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To Feed or Not to Feed: Examining the Effects of Provisioning Tourism on Nurse Sharks in Caye Caulker, Belize

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TO FEED OR NOT TO FEED: EXAMINING THE EFFECTS OF PROVISIONING TOURISM ON NURSE SHARKS (*Ginglymostoma cirratum)* AT A POPULAR PROVISIONING SITE IN CAYE CAULKER, BELIZE

By

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Abstract

Wildlife tourism is increasing in popularity around the world, creating the need to understand alterations in animal behavior and spatial distributions that may occur due to associated anthropogenic disturbances. Nurse sharks (*Ginglymostoma cirratum*, Bonnaterre 1788) are commonly used for wildlife tourism within the Caye Caulker Marine Reserve in Belize. Shark and Ray Village (SRV) is a site within the reserve where nurse sharks are consistently fed by tour/snorkel boats to create an interactive experience with tourists, termed provisioning tourism. Prior to this experiment, no studies had been conducted in SRV to evaluate the impact of provisioning tourism (tourism that provides a food reward to participating animals) on this nurse shark population. The purpose of this study was to assess and quantify the impacts provisioning tourism activities have on the behavior, habituation, and abundance of resident nurse sharks in SRV. In-water video surveys were conducted to examine the effects of provisioning and boat activities on the frequency of five shark behavior types: milling, active swimming, conspecific aggression, interspecific aggression, and shark-initiated human interaction. Underwater cameras were placed within SRV to monitor and determine the extent of habituation displayed by the nurse shark population. The maximum number of individual nurse sharks seen within one frame (MaxN), was compared between SRV and control sites outside of SRV. Results from this study suggest that the nurse sharks are very responsive to the presence of boats, displaying signs of habituation to tour boats and ultimately the tourism operations. The abundance of nurse sharks in SRV was notably and significantly greater than abundance in control sites, suggesting a significant change in habitat use at the site. The conclusions made from this study will be presented to the Caye Caulker Fisheries Department to advise future regulations and management techniques.

Keywords: wildlife, tourism, Belize, biology, behavior, feeding, ecotourism, sharks, conservation, recreation

Introduction

Our planet's oceans are experiencing a global decline in shark populations. Many species are threatened with overexploitation due to high demand for fins and meat, habitat loss from development and various effects of climate change (Roff et al. 2018; MacNeil et al. 2020). Sharks are important contributors to the health of ocean ecosystems by maintaining balance in their prey populations. Declines in shark populations could present ecological consequences such as trophic cascades in the ocean (Heithaus et al. 2008), highlighting the importance of studying how human activities affect shark populations for better management and conservation of species.

Declining shark populations and the threat of climate change on our oceans leads to the desire in tourists to experience or interact with these animals and ecosystems while they are extant (Lemelin et al. 2010). Shark tourism involving snorkeling and diving with sharks is increasing in popularity around the world (Gallagher & Hammerschlag 2011; Abrantes et al. 2018; Richards et al. 2015), creating the need to understand changes in animal behavior and spatial distribution that may occur due to associated tourism-related anthropogenic disturbances. Sharks are target animals in many marine wildlife tourism activities at least in part because of their status as top predators in popular imagination (Clua et al. 2010). Some species most often exploited for wildlife tourism purposes include whale sharks (*Rhincodon typus*), Caribbean reef sharks (*Carcharhinus perizi*), bull sharks (*Carcharhinus leucas*), scalloped hammerhead sharks (*Sphyrna lewini*), and nurse sharks (Brunnschweller et al. 2014; Gallagher & Hammerschlag 2011; Haskell et al. 2015). Although some sharks are considered top predators, many species are naturally shy and elusive in the presence of humans (Bres 1993). Many species of sharks, such as bull sharks and nurse sharks, are more active nocturnally, making daytime sightings more difficult (Bres 1993). Because of this trait, provisioning (i.e., the act of using bait to attract wildlife) is often required to lure sharks into dense aggregations for tourists hoping to observe them during the day (Clua et al. 2010; Laroche et al. 2007). In Belize, shark provisioning is conducted within the Caye Caulker Marine Reserve (CCMR) in an area named Shark Ray Village (SRV), where nurse sharks are the primary target species. While there are many shark species present in Belizean waters (e.g. reef, hammerhead, and bull sharks) nurse sharks are one of the few legally protected shark species due to their economic value for tourism (Gallagher & Hammerschlag 2011).

There is a scarcity of knowledge in regard to the impacts of provisioning tourism on sharks (Healy et al. 2020). Around 16% of global shark tourism activities occur in the Greater Caribbean region (Gallagher & Hammerschlag 2011), however there is a lack of shark tourism studies that have been carried out in this region (Gallagher et al. 2015). Within the shark tourism studies that have been conducted, most focus on socio-economics (e.g. Davis et al. 1997, Smith et al. 2009, Du Preez et al. 2012) and biological effects on target species (e.g. Laroche et al. 2007, Clua et al. 2010, Bruce and Bradford 2013). There are few studies (e.g. Bradley et al. 2017, Brena et al. 2015, Araujo et al. 2014) that focus on shark behavior and ecology. Examining the environmental and biological impacts of feeding sharks for tourism purposes is also crucial for the conservation of target species. This will help determine any short- and long-term effects that could potentially harm this specific population, which may necessitate improved management to aid in future shark conservation efforts. The purpose of this study was to understand and identify effects of provisioning tourism on nurse sharks, in hopes of providing better management recommendations for tourism operators.

Although considered a species exploited by shark tourism practices, there have been no studies involving nurse sharks and shark tourism (Gallagher et al. 2015), including in the provisioning setting at Caye Caulker Marine Reserve. Nurse sharks are physiologically and behaviorally different from many other shark species used for provisioning tourism, making it difficult to draw conclusions about potential effects based on studies of other species. The Western Atlantic population of nurse sharks is listed as Data Deficient by the IUCN, further emphasizing that there is a knowledge gap with this species. It is essential to collect data on how this specific species responds to human disturbance, such as provisioning, in order to fill the knowledge gap and enhance conservation management efforts.

Marine Tourism

Marine tourism encompasses several different sectors within the tourism industry. There remains debate on the universal definition, but marine tourism can be defined as any form of travel and activity in a marine environment (Sakellariadou 2014). Marine tourism includes water-based activities such as recreational fishing, snorkeling, SCUBA diving and whale watching (Sakellariadou 2014). Within marine tourism there is marine wildlife tourism, which focuses more on animal interaction. Marine wildlife tourism includes non-consumptive activities that allow tourists to interact with free-ranging wildlife (Higham & Lück 2008). These interactions can include feeding, swimming with, observing and photographing marine wildlife. There is still discussion as to whether marine tourism is explicitly damaging or beneficial to targeted marine wildlife, and conservation outcomes are likely to be highly context dependent (Krüger 2005; Macdonald et al. 2017). However, there have been some positive and negative outcomes presented throughout the scientific literature (e.g. Semeniuk & Rothley 2008, Sakellariadou 2014).

The benefits of marine tourism are seen in local Belizean communities that directly gain from tourist activities. Belize contains rich and biodiverse ecosystems, such as mangrove estuaries, seagrass beds and coral reef ecosystems. Belize also contains a large part of the Mesoamerican Barrier Reef system, the second largest barrier reef in the world. It is a biodiversity hotspot for fishes, marine mammals, elasmobranchs, and marine turtles (Palomares & Pauly 2011).

The main tourist attractions in Belize are snorkel or SCUBA tours and other marine-life encounters, making tourism an important industry in Belize (Cisneros-Montemayor et al. 2013). Further emphasizing its importance, approximately 156,180 visitors participate in recreational marine ecotourism activities in Belize per year, generating around US$183 million annually (Cisneros-Montemayor et al. 2013). Revenue generated from this industry can provide jobs for the local communities, increasing the standards of living and generating economic opportunities (Cisneros-Montemayor et al. 2013). Other benefits from marine tourism include increased awareness of problems facing marine environments, as revenue can provide funding for local research and conservation projects, creating an indirect positive effect on the marine environment (Sakellariadou 2014; Vianna et al. 2018).

There are some potential negative effects of marine tourism on ecosystems and wildlife; unless sustainably practiced, marine tourism can result in physical damage to the natural environment and harm to the animals that live in those environments (e.g. Farrell & Marion 2001; Diedrich 2007; Haskell et al. 2015). For example, boats with motors may cause physical damage (e.g. propeller strikes) or disrupt movement behavior of marine mammals and other marine megafauna (e.g. altering foraging behavior) (Sakellariadou 2014; Meissner et al. 2015). Southern stingrays (*Hypanus americanus*) in a snorkel-based provisioning site named Stingray City, and whale sharks in the Philippines were found to have injuries from boat propellers on their bodies as a result of heavy boat traffic in high tourism areas (Semeniuk & Rothley 2008; Araujo et al. 2014). Snorkelers and divers can also represent a hazard to coral reefs that are sensitive to physical touch or mechanical damage from fin kicks (Razak et al. 2016). Frequent presence of humans can enhance pressure on the environment and animals, causing altered behavior (Clua et al. 2010; Corcoran et al. 2013). In a study conducted in the Galapagos and Malpelo islands, various species of sharks (including whale sharks, silky sharks (*Carcharhinus falciformis*), and scalloped hammerhead sharks) showed strong behavioral responses, such as evasion, to SCUBA divers' behavior. These divers exhibited different types of behavior that is typical of tourists, including flash photography, sudden movements, noise, and directly approaching the sharks (Cubero-Pardo et al. 2011). Increased regulation of tourist behavior has been a suggested approach to combating the negative effects of marine tourism on wildlife (Smith et al. 2010; Barker et al. 2011; Smith et al. 2014).

Provisioning Tourism

The impacts of provisioning tourism on both terrestrial and marine species remains a controversial topic, with debate on the extent of harm or benefits it can produce and how it can be managed (Murray et al. 2016). Concerning benefits, provisioning has been seen as a useful conservation tool in helping to recover a declining population of wild birds (Jones et al. 1995). In contrast, provisioning has been shown to increase pathogen exposure and transmission between provisioned hosts (Becker & Hall 2014). Some provisioned animals have shown no evidence of being behaviorally affected by the practice (e.g. Laroche et al. 2007).

Shark provisioning tourism (SPT) is increasing in popularity around the world as a marine recreational activity (Gallagher & Hammerschlag 2011). Sharks are popular in tourism due to their reputation as "eating machines" portrayed in the popular media and the resulting presumed potential for aggressive behavior (Bres 1993). However, sharks naturally tend to avoid humans in the wild, as humans may be perceived as a threat or as potential predators (Semeniuk & Rothley 2008). Because of this elusive behavior, it may be difficult to observe these animals in natural settings (Clua et al. 2010), and so provisioning is used to attract animals for close tourism-related encounters and photo opportunities (Brunnschweiler et al. 2014; Richards et al. 2015).

Studies that have examined the various effects of provisioning on sharks and rays have identified some negative effects on species resulting from tourism activity, such as habituation to the presence of divers leading to an association of divers with food, (Richards et al. 2015) and decreases in health and fitness (Semeniuk & Rothley 2008). Concerning negative effects of SPT are the potential to alter behavior and cause adverse effects on sharks' health and body condition (Laroche et al. 2007). Provisioning tourism can cause habituation, which is an unnatural response of animals to repeated stimuli that causes them to ignore their natural flight reaction to humans and predictably aggregate in an area (Knight 2009). This leads to dense aggregations of sharks and rays to a specific area. Negative effects of very dense populations have been reported in southern stingray populations in Stingray City (Semeniuk & Rothley 2008). This species is typically solitary, but individuals in this provisioned population are frequently seen in high densities with diminished body condition, fitness, and health compared to individuals that live outside of Stingray City (Semeniuk & Rothley 2008). A high density of these animals in one area while provisioning could lead to more frequent incidents of conspecific aggression (Clua et al. 2010) and the transfer of disease and parasites between individuals (Semeniuk & Rothley 2008). The Stingray City population showed a higher percentage of conspecific bite marks and ectodermal parasites, as well as poor body condition (Semeniuk & Rothley 2008).

Shark provisioning tourism can also cause sharks to aggregate and show site fidelity to the provisioning site that may otherwise be unsuitable habitat (Brunnschweiler et al. 2014), decreasing mobility and increasing the risks of inbreeding resulting in a decrease in genetic variation (Clua et al. 2010). Other studies have shown sharks may become conditioned to the presence of boats (Laroche et al. 2007), deviate from their natural food sources (Abrantes et al. 2018), and that provisioning may increase the risk of shark bites for tourists (Clua 2018). A risk to tourist's safety can threaten the safety of shark populations in the area. Tourism is economically important in many places, and any risks associated with sharks could reduce tolerance for sharks and result in culling (e.g. Burns & Howard 2003). Deviating from natural food sources could result in health- and fitness-related issues in sharks (Abrantes et al. 2018), especially if provisioned food becomes the main part of their diets. A nine-year study on seven species of sharks at a provisioning site in Fiji found that species composition changed over the years, suggesting that long-term effects of provisioning could lead to some species outcompeting others (Brunnschweiler et al. 2014). There is also evidence that this practice may have dietary effects on non-target species present when sharks are fed (Drew & McKeon 2019; Meyer et al. 2020). More long-term studies are needed in order to determine whether the effects of shark provisioning tourism can have ecosystem-level consequences such as trophic cascades.

The proposed positive impacts from SPT are minimal and include a perceived benefit for consumers and researchers, with minimal benefits to the target species (Sakellariadou 2014). It is an important part of the socio-economics in some communities (Gallagher & Hammerschlag 2011). Benefits have been seen in stingrays in Stingray City, where provisioned stingrays were larger in body size compared to stingrays outside of this tourist site (Semeniuk & Rothley 2008). This could lead to an increase in growth and reproduction rates due to the guaranteed and large supply of food. The area provided by wildlife tourism provides an ideal space for observation, data collection and ecological research for scientists in the field (Gallagher & Hammerschlag 2011). Additionally, tourism has played a role in justifying the establishment of marine reserves to sustain healthy shark populations (Gallagher & Hammerschlag 2011).

Marine reserves, such as the Caye Caulker Marine Reserve (CCMR) that SRV is located in, are very beneficial to the conservation of shark populations (Bond et al. 2017). Acoustic telemetry and Baited Remote Underwater Video (BRUV) surveys show that measures of shark population density are positively affected by implementation of marine reserves (Bond et al. 2012). This may be due to reduced fishing pressure on the shark population in that area or reduced fishing pressure on prey species and improvements in ecosystem health (Bond et al. 2012). Although there is still a lack of information on this topic, tourism within marine reserves is potentially beneficial to shark populations due to the protections and regulations in place, and the economic valuation of shark tourism may drive the creation of reserves (e.g., in the Bahamas; Gallagher & Hammerschlag 2011).

Study Species

Nurse Sharks, *Ginglymostoma cirratum*

Nurse sharks are a species of shark commonly observed in the wildlife ecotourism industry within the CCMR in Belize (McRae 2004). This species resides inshore and is found in subtropical and tropical Atlantic waters, as well as along the western coast of the Americas (Castro 2000). Although listed as data deficient by the IUCN (2019), nurse sharks are abundant in parts of the Western Atlantic and can easily be found in shallow tropical waters (Castro 2000). They are evaluated as data deficient largely due to a lack of information on migratory behavior and lack of data on Eastern Atlantic and Pacific populations (Rosa et al. 2006). The Western Atlantic population is considered to be near-threatened (Rosa et al. 2006). This species of shark is not known to swim long distances and tend to stay within the same area (Compagno 2001). Nurse sharks are mainly a nocturnal benthic species, commonly found resting underneath large rocks and reef ledges during the day and are usually more active and hunt at night (Compagno 2001). These sharks have a specialized ventilation method called buccal pumping that allows them to actively pump water over their gills while resting on the seafloor. With the use of buccal pumping and their specialized crushing teeth, nurse sharks feed mainly on crustaceans such as crab and lobster, as well as small teleosts and other shellfish (Compagno 2001). In Belize, nurse sharks are one of the most common species of shark, abundantly found in shallow lagoons around the islands (Rosa et al. 2006; Pikitch et al. 2005). Nurse sharks, like other marine predators, regulate prey communities through predation and by influencing prey behavior (Abrantes et al. 2018). These predators are considered vital to the health of coral reef ecosystems in Belizean waters due to their ecological role as a predator sustaining prey populations in reef community structure (Heupel et al. 2014).

The greatest threat to nurse sharks is inshore fishing industries and recreational fishing (Rosa et al. 2006). They are caught accidentally and intentionally on long lines and gill nets and are easy targets when fishing, and the site-fidelity seen in this species makes them vulnerable to localized overexploitation (Rosa et al. 2006). Nurse sharks are exploited mainly for their skin, which can be made into leather because of its thickness (Compagno 2001). Through personal communication with the Caye Caulker Fisheries Department, it was discovered that in 2009 nurse sharks in Caye Caulker were being heavily fished and exploited for their skin and meat by fishermen. This practice severely hurt nurse shark populations in tourism areas like SRV, which lead to a decline in the number of tourists (Ali Casino, personal communication). In response to concern shown by tourists, nurse sharks became protected under Belizean law in 2011 (Fisheries-Statutory Instrument No. 78 of 2011), preventing the extraction and killing of nurse sharks (Regulation 26:03). It is important to improve and build upon conservation strategies regarding this species due to its frequent involvement and interaction with tourism.

Research Questions & Hypotheses

The goal of this study was to characterize the possible impacts of provisioning tourism on nurse sharks at a popular provisioning site, Shark Ray Village in Caye Caulker, Belize, by measuring behavior changes and habituation. The five behaviors measured were milling, active swimming, conspecific aggression, interspecific aggression, and shark-initiated human interaction. The following questions were addressed:

1. Do provisioning activities affect the behaviors of nurse sharks in Shark Ray Village?

   Hypothesis: There is a difference in the frequency of behaviors depending on the presence or absence of provisioning.

   H_0: There is no significant difference in the frequency of nurse shark behaviors between the presence and absence of provisioning.

   H_A: There is a significant difference in the frequency of nurse shark behaviors between the presence and absence of provisioning.

2. Does boat presence affect the behaviors of nurse sharks in Shark Ray Village?

   Hypothesis: There is a difference in the frequency of behavior depending on the presence or absence of boats.

H_0: There is no significant difference in the frequency of behaviors between the presence and absence of boats.

H_A: There is a significant difference in the frequency of behaviors between the presence and absence of boats.

3. Do nurse sharks show habituation to tour boats in Shark Ray Village?

   Hypothesis: The number of nurse sharks will differ between the presence and absence of boats in SRV.

   H_0: The number of nurse sharks will be significantly different between the presence and absence of boats.

   H_A: The number of nurse sharks will not be significantly different between the presence and absence of boats.

4. Do the number of nurse sharks present differ between SRV and areas outside of SRV?

   Hypothesis: Nurse sharks will be more abundant in SRV than outside of SRV.

   H_0: Nurse shark numbers will not differ between the locations.

   H_A: The number of nurse sharks will be greater in SRV than outside of SRV.

Methods

In this study, I examined the effects of provisioning tourism on nurse sharks in SRV using snorkel surveys and underwater camera deployments to observe and record shark behavior and abundance. The methods of this study are comparable to the methods of Semeniuk & Rothley (2008), and Barker et al. (2011), in which they assessed the behavioral responses of southern stingrays and grey nurse sharks to provisioning and diver tourism. From July to September 2019, nurse sharks in SRV were observed by video recording behavior in 1-hour surveys during provisioning and non-provisioning periods in order to understand animal behavior and abundance in response to provisioning. Abundance of nurse sharks was measured through the comparison of the maximum number of nurse sharks within a frame (MaxN) between SRV and control sites. Frequencies of five behaviors exhibited by sharks were recorded through video surveys, including shark-human interaction, conspecific and intraspecific aggression, and swimming pattern behaviors (active swimming or milling). These were behaviors of focus because they have been previously used to assess the impacts of tourism and diver interactions on shark behavior (Martin 2007; Smith et al. 2010, 2014). Descriptions of each behavior can be found in Table 1. Habituation was assessed by comparing nurse shark abundance before and after tour boats arrived at the provisioning site.

Study Area

This study was done in collaboration with the United Kingdom based volunteer organization, Frontier. Field research was conducted at the Frontier Belize Marine Conservation and Diving base camp, located on the north end of Caye Caulker, Belize (Figure 1). The Frontier Belize program provided housing at their base camp, research support and all necessary boat travel to study sites. The island of Caye Caulker (Figure 1) is one of many cayes along the coast of Belize. It is a small limestone southwestern Caribbean island approximately twelve miles offshore of the coast of Belize and 20 miles from its capital, Belize City. The island sits approximately one mile west of the second largest barrier reef in the world, the Mesoamerican Barrier Reef. Caye Caulker contains a variety of reef ecosystems such as fringing reefs, offshore atolls and the Barrier Reef itself (Gibson et al. 1998). These habitats are important for many threatened species including marine turtles, marine mammals and large predatory animals (IUCN, WHO 2017). The lagoons, seagrass and algae beds surrounding Caye Caulker are important nursery areas and foraging grounds for many different species (McRae 2004).

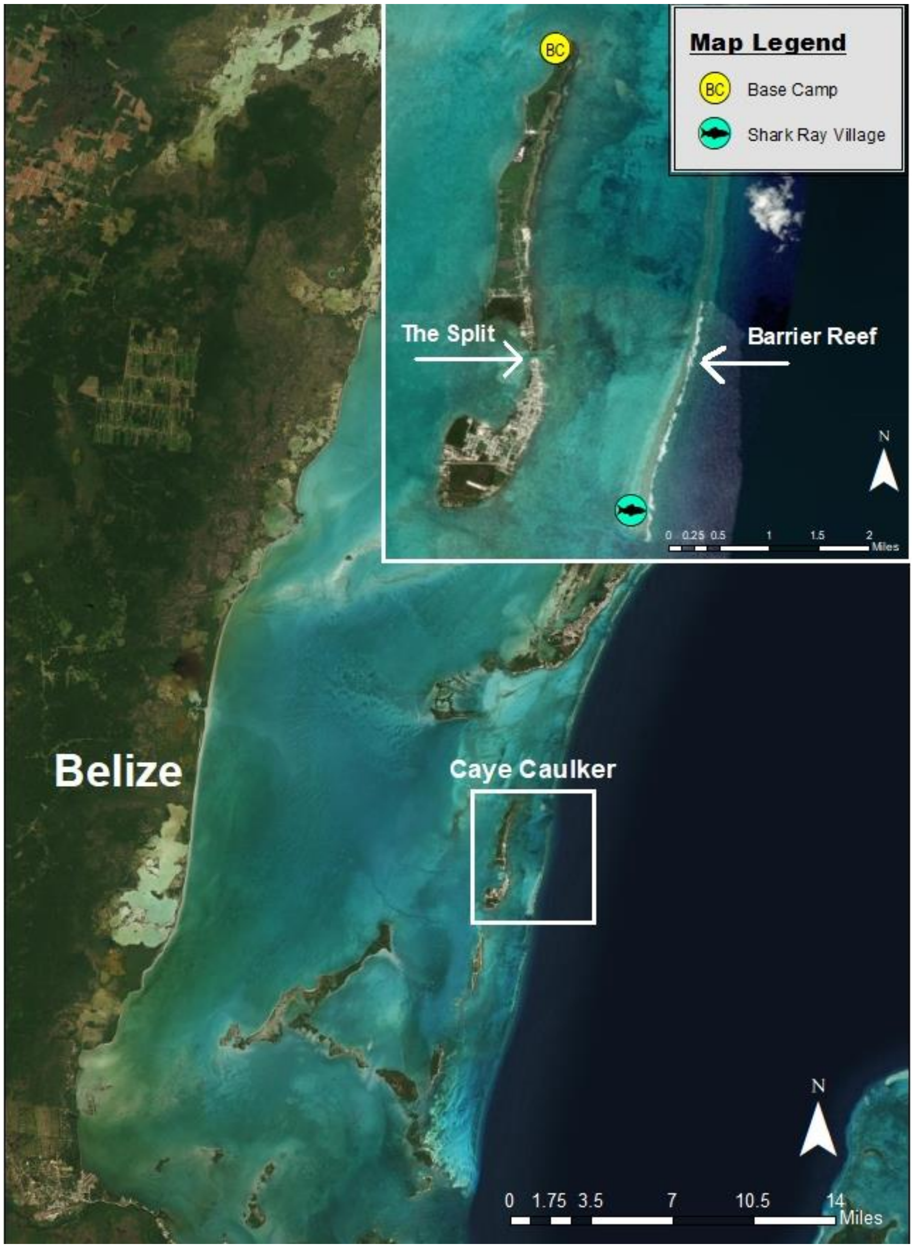

Figure 1. A map image of Caye Caulker in relation to the Belize mainland. The inset map displays the location of housing (base camp), the channel that splits the island into North and South island (The Split), the main study site (SRV), and the Belize Barrier Reef.

The waters surrounding Caye Caulker encompass CCMR (Figure 2). The marine reserve, established in April 1998, is a part of the Belize Barrier Reef system and encompasses over 9,000 acres of the Mesoamerican Barrier Reef (Cho 2005). According to the IUCN (2018), CCMR is a category VI protected area, meaning that the goal of this reserve is to sustainably protect and use its natural resources. This coastal marine area includes a diverse group of ecosystems including mangrove, seagrass and coral habitats (McRae 2004). The areas within the marine reserve support a wide variety of species that are important for commercial fisheries and as tourist attractions (Gibson et al. 1998). CCMR is regulated through zonation (Figure 2) in order to limit the spatial extent of certain recreational activities such as fishing and tourism (McRae 2004). These zones include preservation, conservation and general use zones (McRae 2004). Licensed fishing is allowed in the general use zone, while the preservation zone prohibits all recreational activities including fishing (McRae 2004). The conservation zone is where controlled marine life encounters are allowed to occur, while prohibiting fishing (McRae 2004). These zones were designed to protect the Belizean marine environment, reduce human disturbance and rebuild and support sustainable fish populations (McRae 2004). The Caye Caulker Fisheries Department oversees activities within the zones through daily patrols within the reserve. Located at the northeastern end of the conservation zone is SRV, a popular provisioning site for snorkel tourists and the primary site assessed in this study (Figure 2). The site is located right off of the Barrier Reef, and is marked by six buoys set up in a semi-circle formation approximately 25 meters apart. This site has been a provisioning site for approximately 15 years (Ali Casino, personal communication) and was created when tourism operators intentionally baited the water in that area in order to create a new tourist attraction. The area is made up of very shallow water (less than 2 meters in average depth), consisting primarily of seagrass beds and small patch reefs.

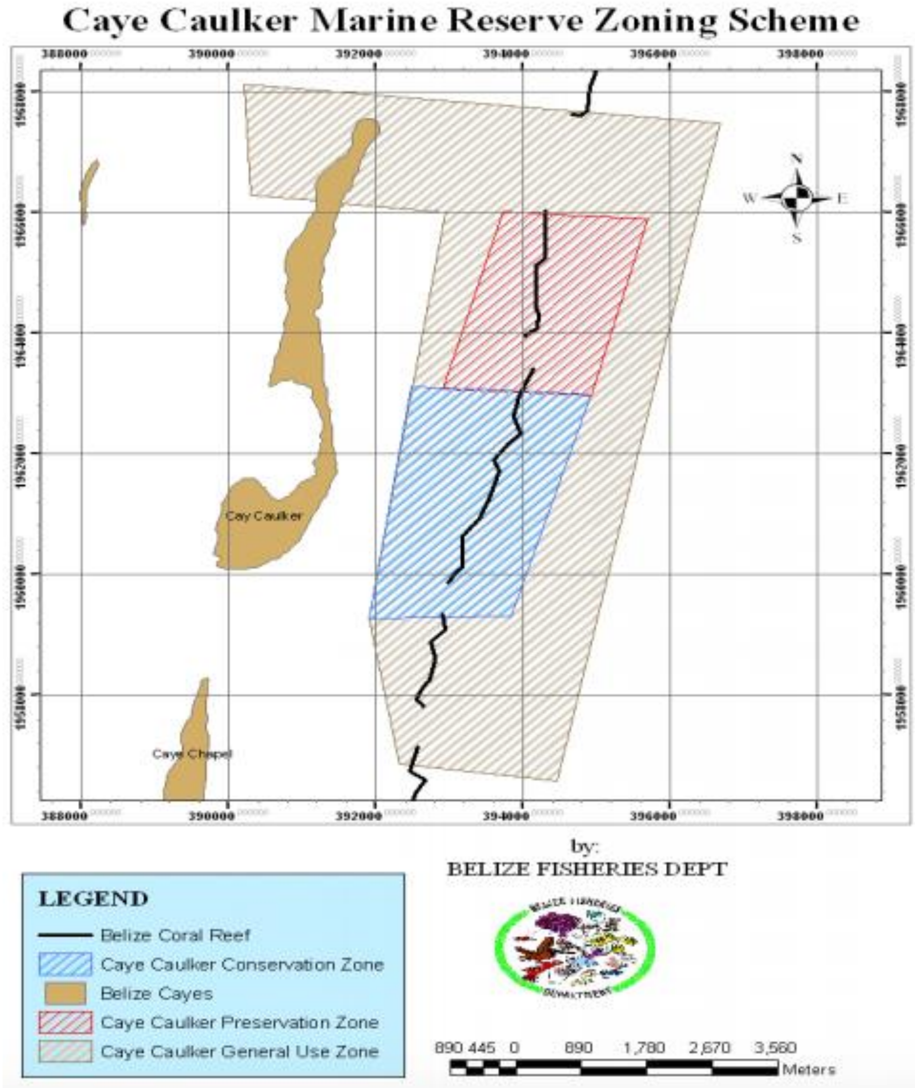

Figure 2. A map of the Caye Caulker Marine Reserve zones provided by the Belize Fisheries Department.

Data Collection

Field data in Caye Caulker was collected from July to September 2019, to increase our understanding of behavior, habituation and abundance of nurse sharks in SRV. The staff of the Frontier Belize program provided housing and assisted with travel and field data. Volunteer surveyors consisted of mostly college-aged gap year students looking for marine field research experience through the Frontier Belize program. All volunteers were thoroughly trained in the sampling methods. They did not participate in regular sampling until they received approval from the principal investigator after completion of all training requirements.

Behavior Study

Behavior data on nurse sharks within Shark Ray Village was collected through the review of video surveys taken during varied tourism hours. Five different behaviors (Table 1) were observed and recorded over the course of a one-hour survey (n=30). Initially, the use of real-time in-water surveys was intended as the main source of data. However, these data were deemed insufficient in accounting for some confounding factors such as inter-observer differences in behavior categorization, and the inability to accurately count sharks during an activity. GoPro® HERO8 cameras were used to conduct surveys. Surveyors worked in groups of two, stationed in separate sections of SRV far enough away from each other that they were not recording the same events and sharks. Survey start-time commenced after the boat captain blew a whistle and all observers were in their respective areas.

While reviewing video from each survey, the frequency of each behavior observed was recorded using the two-minute scanning observational method (Smith et al. 2010). Two minute-scans have been used in observation-based studies as a suitable length of time to accurately record while observing, requiring a low level of effort necessary to capture variation in behaviors as opposed to 1-minute scans (Altmann 1974; Smith et al. 2010). Within each two-minute block, the frequency of behaviors seen was recorded by tallying in the corresponding blocks on survey sheets. Frequency refers to the number of times each behavior was seen within the two-minute block. Since there was no way of distinguishing each shark individually, this method was used to reduce repeated counts of the same shark and put all focus onto overall behaviors. In addition to behavior frequencies, the occurrence and duration of activity were recorded during video review.

The activities recorded included boats feeding, no feeding and no boats. The maximum number of individual nurse sharks within a frame (MaxN) was documented during each of the three provisioning and boating activities. While behavior surveys were being conducted in the water, the boat captain documented tourism activity variables. These variables included the total number of boats, total number of tourists, and the number of boats participating in feeding over the course of the one-hour survey (Table 2). The captain additionally recorded the maximum number of sharks they could see at once when the survey commenced. The rate of tourism activity at the site varied each day due to weather and overall tourist activity on the island. The extent of activity was categorized as either “high” or “low” depending on the amount of boat traffic within SRV. A day was deemed “high” when four or more boats tied off to SRV throughout the entire one-hour survey, and “low” when fewer than 4 boats visited the site during the survey. Other environmental factors such as wind speed and wave height were acquired from the Weather Bug website.

Table 1. Descriptions of each behavior variable.

Behavior	**Definition**
Milling	Low activity, slow movement, frequent directional changes (Smith et al. 2010)
Active Swimming	Swimming in one general direction with no directional change for at least 10 seconds; faster swimming than seen in milling (Smith et al. 2010)
Conspecific Aggression	Any antagonistic behavior between nurse sharks such as biting, pushing and shoving (Martin 2007)
Interspecific Aggression	Any antagonistic behavior between nurse sharks and any other animal such as biting, pushing and shoving (Martin 2007)
Shark-Initiated Human Interaction	Nurse shark actively swims towards a human and either makes physical contact or comes within one foot of the human

Table 2. Survey data displaying values of each tourism activity variable for each survey.

Survey #	Rate of Tourism	Total Boats during sampling period	Total Tourists during survey period	Total Boats Feeding
1	High	5	36	2
2	High	5	36	2
3	High	5	36	2
4	Low	4	37	4
5	High	4	153	4
6	Low	5	35	2
7	Low	6	33	4
8	Low	3	51	2
9	Low	1	7	0
10	High	3	24	3
11	Low	2	4	1
12	High	3	12	2
13	High	3	17	1
14	High	2	9	0
15	Low	3	4	1
16	High	6	65	3
17	High	7	140	4
18	Low	3	16	2
19	Low	3	16	2
20	High	6	65	3
21	Low	3	20	2
22	Low	3	7	0
23	Low	3	7	0
24	Low	3	7	0
25	Low	3	8	0
26	Low	3	8	0
27	Low	3	8	0
28	High	5	30	1
29	High	5	30	1
30	High	5	30	1

Habituation Study

Habituation surveys were conducted by assessing the number of nurse sharks in SRV prior to tourism boats entering Shark Ray Village and comparing the MaxN between boats being present or absent. Tour boats normally first arrived to SRV in the morning, around 0930. In order to reduce the confounding factor of early boat presence, surveyors tied their boat off to a nearby reef approximately 100 meters from SRV and swam the set-up equipment to the site. A GoPro camera was mounted to a tripod and set up in the center of SRV (Figure 3). During each deployment the camera faced the direction of the Barrier Reef (east). A BRUV (Baited Remote Underwater Video) was not considered suitable for this project due to how conditioned to the presence of food the nurse sharks and other marine animals in the vicinity were. The camera was set up at least thirty minutes prior to the first boat arriving in SRV for a total of 8 deployments. After deployment, videos were reviewed, and the number of nurse sharks documented within five-minute intervals was recorded leading up to the arrival of the first tour boat. To reduce any confounding factors human presence may have produced, a five-minute control was given after the camera began recording to give surveyors time to leave the area. Additionally, since this particular data set was so small, data from the behavior surveys was used as a secondary and more reliable tool to assess habituation. The MaxN of nurse sharks was recorded during activities when boats were present (boats feeding and no feeding) and compared to times when no boats were present.

Figure 3. An image of the underwater camera set up during habituation surveys.

The abundance of nurse sharks in Shark Ray Village was compared to that in a total of six different control sites (Figure 4). Some control sites mimicked the habitat in SRV, containing seagrass beds and patch reefs (Table 3). Other control sites consisted of coral gardens in shallow water (<10m), environments considered ideal for nurse sharks (Pikitch et al. 2005). A GoPro camera mounted on a tripod was deployed for one hour in SRV and in each of the control sites. After deployment, videos were reviewed and the MaxN for nurse sharks at each site was recorded.

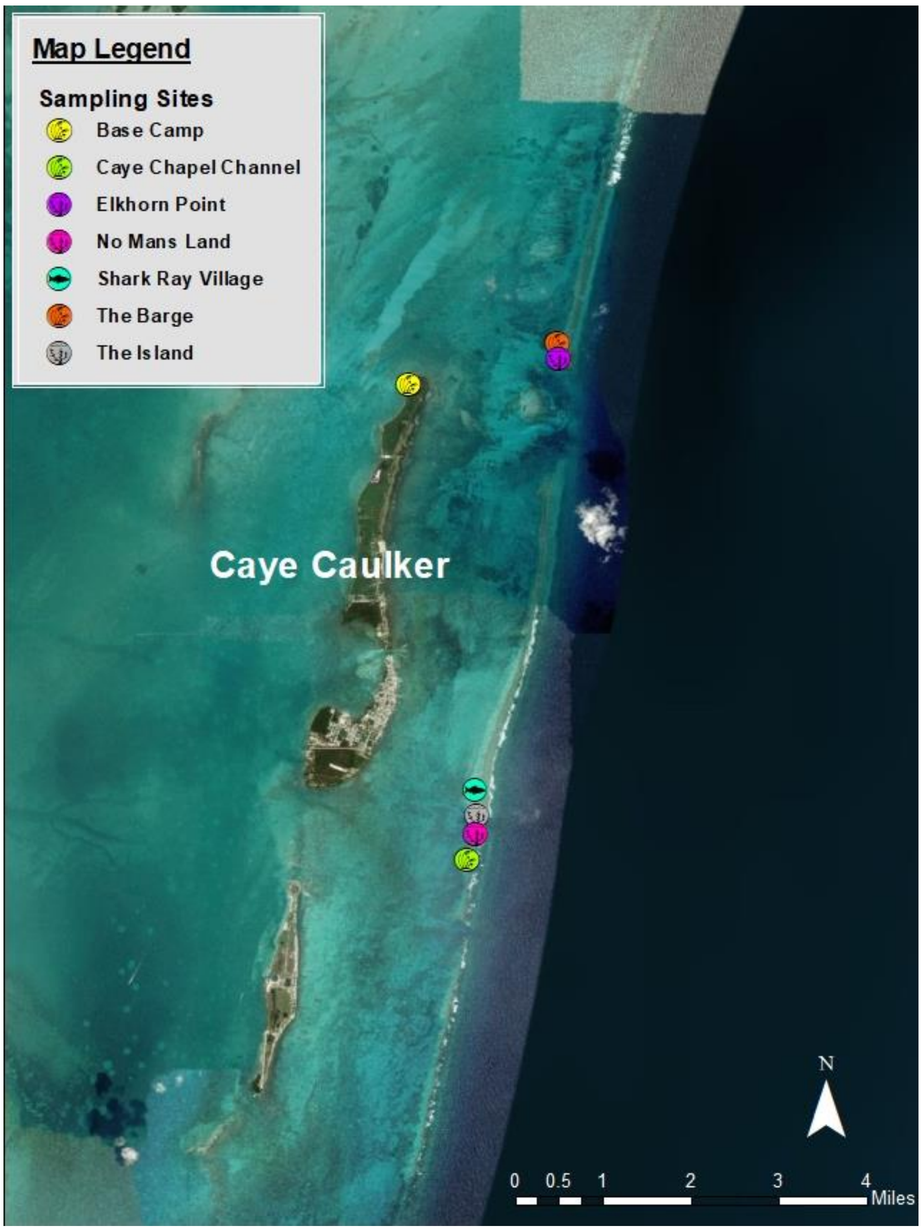

Figure 4. A map image displaying the different sites used for sampling abundance of nurse sharks.

Table 3. A list of each site surveyed for abundance with habitat type, distance from SRV and average depth.

Site Name	Habitat Type	Distance from SRV (miles)	Average Depth (m)
Base Camp	Seagrass, mangroves	4.68	1.36
Caye Channel	Seagrass	0.46	6.00
Elkhorn Point	Coral gardens	4.98	1.50
Shark Ray Village	Seagrass, patch reefs	0	1.50
The Barge	Shipwreck, seagrass	5.18	5.00
The Island	Coral island	0.28	5.00
No Mans Land	Coral island	0.52	3.00

Data Analysis

Models describing the relationship between the frequencies of observed behaviors (number of times each behavior observed per hour) and activity (boats feeding, no feeding, no boats) were fitted using a general linear mixed model (GLMM) with negative binomial distribution. Environmental variables were also included in the models to allow for any environmental effects. Models were fitted in R software (R Core Team 2020) using the MASS (Venables & Ripley 2002) and lme4 (Bates et al. 2015) packages. Data were subset by behavior and each behavior was modeled separately (i.e., milling, active swimming, conspecific aggression, interspecific aggression and shark-initiated human interaction) and tested against nine fixed-effects variables (Table 4). Continuous variables were rescaled in R using the "scale" function, to standardize the range of numeric data. Survey number (S) represented the number designated to each video filmed and reviewed and was included as a random effect in all models to account for variability and lack of independence in behaviors between surveys. An offset term was included as the log-transformed duration of activities (in minutes) multiplied by the MaxN of nurse sharks in each survey for all models to allow for differences in sampling effort. Term selection for each model was conducted by backward-selection using Akaike's information Criterion (AIC) scores. Beginning with the full model containing all variables, each variable was removed and resulted in a reduced model. If the difference in AIC scores between the full model and reduced models (dAIC) was ≤2, the removed variable was not considered an important predictor variable. If the dAIC was >2, then the variable was considered an important predictor variable. The resulting best-fitted models were validated by examining residual plots. A multiple comparisons test using the emmeans package (Lenth 2020) was used to test for differences within the levels of the important categorical predictor variables where they contained more than two levels. Effects of provisioning and boat activity (hypotheses 1 & 2) were analyzed at the same time within a single model by using emmeans to determine the significance between the levels of activity

The habituation data set from the camera set-ups used for habituation was analyzed through descriptive statistics (Figure 6). The second, larger data set was prepared from the behavior video analyses, where the MaxN of nurse sharks was recorded during each activity. The MaxN was compared between the levels of activity using the emmeans package.

Table 4. List of the fixed-effect variables tested against behaviors.

Variable (units)	Levels/Range
Activity	Boats feeding No feeding No boats
Underwater visibility (m)	5-20m
Wind speed (kt)	3-15kt
Wave height (m)	0.4-1.2m
Total number of boats during survey	1-7 boats
Total number of tourists in the water during survey	4-153 tourists
Number of boats feeding	0-4 boats
Type of bait	Sardines Sardines and Snapper
Rate of Tourism	High Low

Results

Hypotheses 1 & 2: Effect of Provisioning and Boat Activities on Behavior

A total of thirty, one-hour survey videos were reviewed and analyzed in order to assess the effect of activities on the behavior of nurse sharks in Shark Ray Village. The average frequencies of each behavior during each activity across all 30 surveys are shown in Table 5 and Figure 5.

Table 5. Descriptive values for the frequencies of each behavior during each level of activity.
Mean=mean behavior frequency, Max=maximum behavior frequency, Min=minimum behavior frequency

Behavior (per hour)	Activity	Mean	Max	Min
Milling	Boat Present Feeding	42.62	112	6
	Boat Present No Feeding	21.33	61	4
	No Boats Present	5.89	30	0
	Overall	22.06	112	0
Active Swimming	Boat Present Feeding	11.06	39	1
	Boat Present No Feeding	60.33	161	0
	No Boats Present	18.47	64	1
	Overall	35.96	161	0
Conspecific Aggression	Boat Present Feeding	2.00	12	0
	Boat Present No Feeding	0.03	1	0
	No Boats Present	0.05	1	0
	Overall	0.52	12	0
Interspecific Aggression	Boat Present Feeding	0.56	5	0
	Boat Present No Feeding	0.10	1	0
	No Boats Present	0.00	0	0
	Overall	0.18	5	0
Shark-Initiated Human Interaction	Boat Present Feeding	0.62	3	0
	Boat Present No Feeding	0.63	3	0
	No Boats Present	0.15	2	0
	Overall	0.50	3	0

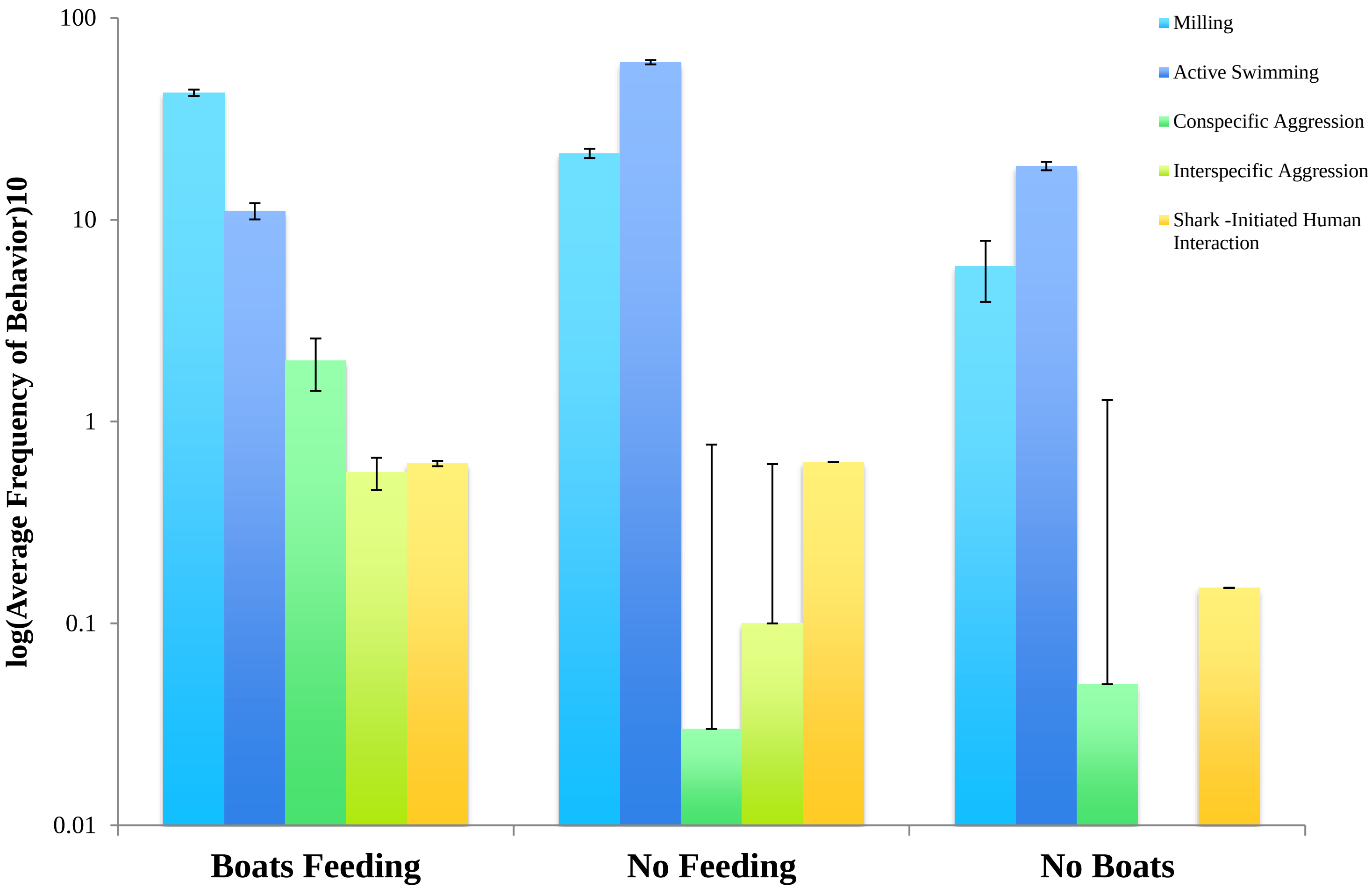

Figure 5. Averages of the total frequencies of each behavior on a log scale during activities of boats feeding, no feeding and no boats. Error bars represent standard deviation.

1. Milling behavior

The best-fit model of milling behavior included activity as an important predictor variable (dAIC=14.39). When comparing milling behavior between levels of activity through emmeans, behavior significantly differed between boats feeding and no feeding (p<0.01). The presence of provisioning was associated with higher observed frequencies of milling behavior (mean observed frequency=42.62 per hour). Nurse sharks would mainly mill at the surface in large "bait balls," or at the seafloor waiting for scraps to fall. There was a marginal significant difference in milling between boats feeding and no boats (p=0.05), and no significance between no boats and no feeding (p=0.81). No other variables were retained in the model.

2. Active Swimming Behavior

Active swimming was the most commonly observed behavior in all surveys (Table 5), and had a higher occurrence when there were no boats (Figure 5). As seen in Table 6, activity was the important predictor variable retained in the model (dAIC=19.90). The emmeans revealed a significant difference in active swimming between boats feeding and no feeding, with higher observed frequencies when there was no feeding and no boats (p<0.01). Active swimming was less frequently observed while boats were feeding, but more frequently observed when there were no feeding events. This behavior was also significantly different between boats feeding and no feeding (p<0.01). These results indicate the effect of provisioning and boat presence on this behavior. There was no significant difference between the activities of no feeding, and no boats (p=0.17), the common variable between these two levels being the absence of feeding.

3. Conspecific Aggression Behavior

The important predictor variables retained when modeled with conspecific aggression included activity (dAIC=30.10), rate of tourism (dAIC=2.95), total boats during survey (dAIC=2.44) and wind speed (dAIC=3.07). Emmeans revealed a significant difference in conspecific aggression between boats feeding and no feeding (p<0.01), with higher observed frequencies while boats were feeding (mean observed frequency=2 per hour). This result indicates that presence and absence of provisioning has an effect on this behavior, which was rarely observed during any other activities. There were no significant differences between the activities of no boats and no feeding (p=0.38), and between no boats and boats feeding (p=0.18), showing no effect of boat presence on this behavior. Conspecific aggression was shown through emmeans to be significantly different between high and low rates of tourism (p<0.01) and was observed more frequently during high rates of tourism. No other variables were shown to be important in the model.

Table 6. dAIC values for GLMM models of behavior after dropping each explanatory variable from the full model. Important explanatory variables (dAIC>2) are bolded.

	Behavior				
Explanatory Variable	Milling	Active Swimming	Conspecific Aggression	Interspecific Aggression	Shark-Initiated Human Interaction
Activity	**14.39**	**19.90**	**30.10**	**2.29**	-1.73
Rate of Tourism	-1.96	-1.70	**2.95**	-2.00	0.03
Total boats during survey	-1.80	-1.88	**2.44**	0.41	-0.43
Total tourists during survey	-1.29	-1.88	-1.98	-1.96	**3.00**
Total boats feeding	-1.53	-1.49	-1.58	-0.94	**2.55**
Visibility	0.45	-1.89	-1.25	0.50	**11.05**
Type of bait	-1.22	-1.83	-1.14	-2.00	1.78
Wind speed	-1.28	0.75	**3.07**	-0.17	-1.95
Wave height	-1.77	1.91	-1.78	-1.97	-1.98

4. Interspecific Aggression

Interspecific aggression was the least frequent behavior observed in all of the surveys (mean observed frequency=0.18 per hour). Similar to conspecific aggression, this behavior was more commonly observed when boats were feeding (mean observed frequency=0.56 per hour). The model best fitted with interspecific aggression included activity as the important predictor variable (dAIC=2.29). From the emmeans test, interspecific aggression was significantly different between boats feeding and no feeding (p<0.01), showing an effect of the presence and absence of provisioning on this behavior. No other variables were retained in this model.

5. Shark-Initiated Human Interaction

When modeling shark-initiated human interaction, the activity level of "no boats" was excluded in analysis due to the absence of interactions with tourists associated with absence of tour boats. Activity was not an important variable retained in the model (Table 6), indicating no effect of provisioning or boating activity on this behavior. The best model included total number of tourists (dAIC=3.00), total number of boats feeding (dAIC=2.55), and visibility (dAIC=11.05) as important explanatory variables. This behavior was mainly observed when boats were feeding (mean observed frequency=0.62), and when no feeding occurred (mean observed frequency=0.63 per hour). Shark-initiated interactions varied over the number of tourists present during a survey and the total number of boats feeding, and no trend was shown in data regarding these variables. In regards to visibility, shark-initiated interactions were sometimes seen in very low visibility. This was due to many tourists stirring up sediment, visually impairing sharks and causing them to run into some tourists. No other variables were included in the model.

Table 7. Multiple comparisons results for each activity using the emmeans package in R.

Behavior	Activity	p-value
Milling	Boats Feeding vs. No Feeding	<0.01
	Boats Feeding vs. No Boats	0.05
	No Boats vs. No Feeding	0.81
Active Swimming	Boats Feeding vs. No Feeding	<0.01
	Boats Feeding vs. No Boats	<0.01
	No Boats vs. No Feeding	0.17
Conspecific Aggression	Boats Feeding vs. No Feeding	<0.01
	Boats Feeding vs. No Boats	0.28
	No Boats vs. No Feeding	0.19
Interspecific Aggression	Boats Feeding vs. No Feeding	<0.01
	Boats Feeding vs. No Boats	1.00
	No Boats vs. No Feeding	1.00

Hypothesis 3: Nurse Shark Habituation to Tour Boats

The results from camera deployment surveys prior to tour boat arrival were described through descriptive statistics (Figure 6). The MaxN of nurse sharks was measured prior to the arrival of the first boat on site, and up to 10 minutes post-arrival. The MaxN was recorded as the maximum number of sharks counted within a frame at each 5-minute interval. Out of all surveys completed (S=8), six showed a peak in the MaxN when boats first arrived to the site (Figure 6). Two surveys showed a peak MaxN prior to boat arrival. During these two surveys, boats pulled in to SRV at angles outside of the camera's range of view, making it difficult to record the MaxN.

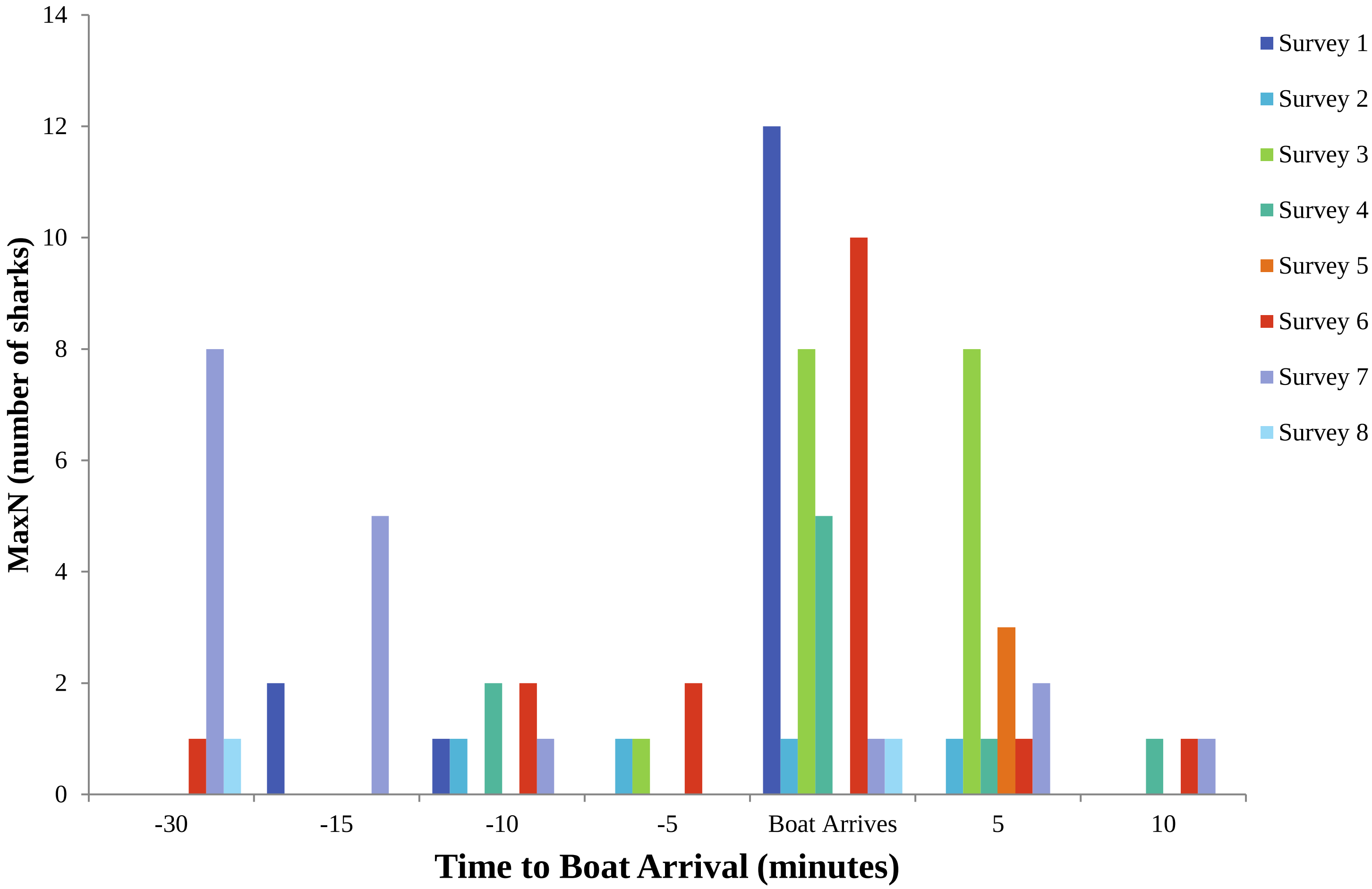

Figure 6. The MaxN of nurse sharks leading up to boat arrival in 5-minute intervals. Each color bar indicates a separate survey.

Habituation was further analyzed by comparing the MaxN of nurse sharks using emmeans between the activities of boats feeding, no feeding, and no boats. The MaxN was significantly different between boats feeding and no boats ($p<0.01$), with more sharks observed in the area when boats were feeding. There was also a significant difference between no feeding and no boats ($p<0.01$), the MaxN being greater when no feeding occurred. In both relationships, regardless of feeding, boat presence was the common variable. The MaxN between no feeding and boats feeding was not significant (p=0.66), emphasizing that boat presence affected the number of sharks observed in the area, not food presence.

Hypothesis 4: Abundance in Shark Ray Village and Control Sites

The MaxN of nurse sharks was compared within SRV during 10 surveys and before boats arrived (8 surveys) to 5 different control sites (10 surveys) around Caye Caulker. Cameras were set up in control sites and the maximum number of nurse sharks within one frame was recorded. Nurse sharks were consistently seen in SRV during survey, while no nurse sharks were ever recorded outside of SRV.

Additional Observations

There were additional, notable observations made during this study. In addition to behaviors focused on in this study, chafing behavior was seen in some of the nurse sharks. Nurse sharks would roll and scratch their backs in the sand, then resume regular swimming. Nurse sharks were seen swimming very close to boat propellers, and multiple nurse sharks were seen with wounds on their fins and body from boat propeller strikes. Lastly, tour guides were observed placing bait inside of conch shells in order to keep nurse sharks near their boats.

Discussion

This study explored the impacts of provisioning tourism on the behavior, habituation and abundance of nurse sharks inhabiting Shark Ray Village in Caye Caulker, Belize. Prior to this research, no study had been conducted on nurse sharks at this specific tourist attraction. Shark Ray Village provided an ideal study area, as it was an easily accessible shallow-water habitat with a steady flow of tourism activity. Through one-hour video surveys, I found that nurse shark behaviors varied based on the provisioning and boat activity occurring. I also observed a greater number of nurse sharks during boat presence in SRV than when boats were absent. Repeated aggregations of nurse sharks to SRV when boats entered the area suggest that nurse sharks are habituated to the tour boats. Nurse sharks were also observed to be in higher numbers within SRV when compared to control sites outside of SRV.

Effects of Provisioning and Boat Activity on Behavior

Milling & Active Swimming Behaviors

The presence or absence of provisioning itself caused changes in these milling and active swimming behaviors. When food was available, sharks would actively swim to boats, with milling behavior quickly taking over once feeding began. When no feeding took place, milling decreased and most of the sharks were seen actively swimming from one boat to another. In the absence of boats sharks were seen swimming the length and width of SRV, confirming the effect of boat presence to produce changes in swimming behavior. Nurse sharks are naturally nocturnal, foraging at night and resting underneath rocks or reefs during the day (Garla et al. 2017). It was very evident that the nurse sharks in SRV exhibited modified behaviors contradicting these natural behaviors and were very active during the day. There was no opportunity to monitor the sharks at night or attach satellite tags, but high activity and feeding during the day reduces the likelihood that these sharks are also actively foraging at night. If these sharks are expending large amounts of energy during provisioning activities during the day, there is less energy being preserved for foraging, reproductive and resting behaviors. If energy needs are not met, this could lead to an overall decrease in fitness for the population (Semeniuk & Rothley 2008). Nurse sharks have very low metabolic rates (Whitney et al. 2016), underlining that they are naturally suited for a low-activity lifestyle. Since they are not RAM ventilators like some shark species, they are dependent on periods of rest and inactivity to balance energy budgets (Whitney et al. 2016). On the contrary, this high cost of movement may be offset by food received from provisioning. Carrier & Luer (1990) compared growth rates of captive nurse sharks to those recaptured over the course of 3 years. Captive nurse sharks were fed sardines three times a week, and showed slightly faster growth rates than nurse sharks recaptured in the wild. Nurse sharks in SRV are provisioned with sardines and other bait multiple times a day almost every day of the week. It is possible that this continuous access to provisioned food in SRV is sustaining energy costs for nurse sharks in SRV. More research would be needed to evaluate the amount of food individual nurse sharks are accessing, and how much of their diet consists of provisioned food.

Conspecific & Interspecific Aggression Behaviors

Aggressive behaviors were the least observed behaviors during this study, and occurred most often during feeding. Instances of biting, shoving and tail whipping were the most common signs of conspecific aggression seen between nurse sharks. Interspecific aggression was seen as nurse sharks head butting, pinning down or shoving southern stingrays and fish while feeding. These interactions were very likely caused by the increased density of sharks and rays and the limited amount of food being provisioned. There was a clear unequal amount of food consumed between sharks and rays, and between sharks of different sizes; larger sharks would have the advantage and easier access to food resources than smaller sharks. The possibility of size-class hierarchy in provisioned species has been documented in some provisioned elasmobranch populations (Newsome et al. 2004; Maljkovic & Cote 2011). This suggests that the “costs” of participating in provisioning tourism may vary across individuals and size classes, with larger individuals potentially experiencing diet supplementation, while smaller individuals may risk injury and waste effort in pursuit of food rewards they are unlikely to receive.

Unnatural aggregations of more than one species to a site may increase the chances of interspecific aggression occurring. Stingrays on the seafloor had a disadvantage in obtaining food since it was distributed at the surface. This disadvantage can cause competition between nurse sharks and stingrays, potentially increasing instances of conspecific and interspecific aggression (Clua et al. 2010). Increased frequency of aggressive behavior is not ideal, as the severity of aggression has the potential to escalate. Thus, aggressive behavior connected to provisioning is a negative effect intensified by human activity. Though the action of conspecific aggression was witnessed during provisioning, there was no physical evidence of this behavior on nurse sharks, contrary to what has been seen in other studies (e.g. Semeniuk & Rothley 2008). Lack of visible bite marks may be due to the extremely thick dermal layer attributed to nurse sharks that would make it difficult to notice bite marks, or to their small teeth that would reduce risk of serious injury resulting from bites (Pratt & Carrier 2001). Additionally, conspecific and interspecific aggression behaviors were very difficult to detect during some video analysis due to poor visibility, mostly due to tourists stirring up sediment or high wind and wave action.

Shark-Initiated Human Interaction Behavior

The presence or absence of food or boats did not affect the frequency of sharks initiating human interaction. This behavior usually presented itself as nurse sharks laying their head on the fins of tourists in anticipation of a food reward. Other instances included sharks swimming towards tourists' legs or hands, without making physical contact but not changing direction until they came within a foot or less of the tourist. Feeding in the presence of many humans may have caused the sharks to link food to humans, reducing natural avoidance behavior and producing this begging response in anticipation of a food reward. Senses used during prey detection may also play a role in their human interactions. Nurse sharks rely mostly on olfactory and electroreception senses when initially detecting prey (Gardiner et al. 2014), and being a naturally nocturnal species, sight is not a sense relied on during initial prey detection. Once prey is in close enough range, nurse sharks switch to relying on secondary senses for detection: vision and touch (Gardiner et al. 2014). In addition, nurse sharks have very small eyes, contributing to poor vision in this species unless within close range of an object. The area of SRV most likely smells of food due to the frequent provisioning events (average of 2 boats feeding per day), and these sharks, due to poor eyesight swim to humans in anticipation of a food reward. Once they were within a very close range to a human and no food reward was presented, they quickly changed course away from the human.

All instances of shark-initiated interactions could possibly increase the risk of bites on humans because of this linkage of humans to food and decrease in avoidance behavior (Levine et al. 2014; Clua 2018), and poor eyesight seen in this species. There are not many reports of shark bites on humans directly linked to provisioning (Meyer et al. 2009), but the possibility still remains.

Nurse Shark Habituation to Boats

There was strong evidence of the habituation of nurse sharks to SRV due to an increase in the number of individuals during boat presence. Many studies confirm habituation phenomenon by reporting an increase in the number of individuals at provisioning sites over long periods of time (i.e. Meyer et al. 2009; Clue et al. 2010; Brunnschweiler et al. 2014). In a contrasting study, Laroche et al. (2007) did not report any signs of behavior modification of provisioned white sharks in South Africa, which they attributed to low levels of tourism throughout the year. The level of tourism activity in SRV is very high, with an average of 4 boats entering the area within an hour every day, therefore encouraging a change in natural behavior. Shark Ray Village has been a hotspot for provisioning tourism for about 15 years (Ali Casino, personal communication), giving these sharks ample opportunity to develop learned responses to tourism activities. Boat arrival to the SRV seemed to act as a cue signaling the sharks to enter that area (Figure 6). The increase in shark numbers when boats arrive to SRV provides evidence that they are using auditory and electroreception senses to associate boat engine noise with food. Furthermore, tour guides would leave their boat engines on while feeding the sharks, maximizing the association of boat engine noise with food. When tour guides turned on their boat engines during non-feeding events, nurse sharks still approached the boat and milled at the surface. This provides evidence that they are using auditory and electroreception senses to associate boat engine noise with food. Human presence did not seem to have the same signaling effect as boats did on these nurse sharks; every time surveyors swam to SRV to set up the underwater camera prior to boat arrival, there were no nurse shark sightings in SRV.

Habituation to boats and the boat engine noise was observed to be problematic in regards to the physical body condition of the nurse sharks in SRV. Many nurse sharks within SRV showed signs of physical trauma from boat propellers. Scars and large notches on dorsal and pectoral fins were seen on multiple sharks, as well as wounds on their mid-bodies. Although there were no direct observations of sharks getting hit by propellers, the association of the boat engine with food, and the close proximity of sharks to boat propellers (Figure 7B) points towards propellers as the likely cause of these injuries. A study on provisioned whale sharks in the Philippines revealed that 47% of provisioned individuals were observed to have propeller scarring (Araujo et al. 2014). Much like the nurse sharks in SRV, these whale sharks were fed at the surface near boats, increasing their chances of collision. Injuries to the fins and bodies of nurse sharks in SRV negatively affect swimming mobility, increasing effort needed to swim, and increases risk of infections. Implementation of propeller guards on tour boats, turning engines off while feeding, and switching the side of the boat food is thrown from could be useful in mitigating propeller injuries.

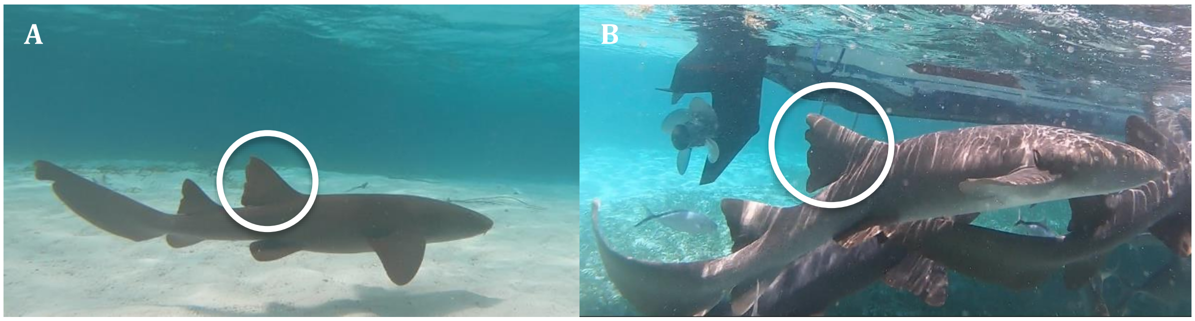

Figure 7. (A) Examples of boat propeller marks observed on both dorsal fins of nurse sharks. (B) Close proximity of provisioned sharks to a boat propeller.

As this is a wild population of nurse sharks, habituation to boats and SRV to this extent could be a problematic modified behavior due to the potential lack of movement from the area. Previously, nurse sharks had not been known to swim long distances, and have usually been shown to have high site fidelity. A recent study by Pratt et al. (2018) revealed that nurse sharks in the Dry Tortugas exhibited partial migratory behavior. Nurse sharks would swim up to 200 miles in the summer to mate on the West coast of Florida. With this new information, questions arise on the ability of nurse sharks in SRV to migrate for reproductive purposes. If these sharks are not migrating for mating purposes, they could potentially be mating within the SRV area or not mating at all. This could lead to problems associated with inbreeding and low gene variation within the population (Clua et al. 2010; Mourier et al. 2013).

The comparison of the MaxN of nurse sharks between boats present or absent provides further insight into the extent of their habituation to the area. Nurse sharks were more frequently observed in the presence of boats. This extremely modified behavior solidifies the point that nurse sharks have identified the source of provisioning and modified their behavior to maximize access to this resource.

Nurse Shark Abundance: SRV vs. Control Sites

Comparison of video surveys in SRV and six other control sites showed an extreme disparity between the frequencies of nurse sharks observed outside and inside of SRV. The control sites varied in terms of benthic habitat type, but all were considered suitable habitats for nurse sharks. Considering camera placement in control sites, it is possible nurse sharks were present at these sites but remained undetected and out of camera range. Nurse sharks outside of SRV may exhibit natural nocturnal behavior by being more active at night and resting during the day, making daytime sightings unlikely during surveys.

Nurse sharks have been documented to show site fidelity to various reefs (Pikitch et al. 2005; Castro 2000; Pratt & Carrier 2001), exhibiting a limited range of movement. The nurse sharks in SRV show site fidelity to SRV, but seem to have an abnormally small range of movement. Nonetheless, this limited range suggests overuse of SRV, potentially causing trophic impacts on nearby reefs with fewer nurse sharks. More long-term studies would be needed in order to confirm or deny this effect.

Additional Observations

<u>Chafing Behavior</u>

An odd and unexpected rolling behavior was noted on almost every behavior survey. Nurse sharks were observed rolling completely onto their dorsal or ventral side, rubbing on either the sandy bottom or seagrass, and then resuming swimming (Figure 8). No event related to provisioning or boat activity seemed to correlate with this behavior. This behavior, termed chafing, has been documented in various species of elasmobranchs (i.e. grey nurse sharks, oscillated eagle rays, lemon sharks, Caribbean reef sharks, and black tip sharks; Smith et al. 2015, Berthe et al. 2017, Bullock et al. 2015, and Ritter 2011). Instances of chafing have been observed in sharks attempting to remove remoras (e.g. Brunnschweiler 2006). However, surveyors in SRV did not detect any remoras on chafing nurse sharks. Some possible reasons for this behavior could be the presence of ectodermal parasites (Smith et al. 2015), which was an issue present with provisioned stingrays in Stingray City in the Cayman Islands (Semeniuk &

Rothley 2008). Parasites can be spread through close contact between individuals, and the high densities of nurse sharks in SRV may allow for parasites to be easily spread. Further research and closer observations of their skin would be needed to confirm the presence of parasites.

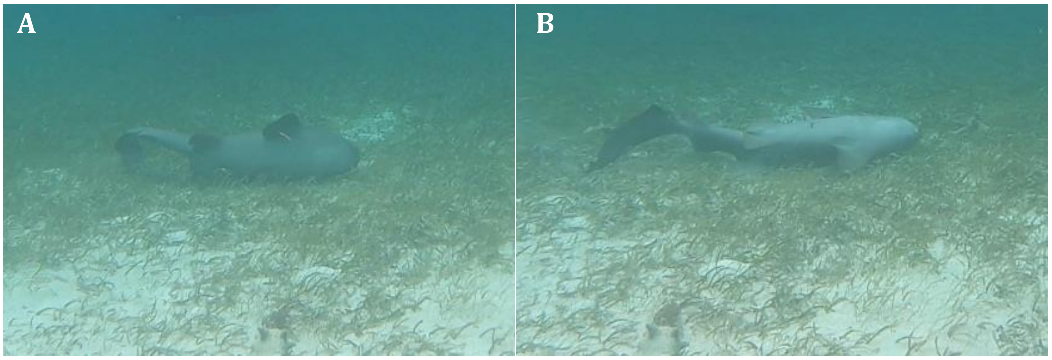

Figure 8. (A-B) Photographic examples of chafing behavior observed by nurse sharks in SRV.

Conch Shells

A common technique tour guides used to keep nurse sharks around their boat was inserting food into conch shells then placing them on the seafloor. Nurse sharks and stingrays were observed swimming over and biting at the food-filled conch shells. Nurse sharks continued this behavior after contents of shell had been removed and boats left SRV, showing that this has become a learned behavior. Introduction of this behavior could lead to an increase in conspecific and interspecific aggression for the contents of the conch shell. Very often nurse sharks and stingrays were observed pushing and shoving each other for access to conch shells. This behavior may also encourage natural foraging behavior, since nurse sharks are known to have a wide trophic range that includes invertebrates in their diets (Castro 2000; Tilley et al. 2013; Shipley et al. 2018). To determine if this technique is harmful or beneficial to nurse sharks in SRV, additional data monitoring levels of aggression and observations of natural hunting behavior outside of SRV would be needed.

Future Research

Many gaps still exist in the knowledge of provisioning tourism on targeted sharks, but this study provides a pathway for future research. Acoustic tags could provide useful information on the movement patterns of nurse sharks in SRV (Lea et al. 2016). This information could help determine the extent of site fidelity nurse sharks show to SRV, if they are using reefs outside of SRV, and if this population shows reduced activity at night. Future research involving stable isotope sampling can help determine the trophic interactions of these sharks and if they are heavily relying on provisioned food rather than foraging. The use of BRUVs could also provide useful information on shark species diversity on surrounding reefs to help determine any effect SRV may have on species distribution. Further evaluation of the physical health condition of these nurse sharks should also be pursued in future research. Social experiments through tour guides and tourist interviews could help gather information on the increased education and awareness needed on the potential effects of provisioning tourism on these nurse sharks.

Conclusion

Many aspects of provisioning tourism were identified to have an effect on nurse sharks in Shark Ray Village. Evidence of modified behavior directly linked to provisioning tourism was shown in this study, concluding that behaviors changed depending on the outside stimuli provided by provisioning activities. Nurse sharks in SRV exhibited a reverse in their natural behavior by being heavily active during the day, and not showing avoidance towards humans. Constant human activity in SRV has led them to develop a learned response to boat engines, causing the association of boats with food. This association resulted in health and fitness costs, as nurse sharks swam too close to propellers leading to injury. Overall there is a very high concentration of nurse sharks in SRV, implying that this population has identified a source of food and modified natural behavior to maximize access to this important resource. The results presented from this study help fill the knowledge gap in provisioning tourism effects on nurse sharks and provides a baseline for future studies within Shark Ray Village. It is essential to understand shark-human interactions, as humans are the greatest threat to shark survival.

Understanding these impacts will assist in improved management, making provisioning tourism safer for targeted species and the humans that participate.

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