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Diel habitat use patterns of a marine apex predator (tiger shark, *Galeocerdo cuvier*) at a high use area exposed to dive tourism

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ABSTRACT

Knowledge of the diel spatial ecology of wild animals is of great interest to ecologists and relevant to resource management and conservation. Sharks are generally considered to be more active during nocturnal periods than during the day; however, few studies have empirically evaluated diel variation in shark habitat use and how anthropogenic disturbances may influence these patterns. In the western central Atlantic Ocean, tiger sharks (*Galeocerdo cuvier*) are highly abundant in the shallow waters of the Little Bahama Bank, Bahamas. Within the northwest edge of the Bank, there is an area nicknamed "Tiger Beach," where tiger sharks are provisioned year-round at spatially discrete ecotourism dive sites spanning ~1.5 km^2. In this study, we used an array of acoustic receivers encircling an area of 102.4 km^2 to evaluate for potential differences in diel spatial habitat use patterns for 42 tagged tiger sharks at Tiger Beach and the surrounding area. Using tracking data from 24 June 2014 to 13 May 2015, we evaluated spatial and diel patterns of shark activity space, centers of activity, residency and the daily proportion of sharks detected within the array. Sharks were detected during both day and night with no significant diel differences in habitat use metrics across the array, although spatial differences in residency existed. Four sharks accounted for 53.8% of residency data throughout the tracking period, with the majority of sharks primarily entering and exiting the array, except during summer months when the most of the tagged tiger sharks were absent from the array. We also found limited empirical support for hypothesized effects of provisioning tourism on tiger shark habitat use. However, additional research at finer, individual scales, may be needed to better resolve the potential influence of provisioning on tiger sharks at Tiger Beach.

1. Introduction

Given large space and high energetic requirements of apex predators, ecosystems can generally support a relatively low density of these enigmatic animals (Colinvaux, 1978). Thus, identifying high use areas by apex predators and understanding the patterns and drivers of their habitat use is of ecological and conservation significance given widespread population declines of many species (Brook et al., 2008; Ripple et al., 2014) and the potential for trophic cascades (Estes et al., 2011; Ritchie and Johnson, 2009). Such knowledge is particularly important in the case of critical habitats, such as feeding areas or gestation grounds, where individuals may be disproportionately vulnerable to exploitation, or that can conversely serve as effective protected areas (Newton, 2008; Queiroz et al., 2016). Sharks are predators in almost all marine environments, and as a group are highly threatened with overfishing (Worm et al., 2013). While large sharks often migrate over expansive areas, some species also exhibit periods of high residency in space and time (Chapman et al., 2015; Speed et al., 2010; Graham et al., 2016).

It is widely assumed and commonly reported that elasmobranchs are more nocturnally active than during diurnal periods; however, few studies have specifically investigated for potential diel patterns in habitat use (reviewed by Hammerschlag et al., 2017a). There is evidence of increased movements of some sharks during nocturnal and/or crepuscular periods (e.g. increased rate of night movement, Campos et al., 2009; deeper night dives, Howey-Jordan et al., 2013; increased crepuscular horizontal movement Papastamatiou et al., 2015), but these patterns are not ubiquitous (Hammerschlag et al., 2017a). Given

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increased anthropogenic impacts on the oceans, there is growing concern as to the potential impacts of humans (noise pollution, light, fishing) on diel patterns of fish habitat use, and the implications this may have on their life histories and ecological roles (reviewed by Hammerschlag et al., 2017b).

One factor that can impact the spatial behavior of sharks is food provisioning from dive tourism, although evidence for this is mixed and appears to be context-dependent (Brena et al., 2015; Gallagher et al., 2015). Some studies have indeed found evidence of habituation and/or increased residency patterns of elasmobranchs at sites exposed to provisioning dive tourism (e.g. Fitzpatrick et al., 2011), while other studies suggest minimal impacts (e.g. Brunnschweiler and Barnett, 2013). In the Cayman Islands, Corcoran et al. (2013) used acoustic telemetry to compare habitat use patterns of Southern stingrays (*Dasyatis Americana*) at sites where provisioning by tourists was present versus absent. Stingrays from the tourism sites demonstrated a reversal of diel activity, with increased activity during the day and minimal nocturnal movements, compared to nocturnally active stingrays from non-feeding sites. Stingrays at tourism sites also utilized significantly smaller activity spaces, which overlapped with the provisioning sites compared to conspecifics from adjacent habitats (Corcoran et al., 2013). Given that changes in diel behavior resulting from provisioning tourism may impact energetics in large elasmobranch fishes (Barnett et al., 2016) and subsequently alter their fitness, it is particularly important to investigate such effects on individuals during important life-history stages (e.g. gravid) and within critical habitats (e.g. gestation grounds) (Gallagher et al., 2015), especially since dive tourism is of growing socio-economic importance to numerous countries around the world (Gallagher and Hammerschlag, 2011).

In the western central Atlantic Ocean, tiger sharks (*Galeocerdo cuvier*) exhibit frequent use of the northern waters of Little Bahama Bank, Bahamas (Hammerschlag et al., 2012; Fig. 1). The area is dominated by female tiger sharks of mixed age classes (Sulikowski et al., 2016). Young female tiger sharks may use the area as a refuge to reach maturity, without the threat of harassment by male sharks, whereas gravid sharks may use the area as a gestation ground, benefiting from year-round calm warm waters that accelerate embryo development (Sulikowski et al., 2016). The northwest edge of the Bank is a popular location for shark diving tourism, nicknamed “Tiger Beach”, where tiger sharks are provisioned year-round by dive-tourists during the day at spatially explicit dive sites spanning an area of 1.5 km^2. Satellite tracking of tiger sharks from the area has suggested that these dive tourism activities do not significantly impact the long-term migration patterns of the tracked animals (Hammerschlag et al., 2012, 2015); however, the potential influences of the tourism activities on diel habitat use patterns of tiger sharks within Tiger Beach and adjacent areas of Little Bahama Bank remains unknown.

Given a general lack of knowledge on diel shark habitat use patterns (Hammerschlag et al., 2017a), paired with a high density of large tiger sharks at Tiger Beach and adjacent area (Hammerschlag et al., 2012), potentially for reproductive purposes (Sulikowski et al., 2016), the primary objective of the present study was to evaluate temporal variability in the spatial patterns of tiger sharks in this area. Moreover, since tiger sharks in the area are exposed to spatially explicit provisioning dive tourism, a second objective was to evaluate if diel habitat use patterns of sharks differed at the dive tourism sites compared to adjacent locations where dive tourism is absent.

To accomplish these two objectives, we used passive acoustic telemetry to test the null hypothesis [H0] that tiger sharks exhibit uniform patterns of spatial habitat use by day and night. Additionally, we tested the following alternative hypotheses: [H1] sharks are more active during night than by day as generally assumed, exhibiting larger nocturnal space use patterns as have been reported for some elasmobranch species (e.g., Papastamatiou et al., 2015); [H2] sharks exhibit increased use of dive tourism sites compared to adjacent areas by both day and night as has been found for elasmobranchs exhibiting habituation/conditioned responses to provisioning tourism sites (e.g. Corcoran et al., 2013) or [H3] sharks exhibit increased use of dive sites compared to adjacent areas only by day (the time in which provisioning occurs) (e.g. Fitzpatrick et al., 2011). We acknowledge that due to the nature of the study system, it is not feasible to experimentally manipulate provisioning activities by dive operators, and accordingly evaluate responses of sharks. Similarly, shark movement data were not available prior to tourism or provisioning commencing. Therefore, we cannot fully resolve the effects of tourism provisioning on tiger shark behavior. However, our experimental approach can provide evidence to support or refute patterns of tiger shark habitat use consistent with known tourism effects on elasmobranch behavior [H2, H3], providing insights into possible tourism effects and avenues for future directed research.

2. Methods

2.1. Study area and Tiger Beach

The shallow banks of the Bahamas Archipelago are mostly composed of underwater carbonate platforms. The Little Bahama Bank extends off Grand Bahama Island. The environment is a shallow (average 5 m deep), and mostly homogenous sand flat, with irregular seagrass patches, and infrequent small patches of coral.

The area known as Tiger Beach is frequented by shark diving operations, and is located within the northwest edge of the Little Bahama Bank (26.86° N, 79.04° W). Here, up to four dive operators may concurrently conduct tiger shark diving activities spanning an area of 1.5 km^2. Tiger shark diving occurs primarily during the day, where sharks are attracted to divers using submerged crates of minced fish (i.e. chumming). During diving activities, tiger sharks are also irregularly fed fish carcasses (Hammerschlag et al., 2012).

To evaluate patterns of tiger shark habitat use in the study area, we used passive acoustic telemetry, whereby sharks were tagged with acoustic transmitters and tracked via an array of stationary hydrophones (detailed in Sections 2.2 and 2.3 below).

2.2. Shark capture and acoustic tagging

Tiger sharks were captured using standardized circle-hook drumlines as described in Gallagher et al. (2014). Briefly, the gear consisted of a submerged weight base tied to a line running to the surface by means of an attached, inflatable buoy float, with a baited circle hook attached to the weight. Once hooked, each shark was slowly brought to the boat and restrained on a dive platform partially submerged in the water. To facilitate respiration, a hose was immediately inserted into the shark's mouth that actively pumped water over the shark's gills. This capture and handling method was selected to promote shark vitality and reduce stress levels during sampling (Gallagher et al., 2014). For each individual captured, sex was recorded and total length (TL) was measured to the nearest cm over a straight line along the axis of the body.

Acoustic transmitters (Vemco V16, 69 kHz, 68 × 16 mm) were surgically implanted into the intracoelomic cavity of sharks through a small incision in the abdominal wall above the pelvic fins. After tag insertion, the incision was closed with several simple interrupted nylon sutures. Twenty tiger sharks were tagged between 18 and 20 October 2013, thirteen sharks were tagged between 12 and 14 May 2014, and nine sharks were tagged between 14 and 16 November 2014 (Table 1). Sharks were then released at their location of capture. When sharks came within detection range of the hydrophones (described below), the tag number and time of detection was recorded on the corresponding receiver.

2.3. Telemetry array

To record the movements of acoustically tagged sharks, an array of