



## Original Articles

# Habitat selection and spatial behaviour of vulnerable juvenile lemon sharks: Implications for conservation

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## ABSTRACT

Nearshore environments represent important habitat for many marine vertebrates during their early-life stages. Globally, these coastal sites are impacted by human activities that have the potential to negatively impact biodiversity in ways we do not yet fully appreciate. To improve our understanding of the relevance of mangrove removal in tropical elasmobranch nursery grounds, we studied the globally Vulnerable lemon shark (*Negaprion brevirostris*) in a mangrove-fringed lagoon in Bimini, The Bahamas, following a decade of coastal development and habitat disruption. We used two years of acoustic telemetry detections and generalised linear mixed models (GLMMs) to evaluate the link between juvenile shark spatial behaviour and six features of their physical environment. AIC-adjusted model-averaged predictions of habitat selection demonstrated that distance from the central mangrove forest was the most important feature for sharks. After updating model averaging to account for overall preference for proximity to the central forest, we found that medium density seagrass was secondarily preferred over all other habitat types (bare sand, sargassum, urban and rocky outcrops, and deep water) within the core use area (probability of use  $\geq 50\%$ ). Locally, our results support including this core area in future marine protected area considerations. More broadly, in the face of rapid global population declines of many elasmobranchs and wide-spread habitat fragmentation in coastal marine nurseries, we identified widely applicable habitat features underpinning an area of high ecological significance for a threatened shark during a vulnerable life stage and outlined a habitat selection framework suitable for using marine vertebrate movement data as ecological indicators for future applied conservation.

## 1. Introduction

Species extinction is a critical threat to marine vertebrate diversity (Herbert-Read et al., 2022). This is acutely felt by elasmobranchs (Pacoureau et al., 2021; Finucci et al., 2024), where slow life histories put species at increased risk from exploitation and population declines (Dulvy et al., 2017). Understanding the spatial behaviour of these marine vertebrates, particularly during vulnerable life stages, is therefore critical to identify and address species-level threats, particularly in light of existential anthropogenic pressures (Queiroz et al., 2016; White et al.,

2019b).

Although many elasmobranchs are being fished at unsustainable rates as adults (Pacoureau et al. 2021), unchecked threats to immature recruitment (Cortés and Brooks, 2018; Hutchinson et al., 2015) and habitat (Yan et al. 2021) can also have strong impacts on population growth. For elasmobranchs in coastal environments, the presence of particular habitat types does not necessarily directly afford species protection from anthropogenic disturbances like fishing pressure (Yan et al. 2021). Therefore in evaluating what is, or could be, critical habitat for coastal elasmobranchs we also must evaluate the strength of the

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relationship between habitat types and species use in light of anthropogenic sources of disturbance and exploitation (e.g. Letessier et al., 2019).

For many shark species, coastal habitats can provide important services in early life (Kinney and Simpfendorfer, 2009; Leurs et al., 2023; Sievers et al., 2019). Mangrove-fringed lagoons are a hot spot of juvenile teleost abundance (Zu Ermgassen et al., 2020), thereby providing reliable prey resources for juvenile elasmobranchs (Wetherbee et al., 1990; Kanno et al., 2019). The physical structure of coastal fringing habitats can also provide protection from predators, as large-bodied sharks may not be able to access the habitat either at all or during particular tidal phases (Guttridge et al. 2012; Kanno et al., 2019). Coastal-fringing habitats and other topographic features may also be used as indicators of reliable access to conspecifics, both at a small scale (Anderson et al., 2023; Guttridge et al., 2011) and a larger regional scale (e.g. Papastamatiou et al., 2021). Aggregation, or more broad social behaviour, is likely to have many positive effects both for reproduction (Anderson et al., 2023), energetics (e.g. Hosegood et al., 2019), anti-predator grouping (Guttridge et al., 2012), and potentially even social information transfer (Brown & Laland, 2003; Crane & Ferrari, 2015).

Despite the numerous hypothesised drivers of the spatially explicit association between juvenile sharks and certain habitat features and the benefit this information could provide for conservation management in the face of increasing extinction risk (Pacoureau et al., 2021; Dulvy et al., 2017), detailed studies of spatial behaviour in juvenile elasmobranchs remain rare (e.g. Edwards et al., 2022). Accordingly, the ecological indicators underpinning spatial aggregations of juvenile elasmobranchs remain a major knowledge gap (e.g. Yan et al., 2021), one which studies of habitat selection could begin to bridge.

Building on previous research (e.g. Dhellemmes et al. 2020a & 2020b), we ask what habitat features drive juvenile shark spatial behaviour in a mangrove-fringed nursery after a decade of habitat disruption, and how we might use this information for evidence-based management of this population and others in tropical coastal environments. To do so, we studied the variation and selection in space use of individual juvenile lemon sharks (*Negaprion brevirostris*, IUCN Red Listed 'Vulnerable'), using passive acoustic telemetry, throughout a semi-tidal mangrove-fringed lagoon, in Bimini, The Bahamas, over a two-year period. Juvenile lemon sharks show high site fidelity to this lagoon year on year (Chapman et al., 2009), and lineage studies have established that this population shows natal philopatry (Feldheim et al., 2002), thereby meeting the criteria for Bimini to be considered a shark nursery ground (Heupel, Carlson, & Simpfendorfer, 2007).

Research evaluating the habitat use of large elasmobranch species in Bimini suggested that establishing a marine protected area (proposed as the North Bimini Marine Protected Area, NBMPA) could significantly contribute to regional elasmobranch management (van Zinnicq Bergmann et al., 2022) and highlighted the importance of Bimini's natural environment for biodiversity conservation and marine protection targets (van Zinnicq Bergmann et al., 2022). However, the implementation of the NBMPA faced complex socio-political challenges and has not progressed (Supporting Information Item 1) (Wise, 2014). Meanwhile, the interior coastline of the lagoon experiences gradual coastal development resulting in the loss of mangrove habitat (Gruber et al., 2001; Jennings et al., 2012; Kessel et al., 2016) coinciding with a decline in the survival of Bimini's lemon sharks (Jennings et al., 2008).

Juvenile elasmobranchs can rely heavily upon coastal environments, therefore their selection of habitats can be proposed as an indicator of nursery quality and reliance, and furthermore as evidence in support of protection from degradation, as observed in other fish species (Goode et al. 2020). So, in the face of local and global coastal habitat loss (Bryan-Brown et al., 2020) and marked declines in elasmobranch populations (Pacoureau et al., 2021; Finucci et al., 2024), we aim to answer the question: given the available habitat in the Bimini lagoon, what spatial habitat features do juvenile elasmobranchs primarily and secondarily associate? In doing so, we provide insight on the habitat

selection of elasmobranchs at a vulnerable life stage, contributing to the global knowledge base for this threatened taxa. Additionally, we justify and outline an analytical approach for including individual level information in modelling spatial behaviour as an indicator of valuable habitat quality, using acoustic telemetry (a common biologging tool in marine ecology). Our statistical methodology considers habitat types individually and evaluates selection at the level of the individual shark, before these are combined in a final analysis to understand the population level processes of habitat selection (Fig. 1). Our analyses reflect the need to consider the hierarchical nature of ecological drivers of marine vertebrate behaviour interacting across scales in marine ecology (for example, the landscape-level effect of tide contrasted with the fine-scale mosaic of seagrass meadow density) (Kressler et al., 2023) and could be widely applied to other acoustic telemetry data sets to help improve our understanding of the indicators and implications of juvenile spatial behaviour in marine vertebrates. Finally, we propose management recommendations based on the fine-scale habitat selection by functionally dependent individuals.

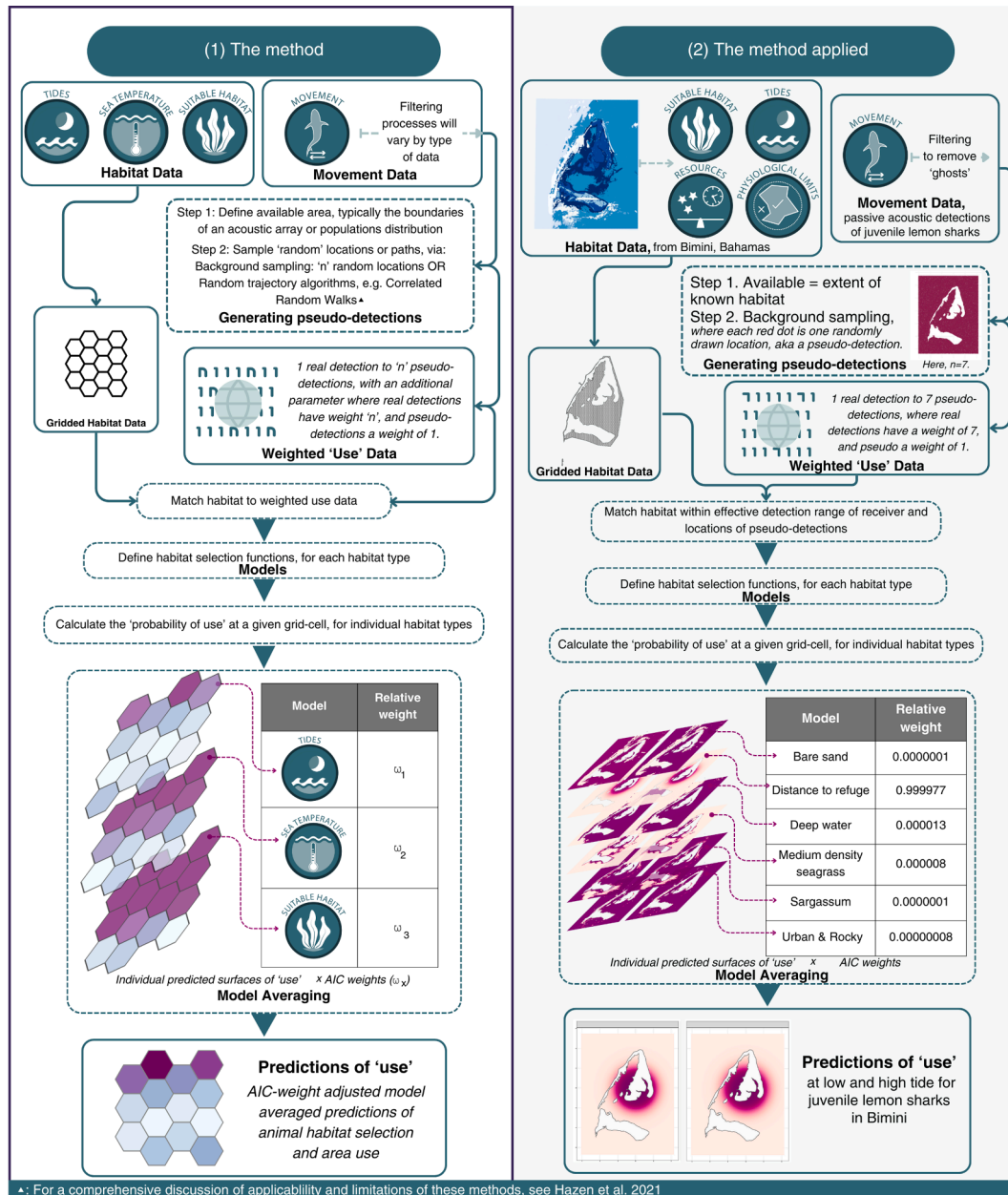
## 2. Methods

### 2.1. Study area

The research was conducted around Bimini, The Bahamas (25.7273° N, 79.2979° W), a mangrove-fringed island located approximately 80 km from the south-eastern coast of Florida, USA (Fig. 2). Bimini sits on the western edge of the Great Bahama Bank in the North Atlantic Ocean, east of the Gulf Stream, and is a productive habitat for many pelagic and coastal species (Grimmel et al., 2020). Juvenile lemon sharks inhabit the waters of Bimini, which they use as nursery grounds (Chapman et al., 2009; Kessel et al., 2013). High site fidelity facilitates repeat capture and long-term monitoring of the local population and individuals (e.g. Dhellemmes et al., 2020a).

### 2.2. Habitat data

Habitat information came from previous work which classified the terrestrial and aquatic environments in Bimini on behalf of the Bimini Biological Field Station Foundation (BBFSF) (Supporting Information Item 2 & 3). Here, five key habitat types were selected that were widely available and represented a diversity of features within the study system: (1) medium-density seagrass (dominated by *Thalassia testudinum*, but can also contain small amounts of *Syringodium* and *Halodule*) (6.1 % total cover, Supporting Information Item 2d), (2) *Sargassum* (5.6 %, Supporting Information Item 2d), (3) urban and rocky habitats (2.9 %, SI Item 2d), (4) deep water (29 %, Supporting Information Item 2d), and (5) bare sand (5.4 %). Deep water in Bimini can be the result of natural bathymetry, like to the west of Bimini as the Bahamian shelf drops into the Gulf Stream (Fig. 2), or it can be man-made and the result of channel dredging as observable on the interior coastline of the North island to facilitate large vessel entry and docking along the western edge of the lagoon (Fig. 2). The remaining habitat types, excluding alternate densities of seagrass (see Supporting Information Item 3), were not considered in the statistical analysis because their limited total availability resulted in rank deficiency and non-convergence of models (Marsh, 3.9 % total cover; mangrove 1.5 %; large sponge, 0.2 %, Supporting Information Item 2d). Given tagging was conducted within nurseries of the northern lagoon, we defined the geographic centre of the dense mangrove forest in the northern lagoon as the central refuge point (pink diamond, Fig. 2b, see Supporting Information Item 2). Juvenile sharks, teleost, and invertebrates can move through areas of these central mangroves, but the area has limited permeability to larger predators and humans, which suggests that this area could offer refuge (Guttridge et al. 2012). Thus, we include distance from this central refuge as our sixth habitat variable. For analyses, the five distinct habitat types identified above and the continuous variable 'distance from refuge' were



**Fig. 1.** The stepwise guide to the method used to generate predictions of habitat selection and marine vertebrate space use, first broadly demonstrated for any (1) movement data, and secondly (2) as specifically applied in this study for juvenile lemon sharks in Bimini, Bahamas. In the figure, solid lines indicate the item is a data frame or output, and hashed lines indicate the item is a data transformation or modelling process. Icons denote types of ecological data as described in Kressler, Dall & Sherley (2023). The method begins with habitat and movement data (in our study, remote sensed habitat features in Bimini, and passive acoustic telemetry detections of juvenile lemon sharks). Habitat data is then organised into a grid. Movement data is filtered before pseudo-absences, or in our case pseudo-detections, are generated; filtering processes will vary by movement data type, in our study they involved filtering for 'ghost detections' (see Supporting Information Item 4). Pseudo-detections are generated via the two steps: in our study, step 1 identified available habitat as all that which is 'known' via remote sensing excluding the land, and in step 2 background sampling was performed to randomly sample 7 pseudo-detections for each 1 real detection. These pseudo-detections/detections are combined into one data frame and assigned a weight relative to the number of pseudo-detections randomly drawn. Gridded habitat data is then matched to the location of detections and pseudo detections, to create a spatial modelling data frame, and in our study this was done across the known extent of habitat data in Bimini. Habitat selection functions, in our case GLMMs, are defined and the probability of use is calculated at a given grid cell for individual habitat types. These predictions are then model averaged with an adjustment to account for their relative AIC weight; the sum of these adjusted predictions is then spatially represented as the model averaged prediction of use of a marine vertebrate in the available study extent given all habitat features considered.

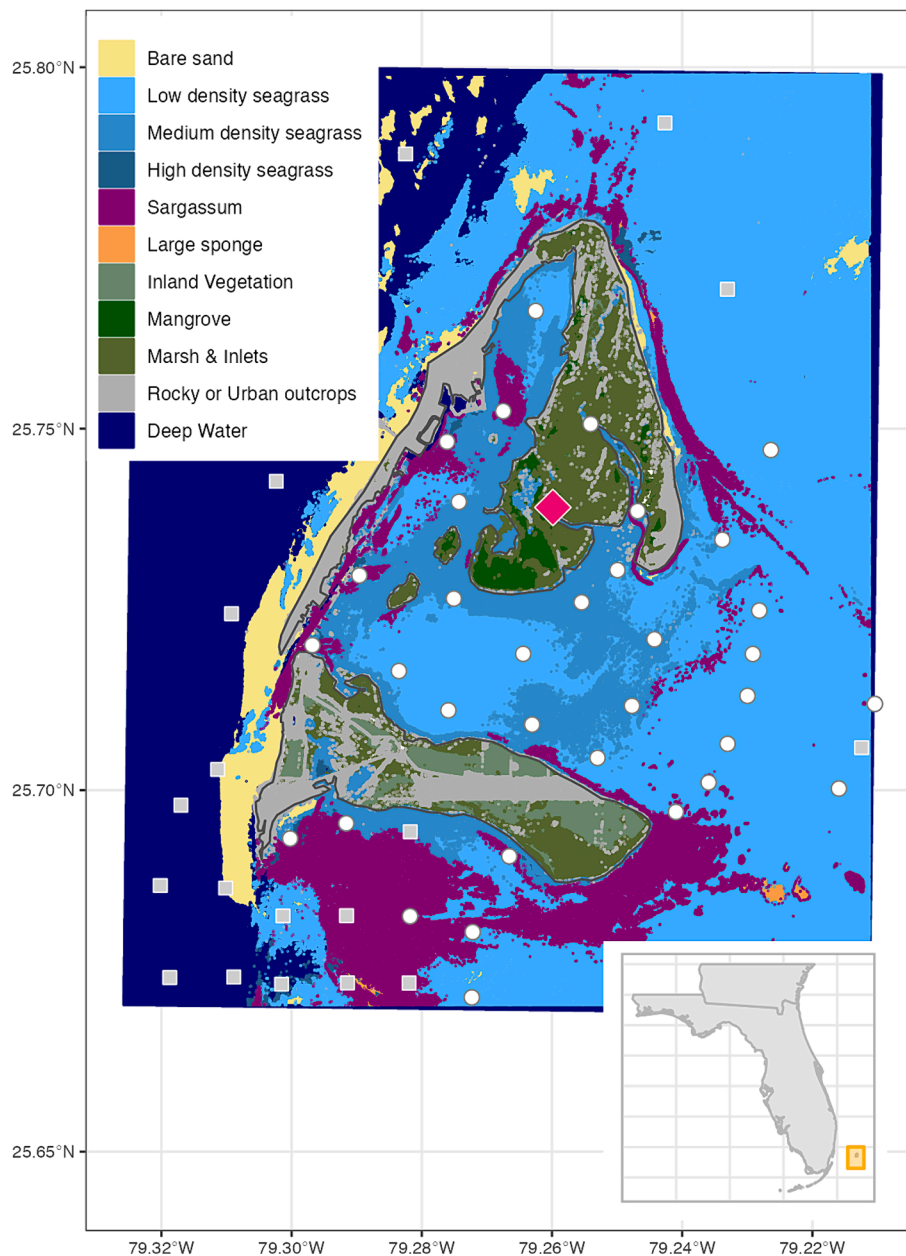
identified as the most parsimonious and comprehensive predictors for describing habitat selection by juvenile sharks.

We conducted all spatial calculations using the *sf* package (version 1.0.9, Pebesma, 2018) for R (version 4.2.0; R Core Team, 2022). We created a hexagon grid of the study site for habitat selection models (Supporting Information Item 5); each grid cell was assigned a proportion for each of the five habitat types by area and the distance from the

central refuge based on its location.

### 2.3. Acoustic telemetry data

Telemetry data were collected using an array of passive acoustic receivers (VR2W, 69 kHz, Innovseas®, Fig. 2, N = 44) anchored to an underwater station and internally implanted acoustic transponders



**Fig. 2.** Map of Bimini, Bahamas and the passive acoustic receiver array. The land of Bimini is outlined in grey. The inset (bottom left) illustrates the location of Bimini (yellow box) off the southeast coast of the USA (grey polygon). Habitat types within the study area are illustrated with different colours. The central point of the mangrove forest is marked by the pink diamond outlined in white. Passive acoustic receivers are marked by white circles ( $n = 35$ ) or grey squares ( $n = 19$ ), indicating that they either did or did not detect study individuals, respectively.

(V13AP Innovsea®, ‘tags’, battery life 524 days) deployed in lemon sharks ( $n = 16$ ) in 2019 and 2020 (Table 1). Sharks were caught as part of an annual mark-recapture survey, separated into a semi-submerged bucket, tagged, sexed, and measured (Table 1). Data were collected from 16 April 2019 to 12 December 2020. A detection occurs when a transmitter enters the detection range of a receiver; receiver effective detection range in this system is estimated as 211 m on average (see Guttridge et al., 2017). We removed duplicate detections caused by overlapping detection ranges of receivers (e.g. van Zinnicq Bergmann et al., 2022). Filtering involved two steps: first, detections not matching our individuals transmitter IDs were excluded; secondly, we excluded singular detections that occurred in isolation, i.e. with no corroborating ‘neighbor’ detections within 6 h either side of the detection in question (see Supporting Information Item 4 for analysis to determine the 6 h threshold). We reconstructed positions of individuals from detection

time and receiver location (e.g. van Zinnicq Bergmann et al., 2022). Acoustic data were processed in R, and data filtering processes and criteria are detailed in Supporting Information Item 4.

Because tidal state affects juvenile shark behaviour within nursery grounds (e.g. Guttridge et al. 2012), we classified individual locations as occurring at low, high, or intermediate tide (National Oceanographic and Atmospheric Association (USA) tidal station ‘TEC4617 North Bimini’, <https://tidesandcurrents.noaa.gov/oaatidepredictions.html?id=TEC4617>). Low and High described the three hours around peak low and peak high times for the central lagoon. Intermediate tide described the time between those two windows around peak tides, sometimes referred to as ‘ebb’ and ‘flood’. Juvenile sharks in the lagoon exhibit resting behaviour during intermediate tides or areas of concentrated tidal flow (Dhellemmes et al., 2020b). Resting behaviour may affect habitat selection estimates, potentially inflating them if

**Table 1**

Biometric data for juvenile lemon sharks: unique identifier (Tag), pre-caudal length (PCL, standardised body length measurement, centimetres), sex (male 'm'/female 'f'), the average, the minimum and the maximum duration between detections (hours), and the Days at Liberty (d = days, H = hours, M = minutes, S = seconds) describes the period over which the individuals were tracked in the array for this study.

Tag	Pre-CaudalLength (cm)	Sex	Average Duration between Detection (hours)	Minimum Duration between Detection (hours)	Maximum Duration between Detection (hours)	Days at Liberty
1	96.0	f	312.478	0.525	2,059.609	517d 5H 17 M 13S
2	86.0	f	35.833	0.522	1,380.403	519d 1H 52 M 11S
3	69.5	f	45.724	0.525	530.593	527d 1H 55 M 6S
4	77.0	f	54.428	0.522	1,502.279	525d 11H 4 M 51S
5	82.5	m	273.650	0.528	1,366.289	528d 14H 26 M 8S
6	62.0	m	120.790	0.525	2,512.698	528d 1H 55 M 41S
7	96.0	m	110.114	0.528	430.611	408d 7H 47 M 14S
8	77.0	m	103.892	0.092	1,080.630	528d 1H 43 M 46S
9	84.0	m	147.922	0.525	2,651.954	358d 15H 32 M 44S
10	99.0	f	70.816	0.522	3,960.448	514d 12H 18 M 12S
11	91.0	f	72.907	0.531	336.885	75d 19H 49 M 11S
12	75.0	f	18.464	0.522	108.703	300d 2H 36 M 46S
13	71.2	m	1,060.953	0.547	778.342	44d 10H 53 M 56S
14	71.5	f	2,328.125	0.611	2,646.917	200d 22H 18 M 14S
15	91.0	m	78.059	0.533	224.641	259d 13H 5 M 39S
16	96.8	f	21.249	0.525	122.673	78d 2H 10 M 35S

individuals rest near receivers. To mitigate this, we excluded intermediate tidal detections (19 % of all detections) and focused on low and high tide detections only.

#### 2.4. Habitat selection models

##### 2.4.1. Defining availability structure and habitat composition

Here we use habitat selection functions with acoustic detection data (e.g. Brownscombe et al., 2022; Griffin et al., 2021) to explore spatial behaviour of lemon sharks. Acoustic telemetry data is presence-only, so for each real detection we generated 7 pseudo-detections from within the available detection area by background sampling (Supporting Information Item 6). This approach provides a higher degree of niche separation than alternative methods, like correlated random walk sampling, and captures the most possible space use (Hazen et al., 2021). We included a weighting coefficient for each detection (real and pseudo) at a ratio of 7:1. Using the hexagon grid and detection range zones, we georeferenced real and pseudo-detections and assigned habitat data accordingly (Supporting Information Item 5; Pebesma, 2018; Wickham et al., 2022).

##### 2.4.2. Defining the habitat selection function & GLMMs

Habitat selection functions were specified using six generalised linear mixed models via the "glmer" function in the R package *lme4* (version 1.1.29, Bates, 2010) – one for each habitat type and one for 'distance to refuge' (Table 2). These six models follow the same structure and were implemented using a binomial error structure with a logit link (Table 2). Habitat selection ('use') was the binomial response (0 = pseudo-detection, 1 = real detection). Tidal state (low or high) was included as a two-way interaction with the habitat variable (the habitat composition does not change at different tidal states, however given the study site is a semi-tidal estuary it is possible that the tidal state influences the selection of habitat types and compositions) (Table 2). To account for pseudo-replication, we included random slopes for each individual and random intercepts for the habitat predictor (Table 2) (Muff et al., 2020). To evaluate selection for each habitat type at the level of the individual and to avoid issues of parameter identifiability that can arise with moderate levels of collinearity (Freckleton 2011) (Supporting Information Item 2c), each habitat type was modelled separately with a random coefficient model (Table 2). This approach also allowed us to reduce individual model's complexity while still allowing for interpretation of random and fixed effects of all relevant habitat types. Models goodness of fit and accuracy were evaluated using Receiver Operating Characteristic (ROC) curves, and the diagnostic statistic Area Under The Curve (AUC) (SI Item 7).

**Table 2**

Generalised linear mixed model (GLMM) formulas for eight habitat variables: proportion of bare sand, of low-density, medium-density, and high-density seagrass, of sargassum, of urban landscape and rocky outcrops, of deep water (>5m depth at low tide), and the distance in metres from the central mangrove forest in the North Sound (see Fig. 2).

Predictor variable	Model	Model formula
Proportion of bare sand, 'baresand'	m1	use ~ baresand + baresand*tidephase + (baresand   PIT), family = binomial(link = logit), weights = w7
Proportion of low-density seagrass, 'lowdensg'	m2	use ~ lowdensg + lowdensg*tidephase + (lowdensg   PIT), family = binomial(link = logit), weights = w7
Proportion of medium-density seagrass, 'meddensg'	m3	use ~ meddensg + meddensg*tidephase + (meddensg   PIT), family = binomial(link = logit), weights = w7
Proportion of high-density seagrass, 'highdensg'	m4	use ~ highdensg + highdensg*tidephase + (highdensg   PIT), family = binomial(link = logit), weights = w7
Proportion of sargassum, 'sargassum'	m5	use ~ sargassum + sargassum*tidephase + (sargassum   PIT), family = binomial(link = logit), weights = w7
Proportion of urban landscape & rocky outcrops, 'urban'	m6	use ~ urban + urban*tidephase + (urban   PIT), family = binomial(link = logit), weights = w7
Proportion of deep water, 'deepwater'	m7	use ~ deepwater + deepwater*tidephase + (deepwater   PIT), family = binomial(link = logit), weights = w7
Distance to refuge, 'distance'	m8	use ~ distance + distance*tidephase + (distance   PIT), family = binomial(link = logit), weights = w7

Where 'use' is a binary response variable (0,1) describing whether a data point is a real detection or a pseudo-absence; 'tidephase' describes the tidal state (low or high); 'PIT' is the individuals' unique identifiers; and 'w7' is a weighting column that assigns a greater weight to 'real' use values (1 s) versus pseudo-use values (0 s) based on the availability structure, here real detections are given a value of 7 and pseudos a value of 1.

To interpret habitat selection at the individual level, we used the 'ggpredict' function in the R package *ggeffects* to calculate the marginal effects conditioned on the group level (i.e. the individual) in the random term for each of the six habitat GLMMs (version 1.3.1; Lüdtke, 2018).

##### 2.4.3. Aic-weight adjusted juvenile shark habitat selection by model averaging

To interpret habitat selection at the population level, we calculated probability of use estimates for each hexagon grid cell using the coefficients from each of the six GLMMs in turn (Table 3, models included

**Table 3**  
Generalised linear mixed model (GLMM) summaries for eight habitat variables.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8
(Intercept)	-0.223*** [-0.326, -0.121]	-1.235*** [-1.336, -1.133]	-1.379*** [-1.438, -1.320]	-0.120** [-0.206, -0.035]	0.050*** [0.036, 0.064]	0.024*** [0.016, 0.032]	0.263*** [0.254, 0.271]	7.257*** [5.982, 8.531]
Habitat Type	-545.873*** [-546.037, -545.710]	2.449*** [2.272, 2.626]	11.002*** [10.856, 11.148]	0.437*** [0.294, 0.580]	-3.791*** [-3.932, -3.649]	-398.153*** [-398.272, -398.033]	-315.459* [-583.962, -46.957]	-0.003*** [-0.004, -0.002]
Tide State	0.195*** [0.180, 0.209]	0.900*** [0.878, 0.922]	-0.040*** [-0.061, -0.018]	-0.319*** [-0.334, -0.305]	-0.015* [-0.030, -0.001]	-0.008 [-0.021, 0.006]	0.003 [-0.011, 0.017]	0.146*** [0.077, 0.216]
Habitat-Tide Interaction	-3.256*** [-3.377, -3.135]	-1.751*** [-1.789, -1.713]	0.456*** [0.342, 0.571]	5.617*** [5.468, 5.765]	1.631*** [1.498, 1.763]	18.641*** [18.519, 18.763]	1.149 [-0.711, 3.009]	0.000*** [0.000, 0.000]
SD (Group Intercept)	0.253	0.651	0.489	0.316	0.034	0.012	0.000	3.270
SD (Habitat Individual)	1300.466	1.217	3.528	8.052	4.393	1193.472	538.444	0.002
Cor (Intercept ~ Habitat Individual)	-0.507	-0.983	-0.973	-0.780	-0.821	-0.978		-0.980
AIC	503258.8	458064.6	366450.5	500624.7	520868.6	525317.2	465152.8	167163.5

Estimates are presented unadjusted by the AIC weights. Model 1 is the model for bare sand; 2 for low-density seagrass; 3 for medium-density seagrass; 4 for high-density seagrass; 5 for sargassum; 6 for urban and rocky outcrops; 7 for deep water; and 8 for distance to the central mangrove forest (i.e. refuge). Models 1, 3, 5, 6, 7 & 8 were included in model averaging in the first instance (i.e. Before-Updating); and Models 1, 3, 5, 6 & 7 were included in model averaging after updating the area of selection (i.e. After-Updating). Analyses were only conducted using the best of the seagrass models, i.e. medium-density of seagrasses (Model 3), thereby excluding low- and high-density seagrasses and associated models (Models 2 & 4, respectively). The delta-AIC (dAIC) between Models 3 and 2 was 91,614.14; and between 2 and 4 was 42,560.09 (SI Item 3).

+ p < 0.1, \* p < 0.05, \*\* p < 0.01, \*\*\* p < 0.001.

in 'Before-Updating'). To do this, a dataset of the proportions of the five habitat types and the distance of each cell from the refuge was constructed for each available hexagon grid cell, at low and at high tide.

Using the 'invlogit' and 'predict' functions from the R packages *arm* and *effects*, respectively, the probability of use at every hexagon cell was predicted for each GLMM individually at both low and high tide based on the proportions of habitat or the distance from the central refuge (Gelman and Hill, 2006; Fox and Hong, 2009). We then applied a model averaging approach to adjust model estimates based on their AIC weights before averaging each hexagon grid cells estimated probability of use for low and high tide (Table 4 'Before'). We used this approach because model averaging provides unbiased parameter estimates when there are low to moderate levels of correlation between explanatory variables, and the variances are generally more reliable than those generated from multiple regression (Freckleton 2011). The model averaging approach prediction dataset was spatially georeferenced to allow mapping of predictions of the probability of use using the R packages *sf* (Pebesma, 2018) and *ggplot2* (Wickham, 2016).

#### 2.4.4. Defining a 'core use area' boundary and updating model averaging

To explore secondary selection within the primarily selected area, we defined a 'core use area' (CUA) as that area where the AIC-adjusted model averaged predictions of use were greater than or equal to 50 %. To do this, we identified the hexagon grids where use was greater than or equal to 50 %; we then used functions in the R package *sf* to identify

**Table 4**  
Akaike Information Criterion (AIC) weights for the six GLMMs used in model averaging.

Model	Before	After
8	0.99995268	
3	0.00004689	0.99102972
7	0.00000034	0.00711090
1	0.00000005	0.00106899
5	0.00000002	0.00043855
6	0.00000002	0.00035183

Model numbers refer to the GLMMs described in Table 2 & 3; 'Before' and 'After' refer to the AIC weights as calculated firstly including the distance from refuge model (Model 8), and subsequently after the model averaging process was updated and performed without Model 8.

the minimum convex polygon encircling this area, hereafter referred to as a 'boundary', or the 'Before'-CUA (Pebesma, 2018).

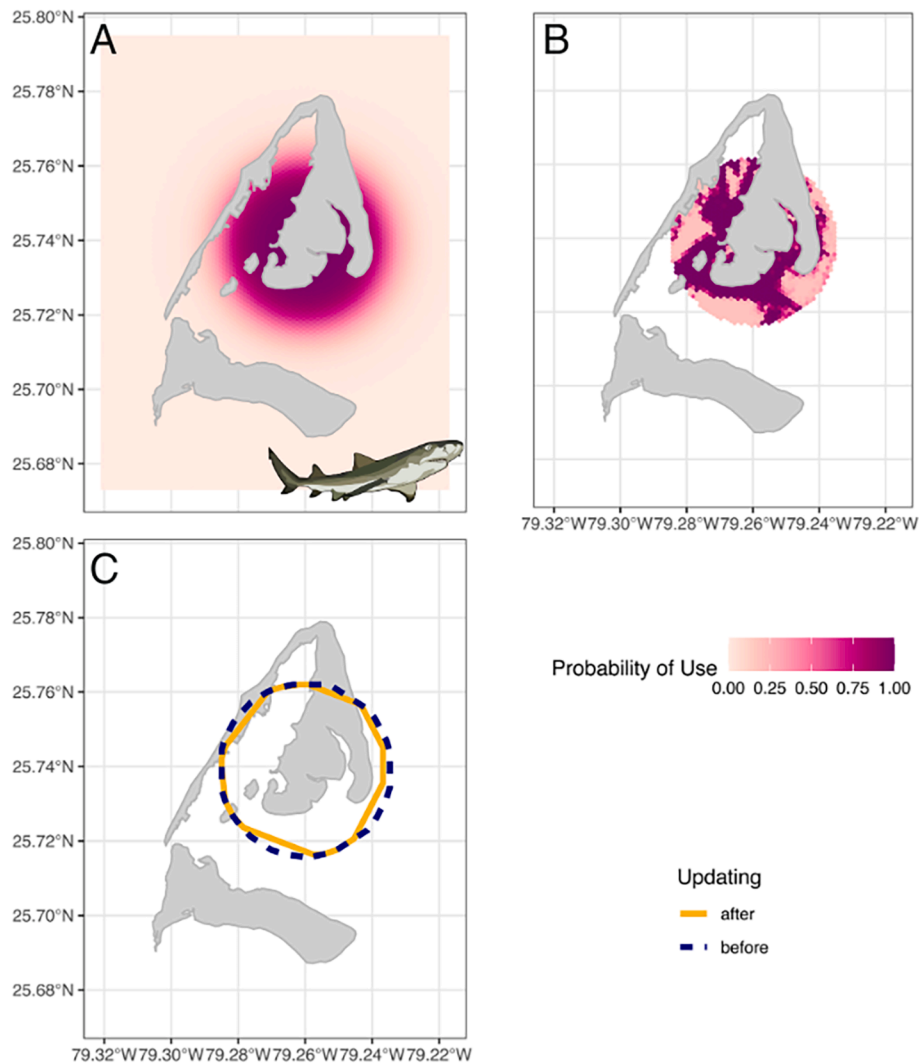
Next, we address the question of secondary habitat selection, within the CUA, via a process we refer to as 'updating'. Updating is the process by which we limited the spatial extent of predictions to the CUA identified in the model averaging process when the model with the largest AIC weight was included, then we re-calculated the model predictions using the same AIC-weighted model averaging approach with the amendment that we excluded the model with the greatest AIC weight (Table 3 & 4). To update predictions within the CUA but also the boundary of the CUA, first we calculated AIC weights for the five 'next best' habitat type GLMMs (Table 4 'After'). Then, using these new weights we re-projected models into the spatial extent of the 'Before'-CUA and identified the new, i.e. After-updating, CUA. The model with the largest AIC weight of the five in the updating process would indicate the habitat type which is selected for secondarily (Table 4, 'After'), within the context of the Before-CUA.

We then calculated the area in the boundary of the After-updating CUA (Fig. 3c.) and compared the area of the Before- and After- CUAs boundaries using a Student's *t*-test (Fig. 3c, Supporting Item 7).

### 3. Results

#### 3.1. Acoustic telemetry data

Telemetry data from 16 individuals ranging from 62 cm to 99 cm precaudal length yielded 28,852 detections across 35 of 44 receivers (Table 1), with an individual being detected on average 1707.5 (±1532.86, standard deviation) times during the study period. Individuals within the array were detected for varying periods based on deployment dates. The minimum and maximum detection durations were 44 and 528 days, respectively. Filtering of acoustic detection data resulted in detection intervals ranging from 0.09 to 165 h (Table 1, Fig. 1, Supporting Information Item 4). All tracked individuals were detected multiple times, and never detected by the outermost receivers, indicating comprehensive coverage of the sub-population within the array in 2019 and 2020.



**Fig. 3.** Predictions from habitat selection models before (A) and after (B) updating of model averaging process, and (C) minimum convex hulls of core use area (CUA). Panel 'A' displays the AIC-weighted model averaging predictions of habitat use. The colour gradient represents the probability of a grid-cell being used at low tide based on habitat composition (for high tide see Supporting Information Item 8). Panel 'B' shows predictions after model averaging was updated to investigate the secondary selection of juvenile sharks within the CUA (Fig. 3a). 'Updating' refers to the process by which we refined models of habitat selection (for methods see Supporting Information Item 9). Updated estimates in panel 'B' suggest a refinement of the CUA by secondary selection, confirmed by comparing the minimum convex hulls, or boundaries, of the CUAs before versus after updating (panel C). The area encompassed by the outline after updating is significantly less than the area before (18.52 km<sup>2</sup> and 20.654 km<sup>2</sup> respectively, Student's *t*-test  $t_1 = 18.87$ ,  $p < 0.05$ ).

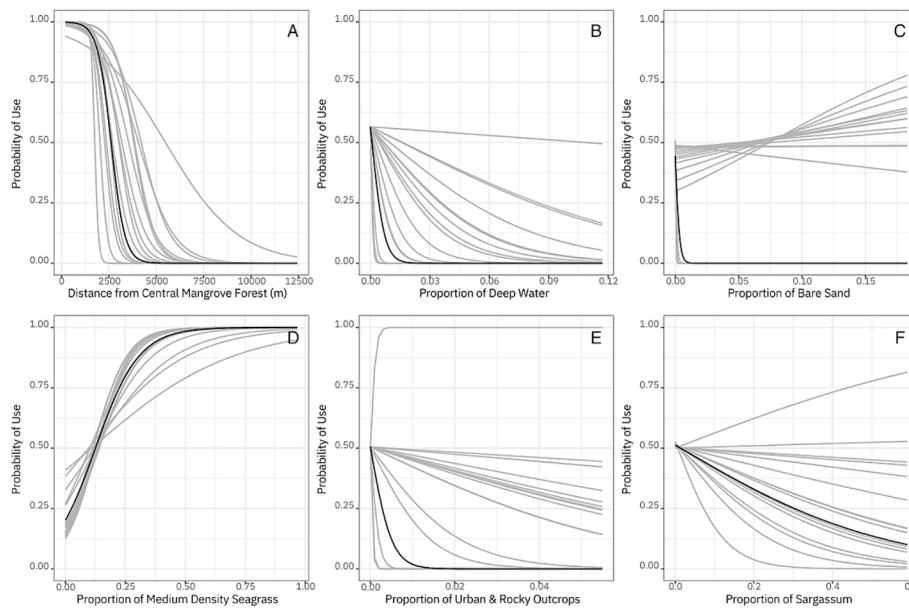
### 3.2. Juvenile shark habitat selection

All results from the AIC-adjusted model averaging approach were geo-referenced and plotted using the R packages *sf* (Pebesma, 2018) and *ggplot2* (Wickham, 2016) (Fig. 2A-C). Using our original model (Models 1, 3, 5, 6, 7 & 8) set, i.e. Before-updating models, and the AIC-weight adjusted model averaging approach, we found a pronounced preference for juvenile sharks to remain within < 2500 m of the central mangrove refuge (estimate = -0.003, CI = -0.004, -0.002,  $p < 0.001$ , Table 3) (Fig. 3A considering the model averaged effect & Fig. 4A considering Model 8 alone), with distance from refuge providing 99.9 % of the relative explanatory power in our model set Before-updating (Table 4, Model 8), and the probability of use dropping away to essentially zero by ~ 4000 m distance from the refuge (Fig. 4A, solid black line). Secondly, juvenile sharks demonstrated a predictable preference for medium density seagrass (estimate = 11.002, CI = 2.272, 2.626,  $p < 0.001$ , Table 3), with 99.1 % contribution from the model in the After-Updating model averaging process to examine selection within the CUA identified (Table 4, Supporting Information Item 9, & Fig. 3B). Both

the refuge (Model 8) and medium-density seagrass (Model 3) models were well supported by diagnostic tests of ROC curves and area under the curve (AUC) statistics revealing excellent accuracy (AUC = 0.964, and 0.928, respectively, SI Item 7).

Marginal effects plots (Fig. 4B), model estimates (Table 3), and the relative weight AIC for the deep water model After-Updating (weight = 0.7 %, Model 7, Table 3), suggest an avoidance of deep water by juvenile sharks (estimate = -315.153, CI = -583.962, -46.957,  $p < 0.1$ , Model 7, Table 3). However, considering ROC curves, the model for deep water was only slightly better than random (AUC<sub>Model 7</sub> = 0.55, SI Item 7), so while the model predictions demonstrate stark avoidance by juveniles (Fig. 4B), the model is not well supported.

Individual models for sargassum (Model 5) and urban and rocky outcroppings (Model 6), were no better than random at predicting juvenile spatial behaviour on their own based on AUCs (AUC = 0.533, and 0.535, respectively; SI Item 7), and had negligible relative weight contributions After-Updating (Table 4). The Model for bare sand (Model 1) was well supported, moderately accurate and better than random based on its AUC (AUC = 0.790, SI Item 7), and suggests avoidance of bare



**Fig. 4.** Marginal effects for each level of the random effects in the final six habitat GLMMs (A-E). Light grey lines show the marginal effects estimates for individual probability of use. The black lines are the population level fixed effect estimates. Predictions are made only up to the maximum proportion observed in the study area.

sand habitats by juvenile sharks (estimate = -545.873, CI = -546.037, -545.710,  $p < 0.001$ , Table 3). While the model for bare sand had a negligible AIC-weight Before-Updating (likely a result of overwhelming influence of Model 8), it was the third top contributor to the model averaging process After-Updating, providing 0.1 % of the explanatory power of juvenile shark space use within the CUA (Table 4).

Although some single-habitat type GLMMs suggest an influence of tidal state on habitat selection either directly or through an interaction (Table 3), the final model averaged predictions demonstrate that the overall effect of tidal state was negligible (Table 3 and Supporting Information Item 8). This is likely driven by the overwhelming AIC-support for the distance from refuge model (Model 8, Table 3 & 4) and the small parameter estimates for the tidal state and the interaction between refuge distance and tidal state (parameter estimates - 0.003 and  $< 0.001$ , respectively,  $p$ -value  $< 0.001$ , Table 3). This is the same effect After-Updating and therefore we have only presented the findings for low tide in the main text (for low and high tide estimates Before- and After-Updating see Supporting Information Items 8 & 10a, respectively). This negligible effect of tide is likely an artefact of the resolution of the receiver's detection capability, the placement being insufficient to capture the variability expected between tidal peaks, or both.

### 3.3. Updating the boundary of the CUA based on secondary selection information

After updating predictions of habitat selection, projecting only within the Before-updating CUA (Supporting Information Item 9a), we found a small but significant reduction in total area within the boundaries of the Before and After predictions of use at low tide (20.6 km<sup>2</sup> and 18.5 km<sup>2</sup>, respectively, Student's  $t$ -test,  $t_1 = 36.08$ ,  $p = 0.01$ , Supporting Information Item 9c) (Fig. 3B & 3C), driven by the strong selection preference for seagrass habitat (Fig. 3B, Table 4, Model 3) narrowing core use area estimates (Fig. 3C, Supporting Information Item 9b).

## 4. Discussion

Many ecological studies have investigated the spatial behaviour of marine vertebrates (e.g. Griffin et al., 2020; Clark et al., 2021; Trevail et al., 2021), including adult elasmobranchs (e.g. van Zinnicq Bergmann et al., 2022). However, relatively few studies have used quantitative

models to study the spatial behaviour of juvenile elasmobranchs (Dhellemmes et al., 2020b; White et al., 2019a). To establish juvenile shark presence as an indicator of habitat value and management, we quantified habitat preferences and associations of a juveniles of a Vulnerable shark species, using passive acoustic telemetry and an innovative analytical approach (Fig. 1). By assessing individuals' multi-year habitat selection at a fine spatial scale, we provide strong evidence to link selection to value and habitat to presence. As a result, we provide support for the importance of coastline fringing habitats in wider marine protected area (MPA) designation and planning in tropical coastal environments, and an ecological indicators to facilitate integration of elasmobranch behaviour into management, both locally and in analogous ecosystems worldwide. Building upon a foundation of long-term research in Bimini, this study provides two key outcomes. Firstly, it identifies the primary and secondary drivers of juvenile shark spatial behaviour relative to habitat features, thereby providing evidence for the importance of certain habitats to lemon sharks in Bimini. For management, our analyses identified a CUA based on these drivers of spatial behaviour (Fig. 3c). Secondly, this study develops a habitat selection modelling framework for acoustic telemetry data, which showcases how to evaluate population spatial behaviour while accounting for individual-level effects and use the outcomes as an indicator of management priorities.

For the first key outcome, we found that juvenile lemon sharks demonstrated preference for mangrove forests (Fig. 3a & 4a), and secondary selection for medium-density seagrass beds within the CUA identified by model averaging (Fig. 2B, Table 4 'After' Model 3, Supporting Information Item 9). These findings are consistent with the literature: juvenile sharks are using the natural and centrally located refuge available to them, behaving akin to central place foragers in other species (e.g. Elliott et al., 2009). Here, tide had a negligible effect on the strength of habitat selection, but we believe this to be an artefact of a limited capacity of the receiver array in capturing the small-scale tidal shifts that are common of this species in tidal habitats (e.g. Wetherbee et al., 2007) (Supporting Information Item 9). Additionally, tagging efforts were biased to the north, which may underestimate mangrove usage in South Bimini. However, we believe our sample size and tagging protocol to be sufficient to draw the above conclusions regarding the central and northern lagoon.

In sub-tropical marine environments, mangroves are vital for



supporting early-life stages of sharks and rays (Kanno et al., 2019), teleosts (Igulu et al., 2014), and invertebrates (Zu Ermgassen et al., 2020). Our study in Bimini suggests that the juvenile lemon sharks use the central mangrove area as a refuge, perhaps for rest (e.g. Wojczulanis-Jakubas et al. 2022) and predator avoidance (e.g. Dhellemmes et al., 2020b), a pattern that may be observed in other regions. Unfortunately, the alarming rate of anthropogenic degradation of mangroves poses a global concern. Comparisons of our study with a study conducted in Bimini pre-coastal development (Morrissey & Gruber, 1993a) suggest a shift in the habitat preference of juvenile sharks, likely influenced by changes in habitat availability and increased human activity since the 1990 s (Fig. 5a-c). The changes in post-1990 s habitat selection could be an artefact of objective classification of habitat data resulting in misleading comparisons, or juveniles' site fidelity despite a changing seascape. But notwithstanding methodological differences, consistency in the sampled population and shark length allow comparisons. The impact of the increase in global anthropogenic activity is yet to be holistically realised, but habitat removal (e.g. Niella et al., 2022; Yan et al., 2021) and avoidance of anthropogenic activity (e.g. Nickel et al., 2021) are both well-documented drivers of behavioural change and may have incited behavioural responses in Bimini's juvenile shark populations (e.g. dynamics in 'emergence behaviour', Sih 1997), specifically their post-1990 s habitat selection. Here we observed overwhelming selection for the remaining pristine mangroves in Bimini, secondary selection for medium-density seagrass meadows (Fig. 3a & 4a), and avoidance of bare sand and deep water. Deep water in the northern lagoon is entirely derived from man-made channels, and bare sand can increase with the removal of seagrass habitats and coastal development which has been marked since the early-2000 s (Fig. 4). Using these preferences, and aversions, as an indicator of the ecological resilience of the system, we can infer that Bimini's marine ecosystem is experiencing detectable ecological impact at the level of individual juvenile sharks from human activity. And in this way, we believe our results exemplify how juvenile elasmobranch spatial behaviour, specifically the strength of their preference, can be used as an indicator of the value of habitat and the vulnerability of marine ecosystems to further anthropogenic habitat removal. Thus, in the face of continued anthropogenic activity, our findings highlight the importance of protecting remaining mangrove habitats against further threat.

The implications of our research are also pertinent to researchers working in analogous habitats worldwide as mangroves are prevalent across numerous ocean coastlines. As climate change continues to exert its influence, there is evidence to suggest that the distribution ranges of mangroves are shifting poleward (Fazlioglu et al., 2020; Godoy and Lacerda, 2015). This phenomenon may lead to the presence of juvenile

elasmobranchs in areas previously unrecorded, mirroring observations seen in certain mangrove-associated crustacean species (Sharifian et al., 2021). The indicator highlighted in our study holds potential applicability in these instances. Therefore, our work serves as a valuable reference point for researchers investigating similar ecological dynamics in mangrove and seagrass ecosystems across the globe. For example, our findings and methodology could provide insight and guidance for real-ised area protection and management goals outlined in Cuba's national plan of action for the conservation of sharks (PAN, 2015), where juvenile elasmobranchs were recently documented amongst diverse habitat features in an estuary on the southern coast (Ruiz-Abierno et al. 2020). Or, in Turks and Caicos, our method could be applied to study the hierarchical importance of habitat features across coastal gradients in South Caicos, allowing researchers to quantify the extent to which current protection efforts capture essential nursery habitat for juvenile elasmobranchs (Henderson et al. 2021). Whether in Bimini or further afield, our findings and approach provide the opportunity to enhance our understanding of the relevance of coastline-fringing mangrove habitats on the behaviour and survival of elasmobranch populations and highlight the management value inherent in particular coastal habitats for the success of elasmobranch conservation.

#### Authors' contributions

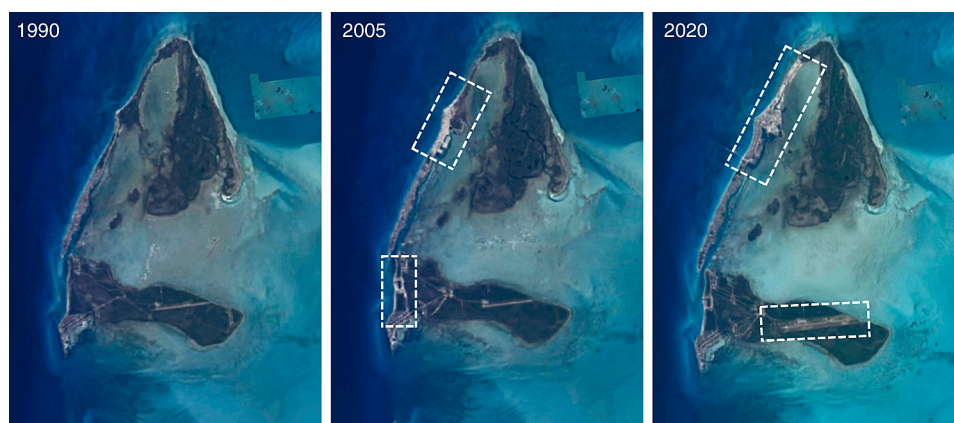
MMK conceived the study idea, with support from MS and RBS. MMK conducted all data analyses with critical input from AT and RBS. Telemetry data was collected and provided by EB, MS, VH, CW, in order of relative contribution. VH conducted all array maintenance, which was essential to the retrieval of all telemetry data. Habitat data was provided by MS. ACG, EB, and MS obtained funding for the research. MMK and RBS led writing of the manuscript. All authors contributed to the drafts and gave final approval.

#### Statement on Inclusion

Our study was conducted by authors from five institutions across five countries, including a scientist based in the country where the study was carried out, but not, unfortunately, a Bahamian national or a Bahamian trained scientist. As data were collected during previous studies, repurposed for this analysis, novel collaborations with Bahamian scientists were not pursued specifically for this project. However, the BBFSF is a Bahamian non-profit, that supports local businesses, trains local scientists, and engages the government, through outreach and internships opportunities offered exclusively to Bahamian early career researchers.

#### CRedit authorship contribution statement

**Molly M Kressler:** Writing – original draft, review & editing, Conceptualisation, Data curation, Funding acquisition, Methodology,



**Fig. 5.** Satellite imagery of study area in (A) 1990, (B) 2005 and (C) 2020. Images taken from Google Earth Timelapse feature (link), showing satellite imagery of Bimini, Bahamas in 1990, 2005 and 2020, respectively. The images show the areas of development that occurred on the western coastline of North Bimini over this time (white hashed boxes). The years selected, 1990, 2005, and 2020, represent the approximate time periods and the associated habitat conditions experienced by individuals from an earlier study (Morrissey and Gruber, 1993b) (A), and our study individuals (C).

Validation, Visualisation, Formal analysis. **Evan E Byrnes:** Writing – review & editing, Resources, Investigation, Funding acquisition, Data curation. **Alice M Trevail:** Writing – review & editing, Visualization, Supervision, Formal analysis. **Clemency E White:** Writing – review & editing, Resources, Investigation, Data curation. **Vital Heim:** Writing – review & editing, Resources, Investigation, Data curation. **Matthew Smukall:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Adrian C Gleiss:** Writing – review & editing, Resources, Methodology, Funding acquisition. **Richard B Sherley:** Writing – review & editing, Visualization, Validation, Supervision, Funding acquisition, Formal analysis, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

## Acknowledgements

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2024.112239>.

## References

- Anderson, A.B., Pinheiro, H.T., Francini-Filho, R.B., Ferreira, C.E.L., Joyeux, J., 2023. Habitat use of five sympatric predatory reef fishes at a remote island in the south-western Atlantic. *J. Fish Biol.* 103, 324–335. <https://doi.org/10.1111/jfb.15433>.
- Bates, D.M., 2010. *lme4: Mixed-effects modeling with R*. Springer.
- Brown, C., Laland, K.N., 2003. Social learning in fishes: a review. *Fish Fish.* 4, 280–288. <https://doi.org/10.1046/j.1467-2979.2003.00122.x>.
- Brownscombe, J.W., Shipley, O.N., Griffin, L.P., Morley, D., Acosta, A., Adams, A.J., Boucek, R., Danylchuk, A.J., Cooke, S.J., Power, M., 2022. Application of telemetry and stable isotope analyses to inform the resource ecology and management of a marine fish. *J. Appl. Ecol.* 59 (4), 1110–1121. <https://doi.org/10.1111/1365-2664.14123>.
- Bryan-Brown, D.N., Connolly, R.M., Richards, D.R., Adame, F., Friess, D.A., Brown, C.J., 2020. Global trends in mangrove forest fragmentation. *Sci. Rep.* 10 (1), 7117. <https://doi.org/10.1038/s41598-020-63880-1>.
- Chapman, D.D., Babcock, E.A., Gruber, S.H., DiBattista, J.D., Franks, B.R., Kessel, S.A., Guttridge, T., Pikitch, E.K., Feldheim, K.A., 2009. Long-term natal site-fidelity by immature lemon sharks (*Negaprion brevirostris*) at a subtropical island. *Mol. Ecol.* 18 (16), 3500–3507. <https://doi.org/10.1111/j.1365-294X.2009.04289.x>.
- Clark, B., Cox, S., Atkins, K., Bearhop, S., Bicknell, A., Bodey, T., Cleasby, I., Grecian, W., Hamer, K., Loveday, B., Miller, P., Morgan, G., Morgan, L., Newton, J., Patrick, S., Scales, K., Sherley, R., Vigfúsdóttir, F., Wakefield, E., Votier, S., 2021. Sexual segregation of gannet foraging over 11 years: Movements vary but isotopic differences remain stable. *Mar. Ecol. Prog. Ser.* 661, 1–16. <https://doi.org/10.3354/meps13636>.
- Cortés, E., Brooks, E., 2018. Stock status and reference points for sharks using data-limited methods and life history. *Fish Fish.* 19, 1110–1129. <https://doi.org/10.1111/faf.12315>.
- Crane, A.L., Ferrari, M.C.O., 2015. Minnows trust conspecifics more than themselves when faced with conflicting information about predation risk. *Anim. Behav.* 100, 184–190. <https://doi.org/10.1016/j.anbehav.2014.12.002>.
- Dhellemmes, F., Finger, J., Smukall, M.J., Gruber, S.H., Guttridge, T.L., Laskowski, K.L., Krause, J., 2020a. Personality-driven life history trade-offs differ in two subpopulations of free-ranging predators. *J. Anim. Ecol.* 90 (1), 260–272. <https://doi.org/10.1111/1365-2656.13283>.
- Dhellemmes, F., Finger, J.S., Laskowski, K.L., Guttridge, T.L., Krause, J., 2020b. 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>.
- Dulvy, N.K., Simpfendorfer, C.A., Davidson, L.N.K., Fordham, S.V., Bräutigam, A., Sant, G., Welch, D.J., 2017. Challenges and priorities in shark and ray conservation. *Curr. Biol.* 27 (11), R565–R572. <https://doi.org/10.1016/j.cub.2017.04.038>.
- Edwards, M., McCallister, M., Brewster, L., Bangley, C., Curtis, T., Ogburn, M., Ajemian, M., 2022. Multi-year assessment of immature bull shark *Carcharhinus leucas* residency and activity spaces in an expansive estuarine nursery. *Mar. Ecol. Prog. Ser.* 695, 125–138. <https://doi.org/10.3354/meps14113>.
- Elliott, K.H., Woo, K.J., Gaston, A.J., Benvenuti, S., Dall'Antonia, L., & Davoren, G. K., 2009. Central-place Foraging in an Arctic Seabird Provides Evidence for Storer-Ashmole's Halo. *Auk* 126 (3), 613–625. <https://doi.org/10.1525/auk.2009.08245>.
- Fazlioglu, F., Wan, J.S., Chen, L., 2020. Latitudinal shifts in mangrove species worldwide: evidence from historical occurrence records. *Hydrobiologia* 847 (19), 4111–4123.
- Feldheim, K.A., Gruber, S.H., Ashley, M.V., 2002. The breeding biology of lemon sharks at a tropical nursery lagoon. *Proc. r. Soc. Lond. B* 269, 1655–1661. <https://doi.org/10.1098/rspb.2002.2051>.
- Finucci, B., Pacoureau, N., Rigby, C.L., Matsushiba, J.H., Faure-Beaulieu, N., Sherman, C. S., VanderWright, W.J., Jabado, R.W., Charvet, P., Mejía-Falla, P.A., Navia, A.F., Derrick, D.H., Kyne, P.M., Pollom, R.A., Walls, R.H.L., Herman, K.B., Kinattumkara, B., Cotton, C.F., Cuevas, J.-M., Daley, R.K., Dharmadi, E.D.A., Fernando, D., Fernando, S.M.C., Francis, M.P., Huveneres, C., Ishihara, H., Kulka, D. W., Leslie, R.W., Neat, F., Orlov, A.M., Rincon, G., Sant, G.J., Volvenko, I.V., Walker, T.I., Simpfendorfer, C.A., Dulvy, N.K., 2024. Fishing for oil and meat drives irreversible defaunation of deepwater sharks and rays. *Science* 383, 1135–1141. <https://doi.org/10.1126/science.ade9121>.
- Griffin, L.P., Smith, B.J., Cherkiss, M.S., Crowder, A.G., Pollock, C.G., Hillis-Starr, Z., Danylchuk, A.J., Hart, K.M., 2020. Space use and relative habitat selection for immature green turtles within a Caribbean marine protected area. *Anim. Biotelem.* 8 (22) <https://doi.org/10.1186/s40317-020-00209-9>.
- Godoy, M.D., Lacerda, L.D.D., 2015. Mangroves response to climate change: a review of recent findings on mangrove extension and distribution. *Anais da Academia Brasileira de Ciências* 87 (2), 651–667.
- Griffin, L.P., Casselberry, G.A., Hart, K.M., Jordaan, A., Becker, S.L., Novak, A.J., DeAngelis, B.M., Pollock, C.G., Lundgren, I., Hillis-Starr, Z., Danylchuk, A.J., Skomal, G.B., 2021. A novel framework to predict relative habitat selection in aquatic systems: applying machine learning and resource selection functions to acoustic telemetry data from multiple shark species. *Front. Mar. Sci.* 8, 631262. <https://doi.org/10.3389/fmars.2021.631262>.
- Grimmel, H.M.V., Bullock, R.W., Dedman, S.L., Guttridge, T.L., Bond, M.E., 2020. Assessment of faunal communities and habitat use within a shallow water system using non-invasive BRUVs methodology. *Aquaculture and Fisheries* 5 (5), 224–233. <https://doi.org/10.1016/j.aaf.2019.12.005>.
- Gruber, S.H., de Marignac, J.R.C., Hoening, J.M., 2001. Survival of juvenile lemon sharks at Bimini, Bahamas, estimated by mark-depletion experiments. *Trans. Am. Fish. Soc.* 130 (3), 376–384. [https://doi.org/10.1577/1548-8659\(2001\)130<0376:SOJLSA>2.0.CO;2](https://doi.org/10.1577/1548-8659(2001)130<0376:SOJLSA>2.0.CO;2).
- Guttridge, T.L., Gruber, S., DiBattista, J., Feldheim, K., Croft, D., Krause, S., Krause, J., 2011. Assortative interactions and leadership in a free-ranging population of juvenile lemon shark *Negaprion brevirostris*. *Mar. Ecol. Prog. Ser.* 423, 235–245. <https://doi.org/10.3354/meps08929>.
- Guttridge, T.L., Gruber, S., Franks, B., Kessel, S., Gledhill, K., Uphill, J., Krause, J., Sims, D., 2012. Deep danger: Intra-specific 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>.
- Guttridge, T.L., Van Zinnicq Bergmann, M.P.M., Bolte, C., Howey, L.A., Finger, J.S., Kessel, S.T., Brooks, J.L., Winram, W., Bond, M.E., Jordan, L.K.B., Cashman, R.C., Tolentino, E.R., Grubbs, R.D., Gruber, S.H., 2017. Philopatry and Regional Connectivity of the Great Hammerhead Shark, *Sphyrna mokarran* in the U.S. and Bahamas. *Front. Mar. Sci.* 4 <https://doi.org/10.3389/fmars.2017.00003>.
- Hazen, E.L., Abrahms, B., Brodie, S., Carroll, G., Welch, H., Bograd, S.J., 2021. Where did they not go? Considerations for generating pseudo-absences for telemetry-based habitat models. *Mov. Ecol.* 9 (1), 5. <https://doi.org/10.1186/s40462-021-00240-2>.
- Henderson, A.C., Smith, C., Bell, K., Gomez, T., Jourdan, A., Lenain, E., 2021. Demographic characteristics of sharks in the sublittoral environment of the Turks and Caicos Islands. *Environ. Biol. Fishes* 104 (9), 1121–1137. <https://doi.org/10.1007/s10641-021-01141-4>.
- Herbert-Read, J.E., Thornton, A., Amon, D.J., Birchenough, S.N.R., Côté, I.M., Dias, M.P., Godley, B.J., Keith, S.A., McKinley, E., Peck, L.S., Calado, R., Defeo, O., Degraer, S., Johnston, E.L., Kaartokallio, H., Macrae, P.I., Metaxas, A., Muthumbi, A.W.N., Obura, D.O., Sutherland, W.J., 2022. A global horizon scan of issues impacting marine and coastal biodiversity conservation. *Nat. Ecol. Evol.* 6 (9), 1262–1270. <https://doi.org/10.1038/s41559-022-01812-0>.

- Hosegood, P.J., Nimmo-Smith, W.A.M., Proud, R., Adams, K., Brierley, A.S., 2019. Internal lee waves and baroclinic bores over a tropical seamount shark 'hot-spot'. *Prog. Oceanogr.* 172, 34–50. <https://doi.org/10.1016/j.pocean.2019.01.010>.
- Hutchinson, M., Itano, D., Muir, J., Holland, K., 2015. Post-release survival of juvenile silky sharks captured in a tropical tuna purse seine fishery. *Mar. Ecol. Prog. Ser.* 521, 143–154. <https://doi.org/10.3354/meps11073>.
- Igulu, M.M., Nagelkerken, I., Dorenbosch, M., Grol, M.G.G., Harborne, A.R., Kimirei, I.A., Mumby, P.J., Olds, A.D., Mgaya, Y.D., 2014. Mangrove habitat use by juvenile reef fish: meta-analysis reveals that tidal regime matters more than biogeographic region. *PLoS One* 9 (12), e114715.
- Jennings, D.E., Gruber, S.H., Franks, B.R., Kessel, S.T., Robertson, A.L., 2008. Effects of large-scale anthropogenic development on juvenile lemon shark (*Negaprion brevirostris*) populations of Bimini, Bahamas. *Environmental Biology of Fishes* 83 (4), 369–377. <https://doi.org/10.1007/s10641-008-9357-3>.
- Jennings, D.E., DiBattista, J.D., Stump, K.L., Hussey, N.E., Franks, B.R., Grubbs, R.D., Gruber, S.H., 2012. Assessment of the aquatic biodiversity of a threatened coastal lagoon at Bimini, Bahamas. *Journal of Coastal Conservation* 16 (3), 405–428. <https://doi.org/10.1007/s11852-012-0211-6>.
- Kanno, S., Schlaff, A., Heupel, M., Simpfendorfer, C., 2019. Stationary video monitoring reveals habitat use of stingrays in mangroves. *Mar. Ecol. Prog. Ser.* 621, 155–168. <https://doi.org/10.3354/meps12977>.
- Kessel, S.T., Gruber, S.H., Gledhill, K.S., Bond, M.E., Perkins, R.G., 2013. Aerial survey as a tool to estimate abundance and describe distribution of a carcharhinid species, the lemon shark, *Negaprion brevirostris*. *Journal of Marine Biology* 2013, 597383. <https://doi.org/10.1155/2013/597383>.
- Kessel, S.T., Hansell, A.C., Gruber, S.H., Guttridge, T.L., Hussey, N.E., Perkins, R.G., 2016. Three decades of longlining in Bimini, Bahamas, reveals long-term trends in lemon shark *Negaprion brevirostris* (Carcharhinidae) catch per unit effort. *J. Fish Biol.* 88 (6), 2144–2156. <https://doi.org/10.1111/jfb.12987>.
- Kinney, M.J., Simpfendorfer, C.A., 2009. Reassessing the value of nursery areas to shark conservation and management. *Conserv. Lett.* 2 (2), 53–60. <https://doi.org/10.1111/j.1755-263X.2008.00046.x>.
- Kressler, M.M., Dall, S.R.X., Sherley, R.B., 2023. A framework for studying ecological energy in the contemporary marine environment. *ICES Journal of Marine Science* 80, 1580–1593. <https://doi.org/10.1093/icesjms/fsad082>.
- Letessier, T.B., Mouillot, D., Bouchet, P.J., Vigliola, L., Fernandes, M.C., Thompson, C., Boussarie, G., Turner, J., Juhel, J.-B., Maire, E., Caley, M.J., Koldewey, H.J., Friedlander, A., Sala, E., Meeuwig, J.J., 2019. Remote reefs and seamounts are the last refuges for marine predators across the Indo-Pacific. *PLoS Biology* 17 (8). <https://doi.org/10.1371/journal.pbio.3000366>.
- Leurs, G., Nieuwenhuis, B.O., Zuidewind, T.J., Hijner, N., Olf, H., Govers, L.L., 2023. Where land meets sea: Intertidal areas as key-habitats for sharks and rays. *Fish Fish.* 24, 407–426. <https://doi.org/10.1111/faf.12735>.
- Lüdtke, D., 2018. ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. *Journal of Open Source Software* 3 (26), 772. <https://doi.org/10.21105/joss.00772>.
- Morrissey, J.F., Gruber, S.H., 1993a. Habitat selection by juvenile lemon sharks, *Negaprion brevirostris*. *Environ. Biol. Fishes* 38 (4), 311–319. <https://doi.org/10.1007/BF00007524>.
- Morrissey, J.F., Gruber, S.H., 1993b. Home Range of Juvenile Lemon Sharks, *Negaprion brevirostris*. *Copeia* 1993 (2), 425. <https://doi.org/10.2307/1447141>.
- Muff, S., Signer, J., Fieberg, J., 2020. Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. *J. Anim. Ecol.* 89 (1), 80–92. <https://doi.org/10.1111/1365-2656.13087>.
- Nickel, B.A., Suraci, J.P., Nisi, A.C., Wilmers, C.C., 2021. Energetics and fear of humans constrain the spatial ecology of pumas. *Proc. Natl. Acad. Sci.* 118 (5), e2004592118. <https://doi.org/10.1073/pnas.2004592118>.
- Niella, Y., Raoult, V., Gaston, T., Goodman, K., Harcourt, R., Peddemurs, V., Smoother, A.F., 2022. Reliance of young sharks on threatened estuarine habitats for nutrition implies susceptibility to climate change. *Estuar. Coast. Shelf Sci.* 268, 107790. <https://doi.org/10.1016/j.ecss.2022.107790>.
- Pacoureau, N., Rigby, C.L., Kyne, P.M., Sherley, R.B., Winker, H., Carlson, J.K., Fordham, S.V., Barreto, R., Fernando, D., Francis, M.P., Jabado, R.W., Herman, K.B., Liu, K.-M., Marshall, A.D., Pollom, R.A., Romanov, E.V., Simpfendorfer, C.A., Yin, J. S., Kindsvater, H.K., Dulvy, N.K., 2021. Half a century of global decline in oceanic sharks and rays. *Nature* 589 (7843), 567–571. <https://doi.org/10.1038/s41586-020-03173-9>.
- PAN-Tiburones: Plan de Acción Nacional de Conservación y Manejo de Condrictos de la República de Cuba (p. 48). (2015). Ministerio de la Industria Alimentaria.
- Papastamatiou, Y.P., Iosilevskii, G., Santo, V.D., Huvener, C., Hattab, T., Planes, S., Ballesta, L., Mourier, J., 2021. Sharks surf the slope: Current updrafts reduce energy expenditure for aggregating marine predators. *J. Anim. Ecol.* <https://doi.org/10.1111/1365-2656.13536>.
- Pebesma, E., 2018. Simple features for R: standardized support for spatial vector data. *The R Journal* 10 (1), 439. <https://doi.org/10.32614/RJ-2018-009>.
- Queiroz, N., Humphries, N.E., Mucientes, G., Hammerschlag, N., Lima, F.P., Scales, K.L., Miller, P.I., Sousa, L.L., Seabra, R., Sims, D.W., 2016. Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots. *Proc. Natl. Acad. Sci.* 113 (6), 1582–1587. <https://doi.org/10.1073/pnas.1510090113>.
- R Core Team. (2022). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. <https://www.R-project.org>.
- Ruiz-Abierno, A., Márquez-Farías, J.F., Hueter, R.E., Macías-Romero, L., Barros-García, J.M., García-Córdova, L., Hurtado, A., Miller, V., 2020. Distribution and length composition of lemon sharks (*Negaprion brevirostris*) in a nursery ground in southern Cuba. *Environ. Biol. Fishes* 103 (12), 1583–1594. <https://doi.org/10.1007/s10641-020-01050-y>.
- Sievers, M., Brown, C.J., Tulloch, V.J.D., Pearson, R.M., Haig, J.A., Turschwell, M.P., Connolly, R.M., 2019. The role of vegetated coastal wetlands for marine megafauna conservation. *Trends Ecol. Evol.* 34 (9), 807–817. <https://doi.org/10.1016/j.tree.2019.04.004>.
- Sih, A., 1997. To hide or not to hide? Refuge use in a fluctuating environment. *Trends Ecol. Evol.* 12 (10), 375–376. [https://doi.org/10.1016/S0169-5347\(97\)87376-4](https://doi.org/10.1016/S0169-5347(97)87376-4).
- Trevail, A.M., Green, J.A., Bolton, M., Daunt, F., Harris, S.M., Miller, P.I., Newton, S., Owen, E., Polton, J.A., Robertson, G., Sharples, J., Patrick, S.C., 2021. Environmental heterogeneity promotes individual specialisation in habitat selection in a widely distributed seabird. *J. Anim. Ecol.* 90 (12), 2875–2887. <https://doi.org/10.1111/1365-2656.13588>.
- van Zinnicq Bergmann, M.P.M., Guttridge, T.L., Smukall, M.J., Adams, V.M., Bond, M.E., Burke, P.J., Fuentes, M.M.P.B., Heinrich, D.D.U., Huvener, C., Gruber, S.H., Papastamatiou, Y.P., 2022. Using movement models and systematic conservation planning to inform marine protected area design for a multi-species predator community. *Biological Conservation* 266, 109469. <https://doi.org/10.1016/j.biocon.2022.109469>.
- Wetherbee, B., Gruber, S., Cortés, E., 1990. Diet, feeding habits and consumption in sharks, with special reference to the lemon shark, *Negaprion brevirostris*. *National Oceanographic and Atmospheric Administration Technical Report NMFS 1990*, 29–47.
- Wetherbee, B., Gruber, S., 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, T.D., Ferretti, F., Kroodsma, D.A., Hazen, E.L., Carlisle, A.B., Scales, K.L., Bograd, S.J., Block, B.A., 2019b. Predicted hotspots of overlap between highly migratory fishes and industrial fishing fleets in the northeast Pacific. *Sci. Adv.* 5 (3), eaau3761. <https://doi.org/10.1126/sciadv.aau3761>.
- White, C.F., Lyons, K., Jorgensen, S.J., O'Sullivan, J., Winkler, C., Weng, K.C., Lowe, C. G., 2019a. Quantifying habitat selection and variability in habitat suitability for juvenile white sharks. *PLoS One* 14 (5), e0214642.
- Wickham, H., 2016. *ggplot2: Elegant graphics for Data Analysis*. Springer-Verlag, New York.
- Wickham, H., François, R., Henry, L., & Müller, K. (2022). *dplyr: A Grammar of Data Manipulation*. <https://dplyr.tidyverse.org>, <https://github.com/tidyverse/dplyr>.
- Wise, S.P., 2014. Learning through experience: Non-implementation and the challenges of protected area conservation in The Bahamas. *Mar. Policy* 46, 111–118. <https://doi.org/10.1016/j.marpol.2014.01.010>.
- Wojczulanis-Jakubas, K., Grissot, A., Devogel, M., Altmeyer, L., Fujisaki, T., Jakubas, D., Kidawa, D., Karnovsky, N., 2022. Post-foraging in-colony behaviour of a central-place foraging seabird. *Sci. Rep.* 12 (1), 12981. <https://doi.org/10.1038/s41598-022-17307-8>.
- Yan, H.F., Kyne, P.M., Jabado, R.W., Leeney, R.H., Davidson, L.N.K., Derrick, D.H., Finucci, B., Freckleton, R.P., Fordham, S.V., Dulvy, N.K., 2021. Overfishing and habitat loss drive range contraction of iconic marine fishes to near extinction. *Sci. Adv.* 7 (7), eabb6026. <https://doi.org/10.1126/sciadv.abb6026>.
- Zu Ermgassen, P.S., Grove, T., Nagelkerken, I., 2020. Global affiliation of juvenile fishes and invertebrates with mangrove habitats. *Bull. Mar. Sci.* 96 (3), 403–414. <https://doi.org/10.5343/bms.2019.0044>.