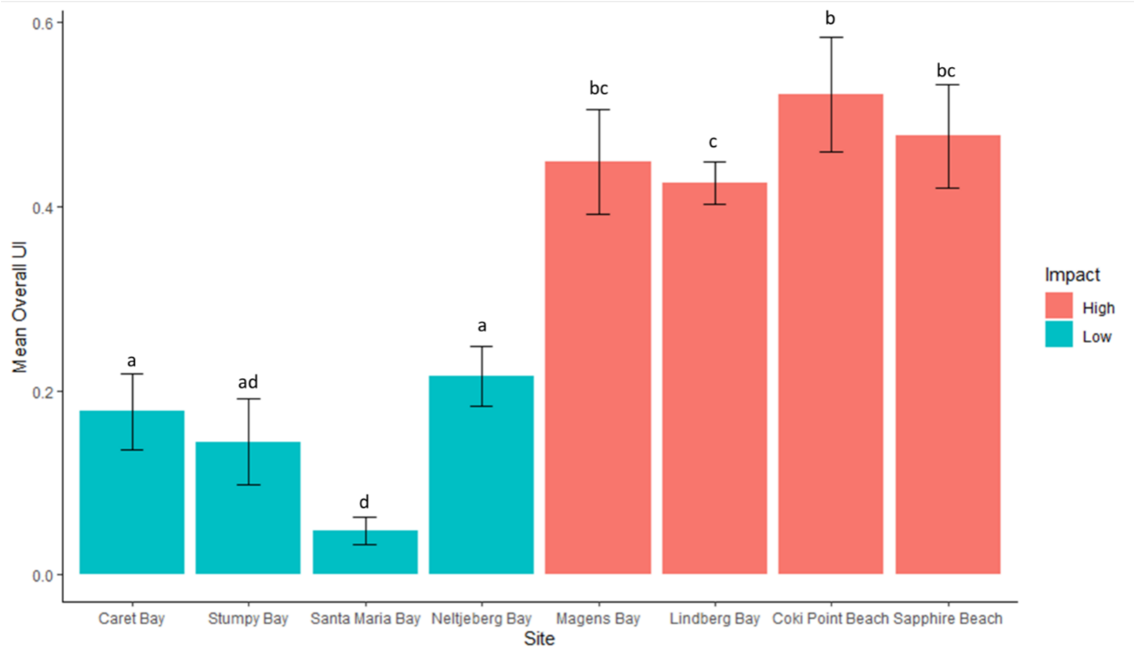


Figure 8: Overall UI across all sites. Kruskal-Wallis results indicated a significant difference between high- and low-impact sites. Letters indicate Dunn Post Hoc significant differences.

A Wilcoxon Rank Sum Test compared overall UI values between high- and low- tourist season across sites and a significant difference was found (Z = 5240, *p* = 0.02). Additional Wilcoxon Rank Sum Test compared overall UI values between high- and low- tourist season across high-impact sites (Lindberg Bay, Magens Bay, Coki Point Beach, Sapphire Beach), and a significant difference was found (Z = 124.5, *p* = 0.002). A Wilcoxon Rank Sum Test that compared overall UI between high- and low- tourist season across low-impact sites (Stumpy Bay, Santa Maria Bay, Caret Bay, Neltjeberg Bay) found no significant difference (Z = 60, *p* = 0.50). These results indicate there was significantly more urbanization during the high- versus low- tourist season at popular tourist sites, beach sites which experience higher urbanization.

Results of the PCA comparing overall UI values from each survey indicated that 77% of the variation in the data could be explained by the first two components. PC1 (eigenvalue of 3.74) accounts for approximately 62% of variation across sites and was driven by the presence of vehicles on sand and buildings on sand, resulting in a separation of high- and low-impact sites (Figure 9). PC2 (eigenvalue of 0.93) was responsible for approximately 15% of variation, primarily driven by beach cleaning and solid waste on the sand.

Figure 9: Biplot of PCA analysis of individual UI variables per survey (beach cleaning, visitor frequency, vehicles on sand, buildings on sand, distance to urban center, and solid waste) across all sites.

A second PCA on high-impact sites (Coki Point Beach, Magens Bay, Lindberg Bay, and Sapphire Beach) further separated each site from one another (Figure 10) indicating the independent variables selected accounted for 59% of variability across high-impact sites. PC1 (eigenvalue of 2.08) was responsible for approximately 34% of variability across high- impact sites and PC2 (eigenvalue of 1.49) was responsible for approximately 25% of variability. This indicates that there was significant variability represented by both principal components, with PC1 distinguishing Coki Point Beach and Lindberg Bay from Magens Bay and Sapphire Beach by greater solid waste and less beach cleaning. PC2 distinguished Sapphire from other high-impact sites by the presence of vehicles on sand and greater visitor frequency separated Coki Point Beach and Magens Bay from Lindberg Bay and Sapphire Beach.

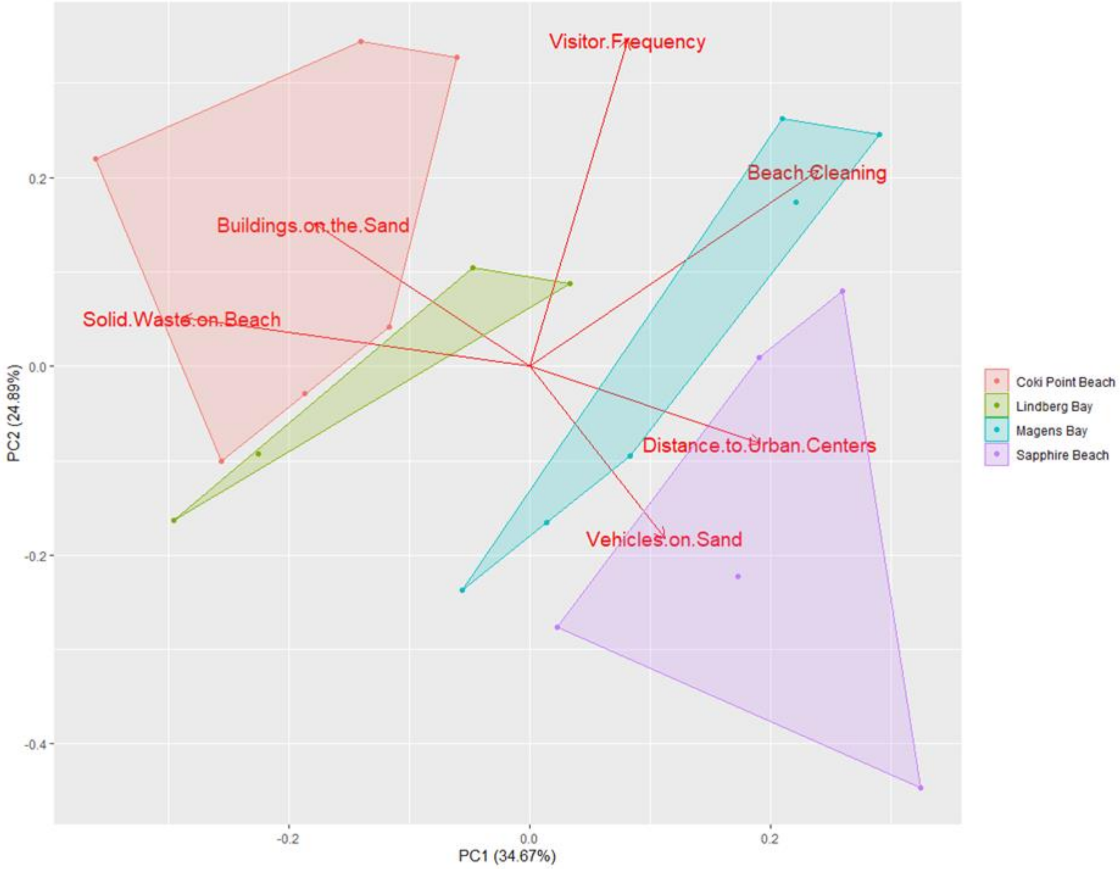


Figure 10: Biplot of PCA analysis of individual UI variables (beach cleaning, visitor frequency, vehicles on sand, buildings on sand, distance to urban center, and solid waste) per survey across high-impact sites.

Ghost Crab Burrow Site Comparisons

Results from a Kruskal-Wallis Test confirmed a significant difference in mean burrow abundance per m^2 across sites ($\chi^2(7) = 70.368$, $p = 3.09\text{e-}11$, Figure 11). Dunn Post Hoc pairwise comparisons indicated Neltjeberg was significantly different from all other sites in mean burrow abundance per m^2 (Table 10). Figure 11 shows that Neltjeberg had the highest mean abundance per m^2, while Magens Bay had the lowest mean burrow abundance per m^2 compared to all other sites except for Lindberg Bay (Table 11). Mean burrow abundance for all other sites was intermediate to Neltjeberg and Magens, and could not be distinguished from one another except forSanta Maria, which was significantly greater than all remaining sites except for Stumpy Bay and Sapphire Beach (Figure 11). Abundance ranged from 0 - 0.19 burrows per m^2, with all sites except Neltjeberg Bay having a minimum of zero burrows during low- tourist season and Neltjeberg having the maximum of 0.31 burrows per m^2 during peak tourist season (Table 11).

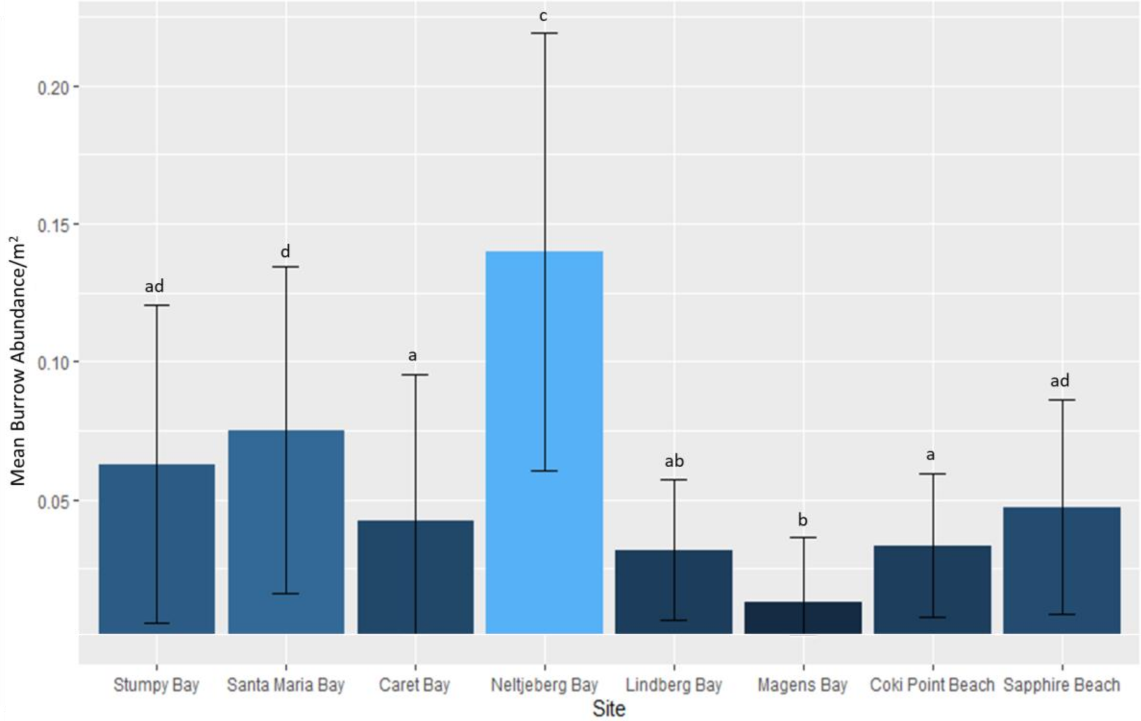


Figure 11: Standardized mean burrow abundance per m^2 by site +/- SEM. Letters represent significant Dunn Post Hoc results.

Table 10: *p*-values from Dunn Post Hoc pairwise comparisons of burrow abundance per m^2 across sites. Significant differences are indicated *.

	Santa Maria Bay	Caret Bay	Neltjeberg Bay	Lindberg Bay	Magens Bay	Coki Point Beach	Sapphire Beach
Stumpy Bay	5.26e-1	1.65e-1	2.38e-3*	1.5e-1	4.33e-4*	1.83e-1	6.44e-1
Santa Maria Bay		4.69e-2*	3.62e-2*	4.58e-2*	4.92e-5*	4.94e-2*	2.77e-1
Caret Bay			4.99e-6*	9.4e-1	4.81e-2*	9.92e-1	3.71e-1
Neltjeberg Bay				5.06e-6*	1.01e-11*	5.62e-6*	3.52e-4*
Lindberg Bay					5.11e-2	9.45e-1	3.45e-1
Magens Bay						4.57e-2*	2.99e-3*
Coki Point Beach							4.0e-1

Wilcoxon Rank Sum Test results indicated no significant differences in mean burrow abundance per m^2 between high- and low- tourist season ($Z = 5078.5$, $p = 0.07$). Further Wilcoxon Rank Sum Test results indicated a significant difference in mean burrow abundance per m^2 between high- and low- human impact sites ($Z = 2195$, $p = 1.479e\text{-}09$) confirming that high- human impact sites have fewer burrows compared to low- human impact sites.

Table 11: Burrow abundance, width, and depth averages, ranges, standard deviations, and standard errors found within study's nested design (transects within eight sites).

Site	Season	Mean Burrow Abundance per m^2	Range of Abundance per m^2	Mean Transect Burrow Width (mm)	Range of Transect Burrow Width (mm)	Mean Transect Burrow Depth (cm)	Range of Transect Burrow Depth (cm)
Stumpy Bay	High	0.08 n=12; SD=0.07; SE=0.02	0-0.19	22.2 n=12; SD=5.65; SE=1.63	16.2-33.8	32.5 n=12; SD=6.63; SE=1.91	23.3-45
	Low	0.05 n=12; SD=0.05; SE=0.01	0-0.18	27.6 n=12; SD=6.40; SE=1.85	21.0-41.8	34.8 n=12; SD=7.95; SE=2.30	23.3-51
Santa Maria Bay	High	0.1 n=8; SD=0.07; SE=0.01	0.02-0.2	17.1 n=8; SD=3.80; SE=1.34	11.8-22.2	22.2 n=8; SD=3.43; SE=1.21	17.7-27
	Low	0.06 n=12; SD=0.04; SE=0.01	0-0.14	20.2 n=12; SD=2.99; SE=0.86	16.5-25.5	33.1 n=12; SD=6.70; SE=1.94	26.8-47.1
Caret Bay	High	0.06 n=12; SD=0.06; SE=0.02	0-0.19	23.2 n=12; SD=7.24; SE=2.09	13.8-33.8	29.1 n=12; SD=15.1; SE=4.4	13-62.7
	Low	0.02 n=12; SD=0.03; SE=0.01	0-0.11	37.5 n=12; SD=22.2; SE=6.41	16.9-69.2	28.3 n=12; SD=4.83; SE=1.40	24-36.5
Neltjeberg Bay	High	0.17 n=12; SD=0.1; SE=0.03	0.03-0.31	20.8 n=12; SD=6.5; SE=1.88	13.8-32.5	34.4 n=12; SD=11.38; SE=3.28	23.6-67.7
	Low	0.11 n=12; SD=0.05; SE=0.01	0.04-0.19	20.3 n=12; SD=3.68; SE=1.06	15.4-27.9	31.8 n=12; SD=5.15; SE=1.49	18.5-39.75
Lindberg Bay	High	0.04 n=12; SD=0.03; SE=0.01	0-0.11	27.5 n=12; SD=18.31; SE=5.29	14.9-78.6	38.5 n=12; SD=14.04; SE=4.05	28-78
	Low	0.03 n=12; SD=0.02; SE=0.004	0-0.05	24.0 n=12; SD=6.97; SE=2.01	16.4-34.6	38.3 n=12; SD=8.67; SE=2.50	23-52
Magens Bay	High	0.01 n=12; SD=0.02; SE=0.006	0-0.067	22.5 n=12; SD=3.79; SE=1.09	19.8-25.2	43.8 n=12; SD=7.42; SE=2.14	38.5-49
	Low	0.02 n=12; SD=0.02; SE=0.007	0-0.07	30.0 n=12; SD=4.73; SE=1.37	25.8-38.0	48.5 n=12; SD=19.02; SE=5.49	28-77
Coki Point Beach	High	0.04 n=12; SD=0.03; SE=0.008	0-0.08	33.6 n=12; SD=4.85; SE=1.4	26.4-42.7	53.7 n=12; SD=23.31; SE=6.73	20-88
	Low	0.03 n=12; SD=0.02; SE=0.007	0-0.05	28.9 n=12; SD=6.19; SE=1.79	21.8-38.1	34.4 n=12; SD=7.90; SE=2.28	23-46.5
Sapphire Beach	High	0.04 n=12;SD=0.03; SE=0.01	0-0.11	26.0 n=12; SD=14.3; SE=4.12	12.1-63.3	43.1 n=12; SD=17.58; SE=5.08	18-82
	Low	0.05 n=12; SD=0.05, SE=0.01	0-0.13	32.9 n=12; SD=7.46; SE=2.15	21.0-41.8	33.7 n=12; SD=8.62; SE=2.49	22-47

Kruskal-Wallis results indicated a significant difference in mean burrow widths across sites ($\chi^2(7) = 37.029$, $p = 4.63e\text{-}06$, Figure 12). Dunn Post Hoc pairwise comparison results indicated significant differences between individual sites (Table 12). Eleven of the twenty-eight pairwise comparisons resulted in a significant difference, with Coki Point Beach being significantly different from all sites except Sapphire Beach and Magens Bay (Table 12). Mean burrow width was greatest at Lindberg Bay during peak tourist season with the maximum width was measured at 78.6 mm. The smallest mean burrow width was recorded at Sapphire Beach during peak tourist season at 12.1 mm (Table 12).

Table 12: *p*-values from Dunn Post Hoc pairwise comparisons of burrow width across sites. Significant differences are indicated*.

	Santa Maria Bay	Caret Bay	Neltjeberg Bay	Lindberg Bay	Magens Bay	Coki Point Beach	Sapphire Beach
Stumpy Bay	2.85e-2*	8.81e-1	7.26e-2	5.45e-1	4.63e-1	4.11e-2*	4.77e-1
Santa Maria Bay		3.98e-2*	5.37e-1	9.06e-2	1.92e-2*	2.08e-5*	4.32e-3*
Caret Bay			1.21e-1	6.58e-1	4.5e-1	4.37e-2*	4.52e-1
Neltjeberg Bay				2.48e-1	3.95e-2*	5.41e-5*	1.31e-2*
Lindberg Bay					2.36e-1	1.15e-2*	2.02e-1
Magens Bay						4.71e-1	7.89e-1
Coki Point Beach							2.06e-1

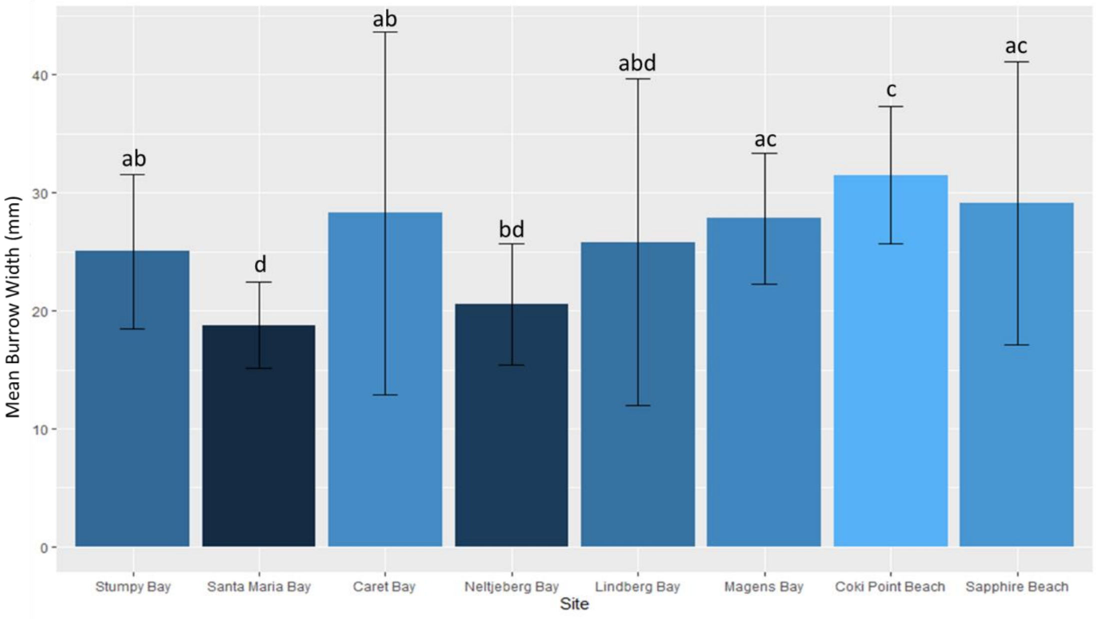


Figure 12: Mean Burrow width across sites with Dunn Post Hoc analysis results indicating significant differences by letters.

Kruskal Wallis results indicated a significant difference in frequency across age groups (juvenile, medium adult, and older adult, $\chi^2(2) = 15.92$, $p = 3.50\text{e-}4$), and Dunn Post Hoc pairwise comparisons indicated a significant difference between the frequency of juvenile and older adult burrows ($p = 0.04$), and between medium adult frequencies and older adult frequencies ($p = 2.07\text{e-}4$), but not between medium adult and juvenile frequencies ($p = 0.08$). Life stage proportions across sites are reported in Table 13. Neltjeberg Bay (62%) and Santa Maria Bay (54%) possessed the largest populations of juvenile crabs on average, while Coki Point Beach (44%) and Sapphire Beach (36%) had the largest proportions of older crabs on average. Large proportions of all populations across all sites were categorized as medium adult crabs (Table 13).

A Kruskal Wallis test results comparing age populations across sites indicated no significant differences in juvenile populations (individuals < 20 mm, $\chi^2(7) = 10.195$, $p = 0.18$), medium adult populations (individuals 20-33 mm, $\chi^2(7) = 3.218$, $p = 0.86$), or older adult populations (individuals > 33 mm, $\chi^2(7) = 9.44$, $p = 0.22$). Wilcoxon Rank Sum test results did however indicate a significant difference in juvenile populations (Z = 375, $p =$

0.01) and medium adult populations (Z = 163, *p* = 0.04) between high- and low-impact season. Differences indicate the growth from a juvenile to a medium crab with juveniles having a larger population during high- tourist season (February-March) and medium crabs having a higher population during low- tourist season (May-June). No significant difference was found in older crabs between high- and low- tourist season (Z = 244, *p* = 0.85).

To observe burrowing spatial patterns, total burrow abundance per life stage were graphed in relation to the supra/mid transition line (Figure 13). Kruskal Wallis test results indicated a significant difference in distance to transition zone across age classifications (juvenile, medium adult, & older adult, $\chi^2(2) = 19.37$, *p* = 6.22e-05). Dunn Post Hoc results indicated a significant difference in distance to transition zones between juveniles and older adults (*p* = 4.56e-5) and medium adults and older adults (*p* = 3.35e-4), but not between juveniles and medium adults (*p* = 4.75e-1). Wilcoxon Rank Sum test results indicated no significant difference in distance to transition zone between high- and low-impact sites (Z = 25339, *p* = 0.45).

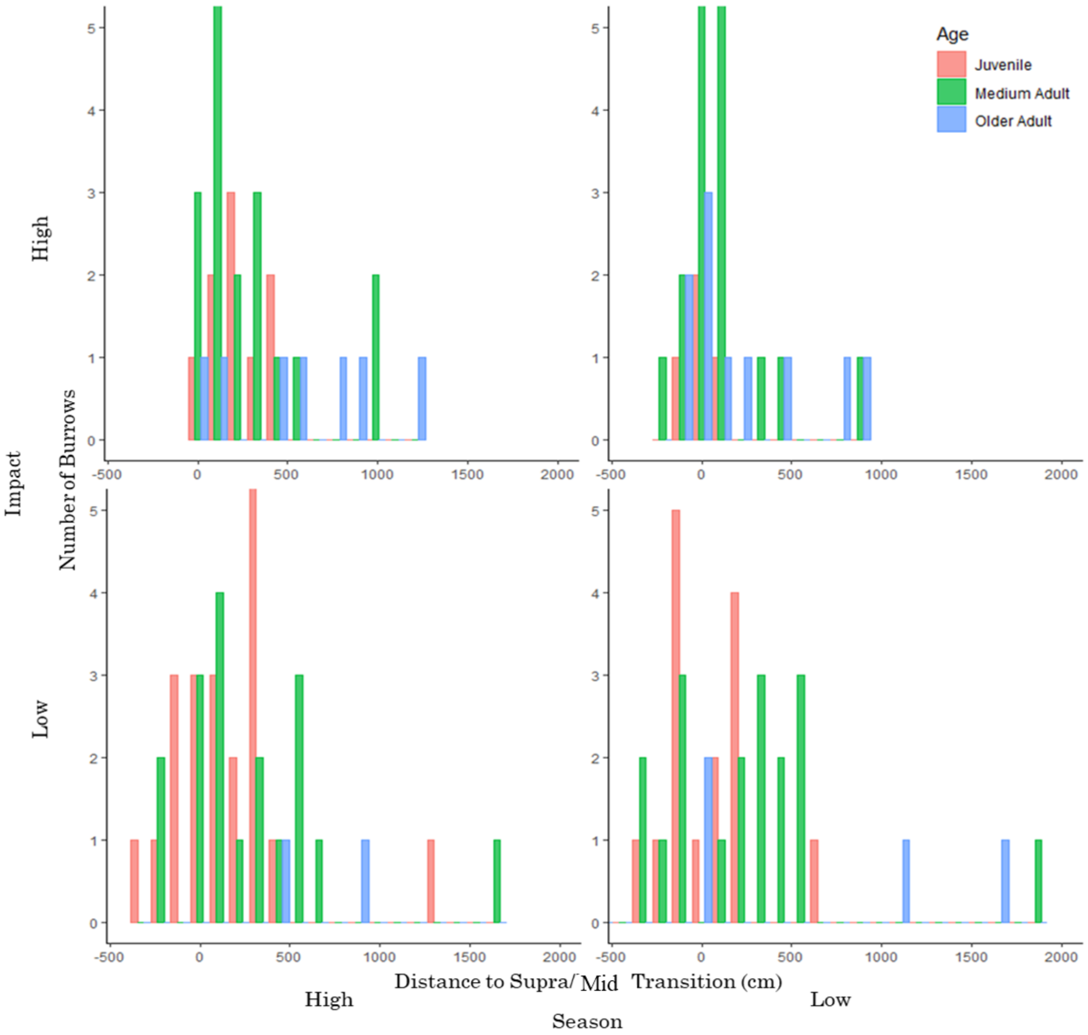


Figure 13: Abundances of juvenile, medium adult, and older adult burrows in relation to the supra/mid transition zone by site impact level. High- impact sites (Lindberg Bay, Magens Bay, Coki Point Beach, and Sapphire Beach; above) Low- impact sites (Stumpy Bay, Santa Maria Bay, Caret Bay, and Neltjeberg Bay; below).

Table 13: Crab standardized abundance, age and activity frequencies of all sites by season 1) Stumpy Bay, 2) Santa Maria Bay, 3) Caret Bay, 4) Neltjeberg Bay, 5) Lindberg Bay, 6) Magens Bay, 7) Coki Point Beach, and 8) Sapphire Beach.

Site	**Season**	**Juvenile Proportions**	**Medium Adult Proportions**	**Large Adult Proportions**	**Strong Activity Frequency**	**Moderate Activity Frequency**	**Subtle Activity Frequency**	**No Activity Frequency**
Caret Bay Low- Impact	High	43% (n=14)	38% (n=13)	19% (n=5)	41% (n=13)	19% (n=6)	34% (n=11)	6% (n=2)
	Low	30% (n=4)	52% (n=4)	19% (n=5)	15% (n=2)	15% (n=2)	23% (n=3)	46% (n=6)
Neltjeberg Bay Low- Impact	High	70% (n=63)	16% (n=14)	15% (n=14)	13% (n=12)	36% (n=33)	37% (n=34)	13% (n=12)
	Low	50% (n=38)	44% (n=30)	6% (n=4)	15% (n=11)	51% (n=37)	28% (n=20)	6% (n=4)
Santa Maria Bay Low- Impact	High	66% (n=35)	31% (n=17)	4% (n=2)	22% (n=12	24% (n=13)	35% (n=19)	19% (n=10)
	Low	33% (n=22)	63% (n=27)	4% (n=3)	47% (n=24	29% (n=15)	14% (n=7)	10% (n=5)
Stumpy Bay Low- Impact	High	56% (n=22)	26% (n=10)	19% (n=5)	11% (n=4)	22% (n=8)	61% (n=22)	6% (n=2)
	Low	7% (n=3)	79 (n=28)	14% (n=3)	41% (n=14)	24% (n=8)	35% (n=12)	0% (n=0)
Coki Point Beach High- Impact	High	20% (n=4)	27% (n=6)	53% (n=10)	68% (n=13)	21% (n=4)	11% (n=2)	0% (n=0)
	Low	12% (n=2)	52% (n=7)	35% (n=5)	36% (n=5)	29% (n=4)	36% (n=5)	0% (n=0)
Lindberg Bay High- Impact	High	43% (n=10)	32% (n=5)	25% (n=4)	42% (n=8)	21% (n=4)	37% (n=7)	0% (n=0)
	Low	22% (n=4)	67% (n=9)	11% (n=2)	53% (n=8)	20% (n=3)	13% (n=2)	13% (n=2)
Magens Bay High- Impact	High	34% (n=2)	67% (n=3)	0% (n=0)	40% (n=2)	60% (n=3	0% (n=0)	0% (n=0)
	Low	17% (n=1)	45% (n=5)	38% (n=4)	40% (n=4)	50% (n=5)	0% (n=0)	10% (n=1)
Sapphire Beach High- Impact	High	33% (n=6)	57% (n=11)	10% (n=3)	60% (n=12)	30% (n=6)	10% (n=2)	0% (n=0)
	Low	14% (n=5)	20% (n=7)	66% (n=13)	46% (n=12)	15% (n=4)	31% (n=8)	8% (n=2)

Results from a Kruskal-Wallis Test indicated a significant difference in mean burrow depth across sites ($\chi^2(7) = 28.56$, $p = 1.74e\text{-}4$). Dunn Post hoc results found that mean burrow depths at Caret Bay and Santa Maria Bay were significantly shallower compared to mean burrow depths at Coki Point Beach, Lindberg Bay, Magens Bay, and Sapphire Beach, but that Stumpy and Neltjeberg had mean burrow depths intermediate to the two groupings (Figure 14). Mean burrow depth was greatest at Coki Point Beach during peak tourist season with the deepest depth recorded being 88 cm. Shallower depths were recorded across sites, with the shallowest mean burrow depth being 13 cm at Caret Bay during peak tourist season (Table 14).

Table 14: *p*-values from Dunn Post Hoc pairwise comparisons of burrow depth across sites. Significant differences are indicated*.

	Santa Maria Bay	Caret Bay	Neltjeberg Bay	Lindberg Bay	Magens Bay	Coki Point Beach	Sapphire Beach
Stumpy Bay	0.11	0.17	0.77	0.31	0.11	0.18	0.34
Santa Maria Bay		0.87	0.19	0.01*	0.01*	0.02*	0.01*
Caret Bay			0.22	0.01*	0.01*	0.01*	0.02*
Neltjeberg Bay				0.18	0.06	0.12	0.21
Lindberg Bay					0.34	0.75	0.9
Magens Bay						0.51	0.31
Coki Point Beach							0.69

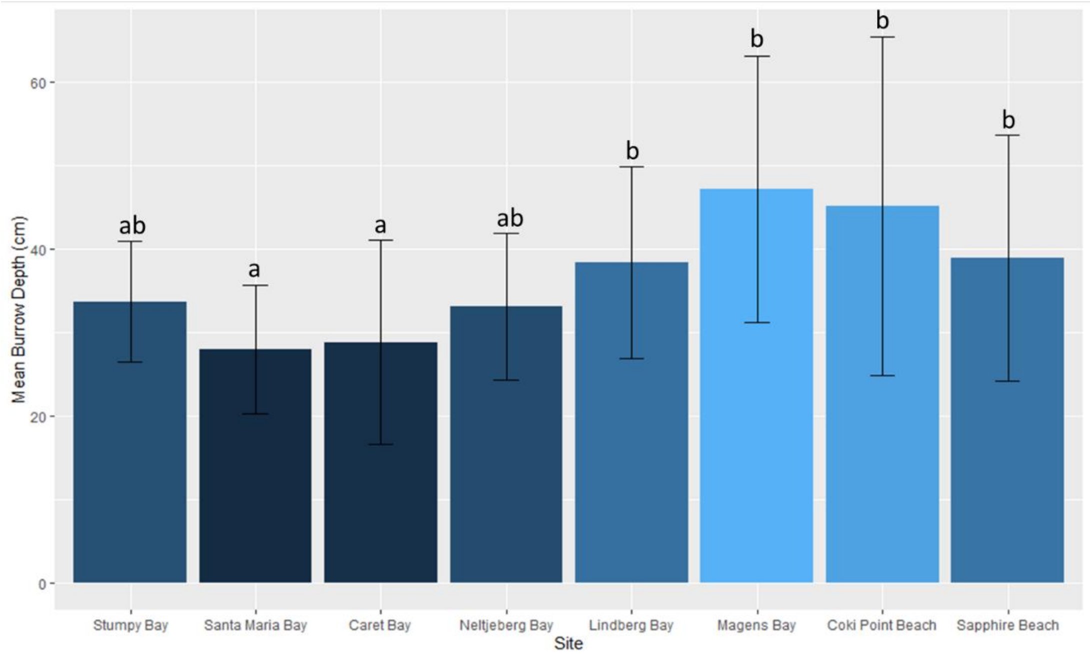


Figure 14: Mean burrow depth by site. Letters indicate Dunn Post significant differences.

Kruskal Wallis results comparing burrow activity frequencies across sites indicated no significant difference in the frequency of moderate ($\chi^2(7) = 13.49$, $p = 0.06$) and no activity ($\chi^2(7) = 12.14$, $p = 0.09$) characterizations of burrows. Significant differences were found in the frequency of subtle activity ($\chi^2(7) = 15.56$, $p = 0.03$) , and Dunn Post Hoc pairwise comparisons indicated a significant difference in subtle activity between Stumpy Bay and Magens Bay ($p = 0.03$), no other differences were detected between individual sites (Table 15). Kruskal Wallis results also found significant differences in strong activity across sites ($\chi^2(7) = 15.98$, $p = 0.03$). Dunn Post Hoc pairwise comparisons indicated the only significant differences were between Neltjeberg Bay and Lindberg Bay ($p = 0.05$), and Neltjeberg Bay and Coki Point Beach ($p = 0.05$) (Table 16). Results indicated Coki Point Beach had significantly more burrows with strong activity compared to sites such as Neltjeberg Bay (Tables 13, 16). Sites such as Stumpy Bay had significantly more burrows with subtle activity compared to beaches such as Magens Bay with no subtle activity (Tables 13, 15).

Table 15: *p*-values from Dunn Post Hoc pairwise comparisons of subtle activity frequency across sites. Significant differences are indicated*.

	Santa Maria Bay	Caret Bay	Neltjeberg Bay	Lindberg Bay	Magens Bay	Coki Point Beach	Sapphire Beach
Stumpy Bay	0.51	0.71	0.62	0.28	0.03*	0.28	0.1
Santa Maria Bay		0.68	0.74	0.7	0.2	0.69	0.49
Caret Bay			0.88	0.48	0.09	0.49	0.27
Neltjeberg Bay				0.54	0.1	0.47	0.28
Lindberg Bay					0.27	0.9	0.68
Magens Bay						0.28	0.49
Coki Point Beach							0.66

Table 16: *p*-values from Dunn Post Hoc pairwise comparisons of strong activity across sites. Significant differences are indicated*.

	Santa Maria Bay	Caret Bay	Neltjeberg Bay	Lindberg Bay	Magens Bay	Coki Point Beach	Sapphire Beach
Stumpy Bay	0.97	1	0.47	0.37	0.78	0.31	0.45
Santa Maria Bay		0.94	0.38	0.31	0.93	0.37	0.33
Caret Bay			0.5	0.27	0.74	0.28	0.31
Neltjeberg Bay				0.05*	0.32	0.05*	0.09
Lindberg Bay					0.45	0.95	0.99
Magens Bay						0.52	0.47
Coki Point Beach							0.98

Drivers of Ghost Crab Abundance

ANOVA comparison of two models 1) GLMM comparing response variable burrow abundance, and predictor variables season with an interaction with overall UI, temperature, wave height, log(1/beach slope), mean grain size, date as a random variable, and a nested effect of transect within site, and 2) GLMM comparing response variable burrow abundance, and predictor variables season, overall UI, temperature, wave height, log(1/beach slope), mean grain size, indicated a significant difference between the two models (Table 17, p < 2.2e-16). AIC was lower for model one, suggesting that model one was the best model to use and indicating an effect of date as a random variable, an interaction of season and overall UI, and a nested effect of transect within site (AIC=1135.8; Table 17).

GLMM results of the first model (burrow abundance with predictor variables season with an interaction with overall UI, temperature, wave height, log(1/beach slope), mean grain size, date as a random variable, and a nested effect of transect within site) indicated that overall urbanization was the only variable that had a significant effect on mean burrow abundance (Table 18, $p = 0.01$, $R^2 = 0.19$), indicating that as urbanization increases, mean burrow abundance decreases (Figure 15).

Table 17: Generalized Linear Mixed Model expressions and comparisons for burrow abundance, width, and depth compared to predictor variables season, overall UI, temperature, wave height, log(1/beach slope), and average grain size. Significant differences are indicated*.

Model Type	**Model Expression**	**df**	**AIC**	**p**
GLMM	Abundance ~ Season*Overall UI + Temperature + (1|Site/Transect) + (1|Date) + Wave Height + Log(1/Beach Slope) + Mean Grain Size (phi)	4	1135.8	<2.2e-16*
	Abundance ~ Season + Overall UI + Temperature + Wave Height + Log(1/Beach Slope) + Mean Grain Size (phi)		1390.6	
GLMM	Burrow Width ~ Season*Overall UI + Temperature + (1|Site/Transect) + (1|Date) + Wave Height + Log(1/Beach Slope)	3	79.82	0.21
	Burrow Width ~ Season + Overall UI + Temperature + Wave Height + Log(1/Beach Slope) + Mean Grain Size (phi)		78.30	
GLMM	Burrow Depth ~ Season*Overall UI + Temperature + (1|Site/Transect) + (1|Date) + Wave Height + Log(1/Beach Slope) + Mean Grain Size (phi)	4	89.74	0.37
	Burrow Depth ~ Season + Overall UI + Temperature + Wave Height + Log(1/Beach Slope) + Mean Grain Size (phi)		85.97	

Table 18: Burrow abundance GLMM against predictor variables season, overall UI, temperature, wave height, log (1/beach slope), mean grain size, and the interaction of season and overall UI. Significant differences are indicated*.

Burrow Abundance Predictor Variables	**Estimate**	**Std. Error**	**Z value**	***p***
Season	-0.95	0.61	-1.55	0.12
Overall UI	-3.01	1.20	-2.51	0.01*
Temperature	-0.02	0.08	-0.32	0.75
Wave Height	-0.32	0.30	-1.06	0.29
Log(1/Beach Slope)	-0.63	0.37	-1.72	0.09
Mean Grain Size (phi)	0.30	0.39	0.078	0.44
Season : Overall UI	1.53	1.13	1.37	0.17

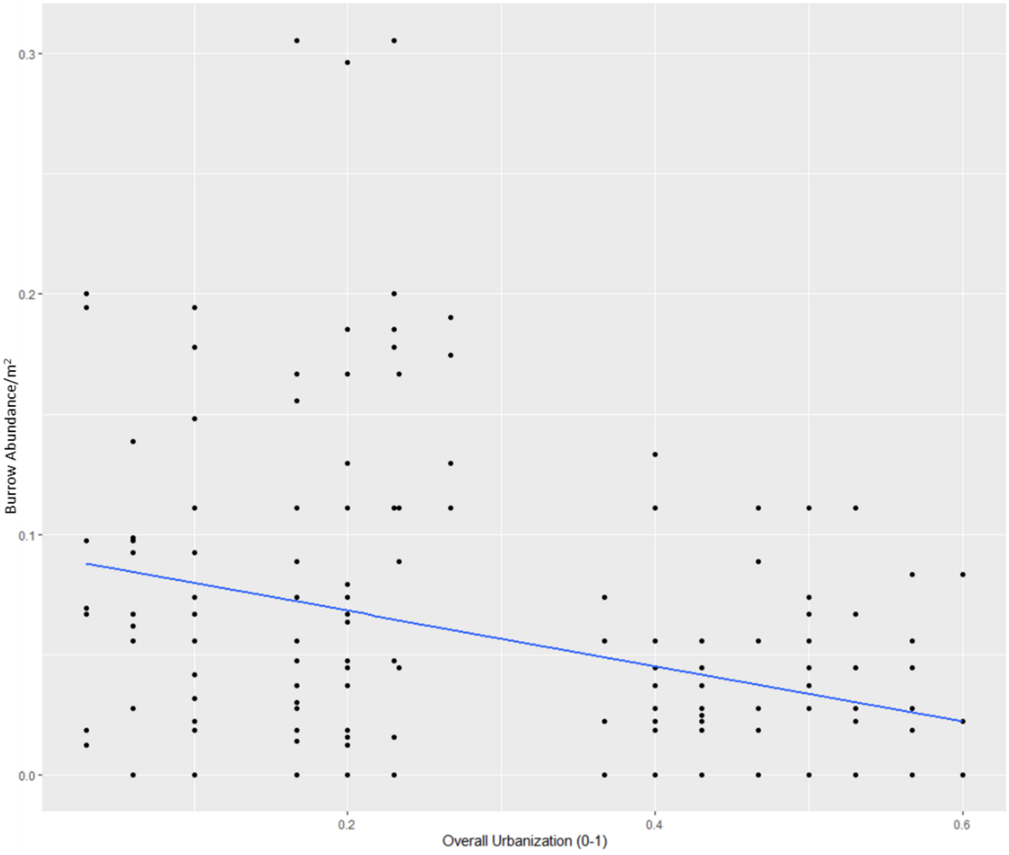


Figure 15: GLMM of burrow abundance per m^2 and overall UI from each site visit.

After the GLMM comparing response variable burrow abundance, and predictor variables season with an interaction with overall UI, temperature, wave height, log(1/beach slope), mean grain size, date as a random variable, and a nested effect of transect within site indicated a significant effect of overall UI, another GLMM was used to compare burrow abundance and urbanization variables (beach cleaning, visitor frequency, distance to urban centers, solid waste on the beach, and vehicles on the sand, Table 19). When results indicated a significant effect of beach cleaning ($p = 0.004$), visitor frequency ($p = 0.01$), and distance to urban centers ($p = 0.009$), a GAM was used to detect any non-linear relationships of mean burrow abundance with predictor variables beach cleaning, visitor frequency, and distance to urban centers (Table 19). GAM results of individual UI variables indicated beach cleaning ($p <$ 2e-16), visitor frequency ($p = 0.005$), and distance to urban center ($p = 0.015$) had a significant effect on mean burrow abundance (Table 19). In both beach cleaning and visitor frequency, as the activity increased mean burrow abundance decreased (Figure 16). However, mean burrow abundance decreased rapidly as distance to urban centers grew until a threshold of UI = 0.35, after which mean burrow abundance decreased less rapidly (Figure 16). This indicates that sites within two to four km from an urban center have lower burrow abundances compared to sites greater than four km or less than two km.

Table 19: GLMM and GAM models of burrow abundance compared to individual urbanization variables. Significant differences are indicated*.

Model Type	Model Expression	Model Variable	p	k	edf
GLMM	Abundance ~ Vehicles on Sand + Beach Cleaning + Solid Waste + Visitor Frequency + Distance to Urban Center	Vehicles on Sand	0.76	-	-
		Beach Cleaning	0.004*	-	-
		Solid Waste	0.17	-	-
		Visitor Frequency	0.01*	-	-
		Distance to Urban Center	0.009*	-	-
GAM	Abundance ~ s(Visitor Frequency, k=3) + s(Distance to Urban Center, k=3) + s(Beach Cleaning, k=3)	Visitor Frequency	0.005*	2.0	1.0
		Distance to Urban Center	0.015*	2.0	1.96
		Beach Cleaning	<2e-16*	2.0	1.0

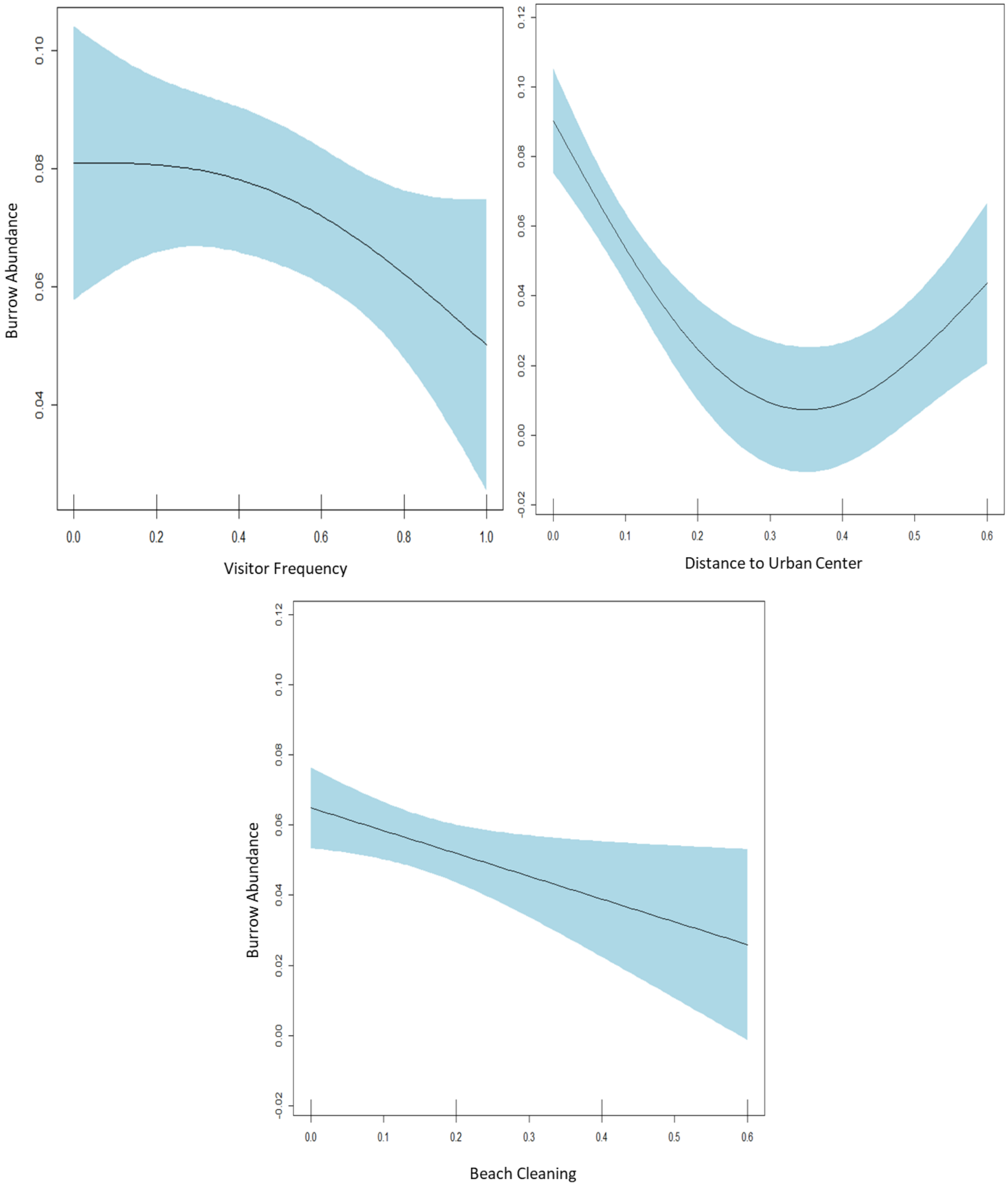


Figure 16: GAM of mean burrow abundance with UI visitor frequency, UI distance to urban center, and UI beach cleaning.

Drivers of Ghost Crab Burrow Width

ANOVA comparison of two models 1) GLMM comparing response variable mean burrow width, and predictor variables season with an interaction with overall UI, temperature, wave height, log(1/beach slope), mean grain size, date as a random variable, and a nested effect of transect within site, and 2) GLMM comparing response variable burrow width, and predictor variables season, overall UI, temperature, wave height, log(1/beach slope), mean grain size, indicated no significant difference between the two models (Table 17, p =0.21).

GLMM results of the first model (burrow width with predictor variables season with an interaction with overall UI, temperature, wave height, log(1/beach slope), mean grain size, date as a random variable, and a nested effect of transect within site) that overall UI and mean grain size had significant effects on mean burrow width (Table 20, Figures 17, 18). Results indicated that mean burrow width was greater under more urbanized conditions (p = 0.005, R^2 = 0.10, Table 20, Figure 17). Mean grain size was found to have a significant effect on burrow widths, with smaller burrows found in finer sand (p = 2.88e-4, R^2 = 0.05, Table 20, Figure 18).

Table 20: Burrow width GLMM against predictor variables season, overall UI, temperature, wave height, log (1/beach slope), mean grain size, and the interaction of season and overall UI. Significant differences are indicated*.

Burrow Width Predictor Variables	**Estimate**	**Std. Error**	**Z value**	***p***
Season	13.68	7.25	1.89	0.06
Overall UI	23.67	8.49	2.81	0.005*
Temperature	-1.69	0.99	-1.70	0.09
Wave Height	0.26	3.02	0.09	0.93
Log(1/Beach Slope)	9.70	6.32	1.54	0.13
Mean Grain Size (phi)	-7.98	1.15	-3.72	2.88e-4*
Season : Overall UI	-11.12	11.79	-0.94	0.35

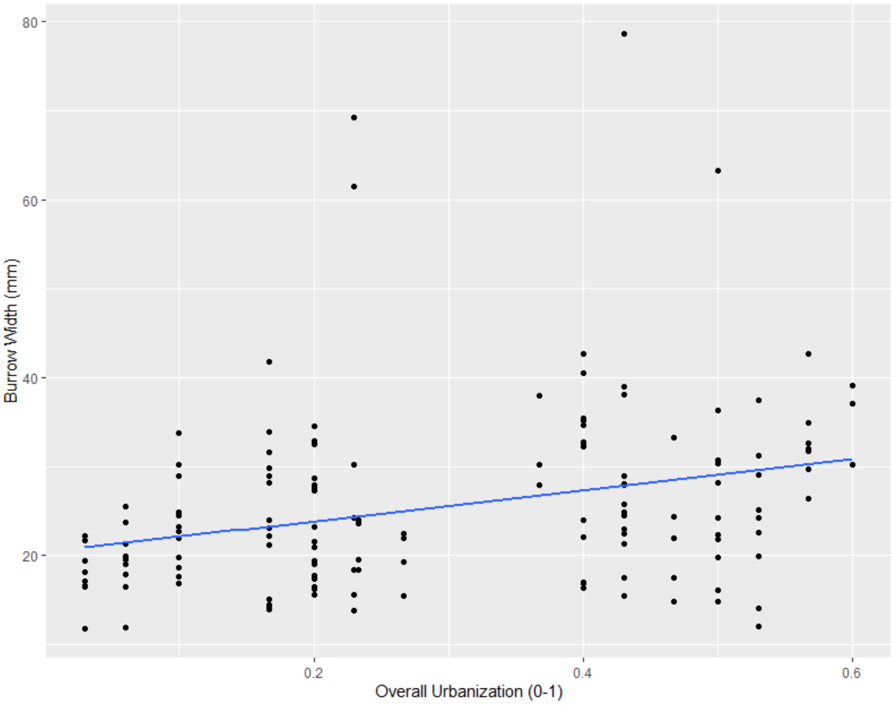


Figure 17: GLMM of mean burrow width (mm) and overall UI from each site visit.

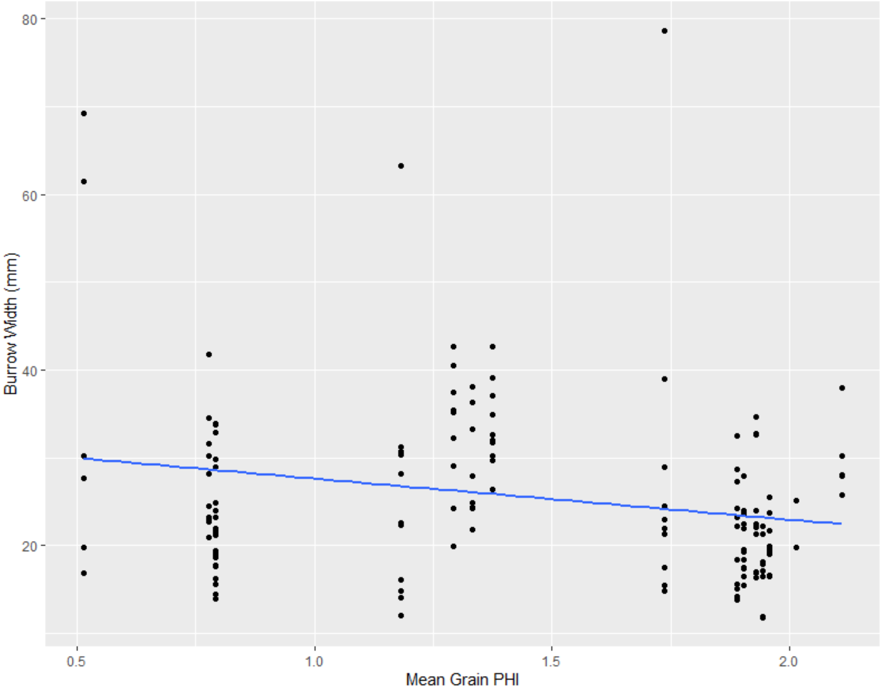


Figure 18: GLMM of mean burrow width (mm) and mean grain size (phi) from each site visit.

After the GLMM comparing response variable mean burrow width, and predictor variables season with an interaction with overall UI, temperature, wave height, log(1/beach slope), mean grain size, date as a random variable, and a nested effect of transect within site indicated a significant effect of overall UI, another GLMM was used to compare mean burrow width and urbanization variables (beach cleaning, visitor frequency, distance to urban centers, solid waste on the beach, and vehicles on the sand, Table 21). When results indicated a significant effect of vehicles on sand (*p* = 0.02), and distance to urban centers (*p* = 0.001), a GAM was used to detect any non-linear relationships of mean burrow width with predictor variables vehicles on sand and distance to urban centers (Table 21). GAM results of individual UI variables indicated vehicles on sand (*p* = 0. 25) had a significant effect on mean burrow width, but there was no significant effect of distance to urban center (*p* = 0.06) on mean burrow abundance (Table 21). GAM results indicated that mean burrow width decreased until a threshold of UI vehicles on sand 0.3, after which burrow width increases indicating larger burrow widths on sites with higher vehicle activity (Figure 19).

Table 21: GLMM and GAM models of burrow width compared to individual urbanization variables. Significant differences are indicated*.

Model Type	**Model Expression**	**Model Variable**	**p**	**k**	**edf**
GLMM	Burrow Width ~ Vehicles on Sand + Beach Cleaning + Solid Waste + Visitor Frequency + Distance to Urban Center	Vehicles on Sand	0.02*	-	-
		Beach Cleaning	0.13	-	-
		Solid Waste	0.78	-	-
		Visitor Frequency	0.38	-	-
		Distance to Urban Center	0.001*	-	-
GAM	Burrow Width ~ s(Distance to Urban Center, k=3) +s(Vehicles on Sand, k=3)	Distance to Urban Center	0.06	2.0	1.63
		Vehicles on Sand	0.025*	2.0	1.90

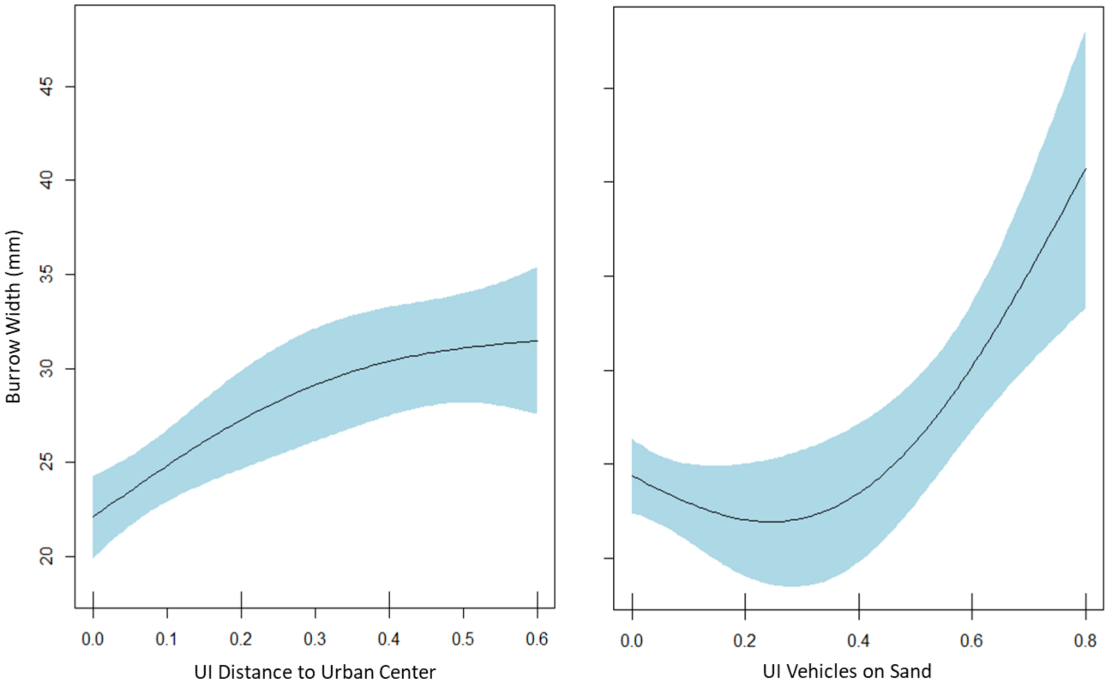


Figure 19: GAM of mean burrow width and UI distance to urban center and UI vehicles on sand.

Drivers of Ghost Crab Burrow Depth

ANOVA comparison of two models 1) GLMM comparing response variable mean burrow depth, and predictor variables season with an interaction with overall UI, temperature, wave height, log(1/beach slope), mean grain size, date as a random variable, and a nested effect of transect within site, and 2) GLMM comparing response variable mean burrow depth, and predictor variables season, overall UI, temperature, wave height, log(1/beach slope), mean grain size, indicated no significant difference between the two models (Table 17, $p = 0.37$).

GLMM results of the first model (mean burrow depth with predictor variables season with an interaction with overall UI, temperature, wave height, log(1/beach slope), mean grain size, date as a random variable, and a nested effect of transect within site) showed that overall UI had a significant effect on mean burrow depth (Figure 20, Table

22). Results indicated that mean burrow depth was greater under more urbanized conditions (p = 5.23e-4, R^2 = 0.10, Figure 20).

Table 22: Burrow depth GLMM against predictor variables season, overall UI, temperature, wave height, log (1/beach slope), mean grain size, and the interaction of season and overall UI. Significant differences are indicated*.

Burrow Depth Predictor Variables	Estimate	Std. Error	Z value	*p*
Season	0.31	0.24	1.30	0.20
Overall UI	1.0	0.28	3.55	5.23e-4*
Temperature	-0.03	0.03	-0.85	0.40
Wave Height	-0.07	0.1	-0.73	0.47
Log(1/Beach Slope)	0.13	0.21	0.60	0.55
Mean Grain Size (phi)	0.006	0.07	0.09	0.93
Season : Overall UI	-0.74	0.39	-1.88	0.06

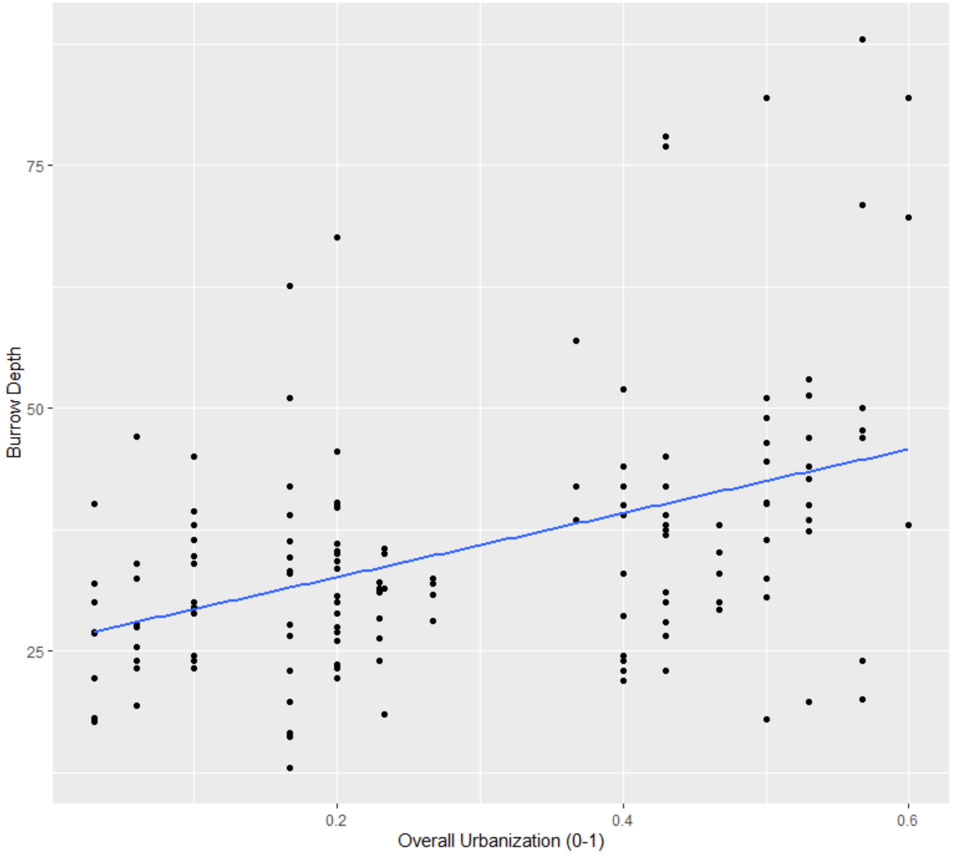


Figure 20: GLMM of mean burrow depth and overall UI from each site visit.

After the GLMM comparing response variable mean burrow depth, and predictor variables season with an interaction with overall UI, temperature, wave height, log(1/beach slope), mean grain size, date as a random variable, and a nested effect of transect within site indicated a significant effect of overall UI another GLMM was used to compare mean burrow depth and urbanization variables (beach cleaning, visitor frequency, distance to urban centers, solid waste on the beach, and vehicles on the sand, Table 23). Results indicated a significant effect of visitor frequency ($p = 0.02$) on mean burrow depth; a GAM was then used to detect any non-linear relationships of mean burrow depth with predictor variable visitor frequency (Table 23). GAM results of individual UI variable indicated visitor frequency had a significant effect on mean burrow depth ($p = 0.011$, Table 23). GAM results indicated that mean burrow depth increased as UI visitor frequency increased (Figure 21).

Table 23: GLMM and GAM models of burrow depth compared to individual urbanization variables. Significant differences are indicated*.

Model Type	**Model Expression**	**Model Variable**	**p**	**k**	**edf**
GLMM	Burrow Depth ~ Vehicles on Sand + Beach Cleaning + Solid Waste + Visitor Frequency + Distance to Urban Center	Vehicles on Sand	0.76	-	-
		Beach Cleaning	0.06	-	-
		Solid Waste	0.42	-	-
		Visitor Frequency	0.02*	-	-
		Distance to Urban Center	0.78	-	-
GAM	Burrow Depth ~ s(Visitor Frequency, k=3)	Visitor Frequency	0.011*	2.0	1.0

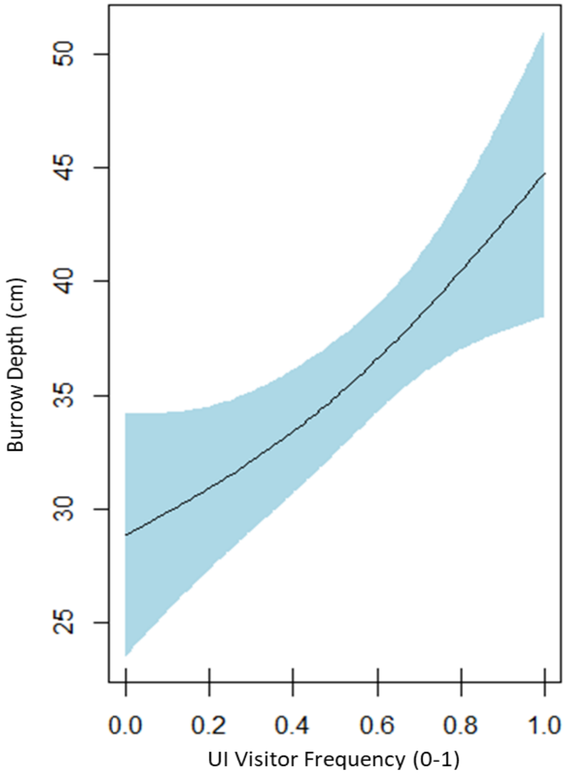


Figure 21: GAM of UI visitor frequency on mean burrow depth.

Discussion

Beach Types Around St. Thomas and UI

I hypothesized that beaches around St. Thomas were reflective/intermediate; however, all sites were found to be wave dominated reflective beaches using the RTR characterization. This was further confirmed by the BI, BDI, and log(1/slope) when all sites resulted in reflective characterizations. Although all beaches ultimately resulted in reflective characterizations, there was variability observed across sites. Variability was observed in the degree of slope, coarseness of sand, and the general shape of the beach, such as the presence or lack of a berm (Figures 5 & 6). The differences across sites distinguished three different reflective beach types during the period of this study. Caret Bay, Coki Point Beach, Magens Bay, and Neltjeberg Bay were all found to be morphologically similar, based on the slopes of the beach and all were the flattest of the reflective beaches. Stumpy Bay was found to be the steepest of the reflective beach types, and Lindberg Bay and Santa Maria Bay were found to be significantly different from both groups, displaying characteristics intermediate to the two other groups. Previous studies have indicated that slope significantly impacts ghost crab populations, with populations decreasing across sites with greater slopes (Defeo & McLachlan, 2005). However, this study indicates that the slight variation in St. Thomas' beach slopes does not have a great enough variation to cause a change in ghost crab populations (Tables 18, 20, & 22).

For morphological categorizations, the RTR method outlined by McLachlan, Defeo, and Short (2018) indicated beach morphology and type of sites around St. Thomas (i.e. WD/TD/TM & reflective/intermediate/dissipative). However, for more detailed differentiation between beaches, log(1/slope) found the greatest site variation due to the similarity in tidal/wave patterns and mean sand grain sizes between sites. This result supports previous studies that have indicated that log(1/slope) finds the greatest variation between sites in a close geographic region (McLachlan & Dorvlo, 2005). Although there were variations detected between sites, model results indicate that this slight variation in reflective characteristics does not affect ghost crab burrow abundance, width, or depth (Figure 6; Tables 18, 20, & 22). The variation found is informative, but not great enough to impact ghost crab populations. Added detail is beneficial when comparing beach slope alone but does not greatly benefit beach morphology classifications or ghost crab population predictions.

St. Thomas beach characteristics align with those described in other studies, including nearby reflective beaches of St. Martin (Boon & Green, 1988). Similarities can be found in the wave/tidal descriptions and in the qualitative descriptions of sediment and beach sizes. St. Martin beaches were described as minimal tidal fluctuations (less than 0.2 m) and steep beach slopes (approximately 0.08-0.19 m), corresponding to reflective characteristics (Boon & Green, 1988). Physical attribute descriptions and beach classifications from this study are similar (St. Martin reportedly possessing reflective beaches mostly shaped by waves and swells, which describes a wave dominated beach); however, this study offers more variation in site descriptions and classifications from multiple newer indices, compared to only using Dean's Parameter (Boon & Green, 1988).

The urbanization index is a popular tool to assess different aspects of human impact across a variety of beaches around the world. The urbanization index values calculated for this study are comparable to previous studies. However, the modifications should be considered, and overall values in other studies may not follow variable definitions perfectly since the index was customized for the St. Thomas sites included in this study. Using the UI, sites such as Folly Beach and Myrtle Beach in South Carolina have been assigned UI values of 0.5 and 0.96, respectively (Gul & Griffen, 2019; Table 24; Figure 22). Folly Beach's overall UI is similar to the overall UI of Sapphire Beach and Coki Point beach, however, when we look at the images of the urbanization of these sites, we can see differences in urbanization and buildings on the sand immediately. Differences can also be observed comparing images of St. Thomas urbanization with sites in Chile (Calenta San Pedro Beach, Playa Changa, and La Herradura; 0.46, 0.89, 0.94, respectively; Gonzalez et al., 2014; Table 24; Figure 22). The most similar overall UI values with Chile are between Magens Bay (0.45) and Calenta San Pedro Beach (0.46), however comparing the images we can see that in Chile there are large city structures right next to the beach and some evidence of trampling; whereas Magens has fewer buildings, but potentially greater visitor frequency for the area. These observed differences in urbanization type emphasize the importance of assessing the specific urbanization variables within the overall index rather than comparing overall values alone.

Table 24: Urbanization index values for beaches in St. Thomas, beaches in South Carolina, and beaches in Chile.

Beach	Overall Urbanization Index
Lindberg Bay	0.43
Magens Bay	0.45
Coki Point Beach	0.52
Sapphire Beach	0.48
Stumpy Bay	0.15
Santa Maria Bay	0.05
Caret Bay	0.18
Neltjeberg Bay	0.2
Calenta San Pedro (Chile)	0.46
Playa Changa (Chile)	0.89
La Herradura North (Chile)	0.94
Myrtle Beach (USA, SC)	0.96
Sullivan’s Island (USA, SC)	0.6
Waties Island (USA, SC)	0.03
Folly Beach (USA, SC)	0.5

Figure 22: Images of urbanized beaches in St. Thomas, South Carolina, and Chile.

St. Thomas Ghost Crab Populations

Analysis of ghost crab populations suggested that mean abundance per m^2 by site was not differentiated into two groups (high- and low- impact) but was significantly different across sites (Figure 11). Low- impact sites Santa Maria Bay and Neltjeberg Bay often had greater average burrow abundances compared to other sites. Previous research comparing abundances between urban beaches (high- impact) and non-urban beaches (low- impact) found greater variation between the two groups of sites and saw greater average numbers of burrows on non-urban sites (1.6 burrows per m^2) compared to the abundances found at low- impact sites in this study (0.13 burrows per m^2; Barros, 2001). These variations in research findings could be due to the different survey methods used by Barros (2001) which potentially inflated the burrow abundances in that study. There are also no comparable ghost crab studies in the USVI, so the variation in ghost crab abundances may be due to geographic differences since Barros (2001) surveyed the east coast of Australia. Further urbanization studies in South Carolina found different burrow width results between high- and low- impact sites. Our study found burrow widths at low- impact sites to be around 20 mm (Figure 12), however, in South Carolina beaches with similar low urbanization impact had an average burrow width close to 30 mm (Gul & Griffen, 2018), suggesting St. Thomas low- impact beaches have smaller individuals compared to South Carolina. When comparing high- impact sites with South Carolina beaches, St. Thomas has slightly wider burrows (approximately 27 - 30 mm) compared to South Carolina (25 mm; Gul & Griffen, 2018). Burrow width results suggest a different balance of juvenile and adult crabs compared to other places, with St. Thomas low- impact sites having larger juvenile populations compared to high- impact sites. Variations between results could be due to survey method, geographical differences, or survey time period. South Carolina was surveyed from late May through September, whereas this study ended in July, potentially capturing August recruitment effects in South Carolina.

Effects of Urbanization on St. Thomas Ghost Crab Populations

All GLMM results indicated that overall UI had a significant negative effect on ghost crab mean abundance, mean burrow depth, and mean burrow width, confirming our hypothesis that urbanization would have a negative effect on these variables (Tables 18, 20, & 22). GAM analysis of UI variables found that beach cleaning and visitor frequency were key UI variables and reduced ghost crab population abundances the most, compared to other anthropogenic impacts captured by the UI (Tables 19 & 23). Beach cleaning had significant effects on ghost crab abundances; sites that practiced frequent beach cleaning possessed smaller populations of larger crabs that burrowed deeper into the beach sand than sites with no cleaning. On St. Thomas due to the lack of heavy machinery use at most beaches, beach cleaning at the study sites was defined as raking of *Sargassum* that drifted ashore at popular tourist sites or general raking of the sand to smooth the beach surface. With the increase in *Sargassum* rafts arriving to St. Thomas, the effect of raking should be considered in future management plans at sites where *Sargassum* is a common occurrence, such as Sapphire Beach and Coki Point Beach. Visitor frequency was also found to have an effect on burrow depth, with higher visitor frequency resulting in deeper burrows (Table 23, Figure 21). This result paired with the finding that increases in overall UI decreased burrow abundance, indicates that high- impact sites like Magens Bay, Coki Point Beach, Sapphire Beach, and Lindberg Bay have smaller ghost crab populations that burrow deeper in the sediment. Deeper burrows are potentially a response to visitor frequency and beach cleaning in an attempt to create safer burrows for the crabs and to create more distance between the beach infauna and anthropogenic impacts. Previous research supports this and has indicated increased urbanization impacted burrow morphology, specifically, resulting in deeper burrows (Gül & Griffen, 2018).

Model results support previous studies that find urbanization and anthropogenic impacts negatively impact ghost crab populations (Barros, 2001; Costa et al., 2019; Costa & Zalmon, 2019; Gül & Griffen, 2018; Gül & Griffen, 2019; Peterson et al., 2000). Our models support that overall urbanization, specifically beach cleaning, decreases ghost crab populations on these St. Thomas beaches. This result coincides with other research results that have found negative impacts from beach cleaning on various infauna species such as shrimp, where cleaned beaches possessed lower population abundances compared to uncleaned beaches (Malm et al., 2004). Ghost crab populations have been reliably used as an indicator of anthropogenic stress on a sandy beach habitat since populations are easily influenced by urbanization and their diets and population reflect the resources available within their habitat (Barros, 2001; Costa et al., 2019; Costa & Zalmon, 2019; Gül & Griffen, 2018; Gül & Griffen, 2019; Peterson et al., 2000; Strachan et al., 1999).

Model results and previous research support that sites on St. Thomas with lower ghost crab populations (Coki Point Beach, Lindberg Bay, and Magens Bay) are experiencing reduction in sandy beach ecosystem diversity due to anthropogenic stress (Huijbers et al., 2015). Specifically, high- impact sites have reduced ghost crab populations and therefore reduced ecosystem services due to the high rates of visitor frequency and beach cleaning. Although high- impact sites are suffering from reduced ecosystem function, there is still infauna activity and with reduced ecosystem stressors, beaches can be restored. Population abundances across high- impact sites were similar, however sites such as Magens Bay frequently had surveys with zero burrows being found, indicating high ecosystem stress and reduction in function. This site should be prioritized in restoration efforts given the lack of infauna and high tourism popularity.

Management Implications

This study confirms that anthropogenic impacts are having a negative impact on urbanized beaches around St. Thomas. Due to the economic and cultural value of all sites, it is not plausible to remove all human impact, so it is important to consider the recreation potential and conservation value when prioritizing specific sites (McLachlan et al., 2013). Conservation value is calculated through observations of natural physical features, presence of endangered/iconic species, and macrobenthic diversity; while recreation potential is based on infrastructure development, safety, and physical carrying capacity of the site (McLachlan et al., 2013). This study can inform management decisions for both priorities. The sandy beach profiles can inform what the current beach structure is and allows for future comparisons to determine if natural structures have been restored or diminished. Ghost crab populations inform the macrobenthic diversity and health, indicating that sites with large ghost crab populations have greater macrobenthic diversity. Urbanization index results can inform recreation potential, particularly infrastructure and development along the beach by the variable buildings on the sand.

High- impact sites (Lindberg Bay, Magens Bay, Coki Point Beach, and Sapphire Beach) would be categorized as recreation intensive, indicating the need for different management goals and outcomes compared to the low- impact sites which would be categorized as multiple use (needing both recreation and conservation interventions) with high conservation value. Low conservation values as a result of high urbanization at Lindberg Bay, Magens Bay, Coki Point Beach, and Sapphire Beach, results in recreation focused management recommendations (McLachlan et al., 2013). Currently, these sites prohibit the use of vehicles on the beach, which creates a safe area for beachgoers. Further health and safety recommendations for these sites include increased the waste/pollution management at these sites. Generally, sites such as Magens Bay and Sapphire beach were found to be clean, however Lindberg Bay and Coki Point beach would benefit from more frequent waste removal, since urbanization results indicated higher waste frequencies at these sites and solid waste pollution reduces the recreational potential of beach sites (McLachlan et al., 2013). Access to amenities and back shore space either is present at all high- impact sites or cannot be further developed.

All low- impact sites resulted in multiple use categorizations indicating the necessity for management of recreation and conservation of these sites. To conserve the natural resources at this site, I recommend a restriction of vehicle access on all sites. Currently, vehicle access is restricted on popular tourist sites; however, sites like Neltjeberg Bay, Stumpy Bay, and Caret Bay all had evidence of vehicle traffic during this study. Under the Virgin Islands Code Title 12 Conservation, Chapter 2 Protection of indigenous, endangered, and threatened fish, wildlife, and plants, no person can harass, injure, or kill any specimen of an endangered species. Vehicle activity on potential turtle nesting beaches or sea bird nesting beaches would violate section 105, Prohibited Activities, under Title 12 of the VI code. Historically St. Thomas has been a nesting site for sea turtles and although turtle populations have declined, beaches still have nesting activity (McClenachan et al., 2006). Further research is needed to confirm specific nesting beaches for the territory. Until that time, all beaches should be treated as if they were active nesting sites; therefore, vehicle traffic on any part of a sandy beach should be immediately prohibited. The restriction of vehicle access would also help preserve the natural beach vegetation further improving the conservation value of all sites (McLachlan et al., 2013). Further beach use surveys are needed to confirm the recreational uses of low- impact sites, however the primary urbanization impacts of visitor frequency and beach cleaning were not problematic at low- impact sites and no additional management of these impacts is needed.

Study Limitations and Future Research Implications

This study successfully characterized the eight beaches selected as study sites, however only one beach was located on the southern side of the island, potentially skewing the results of environmental characteristics such as wave exposure. Future studies are needed to assess beaches on all sides of the island to better determine if there are greater variations of reflective beaches not captured by this study. Beach morphology also fluctuates throughout time depending on environmental variables (i.e. seasons or storm events); this study characterized beaches from February-June, which neglected to assess any environmental changes that occur from June-January. Assessing beaches during this time could be critical for the territory since large storm events that occur during hurricane season (June-November) could significantly change beach morphology through storm-related sediment erosion, deposition, and displacement. Additionally, the locations of the low- impact sites (Stumpy Bay, Santa Maria Bay, Caret Bay, and Neltjeberg Bay) are relatively close to one another, resulting in potential spatial auto-correlation. These geographic similarities may impact the ghost crab populations in that the recruitment may be similar or related since currents that would carry larvae may be shared. If this occurred during this study, it could potentially result in similar population structures at low- impact sites compared to high- impact sites where the populations would be independent from one another.

This study measured ghost crab populations during two seasons, February - March and May - June. It would be beneficial to survey populations year-round to fully assess any recruitment effects or storm effects. Previous studies have indicated a continuous, year-round recruitment of ghost crabs, with an increase during the summer, specifically around August (Negreiros-Fransozo et al., 2002; Pombo & Turra, 2017). Further sampling could confirm whether this is also true for the USVI and could confirm if there is increased recruitment on select sites. Data from this study did not suggest a recruitment pulse, and with the sampling period from May-June a recruitment pulse in August could not be measured. In this study, it was confirmed that high- impact sites possessed larger individuals compared to low- impact sites that possess smaller individuals. It would be beneficial to survey during peak recruitment season to determine if these differences in populations are from a lack of recruitment at high- impact sites, or if the size difference is a result of urbanization impacts.

Further surveys could have also informed how St. Thomas ghost crabs respond to storm impacts by surveying during storm season (June - November). Previous studies have confirmed that there are species-specific population decreases due to storm impacts, and that ghost crab populations recover anywhere from days to weeks after a storm event (Corte et al., 2017), but it is unclear if St. Thomas ghost crab populations relocate or decrease. Surveying after a storm would indicate if St. Thomas crabs persist and relocate after storms or if populations diminish then are replenished over time through recruitment. Consistent and long-term monitoring could track these changes over time and provide critical information for beach management in the territory.

In his study, surveys were conducted during the early mornings. This time of day was selected in order to maximize burrow preservation. Some studies also survey at night to capture active burrows (Costa & Zalmon, 2019). If surveys had been conducted during this time, abundances and widths may have been altered resulting in fewer small individuals and greater amounts of larger individuals. Night surveys would ensure measuring active burrows; however, smaller individuals are more difficult to see and more easily missed resulting in a lower abundance and larger widths reported (Costa & Zalmon, 2019).

Future urbanization assessments could be performed in further detail in continued sandy beach research. This study confirmed that the visitor frequency and beach cleaning played important roles in the reduction of ghost crab populations on the beaches surveyed. These findings are supported by other research findings indicating that beach cleaning practices have a negative effect on ghost crab populations and overall beach health (Defeo et al., 2009; Souza et al., 2017). However, beach cleaning assessments had no variables directly measured and were based on visual observations of rake marks or direct *Sargassum* removal at the time of each survey. To fully assess beach cleaning practices, direct measurements of cleaned beach area, methods, and cleaning duration and frequency, could be used to determine the degree of cleaning occurring at a specific site and test how those relate to the ghost crab metrics measured in this study. The addition of detailed data regarding beach cleaning could be incorporated into current models as an individual variable, separate from the UI, or serve as an additional study building on this research. Additionally, this study surveyed two beaches that were known to remove *Sargassum* via raking, and another beach where raking was conducted to smooth the beach surface, however, there are beaches on St. Thomas where bulldozers are used to move sand and clean the beach area (e.g., Margaritaville Beach, the beach at the Ritz). To better assess cleaning practices, beaches with various levels of cleaning could be included. Increases in beach cleaning frequency could result in lower crab abundances, and differences in practice could also have an impact on crab populations (likely reducing them due to burrow collapse or removal of food sources). Mechanical cleaning using bulldozers would likely have a greater negative impact on ghost crab populations compared to manual raking. Further research could inform management decisions regarding beach cleaning methods and frequency.

Visitor frequency was measured using direct population surveys at high- impact sites between 12-2 pm, and low- impact sites were estimated and ranked using the Gonzalez et al.(2014) low and medium descriptions. Due to the variation in value assignment, there is a risk that the urbanization classifications are not comparable if there were variations in visitor frequency that were not measured. If visitor frequency surveys were conducted at all sites, “intermediate” sites like Neltjeberg may have been classified as high- impact due to greater visitor frequency. Results from this study indicated that there was no change in urbanization between high- and low- tourist season, which shows that local urbanization impact is driving the urbanization more than tourists visiting the beaches. However, surveys were conducted only on weekdays, which makes the visitor frequency measured likely to only include tourist frequency. Knowing now that the local stressors are more important than the tourism stressors, conducting visitor surveys on the weekend or the weekend and weekday would be a better way to assess the visitor use on beaches. If visitor frequency were measured during the week and weekend across all sites, low- impact sites could have potentially been given higher urbanization classifications due to additional visitor frequency being measured and included. Select sites around the island such as Magens Bay and Lindquist Beach require an entrance fee and the number of visitors to those sites are recorded. These records could be used and compared to visitor frequency surveys as a way to determine if the full variability in visitor frequency is being captured. Entrance reports could also verify the seasonal fluctuations in visitor traffic to confirm if fluctuations impact ghost crab populations.

Additional impacts that were not included in this study are the predation of ghost crabs by birds and invasive species. There is limited research on ghost crab predation, but one study in New Zealand indicated that when invasive rats were removed from an island, ghost crab populations reappeared on the beach (Bellingham et al., 2010). Predation by rats was not directly observed in this study, but the results by Bellingham et al. (2010) indicate that the rat population was eliminating ghost crabs on the island (). St. Thomas is home to two invasive rat species, the Norway Rat (*Rattus norvegicus*) and the Black Rat (*Rattus rattus*; Geographic Consulting for the Virgin Islands Department of Agriculture, 2016). On St. Thomas, many rats are attracted to human structures such as homes when scavenging for food (pers. obs.); rats could be attracted to resorts and other beach infrastructure, searching for human food scraps on the beach. Attracting invasive predators could result in these rats also preying on smaller ghost crab populations when food is limited; this might be an unexplored explanation for the patterns observed in this study. The mongoose is also invasive to St. Thomas (Geographic Consulting for the Virgin Islands Department of Agriculture, 2016) and could potentially prey on ghost crabs similar to the rat. If invasive species surveys were taken across sites, results might have indicated an additional driver of reduced populations at high- impact sites.

In 2019, it was observed in South Carolina that the Red Shouldered Hawk preyed on ghost crabs (Mccullough et al., 2019), and although the Red Shouldered Hawk is not observed in St. Thomas, other aviary predators are and represent potential threats to ghost crab populations. In 2020, a Pearly-Eyed Thrasher (*Margarops fuscatus*) was observed attacking and eating a ghost crab on Neltjeberg beach (Kristin Grimes, pers. comm.); a clear indication of aviary predation on ghost crabs at at least one of the beaches included in this study. Large bird tracks were often observed at different sites following ghost crab tracks between burrows across the beach (pers. obs.). From pictures taken during this study, these tracks were later identified to potentially belong to the Little Blue Heron (*Egretta caerulea*), Great Blue Heron (*Ardea hreodias*), Great Egret (*Ardea alba*), or Snowy Egret (*Egretta thula*). The Caribbean islands serve as nesting spots for numerous endangered coastal birds throughout the year or seasonally for select species, however it appears that although full grown adult birds may prey on crabs, chicks and eggs are a common resource for ghost crabs and studies have found ghost crabs pose a threat to nests (Kwon et al., 2018). This makes it unclear if nesting season of certain species is an advantage to ghost crabs because of an increased food resource, or a threat because of an increase in the adult bird population in one place. This study could have taken more images of bird tracks and added information on potential aviary predation to detect if there were different potential aviary predators' pressure across sites. These results could further explain lower population abundances at high- impact sites or indicate that low-impact sites have the same or greater environmental pressures but are still able to have a greater population persist. Further studies of the impacts of predation by coastal birds and invasive species on the ghost crab in St. Thomas would provide beneficial information about the necessity of a project to remove invasives or further investigate the drivers of ghost crab populations.

Chapter 3: Effects of Beach Chairs on Ghost Crab Burrowing Behavior

Sandy beaches compose the majority of open coastlines and are the most popular coast type for human use (Davis & FitzGerald, 2004; Schlacher et al., 2007). Globally, local economies rely on sandy beaches as a source of income through tourism (Davis & FitzGerald, 2004; Schlacher et al., 2007). However, increased visitor frequency can increase the ecological stress on sandy beach ecosystem biodiversity (Barros, 2001; Costa et al., 2019; Costa & Zalmon, 2019; Gül & Griffen, 2018; Gül & Griffen, 2019; Peterson et al., 2000). Direct anthropogenic alterations pose an immediate threat to sandy beach ecosystems and benthic fauna (Defeo et al., 2009; Schlacher et al., 2007). Human development along sandy beaches physically alters habitat and attracts additional visitor frequency, causing a steady increase in visitors and negatively impacting infauna composition (Defeo et al., 2009; Schlacher et al., 2007). Anthropogenic alterations on sandy beaches displace infauna, kill species, limit and degrade habitat, and/or destroy burrows within the sediment (Peterson et al., 2000). Stress from local human disturbance may exert a stronger influence compared to global stressors, such as climate change, for sandy beaches (Schooler et al., 2017). With time, this stress causes continual loss of species and ecosystem services indicating the importance of individual site management of anthropogenic impacts (Schooler et al., 2017).

It has been established that human impact alters species populations, with general trends indicating that human impact decreases the diversity and abundance of sandy beach species (Barros, 2001; Costa et al., 2019; Costa & Zalmon, 2019; Gül & Griffen, 2018; Gül & Griffen, 2019; Peterson et al., 2000). In response to anthropogenic impacts, remaining epifauna have to adapt to the ecosystem stressors and changes or face eventual extinction. Some of these adaptations have resulted in the conditioning of wild animals and have changed instinctual habits to utilize human habitat alterations. Results indicated that the main adaptation to human impact across high profile species (primates, dolphins, stingrays) was alterations in sources and methods of scavenging for food (Corcoran et al., 2013; Gruber et al., 2019; Orams, 2001). Of the limited research conducted on behavioral adaptations resulting from tourism activities, there are none to-date conducted on sandy beach organisms to determine if benthic fauna utilize resources from human impact to benefit their individual wellbeing.

Ecosystem stress and changes caused by human impact on sandy beaches are commonly assessed by measuring populations of the ghost crab (*Ocypode*). The ghost crab is a popular indicator species since many studies have indicated that high anthropogenic alterations and activity on sandy beaches significantly reduces ghost crab populations (Barros, 2001; Costa et al., 2019; Costa & Zalmon, 2019; Gül & Griffen, 2018; Gül & Griffen, 2019; Peterson et al., 2000). Although ghost crabs are used globally as an ecological indicator for sandy beaches and specifically for human impact, information about behavioral adaptations by these crabs to specific types of human activity/infrastructure is limited. Some behavioral changes have been found where ghost crabs utilized human food waste as a resource (Strachan et al., 1999); however, this is the extent of research conducted on ghost crabs utilizing resources from human impacts.

Resorts on St. Thomas, USVI, consistently receive reservation requests and serve visitors to the territory with food, drinks, recreation, and leisure space. Many resorts supply items such as beach chairs and umbrellas for visitors on their beach; however, most resorts leave their beach chairs on the beach area overnight, supplying consistent artificial structure and source of potential anthropogenic disturbance. It is unclear if this persistent structure alters sediment temperatures or if the combination of structure and temperature is a beneficial resource utilized by ghost crabs, resulting in altered behavior.

Within the Caribbean, there is a deficit of ghost crab studies. Specifically, there are no studies within the U.S. Virgin Islands (USVI) regarding specific anthropogenic impacts on ghost crab behavior. To address both global and local data gaps, the aim of this study is to determine if common structures associated with tourism activities (i.e., beach chairs) change sediment temperature, and if the combination of structure and temperature influence ghost crab burrowing behavior.

Previous research has suggested that ghost crabs burrow in response to thermal pressures, specifically burrowing into sediment to escape high daytime temperatures and low nighttime temperatures (Berlino et al., 2018; Lucrezi et al., 2008; Strachan et al., 1999). Therefore, I hypothesized that the presence and type of a beach chair would impact the temperature of the sediment resulting in an increase in crab burrow abundance. Specifically, I hypothesized that sediment temperatures would be significantly cooler under chairs with more seat coverage offering a temperature refuge, resulting in an increased number of burrows under the fully shaded chair condition. Additionally, I hypothesized that smaller juvenile crabs would be more attracted to the refuge of the beach chair since they are more susceptible to predators and other environmental impacts (such as wave impacts and high temperatures) compared to larger adult crabs (Berlino et al., 2018). Observations in the field (Chapter 2) suggested frequent burrowing under beach chairs, and often at the base of chair legs. These observations informed further hypotheses that structure was also impacting ghost crab burrowing behavior. Specifically, I hypothesized that ghost crabs would prefer to burrow near beach chairs compared to areas where no beach chair was present due to burrow protection. Finally, due to the perception of increased protection under beach chairs, I hypothesized that crabs would expend more energy investing in deeper burrows under the no shade condition compared to the part shade and full shade conditions to reach cooler sediment temperatures deeper in the sand.

Methods

Site Selection

Eight beaches on the island of St. Thomas, U.S. Virgin Islands (Chapter 2, Figure 1) were characterized using a modified Urbanization Index (UI; Chapter 2, Table 1; Gonzalez et al., 2014) to determine the site of lowest human impact (see Chapter 2). Of the low- impact sites that were assessed (see Chapter 2), Neltjeberg Bay, Stumpy Bay, and Caret Bay, could be accessed by an unmaintained road or cleared trail. Santa Maria Bay was selected for this study, due to the low overall UI score (0.05, Chapter 2: Table 3) and limited accessibility(by boat or rarely used unmaintained road), in turn, limiting the likelihood of experimental disturbance (Figure 22).

Figure 22: Study site for the Beach Chair Experiment. Santa Maria (18°21’41.1”N 64°59’39.8”W) was selected with the lowest overall urbanization of all sites. Photograph by Kaliegh Schlender.

Sampling Period

To assess the effects of beach chair presence on ghost crab burrowing behavior, a beach chair experiment was conducted from July 6 - August 31, 2020 during low- tourist season to minimize potential human interference or disturbance. Experiment set up occurred every Monday during the sampling period with data collected Wednesday-Friday after an acclimation period. Methods for this experiment were adapted from the resetting methods outlined by Pombo and Turra (2019). Original resetting methods conducted surveys over a two-day period; however, due to the behavioral component of this study, surveys were conducted over a three-day period with two days for acclimation and resetting (per. com., Dr. Maria Pombo).

Experimental Design

To test for the effects of structure and temperature on ghost crab burrowing behavior, four 3 x 3 m plots were established with four different treatments: control plot (no chair; C), no shade (NS), part shade (PS), full shade (FS; Figure 23). Three beach chairs, approximately 200 cm x 50 cm. were modified in the following ways: the FS was a beach chair covered in a plastic tarp to create full shade coverage under the chair; PS was a full length beach chair with standard, plastic strips of material forming the seat; NS was only the frame of a full length chair with the seat material removed. Plots were located 6 m from the highest point on the swash line separated by 5 m (average burrow distance from swash based on Chapter 2, Figure 23) and sampled for a period of seven weeks (July 6 - August 21, 2020) with the chair placed in the center of each plot with the shorter side of the beach chair placed facing the ocean.

During the second week (July 13 - July 17), data collection ended one day early (surveys conducted Monday through Thursday); surveys were then postponed for one week between July 20 and July 24 for safety reasons. Work resumed the following week (July 27 - July 31) when Tropical Storm Isaias hit the U.S. Virgin Islands and data collection occurred Monday through Wednesday only, due to storm activity. Between August 3 and August 21 data were collected Wednesday through Friday after a two-day acclimation period, following the methodology established for this study.

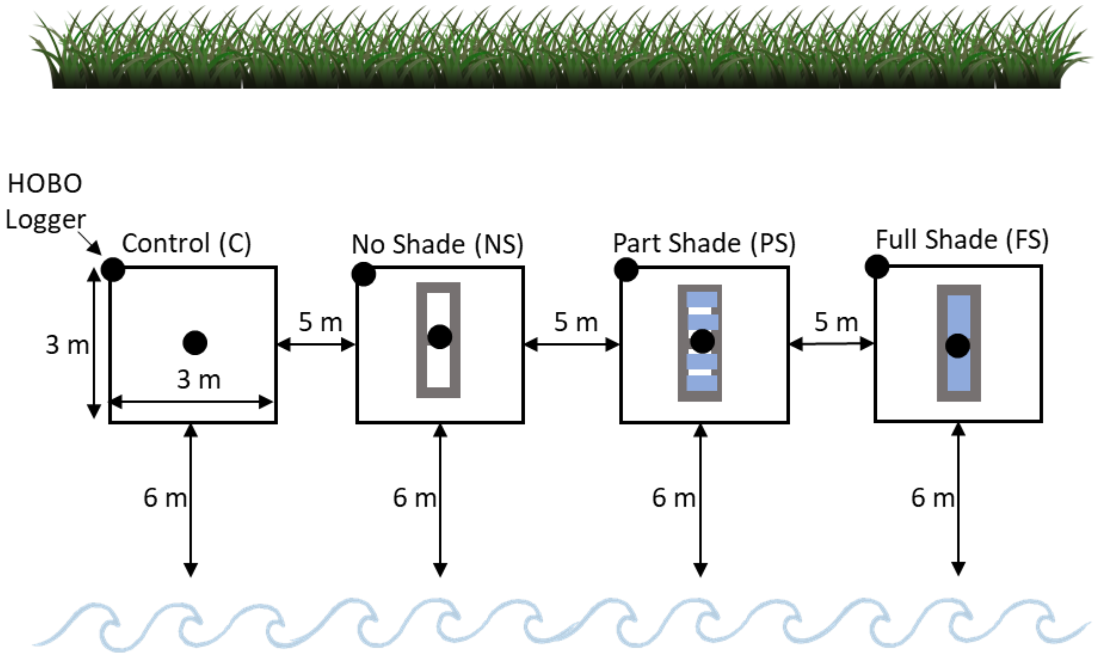


Figure 23: Experimental set up for beach chair experiment on Santa Maria Beach.

Each week, plots were established on Monday to allow for an acclimation period before burrow surveys began Wednesday. During the acclimation period on Monday and Tuesday, any burrows within the 3 x 3 m plots were “reset” by lightly covering any burrow openings with sand (Pombo & Turra, 2019). Resetting burrows has allowed distinguishing up to a 69% difference in active burrow measurements between the initial and secondary surveys (Pombo & Turra, 2019). Wednesday, Thursday, and Friday burrow surveys were conducted in each plot to measure burrow abundance within each plot area, width, depth, and distance to the nearest chair leg. Burrow width was measured with a Vernier caliper. A previously marked zip tie was used to measure burrow depth and distance to the nearest chair leg. Burrows were gently reset at the end of every survey. To control for potential bias related to beach position, each week, the plots were rotated one position relative to the previous week. In addition to quantitative survey data, during each visit qualitative data were recorded. Observations included: perceived or observed changes to environmental conditions (i.e. appearance of *Sargassum* or precipitation events), presence of ghost crab tracks in the plots, presence of ghost crabs within the plots unassociated with burrows in the plots, and general distribution of burrows outside of plots across the beach.

To measure ambient and treatment sediment temperatures, ONSET HOBO Pendant MX water temperature data loggers (MX2201/MX2202) were installed at the corner and center of each experimental plot directly beneath the chair treatment. Each plot contained three HOBO temperature loggers: 1) 33 cm under the chair treatment located in the center of the plot (deep HOBO), 2) 5 cm under the chair treatment located at the center of the plot (surface HOBO), and 3) 33 cm in the corner of the plot which served as a control to confirm if a difference in temperature was occurring due to the presence of the chair treatment (corner HOBO). Temperature recordings (°C) were taken every 15 minutes Tuesday - Friday of each week across the experiment. Loggers were attached to PVC pipes at 5 cm and 33 cm depths because previous burrow surveys at this site found an average burrow depth of 33 cm (n=106).

Data Analyses

Weeks four - six (July 27 - August 14) crab burrowing behavior was observed to be altered by Tropical Storm Isaias and by the arrival of *Sargassum* on the beach. During this time, no burrows were found within the experimental plots. These data were excluded from analysis since uncontrollable environmental variables altered crab behavior. Weeks included in analysis were weeks one, two, and seven (July 6 - July 16, and August 17 - August 21).

To determine if there was a difference in burrow characteristics across chair treatments burrow abundance, width, depth, and distance to chair were averaged daily by plot condition (C, NS, PS, FS, n=32). Shapiro normality tests were used to confirm if data were normal. Days where there were no burrows observed were removed from burrow width, depth, and distance to chair analysis (n=14). When data were normal a nested ANOVA was used to compare the response variable (burrow width, depth, or distance to chair structure) by chair treatment condition (NS, PS, and FS) with a nested effect of the days within a week. No post hoc tests were conducted when no significant differences were found. When data were not normal, a generalized linear regression was applied to the response variable (burrow abundance) and predictor variables chair treatment condition (C, NS, PS, and FS) and week. A power analysis was used to determine if the sample sizes were large enough to detect significant differences within the burrow data. Temperature logger data were analyzed separately due to the very small sample sizes from burrow surveys.

Temperature data were analyzed using a fixed effects repeated-measures analysis of variance (ANOVA) to determine if there was an effect on the response variable temperature by fixed predictor variables HOBO logger conditions and week (n=6). HOBO conditions were defined as plot condition-temperature logger depth, specifically: 1) C-corner, 2) C-surface, 3) C-deep, 4) NS-corner, 5) NS-surface, 6) NS-deep, 7) PS-corner, 8) PS-surface, 9) PS-deep, 10) FS-corner, 11) FS-surface, and 12) FS-deep (n=18,770). A Tukey Post-Hoc analysis was used to determine differences across HOBO conditions and weeks.

Results

Observations

During the course of the study, ghost crabs appeared to prefer burrowing within plots that contained a beach chair compared to plots that had no chair. Across all seven weeks, activity was observed in the form of ghost crab tracks across all conditions except the control plot. When tracks alone were observed, crab activity was clustered around chair legs or the HOBO logger installations. On several occasions, a crab burrowed down the HOBO logger installation (Figure 24). During week four (July 27 - July 24), effects of Tropical Storm Isaias (TS Isaias) were observed: crab burrows that were normally numerous across the beach disappeared. Upon further investigation some crab burrows were observed on the far side of the beach among boulders (outside of the experimental boundaries). There were also multiple occasions where a crab was found superficially covered in sand nestled against a chair leg, but no burrow was present. Ghost crabs were observed superficially covered within the NS plot on August 12, within the FS on August 19, and FS on August 21. These superficially observed crabs were found weeks after TS Isaias, so it is unlikely that this behavior was a result of the storm. However, the first sighting of this behavior coincided with the day *Sargassum* was first observed, indicating this behavior is potentially a response to *Sargassum*. Beach morphology did not drastically change after the storm event. Although crab burrows seemed to reappear within days after the storm across the beach, burrowing behavior did not return to pre-storm burrow patterns within the plots. Approximately one week after the storm, *Sargassum* washed ashore and crab burrows began to be frequently observed in the *Sargassum* near the swash.

Figure 24: Ghost crab burrowing down a HOBO logger installation. Photograph by Kaliegh Schlender.

General burrow metrics by plot condition are reported in Table 24. During the full experiment no burrows were found in the control condition; signs of activity were scarce and if activity was observed it was limited to tracks by the corner stake. Burrow width was similar across plots with the average width of burrows in the NS plot being 23.1 mm, the average width of burrows in the PS plot being 28.8 mm, and the average width of FS plots being 29.6 mm. Burrow depth varied slightly across plot conditions where NS average depth was 12.8 cm, PS was 23.5 cm, and FS was 29 cm. Distance to nearest chair leg also varied, with burrows being closer to chair structures as coverage increased (distance: NS = 0-133 cm, PS = 8-55 cm, & FS = 4-65 cm, Table 24). PS and FS distances from the burrows to the nearest chair leg were similar and smaller, while there appeared to be a larger range in distances for burrows in the NS condition (Table 24).

Table 24: Ranges of ghost crab burrow abundance, width, depth, and distance to nearest chair leg by experimental plot condition per week.

Chair Condition	Total Abundance	Range of Burrow Abundance	Burrow Width Range (mm)	Burrow Depth Range (cm)	Distance to the Nearest Chair Leg Range (cm)	Mean Burrow Abundance	Mean Burrow Width (mm)	Mean Burrow Depth (cm)
Control	0	0	0	0	0	0	0	0
No Shade	15	0-6	10-54.8	8-22	0-133	3.2 SD = 2.6 SE = 0.7	23.1 SD = 14.2 SE = 3.7	12.8 SD = 5.4 SE = 1.4
Part Shade	10	0-6	15-34.6	9-39	8-55	1.4 SD = 1.8 SE = 0.6	28.8 SD = 7.6 SE = 2.4	23.5 SD = 11.7 SE = 3.7
Full Shade	11	0-2	16.5-45.62	14-47	4-65	1.3 SD = 0.9 SE = 0.3	29.6 SD = 10.9 SE = 3.3	29 SD = 13.4 SE = 4.1

Burrow Measurements

Shapiro Wilkes normality test indicated that burrow abundance was not normal, and the data were not able to be transformed. Generalized linear model results indicated no significant effect of chair plot condition on burrow abundance (*p* = 0.77). Burrow width, depth, and distance to nearest chair leg were normal. There was no significant effect of chair plot condition on burrow width (*p* = 0.58), burrow depth (*p* = 0.07), or burrow distance to nearest chair leg (*p* = 0.44; Figure 25). Power analysis results indicated we did not have sufficient samples to detect significant differences in abundance, width, depth, or distance to nearest chair leg across plot chair conditions.

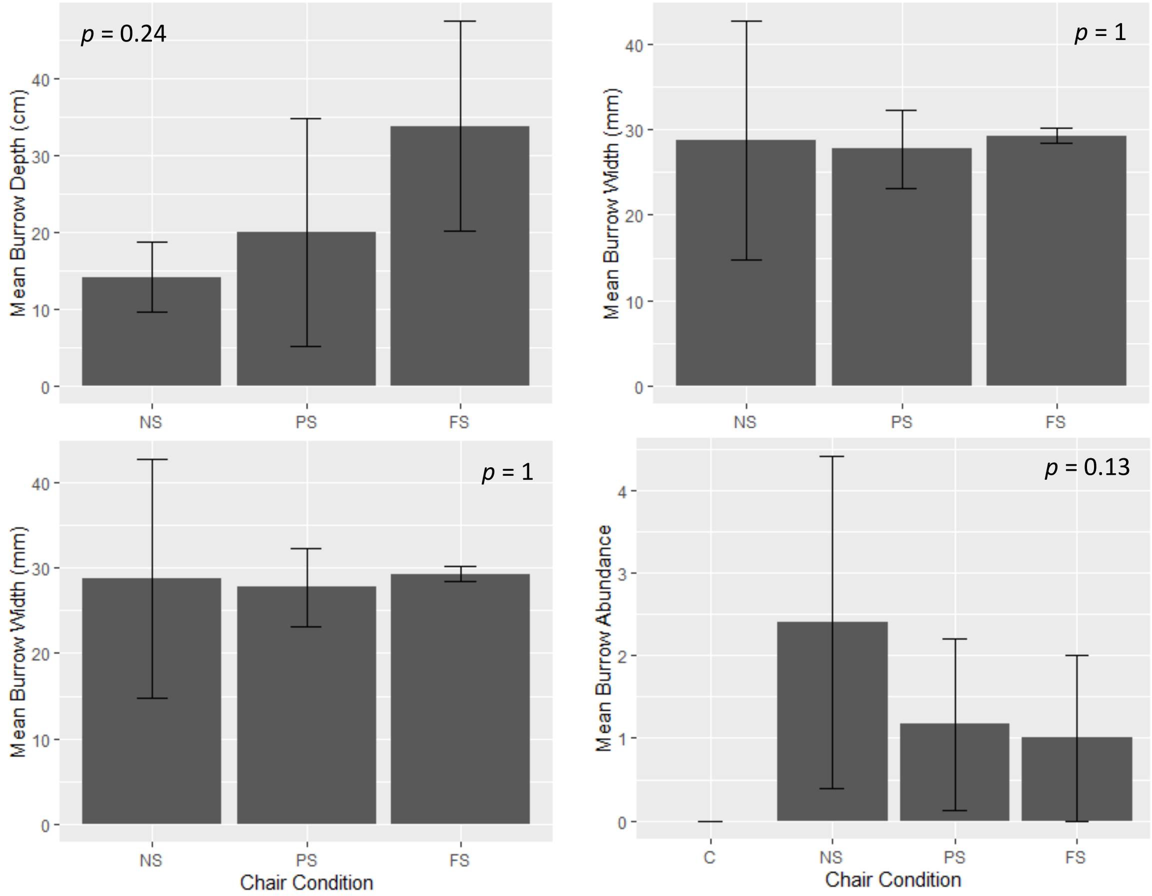


Figure 25 Mean burrow abundance, width, depth, and distance to the nearest chair leg across experimental plot conditions control (C), no shade (NS), part shade (PS), and full shade (FS) +/- standard error. Control plot is not included in width, depth, or distance to the nearest chair since there were no burrows found in those plots. Surveys took place on Santa Maria Beach from July 6 - August 21, 2020.

Temperature logger analysis

Repeated measures ANOVA results indicated a significant difference in temperature across HOBO logger series (F(11) = 1421, *p* < 2.2e-16), weeks (F(1) = 330, *p* < 2.2e-16), and a significant interaction between week and HOBO conditions (F(11) = 77, *p* = 6.37e-12, Figure 26). Results indicated that the NS surface and C surface mean daily temperatures were significantly greater from all other conditions and significantly different from one another (C surface being significantly greater; Table 25, Figure 26)).

Table 25: Tukey Post Hoc analysis results indicating significant differences in temperature across HOBO conditions.

HOBO Condition	**Tukey Post Hoc Group**
FS Surface	a
PS surface	ab
FS deep	ab
PS deep	b
NS deep	c
PS corner	cd
C corner	cd
C deep	cd
FS Corner	cd
NS corner	d
NS surface	e
C surface	f

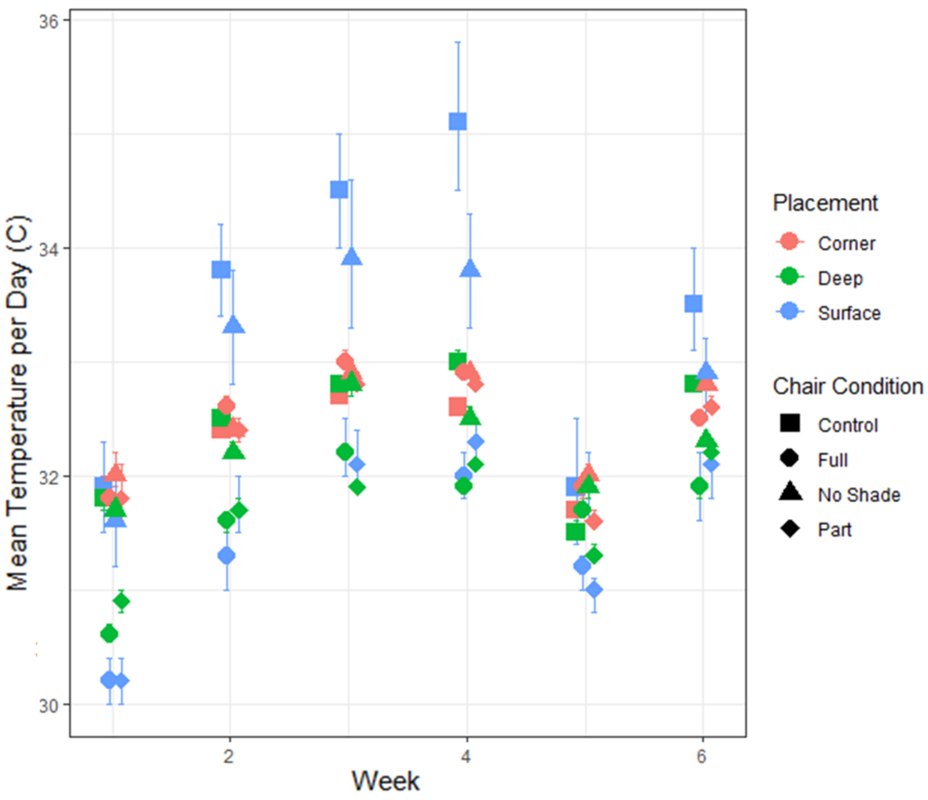


Figure 26: Average weekly temperatures (C°) +/- SEM across chair conditions and depth. Week one was July 6 - 10 and week two was July 13 - 17; there was then a week break due to a safety incident. Work resumed week three on July 27 - 29, then TS Isaias hit so the week was cut short. Week four was August 3 - 7, week five was August 10 - 14, and week six was August 17 - 21.

Tukey Post Hoc results above (Table 25) indicated the corner HOBO series in the NS, PS, and FS conditions were not significantly different than the deep C HOBO series, indicating the controls were effectively established and differences in temperature at 33 cm in depth were due to the presence of the beach chair. Figure 27 compares the no shade HOBO logger series (5 cm, 33 cm, and corner at 33 cm) to the control plot logger series (5 cm & 33 cm). NS deep series and the control deep series were not significantly different, but the NS corner series was significantly warmer compared to the NS deep series. This indicates a slight temperature change due to the chair frame present in the no shade plot (Figure 27).

Overall, the greatest temperature variations were found in the surface C HOBO series, then the surface NS HOBO series; both were significantly warmer compared to the other treatment conditions (Figures 28 and 29). The highest temperatures recorded on these series reached 47°C and the lowest temperature was 25°C, a temperature variation of almost 20°C. The lowest temperature recordings and variation were found in the deep FS HOBO series. The peak temperature within this series was approximately 32°C and the lowest was approximately 30°C, a temperature variation of only 2°C.

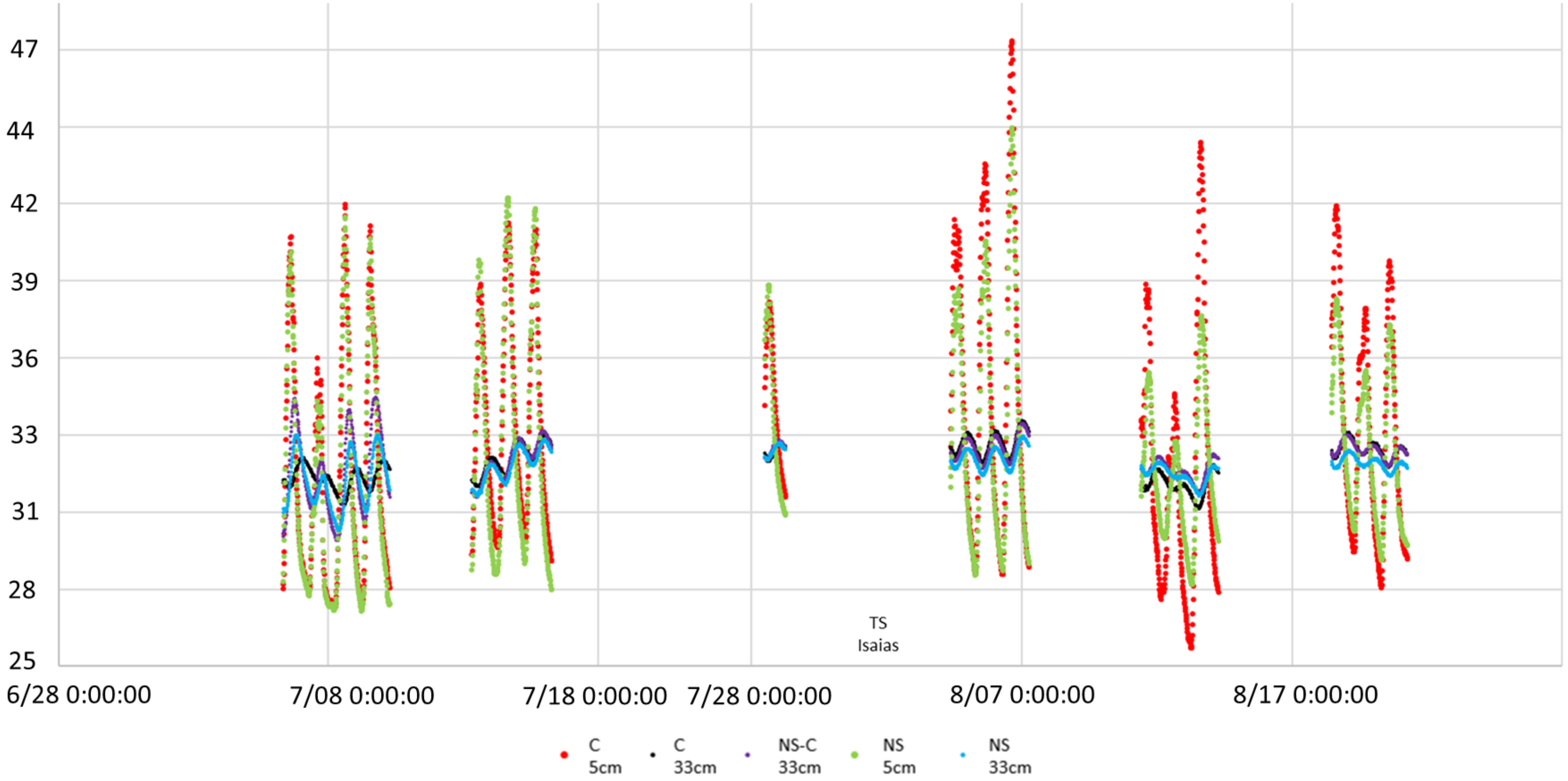


Figure 27: No shade HOBO logger series and control plot hobo logger series. No shade corner 33 cm (purple), no shade 33 cm (blue), no shade 5 cm (green), control 33 cm (black), and control 5 cm (red). Data was collected from Santa Maria Bay from July 6 - August 21, 2020.

The presence of a fully covered and partially covered chair significantly lowered sand temperatures compared to areas without chairs (NS and C). Results of PS and FS HOBO series indicate significantly lower average temperatures under chairs in those conditions at both surface (approximately 10°C cooler) and deep (approximately 1°C cooler) HOBOs compared to all other series (NS and C). Tukey Post Hoc results from the Repeated Measures ANOVA indicated there was no significant difference in average temperature between deep FS and deep PS. However, surface FS was significantly cooler than deep PS (Figures 28 & 29). The significant difference between the surface FS series and deep PS series indicates some variations in temperature between the different shade conditions; however, this difference was not substantial since there was no significant difference between surface FS, deep FS, and surface PS, and there was no significant difference between surface PS, deep PS, and deep FS. Variation within the deep FS and deep C series were approximately the same: 2°C. However, the FS condition was significantly cooler ranging between 30°C - 32°C, while the control plot ranged between 32°C - 34°C (Figure 29).

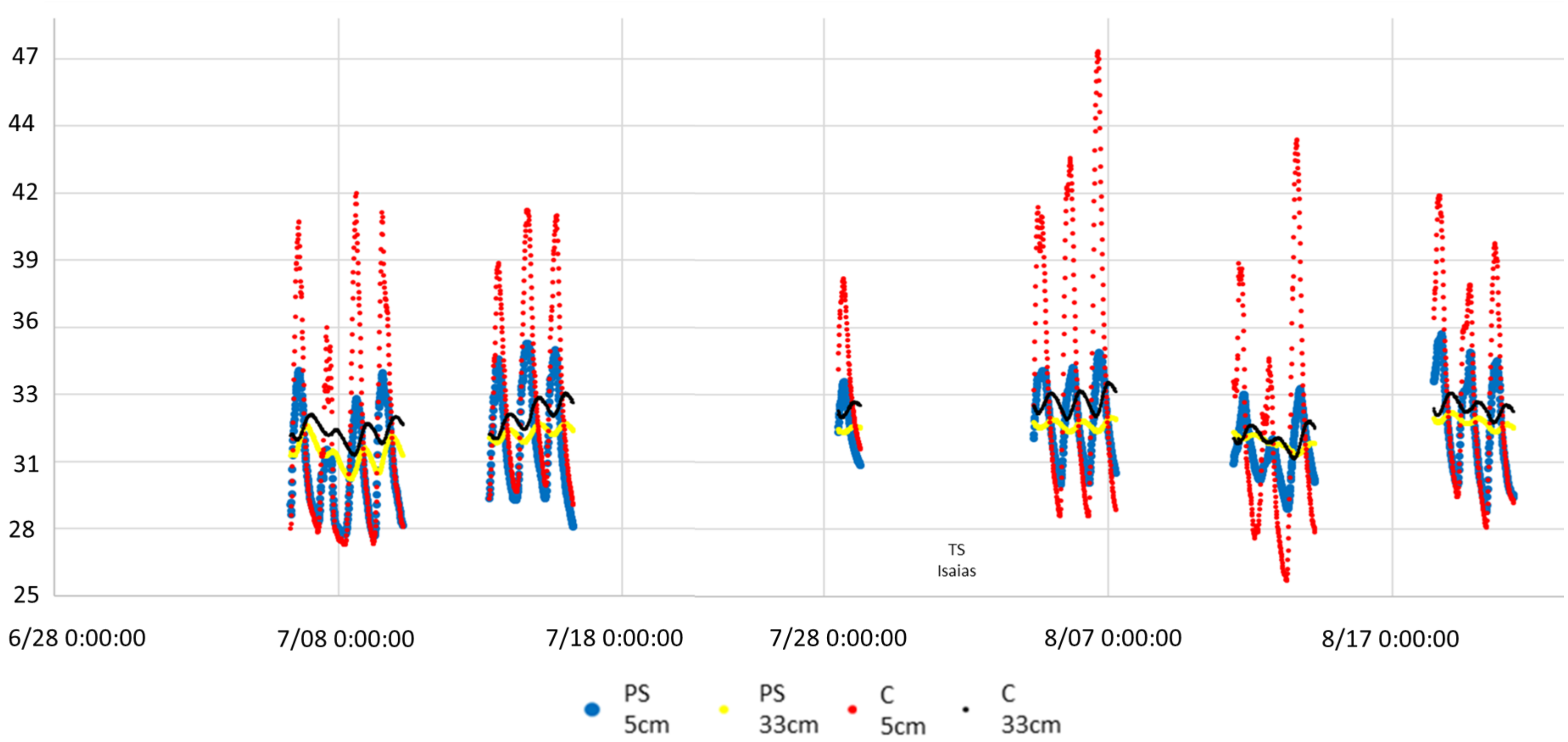


Figure 28: Part shade HOBO temperature series at 5 cm in depth (blue) and 33 cm in depth (yellow) in relation to the control plot temperatures at 5 cm (black) and 33 cm (red). Data was collected from Santa Maria Bay from July 6 - August 21, 2020.

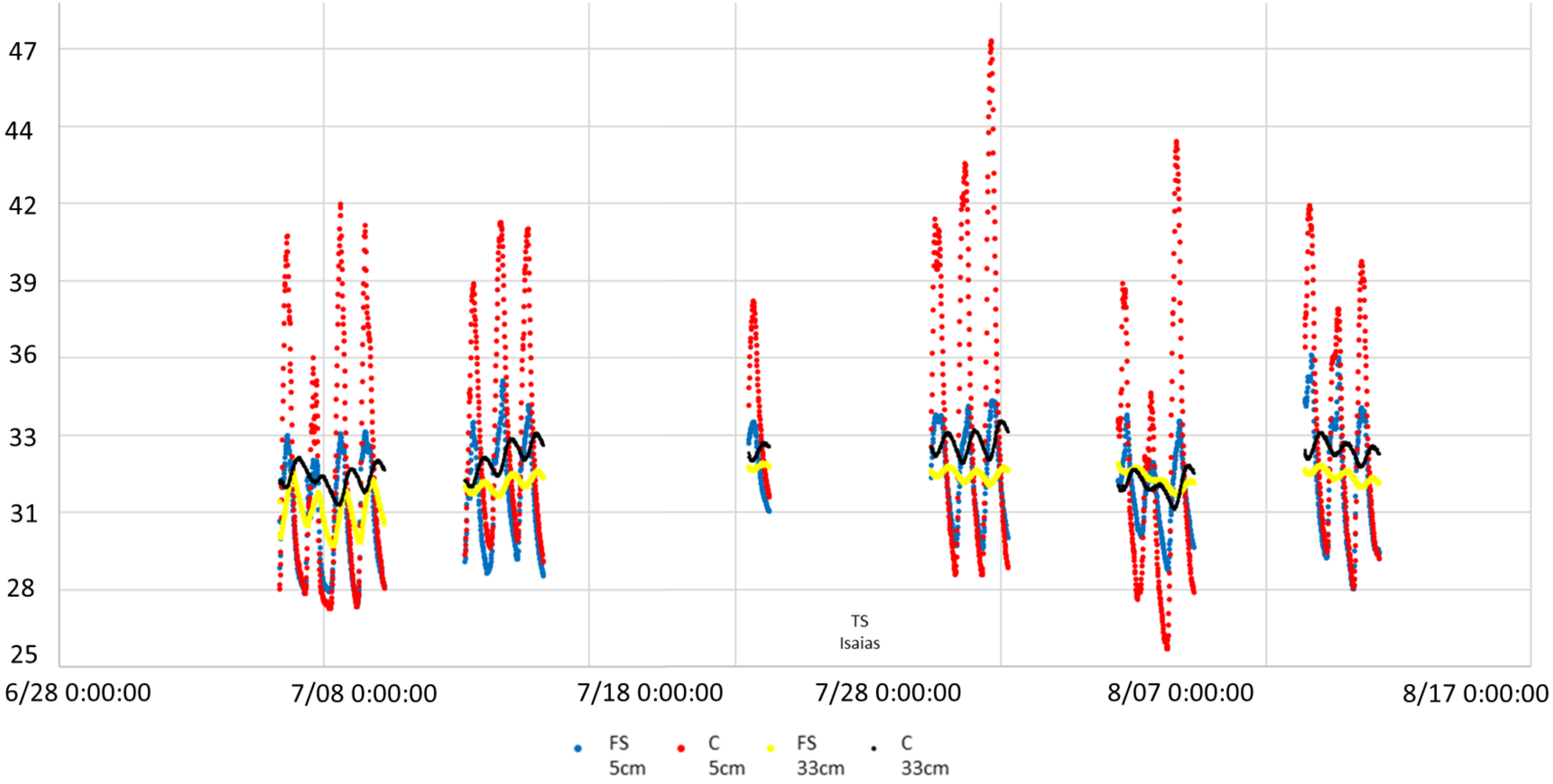


Figure 29: Full shade HOBO logger series at 5 cm in depth (blue) and 33 cm in depth (yellow) compared to the control plot at 5 cm (red) and 33 cm (black). Data was collected from Santa Maria Bay from July 6 - August 21, 2020.

Discussion

Observations

Results indicated that there were no significant effects of beach chairs on burrow abundance, depth, width, or distance to chair leg; these findings were likely due to the limitations in sample size (Figure 25). It was notable that no crab burrows were observed in the control plot over the course of the experiment and all other plots observed some crab burrows, indicating that had more samples been collected, a significant difference between treatments may have been found. Observations at the beginning of the experiment suggested a burrowing preference for the FS and PS condition (week one & two), however, at the end of the experiment, ghost crabs appeared to prefer the NS condition (week six). There is not enough evidence to suggest that this change is due to TS Isaias. TS Isaias occurred weeks after the potential preference for FS or PS, and weeks before the potential preference for the NS condition. Since patterns were observed weeks before or after the storm, it is unlikely that these patterns were due to a storm response. Crustacean population abundances decrease after storm events and take days to weeks to fully recover, however, weeks are needed to recover from major storm events; whereas TS Isaias was not a major storm event (Corte et al., 2017). These observations indicated there is a preference for burrowing under a chair structure, but no preference for condition. Because chair type (NS, PS, & FS) influenced sediment temperature differently, but crabs overall had no clear burrowing preferences under specific chair types, crabs seem to be using the chairs more for their immediate structural benefits over their secondary temperature benefits. However, this relationship changes across crab sizes.

Crab size may influence burrowing behavior around available chair structures on the beach. Burrow width was consistently smaller within the part shade and full shade conditions, while the no shade condition had slightly larger burrows; however, these differences were not significant (Figure 25). This potentially indicates that smaller, younger crabs prefer to burrow under chair conditions with part shade or full shade conditions. This is supported by results from previous studies that found that juvenile crabs were more sensitive to thermal changes compared to older crabs (Berlino et al., 2018). This suggests younger crabs may preferentially burrow under more protected conditions for heightened shelter from the elements and potential predators, or for the increased sediment temperature stability benefits those conditions offer.

Chair conditions may also influence crab burrow depth, however no significant differences among treatments was found (Figure 25). Burrow depth tended to increase with increasing shade (FS > PS > NS). This implies that ghost crabs may be investing more energy in burrow construction under conditions with more protection from burrow threats or greater sediment temperature buffering. Burrowing under the full shade condition and part shade condition for protection purposes was further supported by the average distance to the nearest chair leg. Burrows were located closer to the nearest chair leg under the full shade condition, and farthest from the chair leg under the no shade condition.

Although there were no significant differences found in burrow abundance, width, depth, and distance to chair across treatments, there was a significant effect of chair condition on temperature (Table 25). Temperature at 33cm depth was affected by chair condition. The full shade and part shade conditions were found to be significantly cooler compared to the no shade and control (but not significantly different from each other) at 33 cm in depth. Across all plots temperature varied 2° - 4° at depth between the morning and peak heat of the day (Figures 27, 28, & 29), which was similar to other studies which found similar results indicating ghost crabs burrowed to a depth where there was only a couple degrees fluctuation between the early morning and peak heat of the day (Lucrezi et al., 2008; Strachan et al., 1999; Watson et al., 2018). Cooler temperatures could explain the trends that were observed in burrow abundance width, depth, and distance to chair. If additional samples were collected and a significant difference were found in burrow abundance across chair plots, the temperature difference between the no shade compared to the full shade and part shade condition could indicate a use of structure to mediate sediment temperature by the ghost crab.

Implications of these data could include a potential benefit of urbanization for ghost crabs, or an increased susceptibility to damage. Study results indicated that ghost crabs were using the beach chairs potentially for both physical protection and a temperature refuge. If beach chairs are left in the same place or are stored and not moved, ghost crabs could safely construct burrows under the chairs. However, on high- impact beaches, chairs are constantly moved during the day. So, a burrow may be constructed at night when people are absent but damaged during the day when visitors arrive. Not only do beach chairs potentially attract the ghost crabs, but they attract people as well resulting in an increase in human interaction. People moving or utilizing the same chair as a crab, potentially poses a higher risk to the crab through burrow damage or trampling from beach chair use. It is unclear if ghost crabs would learn to avoid beach chairs when people are absent at night from repeated burrow damage during the day. Over time these interactions and damages to burrows could create a highly susceptible population and decrease ghost crab abundances over time or result in a population adapted to high urbanization.

Research reveals that ghost crabs burrow to escape intense daytime heat (Berlino et al., 2018; Lucrezi et al., 2008; Strachan et al., 1999). The temperature results from this study suggest a climate change adaptation or solution for the ghost crab. Burrows serve as a temperature refuge during the day and a thermal energy source at night, with juvenile crabs expending thermal energy faster compared to large adult crabs (Berlino et al., 2018). This difference in thermal energy usage could suggest a different effect of climate change increasing temperatures by age, with juvenile crabs maintaining activity and daytime scavenging, but needing to return to the burrow more frequently at night, and adult crabs remaining in deep burrows longer during the morning hours, and able to scavenge for longer periods of time at night (Berlino et al., 2018). Increasing temperatures may benefit ghost crabs for a limited window by increasing the thermal energy available, however after the temperature threshold is surpassed, oxygen supply and use becomes more limited and will decrease the metabolic productiveness (Pörtner, 2001). Our study indicated that ghost crab burrows were under 33°C across all plot conditions at 33 cm with just a couple degrees of fluctuation from the peak heat of the day and the nighttime cooler temperatures. This study also confirmed that the variation in temperature from daytime to nighttime did not change across plot types, but the full shade and part shade condition were significantly cooler than the no shade and control conditions. These chairs offer a unique temperature refuge by decreasing high temperatures that lead to a greater heartrate and lower ventilation which could lead to hypoxia (Pörtner, 2001). With the steady increase in temperatures due to climate change we may see an increase in burrowing under human structures as an adaptation to climate change if deeper burrow construction becomes limited due to water table or metabolic energy constraints.

Study Limitations and Future Research Implications

Sample size was a major study limitation, with sample sizes being much smaller than originally anticipated due to exclusion of sampling weeks influenced by conditions outside of the experimental control (i.e., Tropical Storm Isaias and *Sargassum*). Power analysis results indicated we would need approximately 65 more samples than what was collected (n=14) to reach a medium power. General trends in burrowing behavior were observed but were not statistically confirmed likely due to the lack of sufficient samples. Future studies could extend the duration of this experiment to increase the sample size and confirm if a pattern is present. This experiment was conducted from June - August, however the study ended into early August potentially before peak recruitment season. Increasing the duration of the study would have benefitted the sample size limitations, but also would have been able to confirm if juvenile crabs utilize beach chairs more than large adults.

Tropical storm Isaias and *Sargassum* significantly altered the results of this study by altering ghost crab burrowing behavior for over half of the sampling period. After TS Isaias there were no ghost crab burrows in any of the experimental plots, and shortly after, it appeared *Sargassum* located lower on the beach and outside of plots, attracted remaining ghost crabs, post- storm. The observed change in burrowing behavior indicates the need for future research and to build on previous studies that suggest that ghost crabs relocate in response to storms (Hobbs et al. 2008). Ghost crabs are omnivorous scavengers, and appeared to adapt and utilize *Sargassum*, which arrived shortly after the storm. After surveys, ghost crabs were observed burrowing and living in the *Sargassum* along the swash (pers. obs.). Our observations suggest that the lack of data regarding the usage of *Sargassum* by ghost crabs is a data gap deserving of further research. If behavior had not been altered by these unavoidable our sample sizes would have been larger and potentially had been large enough to detect significant differences in abundance, width, depth, or distance to nearest chair leg across experimental plot chair conditions. One method to control for these would be to re-conduct experiments within a lab setting. Within a controlled lab setting, researchers could control the presence or absence of *Sargassum,* and could compare burrowing behavior in similar sandy environments with the only difference being *Sargassum.* Storm effects could be measured by surveying specifically during hurricane season. Studies focused on the recovery after storm events or the effects of *Sargassum* on burrowing behavior would be beneficial for the territory given the increase in storm frequency and increase in *Sargassum*.

The primary objective of this study was to confirm a change in burrowing behavior; it would have been beneficial to conduct this experiment at a high- impact site at the same time to consider additional urbanization effects such as visitor frequency. Conducting the experiment at two sites simultaneously could give insights into the additional urbanization impacts found on high- impact beaches and could confirm if the combination of multiple forms of urbanization increase or decrease beach chair use by ghost crabs. This study captured observational effects of beach chairs, however there is a possibility that ghost crabs on high- impact sites have been conditioned to urbanization and may behave differently compared to crabs on remote beaches where beach chairs have never been introduced in the manner used in this study. This idea is ripe for further investigation.

Chapter 4: Conclusion

Ghost crabs are a popular indicator for ecological stress of sandy beaches due to their predictable and easily-impacted populations, however, most studies are conducted in temperate and subtropical regions resulting in a lack of knowledge about Caribbean beaches and ghost crab populations (Nel et al., 2014). Using environmental characteristics (temperature, mean grain size, log(1/slope), and wave height) with urbanization measurements (i.e. distance to urban center, solid waste on sand, vehicles on sand, beach cleaning, visitor frequency, and buildings on sand) the drivers of ghost crab burrow abundance, width, and depth were assessed to determine the effects of anthropogenic stress on the sandy beach environment for eight St. Thomas beaches. It was confirmed through field observations and modeling, that regardless of slight variations in reflective physical beach morphology, the primary driver of ghost crab population characteristics was urbanization, specifically visitor frequency and beach cleaning practices for these sites. High- impact sites (Magens Bay, Coki Point Beach, Sapphire Beach, and Lindberg Bay), had significantly smaller ghost crab populations, deeper burrows, and larger burrow widths, reflecting the negative impacts that urbanization and tourism has on ghost crab populations across these sites.

All of the high- impact sites had man-made structures and additional equipment for visitors such as beach chairs and umbrellas, with several leaving beach chairs on the beach for prolonged periods of time. Sites such as Lindberg Bay, Sapphire Beach, Magens Bay, Coki Point Beach, Margaritaville, and Bolongo Bay leave individual chairs spread across the beach or in a stack on the beach. The second part of this study investigated the effect of prolonged beach chair exposure on ghost crab burrowing behavior. Observed burrowing behavior suggested an effect of beach chairs on burrowing behavior, however we were unable to statistically confirm these patterns.. The presence of chairs did however, significantly alter sand temperature at burrowing depths, and observations of burrowing behavior indicated that the chairs were potentially being used for additional protection from the elements or predators. Significant differences found in ghost crab populations from urbanization variables, in conjunction with observed behavioral changes from human impact, emphasizes the importance of creating a management plan for beaches within the territory to utilize the ghost crab as an indicator to inform sandy beach ecosystem health and function over time and with changing conditions.

The coastal and marine environment possesses a special cultural value for people who live on St. Thomas. This study provides baseline data on beach morphology, urbanization, and ghost crab populations. At the local scale, establishing a baseline for St. Thomas sandy beach geomorphology and ecology provides a starting point for monitoring sandy beaches and to determine the impacts of urbanization and climate change on these systems. Providing a morphological baseline can also inform management decisions to address specific impacts from storms or other events that would shape the coastline (Vousdoukas et al., 2020). Beach characteristics can be shaped by major storm events through erosion and deposition; by comparing the site-specific profiles created in this study as a baseline, managers can customize recommendations and responses by beaches in response to storm or other events. This study may also serve as motivation for specific urbanization impact studies and considerations by managers. Overall, my results indicate that visitor frequency and beach cleaning should be monitored, but also reflects a potential impact by something as simple as beach chairs, which requires further investigation.

Globally, there is a deficit of beach-related research, and although ghost crabs are a popular ecological indicator, there was still no research conducted within the USVI on this organism until this study. This study provides the first of what will hopefully be many ghost crab-related beach studies for the territory. This research provided a baseline for the USVI and allows other researchers to compare the sandy beach health and morphology around the world with that of the USVI. These results could also inform the impacts of high tourism through the comparisons of the UI values measured in the USVI with sites globally. Research has supported ghost crabs burrowing to escape high temperature fluctuations (Berlino et al., 2018; Lucrezi et al., 2008; Strachan et al., 1999), however, this is the first study reporting temperature changes from beach chairs. This exposes as new knowledge gap between the study of ghost crab ecology and urbanization impacts and is a fruitful, potential avenue for further research.

In light of the threats of climate change, this study provides a unique dataset informing the effect of beach chairs on sediment temperature and the different temperature refuge provided. Although further research is needed to confirm burrowing behavior patterns, previous research supports the variations in sediment surface temperature and deep temperature that were found (Berlino et al., 2018; Lucrezi et al., 2008; Strachan et al., 1999). Additionally, further research on ghost crab metabolic processes indicates that increased temperatures reduce metabolic efficiency, increases heart rate, and increases oxygen demand in crabs (Pörtner, 2001). This suggests that if the chairs do provide a temperature refuge in the face of increased temperatures from climate change, we may see a change in beach chair use in the future, with crabs choosing to burrow closer or underneath these structures. It is unclear from this work whether that will result in positive or negative outcomes for crabs. These results have global implications and suggest potential climate change interventions for sandy beach fauna by providing a temperature refuge from inescapable temperature increases.

Recommended Management Interventions

1. **Increase waste management on beaches**. A primary goal of recreation-focused management includes ensuring a healthy and safe beach for visitors. After comparing the urbanization across sites, one of the primary drivers of variation across high- impact sites was the presence of solid waste. High- impact sites such as Coki Point Beach and Lindberg Bay had higher rates of solid waste (Table 8) that could pose a risk to the health and safety of visitors. Sites such as Magens Bay have multiple locations for waste disposal, making it easy for visitors to discard waste compared to sites with limited overflowing locations.
2. **Regulate beach cleaning practices**. Raking of the beach takes place on Coki Point Beach and Sapphire Beach frequently; with Coki being raked almost daily to smooth the beach surface, and Sapphire being cleaned more frequently when *Sargassum* drifts ashore. There are also limited rake marks observed on Magens Bay. This study identified beach cleaning as a high- impact urbanization variable, suggesting that beach cleaning practices should be monitored. I suggest that raking for the sake of smoothing be limited to only when necessary instead of what appeared to be on a daily basis (pers. obs.). Raking for the removal of *Sargassum* should be limited to only when large amounts accumulate and pose a hazard due to the gases released during decomposition.

3. **Prohibit vehicle access on all beaches.** Currently the VI Code states that vehicle and horse use on highly urbanized sites is prohibited, however this should include all beaches. Restricting vehicle use on all sites will help preserve the natural beach structures such as dunes, protect the ghost crab populations, and protect other endangered species nests.
4. **Change beach chair storage**. It is unclear if there is a significant impact on burrowing behavior, but we did confirm an effect of beach chairs on sediment temperatures. To limit the human alterations and the potential impact on ghost crabs, it would be beneficial to store equipment such as beach chairs within a shed or on a concrete landing near the buildings on high- impact sites.
5. **Establish a long-term ghost crab monitoring program.** Through establishing a citizen science program that monitors select sites (such as sites with high cultural value like Magens Bay and Neltjeberg Bay) over a long period of time, sampling limitations can be address and the fluctuations of ghost crabs over time can be observed. Effects of management actions and storms can be observed to better monitor the ghost crab populations.

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