Marine Biology (2024) 171:132
https://doi.org/10.1007/s00227-024-04447-w

ORIGINAL PAPER

# Movements and habitat use of a nursery area by a widely distributed species of shark in the Southern Caribbean

**Rafael Tavares**[1,2,3] · **Colby D. Kresge**[4] · **Bradley M. Wetherbee**[4,5]

Received: 13 January 2024 / Accepted: 22 April 2024 / Published online: 15 May 2024
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2024


## Abstract

Use of a small tropical nursery in the Los Roques Archipelago by lemon sharks (*Negaprion brevirostris*) was investigated using acoustic telemetry. Twelve juvenile lemon sharks of three size classes were tracked between February 2014 and August 2015 in the Sebastopol Lagoon. Sharks were strongly site attached and remained in the lagoon for the duration of the study. Individuals in the smallest size class exhibited restricted movements within the innermost area of the lagoon in shallow water (< 1 m), over muddy substrate and along mangrove-lined shores. Sharks in the two larger size classes ranged further, in deeper water, over a wider range of substrates and more frequently near the lagoon entrance. Activity space varied among size classes, with home range (95% kernel utilization densities–KUD) of 0.42 $km^2$ and core area (50% KUD) of 0.13 $km^2$ for individuals in the smallest size class. For the medium and large size classes home ranges were 1.11 and 1.15 $km^2$ and core areas were 0.33 and 0.35 $km^2$ respectively. Space use as Minimum Convex Polygons differed among size classes, with overlap between the two largest size classes of 89%, compared with 40% between medium and smallest and 43% for largest and smallest size classes. Space use of lemon sharks in the Los Roques nursery illustrates variable use of habitat with varying environmental characteristics, likely reflecting a balance between predator avoidance and prey acquisition. Greater understanding of the use of nursery habitats for species such as lemon sharks, which use small, discrete nurseries over a broad geographical range can enhance our understanding of relationships between life history traits and environmental variability and management of populations.


**Keywords** Home range · Core areas · Spatial ecology · Los Roques · Lemon sharks · Telemetry

## Introduction

Movement and space use of animals affects their distribution and dispersion and ultimately results in the extent of habitats occupied and environmental conditions encountered (Begon et al. 2006). Many animals display distinct movement patterns during different life stages, resulting in variable interactions between individuals and their habitats (Simpfendorfer and Heupel 2012). Among sharks, many species rely on nearshore and shallow-water environments as nursery areas during the first years of life (Castro 1993; Heupel et al. 2018). Within nurseries, neonates and juveniles often display limited movements and exhibit a high degree of site attachment; behaviors thought to increase survival of juveniles (Holland et al. 1993; Heupel et al. 2004; Garla et al. 2006; Legare et al. 2015). Such lifestyles are of particular relevance for management of shark populations since coastal areas are extremely vulnerable to anthropogenic activities, including fishing, tourism, and development, even in remote

Responsible Editor: J. Carlson.

✉ Rafael Tavares
rtavares@citvenezuela.org

1 Independent Researcher, London, UK

2 Centro Para la Investigacion de Tiburones (CIT), Distrito Capital, Av. Don Bosco, Qta. ABC, No. 10, La Florida 1050, Caracas, Venezuela

3 Instituto Venezolano de Investigaciones Cientificas (IVIC), Avenida Panamericana Kilometro 11, San Antonio de los Altos 1204, Estado Miranda, Venezuela

4 Department of Biological Sciences, University of Rhode Island, Kingston, RI 02881, USA

5 Guy Harvey Research Institute, Nova Southeastern University, Dania Beach, FL 33064, USA

locations and oceanic islands. Reef sharks in particular, have seen significant population declines globally, with almost a quarter of species facing the threat of extinction (Dulvy et al. 2021; White et al. 2015; MacNeil et al. 2020). Therefore, studies of shark nursery areas and factors that influence survival of young individuals may inform management and enhance the recovery of stocks that have been depleted (Knip et al. 2012).

Shark nursery areas have been widely studied and their relationship with survival of juveniles has been broadly discussed (Heithaus 2007; Heupel et al. 2007, 2018). Use of shallow-water nurseries is hypothesized to be driven by two main factors: prey acquisition and predator avoidance (Branstetter 1990; Morrissey and Gruber 1993a; Simpfendorfer and Milward 1993; Hussey et al. 2017). Although these factors are often poorly understood in shark nurseries, predator–prey and competitive relationships are both important ecological interactions that influence community structure and directly impact the distribution and activity patterns of sharks (Heithaus and Vaudo 2012).

The lemon shark, *Negaprion brevirostris*, is a reef-associated species found on continental and insular shelves and is well-known for using shallow lagoons and enclosed bays as nursery areas during the first few years of life (Gruber 1982; Compagno 1984). In the Caribbean and adjacent waters, lemon sharks are common at several groups of islands with suitable coral reef and mangrove habitat, such as Bimini and Eleuthera, The Bahamas (Gruber 1982; Feldheim et al. 2002; Murchie et al. 2010), Atol das Rocas, Brazil (Wetherbee et al. 2007), US Virgin Islands (DeAngelis et al. 2008), Turks and Caicos, British West Indies (Henderson et al. 2010), and Las Aves and Los Roques archipelagos, Venezuela (Tavares 2005; Tavares et al. 2016). Most of the knowledge about spatial ecology of lemon sharks within nursery areas has been obtained from studies conducted in Bimini (Gruber et al. 1988; Morrissey and Gruber 1993a, 1993b; Sundström et al. 2001; Guttridge et al. 2012; Hussey et al. 2017; Finger et al. 2018; Dhellemmes et al. 2020; 2021; Heinrich et al. 2021). Although lemon shark can be considered a well-studied species, they occupy a range of nurseries of variable size and habitat characteristics throughout their distribution. An improved understanding of how variable habitats within nurseries affect life history parameters, such as growth and survival of lemon sharks, can provide insights into population dynamics on a broader scale (Barker et al. 2005; Freitas et al. 2006; Wetherbee et al. 2007; Henderson et al. 2010; Murchie et al. 2010; Tavares et al. 2016).

Los Roques Archipelago is an oceanic insular platform located in the Caribbean and is recognized for its exceptional marine biodiversity, with a fish fauna comprising over 370 species, including 21 species of sharks (Ramirez and Cervigon 2004; Tavares 2009). Lemon sharks use specific regions of the archipelago as nursery areas, most notably the Sebastopol Lagoon, which serves as the main nursery (Tavares et al. 2016; Tavares 2020). Previous studies on use of nursery areas by lemon sharks at Los Roques have provided information on their numbers and life history traits, including high growth rates compared with other nurseries (Freitas et al. 2006; Tavares et al. 2016, 2020). Elevated growth rates observed for lemon sharks at Los Roques may be attributed to warmer water temperature, abundance of prey, a diverse community or low levels of competition and predation compared to other nurseries (Tavares et al. 2020). A greater understanding of nursery use and other factors that directly influence the regulation of population growth will aid in effective assessment and management of lemon shark populations, which is of interest considering their listing as Near Threatened by the IUCN (Sundström 2015).

Variable life history traits of lemon sharks observed among nurseries may be attributable to biotic (e.g. prey abundance, competition and predation) and abiotic (e.g. temperature, salinity and oxygen) variables that are also reflected in the behavior and distribution of sharks (Heupel et al. 2007; Freitas et al. 2009; Simpfendorfer and Heupel 2012; Heupel et al. 2018; Tavaras et al. 2020; Latour et al. 2022). Therefore, the study of movements and activity patterns of lemon sharks at Los Roques will expand our understanding of their ecology and population dynamics in a nursery of variable habitat and over a broader geographic range (southern Caribbean). In this study we investigated the movements of juvenile lemon sharks within the Los Roques nursery area using acoustic telemetry. Objectives of our study were to: (1) estimate core area and home range size, (2) examine variation in space use among size classes, (3) investigate relationships between lemon shark habitat use and environmental variables and fish distribution in the nursery.

## Materials and methods

### Study site

The Los Roques Archipelago is in the southern Caribbean, approximately 160 km north of Venezuela (11º43’–11º58’ N; 66º35’–6º 57’ W; Fig. 1). The archipelago covers an area of approximately 2,251 km$^2$ and comprises more than 40 small and low islands that are distributed around a central lagoon. Los Roques contains diverse coral forms, such as dense and diffuse patch reefs, fringing reefs, and two major barrier reefs, 24 and 30 km in length, located along the southern and eastern edges of the archipelago (Baamonde 2003). The importance of the coral reef ecosystems and diversity of marine fauna of this insular complex led to Los Roques being declared a national park in 1972. Following establishment of the national park, additional conservation

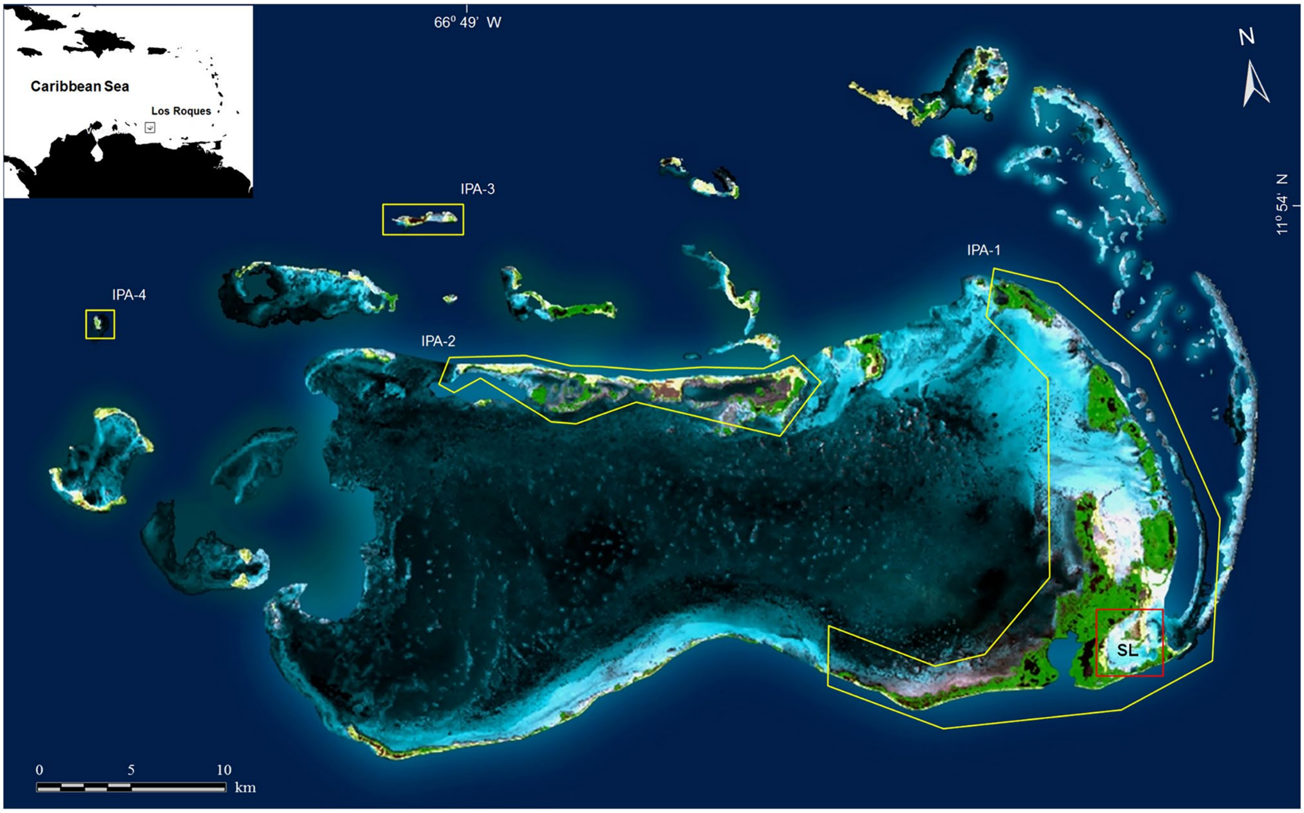


**Fig. 1** Los Roques Archipelago, showing the location of the *IPAs* integral protected areas and the *SL* Sebastopol Lagoon. Satellite image source: Digital Image Processing Center, Ministry for Science and Technology

measures have included the creation of four Integral Protected Areas (IPAs; Fig. 1), which are closed to boats, tourism activities and in 2012 commercial fishing of sharks was banned throughout the entire national park. This study was conducted in the Sebastopol Lagoon, located in the southeastern part of the archipelago within IPA-1 (Fig. 2) and which represents a lemon shark primary nursery area (Tavares et al. 2016).

## Nursery area habitat

Sebastopol Lagoon is a semi-enclosed body of water, with an irregular oval shape, an area of approximately 2.4 $km^2$ and a maximum depth of 2.5 m. The lagoon substrate consists of sand, which dominates the lagoon entrance and central areas, and mud, which dominates the inner parts of the lagoon. The sea bottom of the lagoon is partially covered by patches of seagrasses (*Thalassia testudinum* and *Syringodium filiforme*). Sea water flows into the lagoon, with current strength decreasing from the lagoon entrance to the inner region. Tidal amplitude is modest, with low and high tides of approximately 0.2 m and 0.4 m, respectively. Water temperature was recorded in Sebastopol Lagoon during this study using a data-logger (HOBO water temperature Pro-v2, Onset Computer Corp.) deployed at 2.0 m depth (Fig. 2). Lowest water temperatures during the study were recorded in the month of January 2014 (mean $\pm$ SD = 27.3 $\pm$ 0.80 °C, n = 744) and highest values during the month of September 2015 (mean $\pm$ SD = 30.3 $\pm$ 0.78 °C, n = 744).

Gillnet sampling to document fish abundance in the Sebastopol Lagoon nursery habitat was carried out by the Shark Tagging Program organized by the Centro para la Investigacion de Tiburones and conducted between 2001–2002 and 2005–2014. All fish captured in gillnets were identified to the species level and measured for total length or disc width (in the case of batoids). Details of standardized gillnet fishing methods in the Sebastopol Lagoon are described in Tavares et al. (2016). Relative abundance of fish captured in gillnets was standardized as the number of fish captured by daily fishing operations (fish $day^{-1}$). A gradient of relative abundance of fish in Sebastopol Lagoon was created using ArcGIS version 10.3.1 using the Kriging interpolation method to include estimated abundance values at unsampled locations (ESRI 2017).

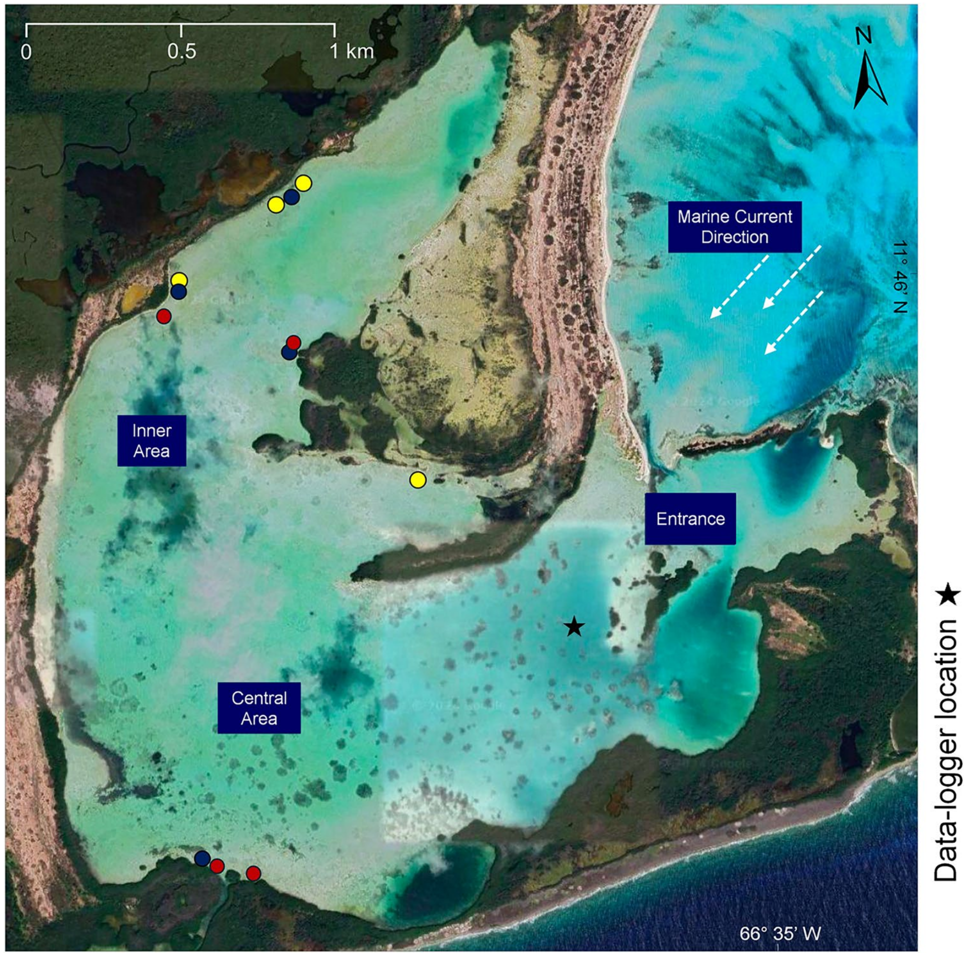


**Fig. 2** The Sebastopol Lagoon showing the capture sites of 12 juvenile lemon sharks, *Negaprion brevirostris*, by size class (smallest = yellow, middle = blue, largest = red). The location of the water temperature data-logger is indicated by the star

## Shark handling and tracking

Previous investigations have indicated that the Sebastopol Lagoon contains 100–120 individual juvenile lemon sharks that range in size between 54.9–118.0 cm total length. These sharks are born in the lagoon between June–August at an average size of 59.5 cm TL and remain in the lagoon until they reach a size of approximately 120 cm TL, which corresponds to an age of four years (Tavares et al. 2016, 2020). The aggregation of lemon sharks in Sebastopol Lagoon is composed primarily of age classes 0, 1 and 2 (Tavares 2005; 2020; Tavares et al. 2016; 2020). Sharks in our study represent a subset of this aggregation and were captured with multi-filament gillnets with 8.9–11.5 cm stretch mesh, 1.0–1.5 m depth and 25–100 m in length. Nets were set perpendicular to the shoreline between 18:00 and 24:00 h and checked for captured sharks and fish at 10–15 min intervals.

Sharks were captured primarily in the central and inner portions of Sebastopol Lagoon (Fig. 2). Sharks were removed from nets and placed in a marine corral, where they were measured (TL), sexed and tagged with an external roto-tag (Premier1 Supplies, USA). Nineteen lemon sharks were captured in gillnet fishing and were assigned to age groups (0 +, 1 +, and 2 +) based on their size, estimated time of parturition and growth rates and age-length relationships for lemon sharks at Los Roques (Tavares et al. 2020). Twelve of the 19 captured lemon sharks were selected for tracking for inclusion of two male and two female individuals of each of the three 0, 1 and 2 age groups. For tracked sharks, those between 64.5 and 71.1 cm TL were considered age class 0 +, sharks between 74.5 and 88.3 cm TL were considered age class 1 + and those 96.1–108.9 cm TL were considered age class 2 + (Table 1).

Acoustic transmitters with unique frequencies between 63 and 80 kHz (V13-1L, 13 × 36 mm, 6 g in water, ping period 3000 ms, nominal life span 183 d, Vemco, Nova Scotia) were implanted into the body cavity of sharks through small incision (2–3 cm) on the ventral body surface, just anterior to the pelvic fins. The incision was closed with 3–4 sutures (3–0 Coated Vicryl, Ethicon Inc.) absorbable suture material. Transmitters and surgical material were submerged in 95% ethanol for 10 min before each surgery. Sharks were placed in tonic immobility to facilitate implantation of transmitters (Watsky and Gruber 1990). Following implantation

**Table 1** Field surveys and numbers of tracking days conducted to the Sebastopol Lagoon, including information on lemon sharks fitted with acoustic transmitters and detection data. Sharks #1–4 were tagged in Feb 2014 and sharks #5–12 were tagged in April 2015

| Field surveys | | Sharks data | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Dates | 24-h tracking days | # | Sex | Length (TL cm) | Age (years) | | Detections | | Schoener index |
| | | | | | Individual | Group | *n* | % | |
| 14 Feb–20 Feb 2014 | 4 | 1 | Male | 64.5 | 0.4 | 0+ | 110 | 85.9 | **1.58** |
| 26 May–31 May 2014 | 4 | 2 | Female | 66.2 | 0.5 | 0+ | 114 | 89.1 | **1.41** |
| 05 Jun–07 Jun 2014 | 3 | 3 | Female | 98.3 | 2.2 | 2+ | 118 | 92.2 | 1.60 |
| 09 Jun–14 Jun 2014 | 5 | 4 | Female | 96.1 | 2.1 | 2+ | 102 | 79.7 | **1.47** |
| | | 5 | Female | 71.1 | 0.8 | 0+ | 144 | 81.8 | 1.82 |
| 21 Apr–25 Apr 2015 | 4 | 6 | Male | 68.9 | 0.7 | 0+ | 138 | 78.4 | 1.78 |
| 30 Abr–05 May 2015 | 4 | 7 | Male | 76.8 | 1.1 | 1+ | 131 | 74.4 | 1.73 |
| 08 Jun–11 Jun 2015 | 3 | 8 | Male | 74.5 | 1.0 | 1+ | 155 | 88.1 | 2.26 |
| 18 Jun–24 Jun 2015 | 5 | 9 | Female | 81.2 | 1.4 | 1+ | 142 | 80.7 | 2.03 |
| 22 Aug–26 Aug 2015 | 4 | 10 | Female | 88.3 | 1.7 | 1+ | 149 | 84.7 | 1.88 |
| 28 Aug–29 Aug 2015 | 2 | 11 | Male | 102.9 | 2.4 | 2+ | 145 | 82.4 | **2.42** |
| | | 12 | Male | 108.9 | 2.6 | 2+ | 136 | 77.3 | 2.25 |

Detections (n and %): monitoring periods during which an individual was detected as a proportion of all monitoring periods. Significant values for the Schoener Index are in bold

of transmitters, sharks were placed in the marine corral and monitored for 24–48 h to verify their recovery before being released at their site of capture. All tracked individuals were in healthy condition before release.

Four sharks were fitted with transmitters in Feb 2014 and tracked during four field surveys between 14 Feb and 15 Jun in 2014 (Table 1). An additional eight sharks were fitted with transmitters in Apr 2015 and tracked during six field surveys between 21 Apr and 29 Aug 2015. During field surveys in 2014 tagged sharks were monitored on 16 different days for 24-h periods and in 2015 tagged sharks were monitored on 22 different days for 24-h periods, representing a total of 304 different 3-h time intervals of monitoring on 38 different days (Table 1). During each 24-h monitoring period, a small boat equipped with an acoustic receiver (VR-100), directional hydrophone (VH-110) and GPS was used to search Sebastopol Lagoon during 3-h intervals (3:00, 6:00, 9:00, 12:00, 15:00, 18:00, 21:00, and 24:00 h). The small size of Sebastopol Lagoon enabled thorough searching of the entire lagoon in well under three hours and acquisition of locations for telemetered sharks that were present during each 3-h time interval. When a shark was detected, the boat was positioned as close as possible to the shark as determined by the directional hydrophone and receiver signal strength. When in proximity to the shark, latitude and longitude of the boat was recorded with the GPS as a proxy for location of the shark during that 3-h time interval (Rechisky and Wetherbee 2003). To minimize disturbance, speed of the boat was kept constant and similar to the speed of the shark. If a shark fitted with a transmitter was not detected during the 3-h search interval it was recorded as not present.

For each shark location, depth (m), bottom type (mud, sand, and seagrass) and surface temperature (using an infrared digital thermometer; General Technologies Corp.) were also recorded. Location data was organized using VUE tracking software (version 1.6.4).

## Space use

Location data was used to construct minimum convex polygons (MCP) and kernel utilization distributions (KUD) for individual sharks and for the three different size classes using the R packages *amt* and *adehabitatHR* (Calenge 2006; Signer et al. 2019). Although MCP tends to overestimate home range size, it is a useful metric for comparison among studies (Worton 1987). KUD is a more robust and conservative method that produces polygons representing levels of use based on probability densities (Worton 1987). KUD values of 50% were used as an estimate of "core area" and 95% KUD was used as an estimate of "home range" (see Heupel et al. 2019; Bouyoucos et al. 2020). Data autocorrelation was examined for each individual shark using the Schoener Index on the basis of the ratio of the mean distance between successive observations and the mean squared distance from the center of activity (Schoener 1981). Significant deviations of the Schoener Index from an expected value of 2.0 (i.e., $<1.6$ or $>2.4$) indicate a strong correlation between distance and time and a pattern of successive locations within a limited area.

Because MCP and KUD values did not differ significantly between sexes (F-test, Zar 1996), we compared 50%, 95% KUD and MCP values among size classes with sexes combined using an Analysis of Variance (ANOVA) and Tukey HSD pairwise test. To investigate temporal patterns of space use, we compared MCP and KUD values for diurnal [6:00–18:00 h] and nocturnal [18:00–24:00 h] time periods for each of the three size classes by applying a two-tail *t*-test. Additionally, mean depths between size classes were also examined for statistical differences using an ANOVA. All statistical analyses were performed using R (R Development Core Team 2020).

## Results

### Shark handling and tracking

A total of 1,584 unique locations were recorded for the 12 sharks tracked, ranging from 102–155 locations per individual. The proportion of 3-h sampling intervals during which individuals were detected as a proportion of total possible intervals detected ranged from 74.4 to 92.2% among sharks. All sharks were detected regularly throughout the study except for shark #9, which was located irregularly during the last 24-h sampling period of August 2015 and shark #7, which was not detected at all during the last two days of monitoring in August 2015.

### Space use

Continual detections of sharks, with few exceptions during all sampling intervals, suggested that all tracked sharks remained within Sebastopol Lagoon for nearly the entire 120 d and 130 d of monitoring in 2014 and 2015 respectively. Movements of individuals of the smallest size class were restricted to a small portion of the inner lagoon, with a core area along mangrove-lined shores, whereas sharks in the larger two size classes moved more extensively throughout the lagoon (Fig. 3). Home range and core area of the smallest size class of sharks were concentrated in the inner part of the lagoon, whereas individuals in the two larger size classes were distributed within both the inner and central portions of the lagoon and included areas more distant from mangrove-lined shores (Fig. 3). Sharks of all three size classes spent limited time in areas near the lagoon entrance, but most detections near the lagoon entrance were from sharks of the largest size class (Fig. 3). Three individuals in the smallest size class and one shark in the largest size class had significant Schoener Indices, indicating limited movement of these individuals during the study period. (Table 1).

The space use data for juvenile lemon sharks in the Los Roques Archipelago are shown in Table 2. Mean (± SD) MCP increased from 0.56 ± 0.44 $km^2$ for the smallest size class to 1.46 ± 0.08 $km^2$ and 1.57 ± 0.05 $km^2$ for middle and largest size classes, respectively. Home range (95% KUD) increased from a mean (± SD) of 0.42 ± 0.25 $km^2$ for the smallest size class to 1.11 ± 0.11 $km^2$ and 1.15 ± 0.22 $km^2$ for individuals in the middle and largest size classes, respectively. Core area (50% KUD) also increased with size, from a mean (± SD) of 0.13 ± 0.08 $km^2$ for the smallest size class to 0.33 ± 0.05 $km^2$ and 0.35 ± 0.07 $km^2$ for the middle and largest size classes, respectively. MCP, 95% KUD and 50% KUD all differed significantly among size classes (ANOVA, $F_{(2,9)} = 15.39–68.7$, $P < 0.05$); however, no significant difference was observed between the middle and largest size classes (Tukey's HSD test, $P > 0.05$). Overlap of MCP between the two largest size classes was 89%, more than double the MCP overlap between the smallest two size classes (40%) and between the smallest and largest size classes (43%). Home range and core areas did not differ between sexes (F-test, $F_{(1,10)} = 0.32–0.40$, $P > 0.05$) or between diel periods for any size class (t-test, $t_{(6)} = 3.02–3.18$, $P > 0.05$), although individuals of the largest size classes tended to utilize the central areas of the lagoon more often during the day and the coastline areas (along the mangroves) more during the night.

### Depth and substrate

Depth of water where sharks were located differed significantly among sizes classes, with shallowest depths for the smallest size class (mean ± SD = 0.36 ± 0.26 m, n = 508) intermediate depths for the middle size class (mean ± SD = 0.67 ± 0.29 m, n = 577) and greatest depths (mean ± SD = 0.94 ± 0.44 m, n = 501) for the largest size class (ANOVA, $F_{(2,1681)} = 434.35$, $P < 0.05$; Tukey HSD test, $P < 0.05$; Table 2). Substrate over which shark locations were recorded differed strikingly among size classes, with a transition from primarily mud for the smallest size class to sand and sea grass substrate for larger size classes (Fig. 4). For the smallest sharks, 94.8% of detections were recorded over mud, compared to only 52.0% and 25.0% of detections over mud for medium and large size classes respectively. Only 2.4% of detections for the smallest size class were recorded over sand, compared with 27.7% and 53.9% for medium and large size classes respectively. Only 2.8% of detections for the smallest size class were recorded over seagrass, whereas similar proportions of detections were recorded over seagrass for medium (20.3%) and large (21.2%) size classes.

### Abundance of fish

A total of 18 species of fishes, belonging to eight families, were captured in gillnet sampling carried out by the Shark Tagging Program between 2001–2002 and 2005–2014. The five most common species as a percentage of all individuals captured were bonefish (*Albula vulpes,* 15.0%), white grunt (*Haemulon plumierii,* 11.8%), yellow fin mojarra (*Gerres*

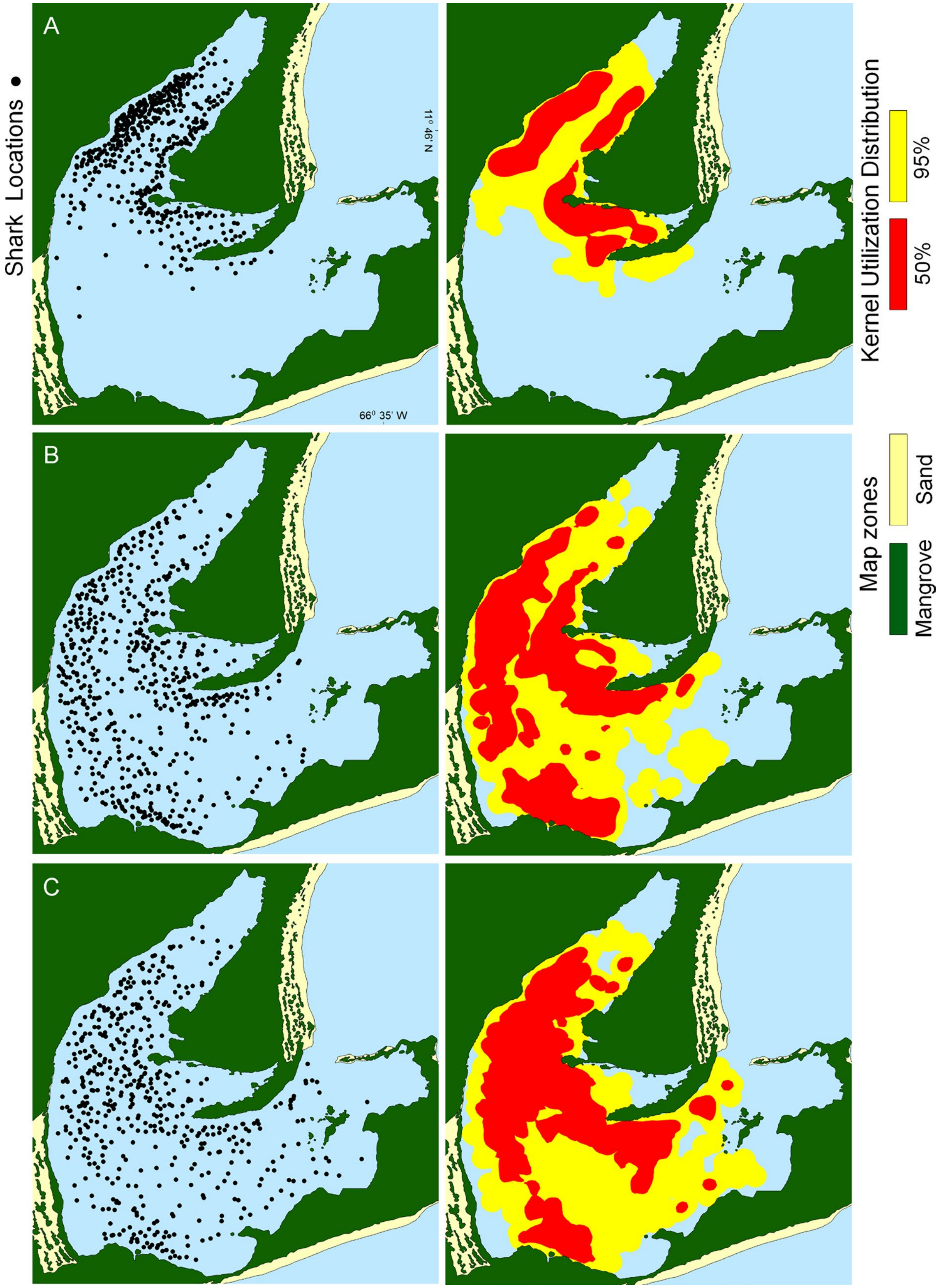


**Fig. 3** Raw locations and kernel utilization density (KUD) estimates (home range 95% and core area 50%) for three size classes (A = smallest, B= middle, C = largest)) of lemon sharks, *Negaprion brevirostris*, in the Sebastopol Lagoon

**Table 2** Mean minimum convex polygon and kernel utilization distributions (KUD, 50% and 95%) estimates for lemon sharks of three size classes tracked with acoustic transmitters in the Sebastopol Lagoon. Significant differences for MCP and KUD values among size classes (Tukey's HSD test, $P < 0.05$) are indicated in bold

| Shark size (TL cm) | Are group (Years) | Mean ± SD | | |
|---|---|---|---|---|
| | | MCP ($km^2$) | KUD 50% ($km^2$) | KUD 95% ($km^2$) |
| 64.5–71.1 | 0+ | **0.56 ± 0.21** | **0.13 ± 0.07** | **0.42 ± 0.12** |
| 74.5–88.3 | 1+ | 1.46 ± 0.08 | 0.33 ± 0.05 | 1.11 ± 0.11 |
| 96.1–108.9 | 2+ | 1.58 ± 0.05 | 0.35 ± 0.07 | 1.15 ± 0.22 |

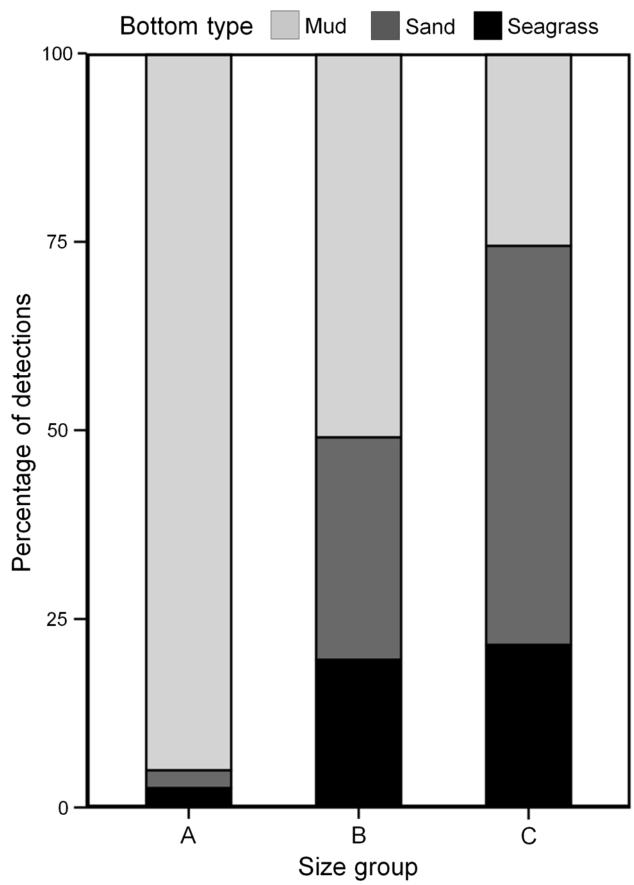


**Fig. 4** Proportion of locations recorded over three substrate types for three size classes (A = smallest, B= middle, C = largest) of lemon sharks, *Negaprion brevirostris*, in the Sebastopol Lagoon

*cinereus*, 11.6%), blue striped grunt (*H. sciurus*, 11.0%) and cravalle jack (*Caranx hippos*, 9.8%). Relative abundance of fishes was highest along the coastline and mangroves fringes, gradually decreasing from the inner lagoon to the lagoon entrance (Fig. 5). Overlap between nocturnal 95% KUD areas of high fish abundance ($\geq 5$ fish day$^{-1}$) increased with size and differences among size classes were most pronounced at night. Overlap between nocturnal 95% KUD and areas of high fish abundance for individuals in the smallest size class (14–31%) were lower than those of the medium size class (36–45%) and largest size class (40–52%).

## Discussion

Monitoring the movements of lemon sharks using acoustic telemetry in this study allowed the examination of spatial and temporal patterns of their use of the Los Roques nursery and revealed temporal consistency of space use, but variation among size classes. Logistics of working at Los Roques made continuous active acoustic tracking methods untenable and use of passive acoustic receivers in the Sebastopol Lagoon would also have been challenging given the potential risk of receiver loss from tourists and illegal fishers. The 3-h sampling intervals used in this study resulted in acquisition of nearly 1600 unique locations of lemon sharks and over 100 locations from each individual fitted with a transmitter and clearly demonstrated that Sebastopol Lagoon functions as a nursery area (Heupel et al. 2007). The observation that sharks were located within the lagoon during 83% of the 3-h time intervals and rare instances of consecutive 3-h time intervals without detection of individuals, supports previous studies suggesting that juvenile lemon sharks spend the majority of their time within the confines of Sebastopol Lagoon (Tavares et al. 2016). Heinrich et al. (2021) reported similar high relocation frequencies for juvenile lemon sharks within a small monitoring area at Bimini.

All lemon sharks in our study displayed repetitive movements within relatively small areas within the Sebastopol Lagoon. Home range sizes as estimated by MCP (1.20 $km^2$) and 95% KUD (0.89 $km^2$) were comparable to relatively small home range sizes reported for lemon sharks in nurseries at other locations. Although different studies have used a variety of methods to estimate activity space for lemon sharks in nurseries, home range sizes between 0.41 and 0.97 $km^2$ have been reported for lemon sharks in nurseries at Bimini (Morrissey and Gruber 1993b; Franks 2007). A relatively small total activity space of 0.11 $km^2$ was estimated for lemon sharks in a nursery in the US Virgin Islands (Legare et al. 2015). The finding that lemon sharks occupy relatively small home ranges has been consistent among studies in various nurseries, however, the nature of movements in different nurseries are influenced by a variety of factors, including the size of the nursery area, habitat type, predation risk and prey availability. For example, the US Virgin Islands nursery is relatively small (1.3 $km^2$), with correspondingly small home range estimates, compared to the North Sound of Bimini (3.3 $km^2$) and Sebastopol Lagoon (2.4 $km^2$) nursery areas and juvenile lemon shark movements differ in nurseries with and without mangroves

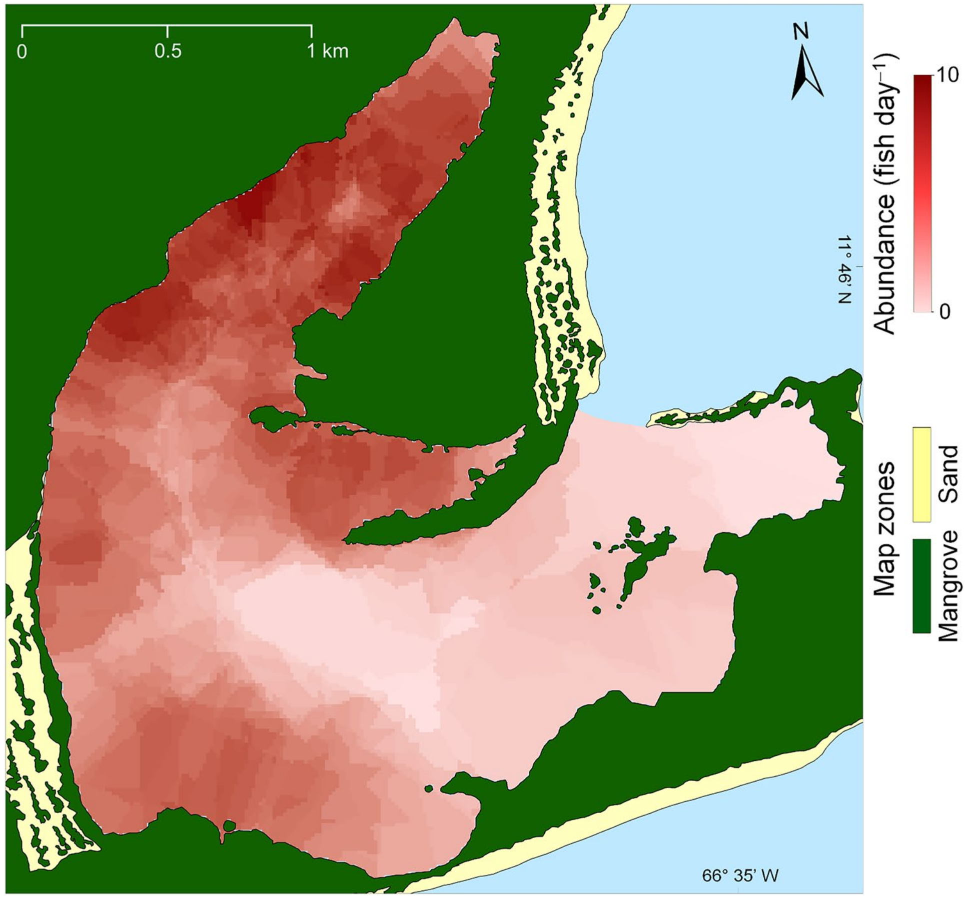


**Fig. 5** Gradient of relative abundance of fish (expressed as fish day$^{-.1}$) captured in gill net sampling conducted in the Sebastopol Lagoon between 2001–2002 and 2005–2014

and with different tidal amplitudes (Morrissey and Gruber 1993b; Wetherbee et al. 2007).

Our study revealed that lemon sharks exhibit size-specific movement patterns within the nursery at Los Roques. Sharks of sizes corresponding to young of the year (64.5–71.1 cm) were detected predominantly within the innermost portion of Sebastopol Lagoon, whereas sharks of sizes corresponding to age 1 + (74.5–88.3 cm) were located in both inner and central portions of the lagoon and sharks estimated to be 2 + year olds (96.1–108.9 cm) were located throughout the entire lagoon, including the near the entrance. Our study and previous investigations (Tavares 2005, 2009; Tavares et al. 2016, 2020) provide evidence that lemon sharks largely restrict their movements to Sebastopol Lagoon and typically leave the nursery area around four years of age and at a size of approximately 120 cm TL. When lemon sharks leave their nurseries, they continue to expand their habitat use (Gruber et al. 1988; Tavares et al. 2016). Activity space expansion with age/size have been observed for lemon sharks at Bimini (Morrissey and Grubber 1993b; Sundström et al. 2001; Franks 2007) and Atol das Rocas, Brazil (Wetherbee et al. 2007). Yeiser et al. (2008) also reported much larger home ranges (6.07–63.57 km$^2$) for sub-adult lemon sharks (195–280 cm TL) compared to those of juveniles. Increased activity space with age has been documented in other species of sharks, including blacktip (*Carcharhinus limbatus*), pigeye (*C. amboinensis*) and blacktip reef (*C. melanopterus*) sharks (Heupel et al. 2004; Knip et al. 2011; Bouyoucos et al. 2020). Home range expansion with age is exhibited by many marine vertebrates and is thought to reflect a need for acquisition of more energy, reduced vulnerability to predation and an increased ability to capture prey as individuals attain greater experience and larger sizes (Wetherbee et al. 1990; Lowe et al. 1996; Makowski et al. 2006; Guttridge et al. 2012).

Variability in use of the Los Roques nursery among size classes of lemon sharks also extended to depth of water and substrate characteristic of areas within the lagoon where they concentrated their movements, as well as overlap with areas of high fish abundance. The smallest size class of lemon sharks largely restricted their movements to the inner portion of Sebastopol Lagoon, predominantly in shallower water, over muddy substrate and along mangrove-lined shores. Locations of the two larger size classes shared some characteristics, but also demonstrated differences in the use of the nursery area. These larger size classes were located in slightly deeper water and occurred more frequently over sand or seagrass substrate and less frequently along mangrove-lined shorelines compared with the smallest size class. Space use, depth, substrate type and overlap with fish abundance data all indicated that as lemon sharks increase in size, they expand their movements within the Sebastopol Lagoon to include more central portions of the lagoon, eventually occurring near the lagoon entrance with access to a variety of other habitats.

The majority of fishes captured in gill nets in Sebastopol Lagoon (families Gerridae, Lutjanidae, Carangidae, Haemulidae, and Scaridae) closely resemble major prey of lemon sharks in other nurseries (Cortes and Gruber 1990; Newman et al. 2010). Mean sizes of fishes captured in the Sebastopol Lagoon were also similar to size of prey consumed by lemon sharks in Bimini nurseries (Newman et al. 2010, 2012). High use of areas of the Sebastopol Lagoon by lemon sharks where high fish abundance was recorded, especially near mangrove-lined shores, suggest that these areas confer a benefit of access to abundant prey as well as refuge from predators. Other species such as blacktip and blacktip reef sharks have also shown movement patterns that demonstrate trade-offs between predator avoidance and access to prey (Heupel and Simpfendorfer 2005; Papastamatiou et al. 2009). Although apparently of little significance at Los Roques, specific environmental conditions (i.e. water temperature, salinity, currents, and anthropogenic disturbances) in individual nursery areas may also influence temporal and spatial patterns of habitat use in lemon sharks and other species of sharks (Tricas 1979; Morrissey and Gruber 1993a; Heithaus 2001; DiBattista et al. 2011).

Affinity for shallow water near mangrove-lined shores, such as observed in our study, is a common behavior for lemon sharks in multiple lemon shark nurseries and thought to reflect strong selection pressure for predator avoidance (Morrissey and Gruber 1993a; Wetherbee et al. 2007; Murchie et al. 2010; Legare et al. 2015; Hussey et al. 2017; Dhellemmes et al. 2021). Morrissey and Gruber (1993a) reported that lemon sharks in the Bimini nursery were found primarily over rocky/sandy substrate, suggesting that shallow depth and proximity to mangroves may outweigh substrate type in importance for predator avoidance and access to prey. Mangroves are one of the most important and productive coastal ecosystems of the tropical and subtropical regions, providing substrate stability, source of food, breeding grounds for many food fishes, as well as protection against predators and refuge, not just for lemon sharks, but for a variety of fauna and flora (Feller et al. 2010; Kathiresan 2012; Kanno et al. 2023).

Use of nursery areas by juvenile lemon sharks is characterized by both flexibility and consistency, depending on environmental and biological characteristics of the nursery. In our study, consistency of habitat use of lemon sharks in the Los Roques nursery was evident in their movements being independent of time of day, water temperature and sex; but they clearly altered their use of the nursery as they increased in size. In contrast, lemon sharks in the Bimini nursery appear to be more active at crepuscular and night periods (Gruber 1982; Gruber et al. 1988; Sundström et al. 2001), but they also occupied water within a narrow temperature range (Morrissey and Gruber 1993a). Lemon sharks at Atol das Rocas moved regularly between a protected tidal creek at high tide and small tide pools at low tide in response to dramatic tidal fluctuations at the nursery (Wetherbee et al. 2007).

Our study contributes to the body of evidence indicating that lemon sharks consistently use small discrete bodies of water such as lagoons and tidal creeks as nursery areas during the initial years of their lives throughout their range. These nurseries, which are often mangrove-lined, function to optimize prey availability and refuge from predators. Although lemon sharks typically limit their movements to shallow water, near mangrove-lined shores (Morrissey and Gruber 1993a, 1993b; Franks 2007; Guttridge et al. 2012), they are also able to take advantage of nurseries where mangroves are absent through nursery-specific habitat selection that also reduces risk of predation but ensures adequate access to prey (Wetherbee et al. 2007). Strong selective pressure for predator avoidance appears to be a primary driver of small home ranges and restricted habitat use observed for lemon sharks within the various nursery areas used. As lemon sharks age, predation risk declines and they expand their movements and after several years they depart nurseries and move to deeper, reef-associated habitats. Ontogenetic shifts in habitat use, as observed for lemon sharks, are thought to offer advantages for enhanced prey capture by older, larger and more experienced sharks (Wetherbee et al. 1990).

Results of our study corroborate general patterns of habitat use described for lemon sharks within nurseries in previous studies and add to the body of knowledge on the spatial ecology of juvenile lemon sharks (Morrissey and Gruber 1993a; Wetherbee et al. 2007; Murchie et al. 2010; Legare et al. 2015). Habitat use of lemon sharks within nurseries in general is characterized by restricted movements, small home ranges and often, a strong association with mangrove systems. These patterns of movement as well as adequate availability of such habitat are presumably important for reduced mortality of lemon sharks during their first few years of life. Therefore, given the widespread decline of many shark populations (Dulvy et al. 2021), concerns regarding the sustainability of lemon shark populations (Sundström 2015) and the wide-spread degradation of mangrove habitats (Bryan-Brown et al. 2020), there is a growing interest in understanding the role of nurseries in enhancing species survival and contributing towards improved management of shark populations. For species such as lemon sharks, which occupy small, discrete and variable nurseries, temporal and spatial patterns of habitat use across multiple nurseries are important considerations for achieving long-term sustainability of their populations.

**Acknowledgements** Logistic support for this study was provided by Casita La Macuira (owned by P. Marquez), Línea Turística Aerotuy, Aquatic Dive Center, Eco-buzos, Arrecife Dive, Aquarena, La Chuchera, Oscar Shop, and Aguasal. We thank the volunteers and students who participated in the field work, and the captains "Felo", "Tonga" and "Parape" who also contributed to the study. We also thank M. Hoyos for providing advice about telemetry equipment and G. Velazquez and O. Fleischer for help with spatial analysis and mapping.

**Author contributions** RT conceived the study and led fundraising efforts. RT and CDK performed data collection and analysis. The first draft of the manuscript was written by RT and all authors commented on previous versions of the manuscript. The final draft of the manuscript was written by BMW. All authors read and approved the final manuscript.

**Funding** This study was supported by the Fondo Nacional de Ciencia, Tecnologia e Innovacion through the research Grants No.73-0101-10 73-0 and 3-181-06-436 3 Additional funds were provided by the Instituto Venezolano de Investigaciones Cientificas , Centro para la Investigacion de Tiburones, The Ocean Foundation and Pew Charitable Trusts

**Data availability** The data used in this study are available from the corresponding author upon request.

## Declarations

**Conflicts of interest** The authors have no relevant financial or non-financial interests to disclose.

**Ethical approval** This research was conducted under research permits from the Instituto Nacional de Parques (INPARQUES) and Instituto Nacional de Pesca, and under the animal ethics guidelines of the Instituto Venezolano de Investigaciones Cientificas.

**Consent for publication** All authors consent to the publication of this manuscript.

## References


Baamonde JM (2003) Origen y formación del archipiélago. In: Los PNA (ed) Zamarro J. Roques, Agencia Española de Cooperación Internacional Caracas, pp 85–98

Barker MJ, Gruber SH, Newman SP, Schluessel V (2005) Spatial and ontogenetic variation in growth of nursery-bound juvenile lemon sharks, *Negaprion brevirostris*: a comparison of two age-assigning techniques. Environ Biol Fish 72:343–355. https://doi.org/10.1007/s10641-004-2584-3

Begon M, Townsend CR, Harper JL (2006) Ecology: from individuals to ecosystems, 4th edn. Blackwell Publishing, Oxford

Bouyoucos IA, Romain M, Azoulai L, Eustache K, Mourier J, Rummer JL, Planes S (2020) Home range of newborn blacktip reef sharks (*Carcharhinus melanopterus*), as estimated using mark-recapture and acoustic telemetry. Coral Reefs 39:1209–1214. https://doi.org/10.1007/s00338-020-01965-z

Branstetter S (1990) Early life-history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. In: Pratt HL Jr, Gruber SH, Taniuchi T (eds) Elasmobranchs as living resources: advances in biology, ecology, systematics and the status of the fisheries, NOAA Technical Report 90, National Marine Fisheries Service, Silver Spring, MD, pp 17–28.

Bryan-Brown DN, Connolly RM, Richards DR, Adame F, Friess DA, Brown CJ (2020) Global trends in mangrove forest fragmentation. Sci Rep 10:7117. https://doi.org/10.1038/s41598-020-63880-1

Calenge C (2006) The package "*adehabitat*" for the R software: a tool for the analysis of space and habitat use by animals. Ecol Modell 197(3–4):516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Castro JI (1993) The shark nursery of bulls bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Environ Biol Fishes 38:37–48. https://doi.org/10.1007/BF00842902

Compagno LJV (1984) Sharks of the world: an annotated and illustrated catalogue of shark species known to date. FAO Fisheries Synopsis

Cortes E, Gruber SH (1990) Diet, feeding habits and estimates of daily ration of young lemon sharks, Negaprion brevirostris (Poey). Copeia 1:204–218. https://doi.org/10.2307/1445836

DeAngelis BM, McCandless CT, Kohler NE, Recksiek CW, Skomal GB (2008) First characterization of shark nursery habitat in the United States Virgin Islands: evidence of habitat partitioning by two shark species. Mar Ecol Prog Ser 358:257–271. https://doi.org/10.3354/meps07308

Dhellemmes F, Finger JS, Laskowski KL, Guttridge TL, Krause J (2020) Comparing behavioural syndromes across time and ecological conditions in a free-ranging predator. Anim Behav 162:23–33. https://doi.org/10.1016/j.anbehav.2020.01.009

Dhellemmes F, Smukall MJ, Guttridge TL, Krause J, Hussey NE (2021) Predator abundance drives the association between exploratory personality and foraging habitat risk in a wild marine meso-predator. Func Ecol 35(9):1972–1984. https://doi.org/10.1111/1365-2435.13874

DiBattista JD, Feldheim KA, Garant D, Gruber SH, Hendry AP (2011) Anthropogenic disturbance and evolutionary parameters: a lemon shark population experiencing habitat loss. Evol Appl 4(1):1–17. https://doi.org/10.1111/j.1752-4571.2010.00125.x

Dulvy NK, Pacoureau N, Rigby CL, Pollom RA, Jabado RW, Ebert DA, Finucci B, Pollock CM, Cheok J, Derrick DH, Herman KB, Sherman CS, VanderWright WJ, Lawson JM, Walls RH, Carlson JK, Charvet P, Bineesh KK, Fernando D, Ralph GM, Matsushiba JH, Hilton-Taylor C, Fordham SV, Simpfendorfer CA (2021) Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. Curr Biol 31(21):4773–4787. https://doi.org/10.1016/j.cub.2021.08.062

ESRI (2017) ArcGIS Online10.3.1. Redlands C.A., Environmental System Research Institute

Feldheim KA, Gruber SH, Ashley MV (2002) The breeding biology of lemon sharks at a tropical nursery lagoon. Proc Biol Sci 269:1655–1661. https://doi.org/10.1098/rspb.2002.2051

Feller IC, Lovelock CE, Berger U, McKee KL, Joye SB, Ball MC (2010) Biocomplexity in mangrove ecosystems. Annu Rev Mar Sci 2:395–417. https://doi.org/10.1146/annurev.marine.010908.163809

Finger JS, Guttridge TL, Wilson ADM, Gruber SH, Krause J (2018) Are some sharks more social than others? Short-and long-term consistencies in the social behavior of juvenile lemon sharks. Behav Ecol Sociobio 72:1–10. https://doi.org/10.1007/s00265-017-2431-0

Franks BR (2007) The spatial ecology and resource selection of juvenile lemon sharks (*Negaprion brevirostris*) in their primary nursery areas. Drexel University

Freitas RHA, Rosa RS, Gruber SH, Wetherbee BM (2006) Early growth and juvenile population structure of lemon sharks *Negaprion brevirostris* in the Atol das Rocas Biological

Reserve, off north-east Brazil. J Fish Biol 68(5):1319–1332. https://doi.org/10.1111/j.0022-1112.2006.00999.x

Freitas RHAD, Rosa RS, Wetherbee BM, Gruber SH (2009) Population size and survivorship for juvenile lemon sharks (*Negaprion brevirostris*) on their nursery grounds at a marine protected area in Brazil. Neotrop Ichthyol 7:205–212. https://doi.org/10.1590/S1679-62252009000200011

Garla RC, Chapman DD, Wetherbee BM, Shivji MS (2006) Movement patterns of young Caribbean reef sharks, *Carcharhinus perezi*, at Fernando de Noronha Archipelago, Brazil: the potential of marine protected areas for conservation of a nursery ground. Mar Biol 149:189–199. https://doi.org/10.1007/s00227-005-0201-4

Gruber SH (1982) Role of the lemon shark, *Negaprion brevirostris* (Poey), as a predator in the tropical marine environment: a multidisciplinary study. Fla Sci 45:46–75

Gruber SH, Nelson DR, Morrissey JF (1988) Patterns of activity and space utilization of juvenile lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian lagoon. Bull Mar Sci 43(1):61–76

Guttridge TL, Gruber SH, Franks BR, Kessel ST, Gledhill KS, Uphill J, Krause J, Sims DW (2012) Deep danger: intraspecific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris*. Mar Ecol Prog Ser 445:279–291. https://doi.org/10.3354/MEPS09423

Heinrich D, Dhellemmes F, Guttridge TL, Smukall M, Brown C, Rummer J, Rummer J, Gruber SH, Huveneers C (2021) Short-term impacts of daily feeding on the residency, distribution and energy expenditure of sharks. Anim Behav 172:55–71. https://doi.org/10.1016/j.anbehav.2020.12.002

Heithaus MR (2001) The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. Environ Biol Fish 61:25–36. https://doi.org/10.1034/j.1600-0706.2001.920315.x

Heithaus MR (2007) Nursery areas as essential shark habitats: a theoretical perspective. Am Fish Soc Symp 50:3–13

Heithaus MR, Vaudo JJ (2012) Predator–prey interactions. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, New York, pp 505–546

Henderson AC, McClellan K, Calosso M (2010) Preliminary assessment of a possible lemon shark nursery in the Turks and Caicos Islands, British West Indies. Carib J Sci 46:29–38

Heupel MR, Simpfendorfer CA (2005) Quantitative analysis of aggregation behavior in juvenile blacktip sharks. Mar Biol 147:1239–1249. https://doi.org/10.1007/s00227-005-0004-7

Heupel MR, Simpfendorfer CA, Hueter RE (2004) Estimation of shark home ranges using passive monitoring techniques. Environ Biol Fish 71:135–142. https://doi.org/10.1023/B:EBFI.0000045710.18997.f7

Heupel MR, Carlson JK, Simpfendorfer CA (2007) Shark nursery areas: concepts, definition, characterization and assumptions. Mar Ecol Prog Ser 337:287–297. https://doi.org/10.3354/meps337287

Heupel MR, Kanno S, Martins AP, Simpfendorfer CA (2018) Advances in understanding the roles and benefits of nursery areas for elasmobranch populations. Mar Freshwat Res 70(7):897–907. https://doi.org/10.1071/MF18081

Heupel MR, Munroe SEM, Lédée EJI, Chin A, Simpfendorfer CA (2019) Interspecific interactions, movement patterns and habitat use in a diverse coastal shark assemblage. Mar Biol 166:1–17. https://doi.org/10.1007/s00227-019-3511-7

Holland KN, Wetherbee BM, Peterson JD, Lowe CG (1993) Movement and distribution of hammerhead shark pups on their natal grounds. Copeia 1993(2):495–502. https://doi.org/10.2307/1447150

Hussey NE, DiBattista JD, Moore JW, Ward EJ, Fisk AT, Kessel S, Guttridge TL, Feldheim KA, Franks BR, Gruber SH, Weideli OC (2017) Risky business for a juvenile marine predator? Testing the influence of foraging strategies on size and growth rate under natural conditions. Proc Roy Soc B: Biol Sci 284(1852):20170166. https://doi.org/10.1098/rspb.2017.0166

Kanno S, Heupel MR, Sheaves M, Simpfendorfer C (2023) Mangrove use by sharks and rays: a review. Mar Ecol Prog Ser 724:167–183. https://doi.org/10.3354/meps14452

Kathiresan K (2012) Importance of mangrove ecosystem. Int J Mar Sci 2(10):70–89. https://doi.org/10.5376/ijms.2012.02.0010

Knip DM, Heupel MR, Simpfendorfer CA, Tobin AJ, Moloney J (2011) Ontogenetic shifts in movement and habitat use of juvenile pigeye sharks *Carcharhinus amboinensis* in a tropical nearshore region. Mar Ecol Prog Ser 425:233–246. https://doi.org/10.3354/meps09006

Knip DM, Heupel MR, Simpfendorfer CA (2012) Evaluating marine protected areas for the conservation of tropical coastal sharks. Biol Conserv 148:200–209. https://doi.org/10.1016/j.biocon.2012.01.008

Latour RJ, Gartland J, Peterson CD (2022) Ontogenetic niche structure and partitioning of immature sandbar sharks within the Chesapeake Bay nursery. Mar Bio 169(76):1–17. https://doi.org/10.1007/s00227-022-04066-3

Legare B, Kneebone J, DeAngelis B, Skomal G (2015) The spatiotemporal dynamics of habitat use by blacktip (*Carcharhinus limbatus*) and lemon (*Negaprion brevirostris*) sharks in nurseries of St. John. United States Virgin Islands Mar Biol 162:1–18. https://doi.org/10.1007/s00227-015-2616-x

Lowe CG, Wetherbee BM, Crow GL, Tester AL (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Environ Biol Fish 47:203–211. https://doi.org/10.1007/BF00005044

MacNeil MA, Chapman DD, Heupel M et al (2020) Global status and conservation potential of reef sharks. Nature 583(7818):801–806. https://doi.org/10.1038/s41586-020-2519-y

Makowski C, Seminoff JA, Salmon M (2006) Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas* L.) on shallow reef habitats in Palm Beach, Florida, USA. Mar Biol 148:1167–1179. https://doi.org/10.1007/s00227-005-0150-y

Morrissey JF, Gruber SH (1993a) Habitat selection by juvenile lemon sharks, *Negaprion brevirostris*. Environ Biol Fish 38:311–319. https://doi.org/10.1007/BF00007524

Morrissey JF, Gruber SH (1993b) Home range of juvenile lemon sharks. Negaprion Brevirostris Copeia 2:425–434. https://doi.org/10.2307/1447141

Murchie KJ, Schwager E, Cooke SJ, Danylchuk AJ, Danylchuk SE, Goldberg TL, Suski CD, Philipp DP (2010) Spatial ecology of juvenile lemon sharks (*Negaprion brevirostris*) in tidal creeks and coastal waters of Eleuthera, The Bahamas. Environ Biol Fish 89:95–104. https://doi.org/10.1007/s10641-010-9693-y

Newman SP, Handy RD, Gruber SH (2010) Diet and prey preference of juvenile lemon sharks, *Negaprion brevirostris*. Mar Ecol Prog Ser 398:221–234. https://doi.org/10.3354/meps08334

Newman SP, Handy RD, Gruber SH (2012) Ontogenetic diet shifts and prey selection in nursery bound lemon sharks, *Negaprion brevirostris*, indicate a flexible foraging tactic. Environ Biol Fish 95:115–126. https://doi.org/10.1007/s10641-011-9828-9

Papastamatiou YP, Lowe CG, Caselle JE, Friedlander AM (2009) Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. Ecology 90(4):996–1008. https://doi.org/10.1890/08-0491.1

R Development Core Team (2020) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://R-project.org/, Accessed 12 Nov 2022.

Ramirez HN, Cervigon F (2004) Los peces del Archipiélago Los Roques. Agencia Española de Cooperación, Caracas

Rechisky EL, Wetherbee BM (2003) Short-term movements of juvenile and neonate sandbar sharks, *Carcharhinus plumbeus*, on their nursery grounds in Delaware Bay. Environ Biol Fish 68:113–128. https://doi.org/10.1023/B:EBFI.0000003820.62411.cb

Schoener TW (1981) An empirically based estimate of home range. Theor Popul Biol 20:281–325. https://doi.org/10.1016/0040-5809(81)90049-6

Signer J, Fieberg J, Avgar T (2019) Animal movement tools (*amt*): R package for managing tracking data and conducting habitat selection analyses. Ecol Evol 9(2):880–890. https://doi.org/10.1002/ece3.4823

Simpfendorfer CA, Heupel MR (2012) Assessing habitat use and movement. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, New York, pp 579–601

Simpfendorfer CA, Milward NE (1993) Utilization of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. Environ Biol Fish 37:337–345. https://doi.org/10.1007/BF00005200

Sundström LF (2015) *Negaprion brevirostris*: the IUCN red list of threatened species 2015, e.T39380A81769233. https://doi.org/10.2305/IUCN.UK.2015.RLTS.T39380A81769233.en

Sundström LF, Gruber SH, Clermont SM, Correia JPS, de Marignac JRC, Morrissey JF, Lowrance CR, Thomassen L, Oliveira MT (2001) Review of elasmobranch behavioral studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. Environ Biol Fish 60:225–250. https://doi.org/10.1023/A:1007657505099

Tavares R (2005) Abundance and distribution of sharks in Los Roques Archipelago National Park and other Venezuelan oceanic islands. Cienc Mar 31:441–454. https://doi.org/10.7773/cm.v31i2.62

Tavares R (2009) Análisis de abundancia, distribución y tallas de tiburones capturados por pesca artesanal en el parque nacional Archipiélago Los Roques. Venezuela Interciencia 34(7):463–470

Tavares R (2020) Survival estimates of juvenile lemon sharks based on tag-recapture data at Los Roques Archipelago. Southern Caribbean. Carib J Sci 50(1):171–177. https://doi.org/10.18475/cjos.v50i1.a17

Tavares R, Rodriguez JP, Morales M (2016) Nursery area and size structure of the lemon shark population, *Negaprion brevirostris* (Poey, 1868), in Los Roques Archipelago National Park. Venezuela. Univ Sci 21(1):33–52. https://doi.org/10.11144/JAVERIANA.SC21-1.NAAS

Tavares R, Wetherbee BM, Rodriguez JP (2020) Age and growth of juvenile lemon sharks (*Negaprion brevirostris*) at an insular nursery in the southern Caribbean. Mar Freshwat Res 72(2):163–172. https://doi.org/10.1071/MF20070

Tricas TC (1979) Relationships of the blue shark, *Prionace glauca*, and its prey species near Santa Catalina Island. California Fish Bull 77(1):175–182

Watsky M, Gruber S (1990) Induction and duration of tonic immobility in the lemon shark, *Negaprion brevirostris*. Fish Physiol Biochem 8:207–210. https://doi.org/10.1007/bf00004459

Wetherbee BM, Gruber SH, Cortes E (1990) Diet, feeding habits, digestion and consumption in sharks, with especial reference in lemon shark, *Negaprion brevirostris*. In: Pratt HL Jr, Gruber SH, Taniuchi T (eds) Elasmobranchs as living resources: advances in biology, ecology, systematics and the status of the fisheries. NOAA Technical Report 90, National Marine Fisheries Service, Silver Spring, pp 29–47.

Wetherbee BM, Gruber SH, Rosa R (2007) Movement patterns of juvenile lemon sharks *Negaprion brevirostris* within Atol das Rocas, Brazil: a nursery characterized by tidal extremes. Mar Ecol Prog Ser 343:283–293. https://doi.org/10.3354/meps06920

White ER, Myers MC, Flemming JM, Baum JK (2015) Shifting elasmobranch community assemblage at Cocos Island: an isolated marine protected area. Conserv Biol 29(4):1186–1197. https://doi.org/10.1111/cobi.12478

Worton BJ (1987) A review of models of home range for animal movement. Ecol Model 38:277–298. https://doi.org/10.1016/0304-3800(87)90101-3

Yeiser BG, Heupel MR, Simpfendorfer CA (2008) Occurrence, home range and movement patterns of juvenile bull (*Carcharhinus leucas*) and lemon (*Negaprion brevirostris*) sharks within a Florida estuary. Mar Freshwat Res 59:489–501. https://doi.org/10.1071/MF07181

Zar J (1996) Biostatistical Analysis. Prentice Hall, New Jersey


**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.