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Habitat preferences of the sicklefin lemon shark (*Negaprion acutidens*) in the Dongsha Atoll National Park: a preliminary assessment

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ABSTRACT: Collecting basic biological information of a species is crucial for developing effective conservation strategies and ensuring its sustainable management. Dongsha Atoll is considered a vital, possibly the primary, nursery ground for the endangered sicklefin lemon shark (*Negaprion acutidens*) in the South China Sea. In this study, we employed acoustic telemetry to investigate the habitat utilization and preferences of *N. acutidens* at different life stages in Dongsha Atoll. A total of 44 sharks, including 16 juveniles, 14 small sharks, 11 sub-adults, and three adults, were tagged and tracked for 1–848 days. Results of this preliminary assessment revealed that: (1) juvenile and small sharks commonly utilize the shallow seagrass flats around Dongsha Island, with juveniles spending a significant amount of time in the embedded lagoon; (2) sharks of all sizes utilize the lagoon mouth area, especially small and sub-adult sharks; (3) adult sharks exhibit a broader activity range within the atoll and are unlikely to enter the embedded lagoon. We hypothesize that the embedded shallow lagoon of Dongsha Island serves as a shelter area for newborns and juveniles, while the lagoon mouth may function as an important hunting ground for small and sub-adult sharks. Adult sharks may have the broadest home range around the atoll and close to Dongsha Island during the breeding season. This study underscores the importance of considering habitat shifts and changes in home range size throughout the ontogeny of *N. acutidens* when planning effective spatial management strategies.

KEY WORDS: Acoustic telemetry, elasmobranch, habitat utilization, requiem shark, site fidelity.

INTRODUCTION

Sharks are undisputed apex predators that play a crucial role in maintaining the balance of marine ecosystems through their strong top-down effects (Ferretti *et al.*, 2010). However, they are also highly vulnerable to fishing pressure due to their slow growth, late maturity, and low offspring production per pregnancy (Stevens *et al.*, 2000; Ferretti *et al.*, 2010). Identifying critical habitats and understanding their use by different shark life stages are essential for conservation and species-specific management (Filmlalter *et al.*, 2013).

Negaprion acutidens (sicklefin lemon shark) and *N. brevirostris* (lemon shark) are the only two species of the genus that allopatrically inhabit tropical and sub-tropical waters (Indo-Pacific vs. Eastern Pacific and Atlantic) around the world (Schultz *et al.*, 2008). Both species are considered threatened with extinction on the IUCN Red List (Endangered for *N. acutidens* and Vulnerable for *N. brevirostris*) (Carlson *et al.*, 2021; Simpfendorfer *et al.*, 2021). They display strong site fidelity to shallow coastal environments such as mangroves and atoll lagoons, with juveniles remaining restricted to their natal areas for a few years after birth (Chapman *et al.*, 2009). Their dispersal after leaving the nursery is also slow compared to other shark species. Small sharks often maintain a close association with their natal sites for many years and gradually expand their ranges as they grow (Chapman *et al.*, 2009; Filmlalter *et al.*, 2013). Some studies have even found that adult lemon sharks exhibit greater residency

than juveniles (Pillans *et al.*, 2021). The restricted dispersal patterns, combined with fragmented habitats and a lower number of breeders, may have resulted in potentially isolated and vulnerable small populations of lemon sharks (Schultz *et al.*, 2008; Mourier *et al.*, 2013; Liu *et al.*, 2023).

The Dongsha Atoll is remotely located on the northern boundary of the South China Sea approximately 450 km from the main island of Taiwan. The diameter of the atoll is around 25 km and its whole range is protected by the Dongsha Atoll National Park (DANP) established in 2007. As a strict no-take marine protected area (MPA), the DANP has successfully prevented most forms of anthropogenic exploitation, thereby significantly preserving the habitat integrity of the atoll (Yu *et al.*, 2022). Dongsha Island, a horseshoe-shape island 2.8 km in length and 0.9 km in width with an embedded lagoon, is a part of the Dongsha Atoll that is famous for thriving seagrass beds and abundant cartilaginous fishes, including *N. acutidens* (Fig. 1). A long-term monitoring study conducted since 2012 has demonstrated a small but well-established population of juvenile *N. acutidens* inhabits the lagoon and lagoon mouth of Dongsha Island. Heavily pregnant females are also observed near the lagoon mouth during high tide in the spring tide period, from the end of March to early May. Then a lot of newborn juveniles appear from April until November when the temperature drops. Based on these observations, *N. acutidens* around this area may also exhibit a philopatric behavior, and Dongsha Island is believed to

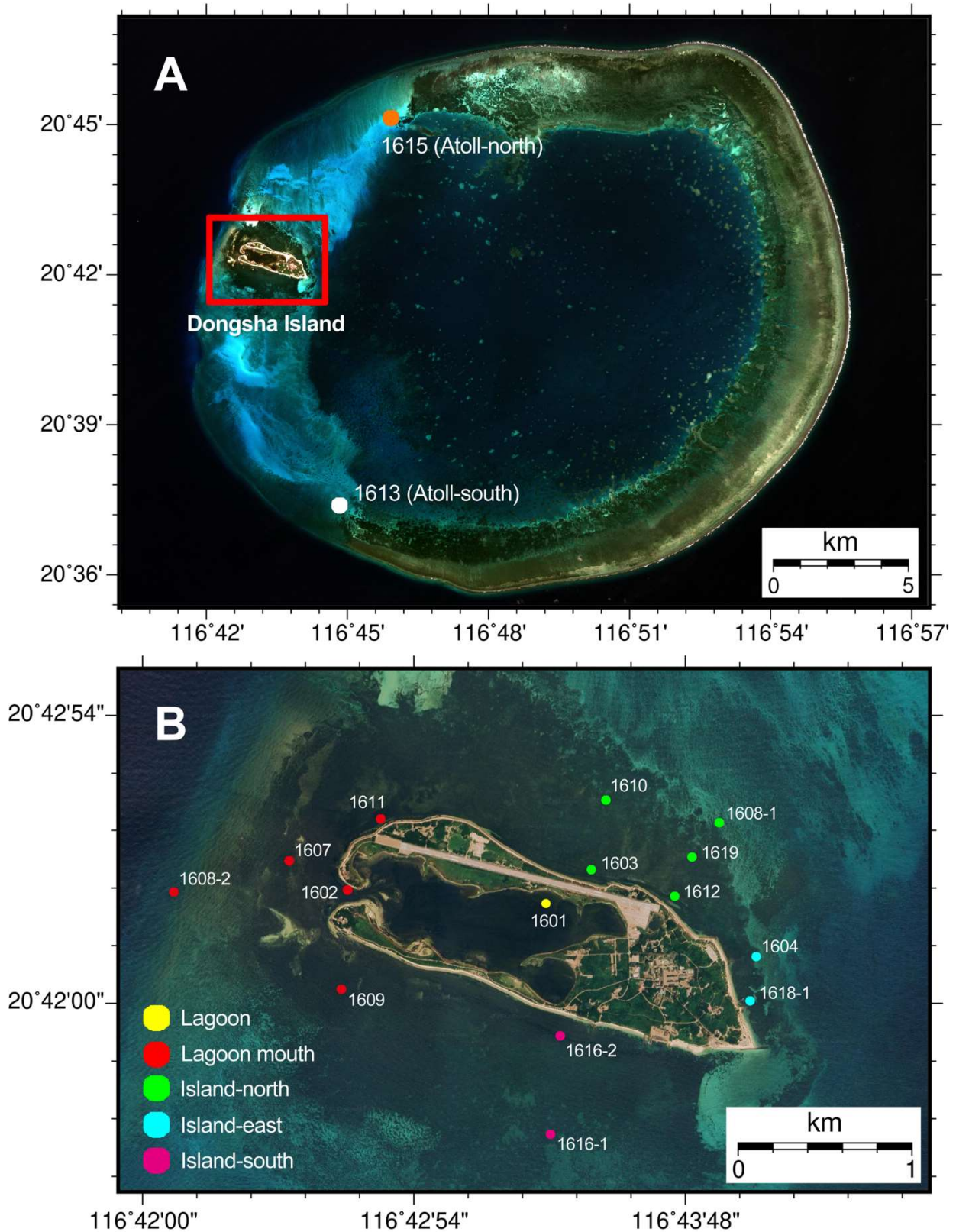


Fig.1. Maps showing locations of receivers arranged along **A.** Dongsha Atoll, and **B.** Dongsha Island. Receivers are grouped based on their locations shown with different colors. The satellite imagery in A was obtained from Sentinel-2 on the Google Earth Engine (GEE) platform, and in B, it was obtained from Google Maps. Detailed information about the receivers is provided in Table S1.

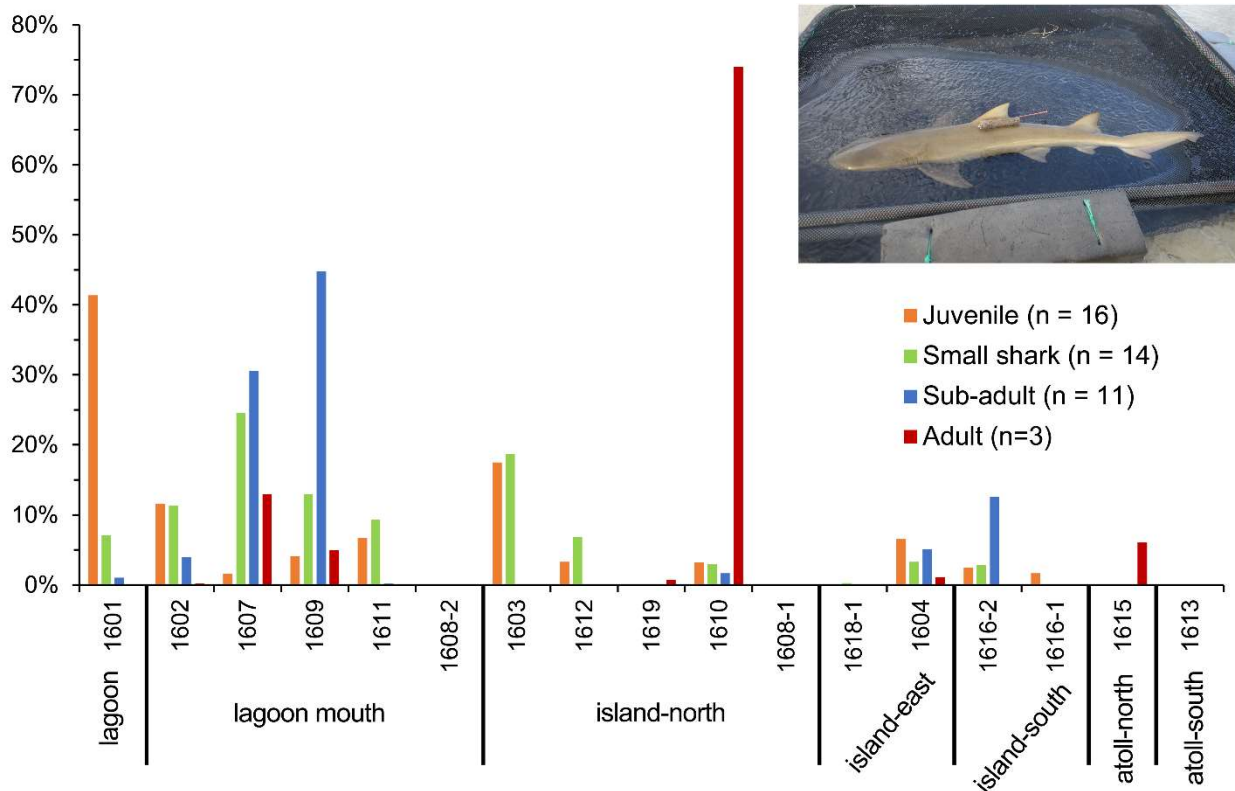


Fig. 2. Frequency distribution of detected signals for each receiver in each shark size category. The top right inset demonstrates how the transmitter is sewn onto the shark's first dorsal fin base.

serve as an important nursery ground for the population.

Once abundant throughout tropical and subtropical Indo-West Pacific, the population of *N. acutidens* has experienced a decline of 50–79% over the past few decades due to overexploitation and habitat degradation, particularly in Asian and African regions (Simpfendorfer *et al.*, 2021). As of now, Dongsha Island may stand as the first and potentially the sole recognized nursery ground for *N. acutidens* within the South China Sea. While the waters of Dongsha Atoll are protected under national park regulations, the threats of poaching and local construction projects pose significant risks to the survival of *N. acutidens* population (Yu *et al.*, 2022). In the present study, we employed an acoustic telemetry to investigate habitat utilization and preferences of *N. acutidens* at different life stages in the Dongsha Atoll. This information is crucial for establishing conservation policies at both international and local levels (Schultz *et al.*, 2008; Filmlalter *et al.*, 2013).

MATERIALS AND METHODS

The data shown in this study were collected based on a 7-year experimental period from September 2016 to August 2023. Sharks were caught using baited net traps and longlines along the coast of Dongsha Island and within the lagoon (Fig. S1). Captured sharks were

measured for total length (TL) and precaudal length (PCL), and then tagged with Lotek MAP-Series coded acoustic transmitters (MM-M-16-50; 16 mm in diameter, 80 mm in length, 35 g in weight, 30 sec trans interval, battery life 2439 days). Three approaches to attaching transmitters have been tested during the experiment. Before 2019, for sharks smaller than 80 cm TL, transmitters were sealed inside finger gloves and sewn onto the first dorsal fin base using sanitized sutures (Fig. 2); for sharks larger than 80 cm TL, transmitters were surgically implanted into the space between muscle layers on the first dorsal fin base. After 2019, all transmitters were surgically implanted into the peritoneal cavity following Filmlalter *et al.* (2013). The sharks were released on site after their measurements and surgeries, which typically took no longer than five minutes.

A total of 17 acoustic receivers (WHS 3250; 380 mm in length, 1,100 g in weight, battery life 168 days, effective detection radius 300–400 m) have been arranged inside the lagoon, at the lagoon mouth, along the coast of Dongsha Island, and at the atoll (Fig. 1, Table S1). To secure the receivers, each one was attached to a 2 kg lead weight and firmly fastened to a 1.5 m galvanized steel pipe (with an outside diameter of 35 mm and a wall thickness of 5 mm) using stainless steel hose clamps and cable ties. The sharpened end of the pipe was then inserted deeply into the sediment with the receiver



positioned in the water column. Receiver data were regularly downloaded, and batteries were replaced every three to five months. Most receivers were deployed simultaneously at the beginning, although a few had their codes changed or locations slightly adjusted during the experimental period. Data from these instances were adjusted and combined with data from the nearest adjacent receivers. Only three receivers could not be retrieved, likely due to drifting away, and new receivers with the same codes were then placed at those locations.

In data analyses, sharks were catalogued in four size groups according to their TL, including juveniles (< 100 cm TL, approximately 0–3 years old), small sharks (100–149 cm TL, 4–6 years old), sub-adults (150–220 cm TL, 7–11 years old), and adults (>220 cm TL, \geq 12 years old). Considering the lack of growth and mature information for *N. acutidens*, we adapted this age categorization according to its closely related congener, *N. brevirostris* (Brown and Gruber, 1988; Chapman *et al.*, 2009). However, due to the possibility of different biological or life history states between the two species, it should be emphasized that this categorization is a pragmatic approach given the limitations of available data. We also estimated the TL at the end of tagging for each shark by applying the von Bertalanffy growth function of *N. brevirostris* (Brown and Gruber, 1988), to evaluate the potential impact on the data if some individuals had entered the next life history stage during the tracking period.

To standardize and simplify the data, we combined all detections of each size group and calculated the detection proportion of each receiver in each group. A higher detection rate of a receiver suggests that sharks are more frequently present in that area, which may indicate a higher preference or utilization. In addition, the mean detections per day for each size group was calculated to assess the efficiency of receiving shark signals. Higher values imply that sharks are closer to the effective detection range of the receiver, while lower values suggest a broader activity range.

RESULTS

During the project conducted from October 2016 to the latest collected data on August 2023, a total of 44 sicklefin lemon sharks (70–273 mm TL) have been tagged, including 16 juveniles, 14 small sharks, 11 sub-adults, and three adults (Table S2). Sharks were monitored for 1–848 days (291 ± 39 days, mean \pm standard error) and the number of detections ranged from 2 to 233148 (32697 ± 6914). Only six juveniles and two small sharks were estimated to enter the next size group by the end of their detections (Table S2).

Based on the detection results, it appears that sharks may be active around Dongsha Island and within the lagoon (Fig. 2). Juveniles were mainly detected within the

lagoon (41.4% of detections), while small sharks and sub-adults exhibited higher detection rates in the lagoon mouth area (58.1% and 79.5%, respectively). Despite the small sample size, adult sharks were never detected in the lagoon, and they are the only size group that has been detected in the atoll area (receiver 1615). The efficiency of receiving shark signals decreases as the size of the sharks increases (400 ± 126 day⁻¹ in juveniles; 100 ± 28 day⁻¹ in small sharks; 78 ± 28 day⁻¹ in sub-adults; and 26 ± 18 day⁻¹ in adults), suggesting that the activity ranges of sharks may expand from Dongsha Island as they grow larger. The habitat preferences of *N. acutidens* in Dongsha waters can be summarized as follows: (1) juvenile and small sharks commonly use the shallow seagrass flats around the island, with juveniles spending a significant amount of time in the lagoon; (2) sharks of all sizes utilize the lagoon mouth area, especially small and sub-adult sharks; (3) adult sharks exhibit a broader activity range within the atoll, mainly staying in peripheral regions when close to the island and are unlikely to enter the lagoon.

DISCUSSION

No death was observed during the surgical procedures for attaching transmitters using any of the three methods. However, there is a concern that external transmitters may be more prone to falling off because lemon sharks are known to rub their bodies against the bottom or rocks to dislodge parasites (Poynton *et al.*, 1997; Sabalones *et al.*, 2004). On the other hand, surgically implanting transmitters into the space between muscle layers presents the most challenging procedure. Therefore, internal surgical implantation into the peritoneal cavity was selected as the final method, which has been commonly used in acoustic telemetry studies (e.g., Filmlalter *et al.*, 2013; Pillans *et al.*, 2021).

During the long-term tracking process, only six juveniles (tracked for 159–847 days) and two small sharks (tracked for 559 and 686 days) were estimated to have reached the next life history stage (Table S2). Unfortunately, our recapture data are not sufficient to verify their estimated TL. Although changes in the life history stage may affect sharks' behavior and result in minor tracking data biases, the transition in shark behavior is a slow and gradual process (Chapman *et al.*, 2009). Therefore, we believe that any error associated with size transition should be within an acceptable range.

Our previous investigations (Y.Y. Chen unpublished data) revealed that recaptured juvenile *N. acutidens* around Dongsha Island were often emaciated with minimal increase in length and decreased weight, and dissection of accidentally died individuals showed that their stomachs were usually empty. This observation is similar to discoveries from other studied regions (e.g. White *et al.*, 2004; Newman *et al.*, 2010; Weideli *et al.*,



Fig. 3. A heavily pregnant female (256 cm TL) caught from lagoon mouth on 28 April 2019. Released immediately after being measured and tagged with an acoustic transmitter. No further signals were detected from this individual.

2023). A high stomach empty rate implies that the predatory capability of juveniles may be limited. Additionally, juvenile and small sharks were observed to be active and aggregate at the lagoon mouth to forage during mid-tide when the water depth was around 40–60 cm, with both dorsal fins exposed above the water. In contrast, they showed no interest in feeding at high water levels. The shallow waters may limit the movement of their prey and further increase the chances of successful hunts. On the other hand, shallow waters can also limit the access of large predators that may prey on small lemon sharks (Morrissey and Gruber, 1993), such as the tiger shark *Galeocerdo cuvier*, which has been frequently observed around Dongsha Island (Y.Y. Chen pers. obs.). Moreover, the lagoon mouth region is the only narrow pass for water exchange, resulting in large amounts of organic matter flowing out from the lagoon during ebbing. This attracts a variety of potential teleost prey species for juvenile, small, and sub-adult sharks, such as families Atherinidae, Carangidae, Chanidae, Labridae, Lethrinidae, Lutjanidae, Mugilidae, and Terapontidae (White *et al.*, 2004; Chang *et al.*, 2012; Weideli *et al.*, 2023). Small and sub-adult sharks, after they leave the nursery at around age 3, may slowly expand their range as they possess sufficient hunting and predator avoidance capabilities, or due to the source of the lagoon mouth area being unable to support larger sharks (Chapman *et al.*, 2009; Hodgkiss *et al.*, 2017).

The gestation of *N. acutidens* is around 10–11 months, and each female can reproduce 6–12 well-developed pups every 1–2 years in shallow nursery areas (Stevens, 1984; Mourier *et al.*, 2013). From March to May, many heavily pregnant females can be observed cruising around Dongsha Island and moving from subtidal zones to the shallow seagrass flat during high tide periods, sometimes

even becoming stranded (Fig. 3). The behavior is speculated to be related to parturition, as a significant number of newborn pups appear after this period. Our acoustic telemetry revealed that adult *N. acutidens* were detected from the lagoon mouth from April to May, which seems to support the hypothesis. However, due to extremely limited budgets and manpower, the receiver array was prioritized around Dongsha Island, resulting in many blind areas of detection. The home range, migration routes, and habitat preferences of larger sharks, especially adults, remain unclear. For example, only one tagged adult (acoustic ID code 12-2) was detected by a receiver at the northwestern atoll (receiver 1615), while no shark signal was received from the southwestern atoll (receiver 1613). In this case, we could not determine whether the observed pattern indicated a potential preference for adults moving northward or whether it was simply due to the limited number of tagged individuals or receivers. Expanding the receiver array within the atoll area and tagging additional adult sharks to monitor their movement patterns constitute the primary focus of our future research. With these improvements, we are confident that Dongsha Atoll can serve as a foundational site for future investigations into the natal philopatry of this species in the South China Sea.

To summarize, the present study supports the hypothesis that Dongsha Atoll is an important nursery ground for *N. acutidens*. The embedded shallow lagoon of Dongsha Island can serve as a shelter area for newborns and juveniles, while the lagoon mouth may be an important hunting ground for small and sub-adult sharks. Adult sharks may have the broadest home range around the atoll and close to the island during the breeding season. This study offers the first habitat preference assessment of *N. acutidens* inhabiting Dongsha Atoll using acoustic telemetry, which is a critical contribution to their conservation and sustainable management. The findings also emphasize that planning effective spatial management strategies for *N. acutidens* must consider habitat shifts and expansion in home range size throughout ontogeny.

Ethics statement

Negaprion acutidens is not a protected species in Taiwan. We exercised additional caution during tagging procedures, ensuring no sharks were sacrificed. Sharks were measured and tagged in water, with close observation and maintenance of their normal breathing throughout. Upon release into the wild, we checked the tagged sharks' swimming behavior for normalcy. Typically, sharks initially swam toward the shore before transitioning to shallow waters and finally swimming out to sea. The sampling/experiment process was conducted under permits No. 1036780269, 1051000471, 1060000672, 1070000741, 1080001321, 1090000677, 1100003219, 1110001638, and 1120000059, granted by the Marine National Park Headquarters.



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