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# Where giants roam: The importance of remote islands and seamount corridors to adult tiger sharks in the South Pacific Ocean

Jordan K. Matley [a,*], Lauren Meyer [a,g], Adam Barnett [b,c], Mark Scott [d], Elizabeth A. Dinsdale [a], Michael P. Doane [a], David Harasti [e], Lisa A. Hoopes [f], Charlie Huveneers [a]

[a] College of Science and Engineering, Flinders University, Adelaide, SA, 5042, Australia
[b] Biopixel Oceans Foundation, Cairns, 4878, Australia
[c] Marine Data Technology Hub, College of Science and Engineering, James Cook University, Townsville City, QLD, Australia
[d] Norfolk Island National Park, Burnt Pine, Norfolk Island, 2899, Australia
[e] Fisheries Research, NSW DPIRD, Port Stephens Fisheries Institute. Taylors Beach, NSW, Australia
[f] IUCN Center for Species Survival, Georgia Aquarium, Atlanta, GA, USA
[g] Georgia Aquarium, Atlantic, GA, USA

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A B S T R A C T

The movements of tiger sharks (*Galeocerdo cuvier*) across their global distribution are diverse and complex, and there remains a dearth of information about the cues that influence migrations of adults to and from offshore islands. We aimed to delineate broad-scale movements of a seasonally abundant tiger shark aggregation at Norfolk Island, a remote small island in the South Pacific Ocean, by identifying migratory pathways and important areas, as well as quantifying the association between space use and environmental factors. We satellite tracked 35 tiger sharks, consisting of some of the largest individuals ever monitored (median total length: 4.0 m), between February 2020 and April 2023. Tracking periods averaging 305 days (14 – 686 days) showed movements throughout large parts of the South Pacific Ocean including near New Caledonia, the Great Barrier Reef, Papua New Guinea, Chesterfield Islands, Vanuatu, Fiji, and New Zealand. The longest track was close to 17,000 km over 468 days. There was high seasonal fidelity to Norfolk Island with 88% of sharks tracked across multiple seasons returning at least once, mainly from New Caledonia. The median date of arrival and departure from Norfolk Island were in December and May, respectively. Coastal use of islands was the most important factor across monthly habitat suitability models, whereas sea surface temperature explained seasonal departures/arrivals from/to Norfolk Island. The findings of our study show diverse potential movement trajectories and cues used by tiger sharks, but importantly highlight the critical role of Norfolk Island and other nearshore areas in supporting large adult female tiger sharks.

## 1. Introduction

The movements of animals are influenced by numerous factors related to internal (energy acquisition, endocrinology, reproduction, and homeostasis) and external (biotic and abiotic) cues (Bauer et al., 2011; Cooke et al., 2022; Lubitz et al., 2022). Similarly, the ability to move over different spatial scales is limited by the animal's functional and anatomical capacity (Nathan et al., 2008). Movement decisions, such as navigation and pathway selection, are also constrained by an animal's ability to sense and react to surrounding physicochemical conditions (Horodysky et al., 2015) and environmental signals (Bauer et al., 2011; Lubitz et al., 2024). Consequently, small- and large-scale movements rely on a complex interplay of cognitive, sensory, and biomechanical tools that are responsive to both internal and external environments. Migration, defined here as the movement between disparate locations as an adaptation to spatiotemporally fluctuating resources (e.g., habitat, food, reproductive partners, thermal windows; Dingle and Drake, 2007), is a critical process in the spatial dynamics of animal populations globally and across terrestrial and aquatic environments. Migratory behavior often includes directed movements on the scale of hundreds or thousands of kilometres, supported by highly adapted navigation/sensory, motion, and propagation capacity (Bauer et al., 2011; Cooke et al., 2022). Like all movement decisions, migrations are influenced by individual, population, and environmental factors,

* Corresponding author.
*E-mail address:* jordan.matley@flinders.edu.au (J.K. Matley).

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with resultant behaviors shaping fitness and survival by optimising biological and physiological states (Dingle, 2014; Bauer et al., 2011).

Describing the distribution, movement patterns, and migration routes of highly mobile predators is a vital step towards understanding how internal and external cues impact spatiotemporal behavior and subsequent ecological interactions (Barnett and Semmens, 2012; Lubitz et al., 2023). Whereas knowledge of localized movements of sharks has important bearing on local ecology (Espinoza et al., 2015; Heupel et al., 2018), tracking broad-scale movements or migrations throughout their entire spatial extent facilitates a more holistic view of the factors driving behavior and resultant implications for conservation and management (Huveneers et al., 2021; Lédée et al., 2021). For example, evaluation of broad-scale movements helps predict how seasonal or climate-induced changes may affect the distribution of species in the future (Niella et al., 2022). The capacity to identify seasonally important areas (e.g., foraging or reproductive) and associated migratory pathways further increases the ability to protect vulnerable species and habitat (Doherty et al., 2017; Dwyer et al., 2020). Furthermore, a greater comprehension of the ecological role of predators can be deciphered from broad-scale tracking, particularly in relation to spatial subsidies (i.e., consumer-mediated movement of nutrients or waste from one location to another), and their influence on foodwebs across the extent of migration routes (Meyer et al., 2010; Afonso et al., 2017).

The tiger shark (*Galeocerdo cuvier*) is a wide-ranging large-bodied generalist predator occurring throughout tropical and subtropical marine waters worldwide. Broad-scale movements (e.g., >500 km) of tiger sharks have been documented using satellite telemetry throughout much of their range, including the Hawaiian Islands (Meyer et al. 2010, 2018), the east coast of Australia (Fitzpatrick et al., 2012; Holmes et al., 2014; Lipscombe et al., 2020; Niella et al., 2022; Barnett et al., 2022), Western Australia (Heithaus et al., 2007; Ferreira et al., 2015), the northwestern Atlantic Ocean (Lea et al., 2015; Hammerschlag et al., 2022; Smukall et al., 2022), the southwestern Atlantic Ocean (Afonso and Hazin, 2014; Afonso et al., 2017), the Gulf of Mexico (Ajemian et al., 2020), the western Indian Ocean (Daly et al., 2018; Barkley et al., 2019), the Galapagos Archipelago (Acuña-Marrero et al., 2017), and the Coral Sea (Werry et al., 2014). Overall, there is considerable diversity in movement patterns and migration strategies within (e.g., ontogenetically or between sexes) and across tiger shark populations ('population' used throughout for practicality referring to sharks tagged in different areas and independent of population genetics). Spatial segregation among juveniles, adult males, and adult females is often observed and typically associated with reproduction (Meyer et al., 2014). For example, Vossgaetter et al. (2024) characterised a female-dominated aggregation of tiger sharks in the Maldives, attributing the sex-based differences and strong site fidelity to suitable conditions (e.g., food provisioning) for gestation. In the Bahamas, large juveniles and adults are more resident than small juveniles, with increased residency of females during winter months posited to be associated with pupping (Smukall et al., 2022). Juveniles and sub-adults have also displayed reduced migration propensity compared to adults in Bermuda (Lea et al., 2015), Hawaii (Papastamatiou et al., 2013), and Chesterfield Islands (Werry et al., 2014). Partial migration, where some individuals of a population migrate and others do not, has also been documented within a cohort of mature females in Hawaii (Papastamatiou et al., 2013). Conversely, some populations appear to be largely non-migratory (at least during tracking periods), or highly variable across age/sex classes despite large home ranges (Fitzpatrick et al., 2012; Werry et al., 2014; Ferreira et al., 2015; Acuña-Marrero et al., 2017; Meyer et al., 2018; Salinas-de-León et al., 2019).

The intraspecific variability in tiger shark movements complicates the characterisation of migration strategies for regional populations, as well as a unifying migration strategy for the species. The ability to characterize migratory patterns within or across populations are compounded by small sample sizes, limited tracking periods, and studies/captures that are biased towards specific sexes or life stages. In particular, there are limited studies where large-bodied adults are the predominant life stage tracked. Interestingly, studies where the most pronounced seasonal movements away from and returning to specific high-use areas have typically occurred when larger data sets of adults were tracked over multiple years, highlighting potential sampling limitations. For example, when adult tiger sharks (n = 23) were tracked in Hawaii for periods up to 595 days, there was a high occurrence of core-structured home ranges with intermittent visits to adjacent islands (Meyer et al., 2018). Similarly, adult tiger sharks (n = 9) undertook annual roundtrip migrations over 7500 km back to specific insular overwintering habitats in the Caribbean when tracked up to 1101 days (Lea et al., 2015).

Despite a relatively high focus of tracking research on tiger sharks with satellite (Renshaw et al., 2023) and acoustic (Matley et al., 2024) telemetry, the assembly of these studies still only offer a peek into a complex behavioral realm that we know little about (Holland et al., 2019). For example, drivers of tiger shark migrations and broad-scale movements have been attributed to foraging (Meyer et al., 2010; Lea et al., 2015), temperature (Holmes et al., 2014; Lipscombe et al., 2020; Hammerschlag et al., 2022; Niella et al., 2022), and demography (e.g., sex and ontogeny; Werry et al., 2014; Ajemian et al., 2020; Smukall et al., 2022), or a combination thereof (Lubitz et al., 2022). However, the specific and relative influence of drivers is difficult to test, limiting our understanding of how tiger sharks react to internal or external cues (Lubitz et al., 2022). Furthermore, while broad-scale tracking of such a wide-ranging animal has covered large swaths of the ocean, some populations (or sub-populations) and demographics remain unaccounted for, particularly near remote offshore islands. One such example pertains to tiger sharks that are seasonally present (e.g., Austral summer) at Norfolk Island, a small and remote island in the South Pacific Ocean (~700 km from the nearest land, and 1400 km east of Australia). Norfolk Island offers an intriguing study system given its distance from any other islands (i.e., possible population segregation), and high abundance of large migratory female tiger sharks (Tofts, 2001; M. Scott pers. obs.). The overall aim of our study was to identify broad-scale movements of tiger sharks after they leave Norfolk Island and identify the proclivity of this population to make large-scale migrations, quantify the importance of certain areas (e.g., Norfolk Island, other islands/nations, hotspot locations), and evaluate how their movements and distribution are associated with geographic and environmental factors. The high number of large adults (immature sharks are rarely seen/caught) at this remote island provides a unique opportunity to identify habitat use and characterize migration patterns for this understudied life stage, while providing new information regarding the spatial dynamics around a small remote island and movements of adult tiger sharks throughout the South Pacific Ocean.

## 2. Methods

### 2.1. Study area

We tagged and tracked tiger sharks from Norfolk Island across their range in the South Pacific Ocean. Norfolk Island is a small (~8 km$^2$) remote island (~700 km to nearest land) in the South Pacific Ocean surrounded by rock, sand, and coral reef habitat. Norfolk Island forms a part of the Norfolk Island Seamounts Area which encompasses seamounts rising along the Norfolk Ridge (Fig. 1) from >1500 m to <200 m primarily north and south of Norfolk Island (Williams et al., 2006). The Norfolk Ridge is a contiguous feature at depths between 1000 and 2000 m, extending from New Zealand north to New Caledonia (~1000 km long and 70 km wide). Both the Norfolk Ridge and Norfolk Island Seamounts Area sustain rich and diverse biological communities with high levels of endemism (Williams et al., 2006). Norfolk Island (IUCN 2024a) and Norfolk Ridge (IUCN 2024b) are listed as Important Shark and Ray Areas (ISRA).

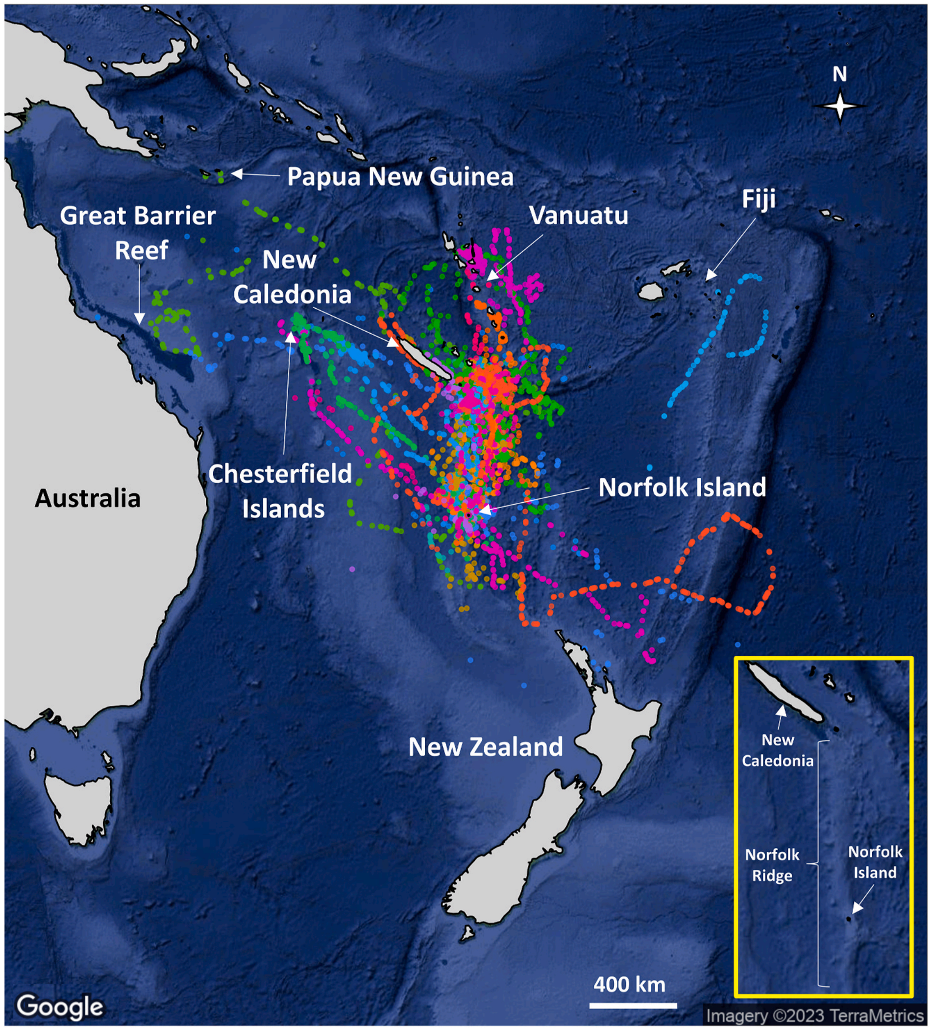


**Fig. 1.** Study area in the western South Pacific Ocean with estimated (fitted) tiger shark (n = 32) locations (points; n = 9377) derived from satellite telemetry. Locations are colored by individuals. A subset map showing the northern part of the Norfolk Ridge (without shark locations) is enclosed in a yellow box at the bottom right. The ggmap R package (Kahle and Wickham, 2013) was used to plot Google-based satellite imagery. All sharks were tagged and released at Norfolk Island.

### 2.2. Shark tagging

We captured tiger sharks (n = 35; 28 female and 7 male) at Headstone Bay (29.046169°S, 167.921167°E), located on the western side of Norfolk Island, via floating drumline baited with a fish carcass on a 16/0 circle hook. Females and males were between 3.1 – 4.5 m and 3.5 – 4.1 m total length, respectively (Table 1), representing one of the largest sized cohorts of tiger sharks to be tagged using satellite telemetry (Fig. 2). Sharks were pulled alongside the vessel and tagged externally with a dorsal fin-mounted satellite-linked radio transmitter (SPOT-420 tag, maximum battery life 370 d, 62 g; Wildlife Computers, Redmond, WA, USA), prior to release. SPOT tags transmit a signal to the Argos satellite array when the animal surfaces (i.e., the tag is exposed to air), providing a near real-time estimate of position. Accuracy of position estimates vary based on the number and time between transmissions received by satellites and are classified based on position error estimates (i.e., 3, 2, 1, 0, A, B, Z; static.wildlifecomputers.com/Spreadsheet-File-Descriptions-4.pdf).

### 2.3. Analysis

#### 2.3.1. Location estimates

We used the AniMotum R package (Jonsen et al., 2023) to predict locations between satellite-derived detections, estimate positional error of fitted and predicted detections based on error classifications and spatial/temporal gaps between detections, and to filter unrealistic positions using a maximum tiger shark sustained swimming speed of 5 m $s^{-1}$ (Barnett et al., 2022). A daily position (per individual) during each 24-h period of tracking was estimated to reduce biases associated with autocorrelation between successive detections. The 24-h period was selected because it was the mean duration between consecutive detections across individuals, ensuring that positions were not interpolated at a temporal resolution incongruous with the data (e.g., 85 % of consecutive detections were within a 24-h period). Daily positions were estimated using the 'move persistence' movement process model (Jonsen et al., 2023), which accounts for variation in time associated with direction and step length (distance travelled during each 24-h period). Any positions that were estimated on-land were moved to the nearest point 100 m offshore.

#### 2.3.2. Broad-scale movements

Broad-scale movements were described and quantified, including movements from/to Norfolk Island to/from different island nations and major bathymetric areas (i.e., the Great Barrier Reef and the Chesterfield Islands). An individual was considered present in a location if the estimated locations were within 100 km of these areas. Predicted locations were used to provide a continuous daily track of animals throughout the possible areas (including >100 km from land).

**Table 1**

Summary information of tiger sharks satellite tracked from Norfolk Island, Australia. Location estimates are based on interpolated daily positions between each animal's first and last detection (n = 9739). Three individuals were not included in analyses because they were either never detected after release (Meg and Scotty), or only had three detections over ~2.5 years (Fletcher).

| ID | Sex | Total Length (m) | Tagging Date | First Detection | Last Detection | No. Daily Location Estimates | Median Position Error (±SE; km) | Estimated Distance Moved (km) | Distance Moved Per Day (km) | Maximum Linear Distance (km) |
|---|---|---|---|---|---|---|---|---|---|---|
| Headstone | F | 3.8 | February 19, 2020 | February 21, 2020 | May 8, 2021 | 443 | 15.5 ± 2.1 | 16347 | 36.9 | 2768 |
| David | M | 3.8 | February 27, 2020 | February 27, 2020 | January 28, 2021 | 337 | 26.5 ± 2.7 | 6233 | 18.5 | 817 |
| MiaMiti | F | 4.3 | February 26, 2020 | February 27, 2020 | May 26, 2020 | 90 | 18.9 ± 4.6 | 1695 | 18.8 | 695 |
| Norfolk | F | 4.1 | February 26, 2020 | February 27, 2020 | December 5, 2021 | 648 | 128.8 ± 18 | 15569 | 24.0 | 3080 |
| Emma | F | 3.1 | February 28, 2020 | February 28, 2020 | May 13, 2021 | 441 | 25 ± 2.1 | 5738 | 13.0 | 199 |
| Fitzy | M | 4.1 | February 25, 2020 | February 29, 2020 | May 13, 2021 | 440 | 12.2 ± 2.8 | 13888 | 31.6 | 1347 |
| Tintoela | F | 3.2 | February 25, 2020 | February 29, 2020 | June 28, 2021 | 486 | 81.5 ± 8.8 | 9970 | 20.5 | 1421 |
| Koru | F | 3.6 | February 28, 2020 | March 10, 2020 | March 6, 2021 | 362 | 49.5 ± 11.7 | 6305 | 17.4 | 1503 |
| Geoff | F | 3.7 | February 23, 2021 | February 23, 2021 | April 1, 2021 | 38 | 14.6 ± 3.6 | 333 | 8.8 | 87 |
| Jap | M | 3.7 | February 24, 2021 | February 25, 2021 | November 16, 2021 | 265 | 15.1 ± 1.5 | 9218 | 33.9 | 893 |
| Philip | F | 4.2 | February 26, 2021 | February 27, 2021 | June 9, 2022 | 468 | 82.3 ± 10.4 | 16984 | 36.3 | 3342 |
| Scotty 2 | F | 4.4 | February 26, 2021 | March 1, 2021 | November 17, 2021 | 262 | 10.4 ± 2.4 | 7007 | 26.7 | 1657 |
| Isla Belle | F | 4.2 | February 24, 2021 | March 2, 2021 | August 31, 2022 | 548 | 47.1 ± 5 | 15337 | 28.0 | 1531 |
| Nepean | F | 4.0 | February 26, 2021 | March 2, 2021 | August 17, 2021 | 169 | 25.9 ± 2.7 | 3318 | 19.6 | 830 |
| Nehsi | F | 4.0 | February 24, 2021 | March 5, 2021 | June 8, 2022 | 461 | 42.1 ± 11.4 | 9465 | 20.5 | 2141 |
| Nomad | F | 3.8 | February 26, 2021 | March 5, 2021 | January 19, 2023 | 686 | 47.5 ± 5.7 | 9957 | 14.5 | 1811 |
| Freidi | F | 3.9 | February 24, 2021 | March 27, 2021 | June 6, 2021 | 72 | 57.9 ± 3.1 | 1259 | 17.5 | 1049 |
| Kimmy | F | 3.9 | February 15, 2022 | February 15, 2022 | April 9, 2023 | 419 | 34.1 ± 4.2 | 12307 | 29.4 | 1656 |
| Suki | F | 3.8 | February 17, 2022 | February 17, 2022 | October 19, 2022 | 245 | 62.6 ± 8.1 | 5881 | 24.0 | 845 |
| Nate | F | 3.8 | February 20, 2022 | February 20, 2022 | September 20, 2022 | 213 | 99.7 ± 14.6 | 1251 | 5.9 | 743 |
| Theodosia | F | 3.8 | February 18, 2022 | February 20, 2022 | January 24, 2023 | 339 | 89.9 ± 32.5 | 12386 | 36.5 | 2055 |
| Jess | F | 4.0 | February 21, 2022 | February 21, 2022 | April 18, 2022 | 57 | 4.8 ± 1.6 | 588 | 10.3 | 80 |
| Jens | M | 3.5 | February 17, 2022 | February 22, 2022 | March 7, 2022 | 14 | 5 ± 2.1 | 72 | 5.1 | 21 |
| Tinka | F | 3.4 | February 17, 2022 | February 22, 2022 | January 11, 2023 | 324 | 62 ± 10.8 | 6273 | 19.4 | 1394 |
| Robert | F | 4.2 | February 23, 2022 | February 23, 2022 | February 22, 2023 | 365 | 45.2 ± 4.7 | 11085 | 30.4 | 1264 |
| Birgit | F | 4.3 | February 24, 2022 | February 24, 2022 | October 3, 2022 | 222 | 49.8 ± 4 | 2125 | 9.6 | 1105 |
| Sharky McShark Face | F | 4.1 | February 26, 2022 | February 26, 2022 | March 28, 2022 | 31 | 4.6 ± 0.9 | 1738 | 56.1 | 1413 |
| Aatuti | F | 4.1 | February 24, 2022 | March 2, 2022 | December 23, 2022 | 297 | 6.4 ± 0.5 | 13551 | 45.6 | 2593 |
| Lacky | M | 3.5 | February 21, 2022 | March 3, 2022 | March 28, 2022 | 26 | 23.5 ± 3.3 | 1174 | 45.2 | 513 |
| Rocket | F | 4.1 | February 26, 2022 | March 8, 2022 | November 16, 2022 | 254 | 13.1 ± 2.6 | 3613 | 14.2 | 1539 |
| Tigger | F | 4.1 | February 26, 2022 | March 11, 2022 | April 15, 2023 | 401 | 192.1 ± 52.9 | 11779 | 29.4 | 981 |
| Ali-Bel | F | 4.5 | March 8, 2022 | March 14, 2022 | January 23, 2023 | 316 | 12.6 ± 2 | 4627 | 14.6 | 1333 |
| Fletcher | M | 4.1 | February 28, 2020 | July 23, 2022 | December 14, 2022 | 3 | – | – | – | – |
| Meg | F | 3.6 | – | – | – | – | – | – | – | – |
| Scotty | M | 4.0 | – | – | – | – | – | – | – | – |
| **Mean (± SE)** | | | | | | **305 ± 32** | **43.9 ± 7.6** | **7408 ± 946** | **24.0 ± 2.2** | **1334 ± 146** |

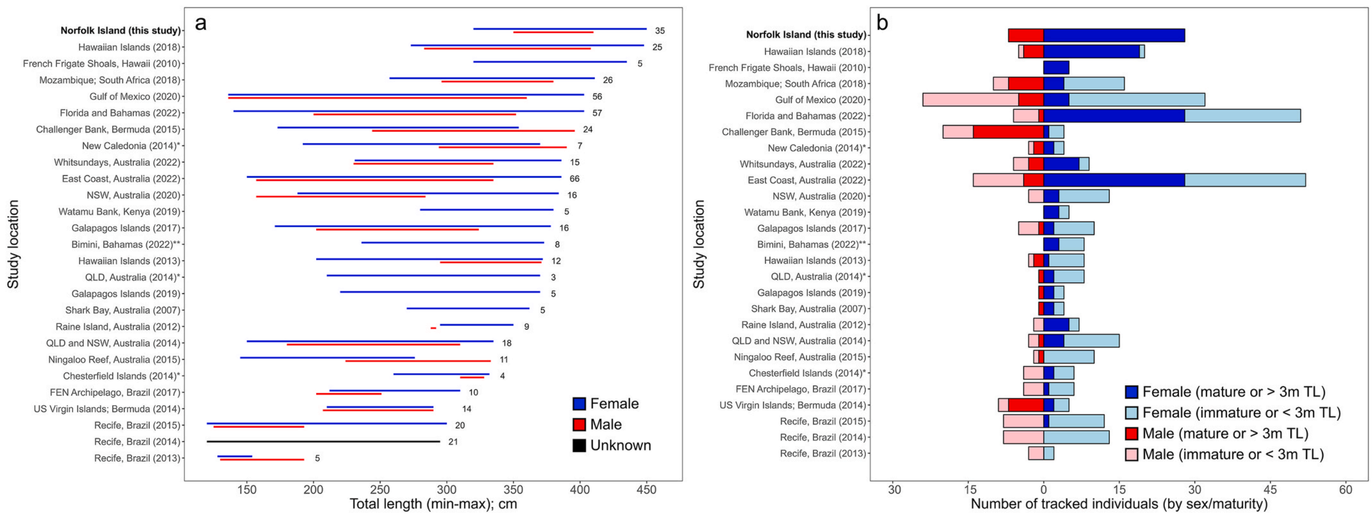


**Fig. 2.** Summary of size (a) and maturity (b) of satellite tagged tiger sharks from peer-reviewed articles.

Hotspot areas and migratory pathways used by tiger sharks at the population level were identified based on overlap between 95 % activity space utilisation distributions (UDs) across individuals (sex or size was not distinguished given the low number of males and small individuals). The Dynamic Brownian Bridge Movement Model (dBBMM) was selected (Move R package; Kranstauber et al., 2023) to quantify activity spaces given that it considers error associated with position estimates, incorporates trajectory and travel time, and minimizes spatial and temporal autocorrelation within movement data (Horne et al., 2007). Positional error for each daily position was derived from the associated mean 'x' and 'y' error provided during AniMotum processing. We selected a grid cell size of 10 km × 10 km to measure overlap. Positions that had an estimated error >10 km, or were not detected again within 10 days, were removed to reduce uncertainty about location positively biasing UD estimates. Overlap was calculated as the number of individuals with overlapping UDs in each 10 km × 10 km cell, independent of time.

### 2.3.3. *Seasonal presence at Norfolk Island*

Seasonal changes in the presence and timing of arrival/departure at Norfolk Island were quantified to investigate the frequency and duration of tiger sharks aggregating at Norfolk Island. Animals that were only detected <100 km from Norfolk Island were removed for this analysis due to their inability to provide absence information.

Seasonal presence at Norfolk Island, defined as the proportion of days present each month (adjusted for incomplete months before tagging and after last detection) was modelled against month (i.e., explanatory variable) using a generalized additive mixed-effect model (GAMM; *gam* function in mgcv R package; Wood, 2017) with binomial distribution (link = logit). Cyclic cubic regression splines were used to connect consecutive monthly periods together (k = 11). The *gam.check* function was used to run diagnostic tests to ensure basis dimensions were adequately chosen. Shark ID was included in the model as a random effect, as was the annual period (defined below), because there was considerable variation in tagging periods between years limiting our ability to test for year-specific behavioral patterns. Additionally, females and males were evaluated together given the limited detections of males at Norfolk Island. Thus, we present a global model evaluating seasonal presence across the entire sample population independent of year.

The timing of arrival at and departure from Norfolk Island were identified for each individual during each distinct annual period between October and September (e.g., October 1, 2019–September 30, 2020). These periods were identified after exploring patterns of arrival/departure each year, in which all animals were first detected (after several months of absence) at Norfolk Island after October 1 and departed before October 1 the following year. Therefore, for each individual and annual period, the first date represented the date of arrival and the last date represented the date of departure. To ensure arrival and departure dates were not biased by tagging (i.e., animals tagged were already 'present' at Norfolk Island) or battery life (i.e., battery died while at Norfolk Island), respectively, arrivals were not used in the tagging year and only departure periods with a final position >100 km from Norfolk Island (i.e., evidence it had departed the island) were used. The duration between the arrival and departure was also calculated. In a few cases, an animal was only detected one day in a period; these instances were removed because they likely represented transitory movements nearby or lacked sufficient detections to distinguish resident behavior.

### 2.3.4. *Move persistence*

Move persistence is an index of movement behavior derived from changes in autocorrelation between detections (based on speed and direction; Jonsen et al., 2019) and was estimated within AniMotum (Jonsen et al., 2023) during preliminary filtering and position estimates. Each position is assigned a persistence value ranging between 0 and 1, with values closer to 0 representing uncorrelated movements (e.g., simple random walk) and values closer to 1 representing correlated movements (e.g., correlated random walk). We chose move persistence as a behavioral indicator because it effectively identifies changes in movement patterns without any prior knowledge of the behavioral states (Jonsen et al., 2019). We used the 'normalized' move persistence method, which scales the values of each individual between 0 and 1 as opposed to absolute values because we wanted to increase our ability to identify changes in behavior pertinent to each individual (i.e., higher sensitivity to individual variation when scaled between 0 and 1).

A general additive mixed-effects model (GAMM; Gaussian distribution) was used to evaluate the relationship between the response variable persistence (daily; continuous 0–1) and various covariates that were hypothesized to influence movement patterns based on previous studies. The covariates initially chosen (including variable structure and references supporting their inclusion) were: sex (static, discrete; Werry et al., 2014), total length (TL; static, continuous; Rangel et al., 2022), month (temporally variable, integer; Ajemian et al., 2020), depth (spatially variable, continuous; Afonso and Hazin, 2015), bathymetrical slope (spatially variable, continuous; Holmes et al., 2014), distance to nearest land (spatially variable, continuous; Meyer et al., 2018), sea surface temperature (SST; spatiotemporally variable, continuous; Payne et al., 2018), and chlorophyll (spatiotemporally variable, continuous;

Papastamatiou et al., 2013). Latitude was also initially included as a model variable but was removed because it was correlated with sea surface temperature. Although water temperature was limited to SST, tiger sharks often spend substantial time near the surface and only occupy a narrow daily temperature range (Vaudo et al., 2014; Andrzejaczek et al., 2020). Thus, SST, which is widely available, is a suitable parameter to use in these models. Bathymetry data were obtained from GEBCO (download.gebco.net; grid version: GEBCO, 2023, resolution: ~400 m [15 arc-second]). The same source was used for bathymetrical slope and was calculated as the maximum depth minus the minimum depth within each 10 × 10 km grid. Sea surface temperature and chlorophyll data were obtained from the NASA Earth Observations portal (neo.gsfc.nasa.gov; 1 Month – AQUA/MODIS, resolution: ~10 km [0.1°]). Highly correlated variables, identified using variance inflation factors (VIFs) ≤3 (car R package; Fox and Weisberg, 2019), were not included in the final model. Tiger shark ID was included as a random factor. A daily autocorrelation structure was incorporated in the model by applying correlation parameter estimates (i.e., rho argument) derived from preliminary model runs (Baayen et al., 2018). Model selection was iterative with all covariate combinations explored using the *dredge* function (MuMIn R package; Bartoń, 2023) and compared using Akaike's information criterion corrected for small sample size ($AIC_c$; Anderson and Burnham, 2002); only models with $\Delta AIC_c$ <2 were considered informative. Model fit was evaluated based on the coefficient of determination ($R^2$). Diagnostic plots were evaluated to ensure residuals of explanatory variables were homogenous. The *gam.check* function was used to run diagnostic tests to ensure basis dimensions were adequately chosen.

#### 2.3.5. Habitat suitability modelling

The relative suitability of different habitats (i.e., combination of abiotic factors) throughout the distribution of tracked tiger sharks was quantified using MaxEnt's Dismo R package (Hijmans et al., 2023). MaxEnt models species distributions based on presence-only occurrence data. Similar to other species distribution modelling (SDM) approaches for spatial data without true absences, a number of pseudo-absences are compared to presences across different environmental or habitat variables to quantify areas of importance relative to those variables (Elith et al., 2010). Due to the nature of presence-only data, MaxEnt modelling is appropriately viewed as a tool to estimate or predict habitat preference of species as opposed to probability of occurrence, providing a measure of habitat suitability, known as the habitat suitability index (HSI; Stephenson et al., 2021). Habitat suitability indices range from 0 to 1 with higher values indicating a more suitable environment (e.g., <0.4 = low suitability, 0.4–0 0.8 = moderate suitability, and >0.8 = high suitability; Georgian et al., 2019). MaxEnt has been shown to be effective with satellite telemetry data, which is often characterized by small and unbalanced sample sizes with varying confidence in position estimates (Elith et al., 2006; Graham et al., 2008; Edrén et al., 2010).

Presence (and pseudo-absences), and environmental variables were identified in 10 × 10 km grids as described above at monthly intervals. Depth, slope, distance to nearest land, SST, and chlorophyll (collinearity across all variable combinations were <0.41 Pearson's coefficient) were the selected environmental variables used to model habitat suitability. To identify broad-scale seasonal changes in habitat selectivity, we combined monthly animal locations across years and averaged monthly environmental variables across years, reducing the effects of limited and unequal sampling across years. Monthly presence within a 10 $km^2$ grid was based on whether any individual was detected within the area in each month, indicating the area contained 'suitable habitat' for the population. The maximum number of background (i.e., pseudo-absence) locations was chosen to be 10,000 (randomly selected from all grids without presences; Phillips and Dudík, 2008). The 100 % minimum convex polygon of all individuals' locations was used to delineate potential absences and avoid bias associated with sampling unrealistic background locations (Elith et al., 2010). Otherwise, a logistic output with 10-fold cross-validation (70:30 training:testing split) with default regularisation settings, jackknife tests of variable importance, and feature class types were selected. Model performance was evaluated using the AUC (area under the receiver-operating-characteristic curve), which assesses the predictive power of the model to discriminate against true positives (i.e., sensitivity) and false negatives (i.e., 1 – specificity) within the test data. Parameter estimates from the 10 output scenarios (i.e., cross-validation replicates) were averaged to obtain a more robust representation of the data compared to single split approaches (Phillips, 2005). Area under the curve values from testing and training datasets were compared to evaluate predictive ability of each monthly model. Finally, two threshold metrics (i.e., HSI values distinguishing unsuitable habitat-areas from suitable habitat-areas) were reported for each month, the '10th percentile training presence' (i.e., omits regions with HSI values in the lowest 10% of occurrence records) and the 'maximum training sensitivity plus specificity' (i.e., the sum of sensitivity and specificity is maximized) thresholds.

## 3. Results

### 3.1. Broad-scale movements

Thirty-two of the 35 tagged individuals produced fitted data that were used in further analysis (Table 1). Specifically, two individuals (one female and one male) were never detected due to tag failure or post-release mortality and one male was removed from analyses because it was only detected three times over a five-month period and thus no reliable movement paths could be determined. The remaining individuals had 9739 combined daily detections (i.e., predicted locations; Table 1), representing 26.7 years of cumulative tracking data and included 27 female and 5 males. These individuals were primarily detected around or between Norfolk Island and New Caledonia in an area approximately 400 km wide (west-east; Fig. 1). Males were rarely detected outside of this region (Fig. S1). Across all individuals, seven were only detected at Norfolk Island or within oceanic waters >100 km away (Fig. 3). Twenty-five individuals made large-scale movements from Norfolk Island (where they were tagged) directly or indirectly to within 100 km of either New Caledonia (France), the Great Barrier Reef (Australia), Papua New Guinea, Chesterfield Islands (France), Vanuatu, Fiji, and New Zealand (Fig. 1; Fig 3). Specifically, 19 individuals moved from Norfolk Island directly to New Caledonia (median duration = 15 days). Five of these sharks (and an additional individual) also moved to New Caledonia through Vanuatu (n = 3; median duration = 17 days), Chesterfield Islands (n = 3; median duration = 19 days), Fiji (n = 1; duration = 70 days), and New Zealand (n = 1; duration = 37 days; Fig. 4). Therefore, a total of 20 individuals (~63 % of all tracked sharks) were detected at some point near (<100 km) New Caledonia. Of the 25 individuals that departed Norfolk Island (and were detected near other islands), 17 returned to Norfolk Island, including 12 directly from New Caledonia (median duration = 13 days), three from the Chesterfield Islands (median duration = 68 days), one from Vanuatu (duration = 13 days), one from the Great Barrier Reef (duration = 29 days), and one from New Zealand (duration = 50 days; Fig. 4). In addition to Norfolk Island (n = 12 individuals), other areas had high connectivity with New Caledonia including Vanuatu (n = 4 individuals), Chesterfield Islands (n = 2 individuals), Papua New Guinea (n = 1 individuals), New Zealand (n = 1 individuals), and Fiji (n = 1 individuals; Fig. 4). Estimates of total distances moved across the 32 individuals were between 72 km and 16,984 km (mean ± standard error: 7456 ± 951 km; Table 1). Daily distances moved were between 5.1 km $d^{-1}$ and 56.1 km $d^{-1}$ (24.0 ± 2.2 km $d^{-1}$). Maximum linear extent ranged between 21 km and 3342 km (1374 ± 148 km) across individuals. The average median (± standard error) 'x' and 'y' error associated with each detection was ~44.0 (±7.6) km (Table 1).

An additional individual was removed (ID: Jens) for the activity space analysis (n = 31) because the sample size was too low (detected

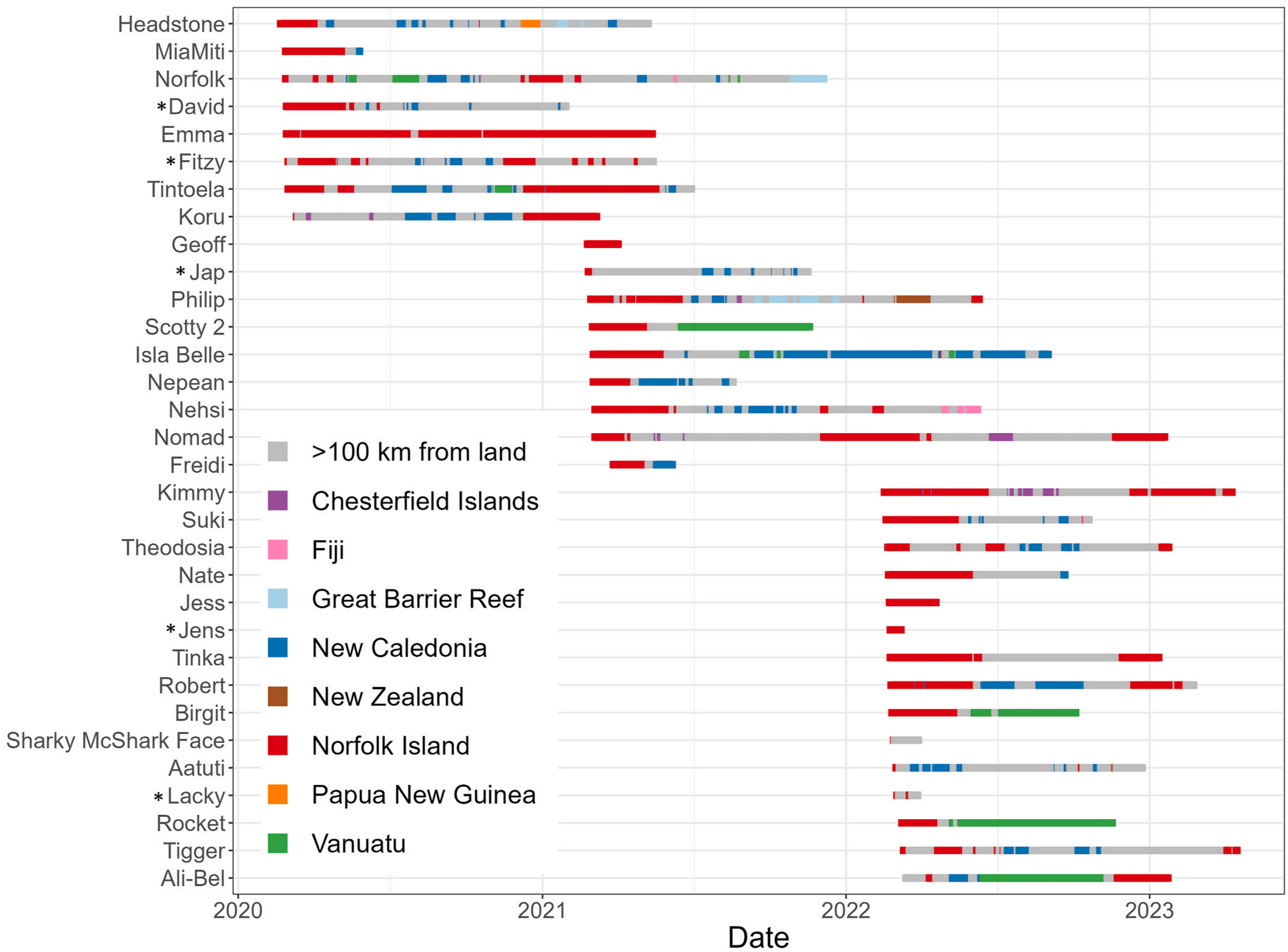


**Fig. 3.** Detection plot of predicted daily locations (n = 9739) for each individual (n = 32) based on proximity (<100 km) to a major land or bathymetric area. An asterisk (*) denotes a male individual.

for 14 days) to process without losing model stability. After filtering for predicted positions with an estimated error <10 km, activity space was calculated from 2480 estimated locations. The maximum number of individual UDs overlapping within 10 km × 10 km cells at any period was 27, which only occurred around Norfolk Island (Fig. 5). Otherwise, the main areas of overlap among individuals were near seamounts southeast of New Caledonia, where as many as 13 individuals had shared UDs within a cell (Fig. 5). The area between Norfolk Island and southeast New Caledonia was also populated with overlapping UDs indicating movement between these areas. Outside of these main areas, there was some overlap (a few individuals) at the Chesterfield Islands and Vanuatu, and the area south of Norfolk Island towards New Zealand.

### 3.2. Seasonal presence at Norfolk Island

Seasonal presence at Norfolk Island was explored based on monthly changes in presence and timing of arrival/departure. Four sharks (ID: Jens, Jess, Emma, Geoff) were excluded because they were only detected at Norfolk Island or only left for a short period before returning (i.e., Emma). The GAMM showed a significant non-linear relationship of presence relative to month (k = 11, edf = 4.7, F = 28.9, $p < 0.001$, $R^2 = 0.45$; Fig. S2a). The predicted smoothers between individuals (Fig. S2b) and between annual periods (Fig. S2c) were generally similar. Based on the global model (Fig. S2a), presence peaked in January – February, with ~50 % predicted monthly presence between December and March.

The median date of arrival at Norfolk Island across years was the 12th of December (n = 13 individuals; 15 observations), while the median date of departure was the 8th of May (n = 28 individuals; 34 observations; Fig. S3). Typically, the range in arrival dates was smaller (~mid-November to end-January) compared to departure dates (~mid-February to end-June). Arrivals and departures were consistent across years (Fig. S2c; Fig. S3). A few individuals arrived at (Nomad, Kimmy) or departed from (Fitzy, Nomad, Nehsi, Norfolk, Tintoela, Robert) Norfolk Island on multiple occasions. Tintoela showed a strong pattern of repeatability departing Norfolk Island two days apart in 2020 and 2021, while Nomad arrived and departed two weeks and three days apart, respectively, in 2021 and 2022 (the remaining arrived/departed >40 days apart). Although a small sample size, the mean residency (i.e., duration between arrival and departure times) at Norfolk Island was 113 days (n = 7 individuals/observations; range: 61–163 days)

### 3.3. Move persistence

Correlation among covariates was marginal (VIF <2) and were thus all included in the global model for move persistence. The candidate models with $\Delta AIC_c < 2$ (n = 4) included all the smooth terms and only varied by the biotic parametric factors included (i.e., sex and TL; Table S1). Based on the best fitting model, $R^2$ (adjusted) was 0.43; all smooth terms were significant (i.e., non-zero effect on population-level persistence values; $p < 0.0001$), and sex and TL were not included (Table S2), but there was a low number of males and small sharks sampled. In terms of trends, the covariates distance to nearest land,

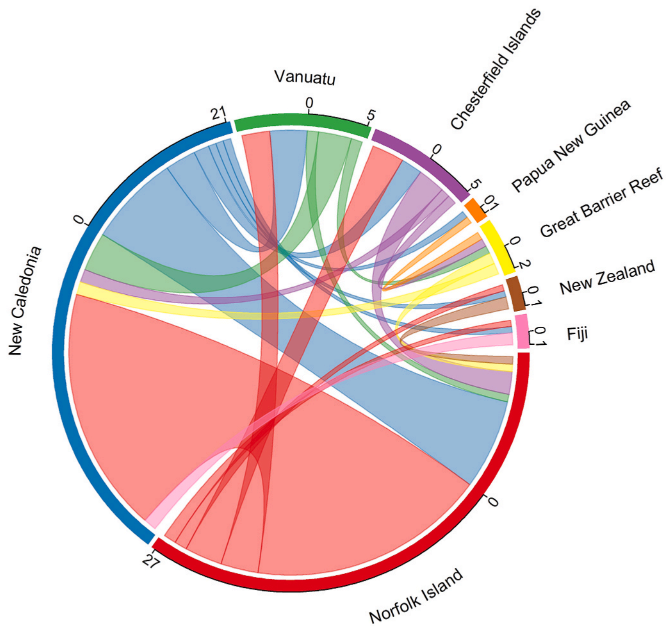


**Fig. 4.** Connectivity of tiger sharks, using direct movements between the areas visited. Matching colored lines and outer sectors indicate individuals moving from one area to another area (of different color). The thickness of lines is weighted by the number of individuals making the movement. Note that individuals may appear more than once if they had multiple unique movement pathways.

chlorophyll, and depth showed a positive non-linear relationship to persistence values, while slope was negatively associated with persistence (Fig. S4). Month and days since tagging had cyclical patterns with lower (than average) persistence values between August and February, and higher (than average) persistence values between March and July. Finally, SST was highly variable, from 18 to 30 °C, but primarily showed a decrease in persistence as temperature increased from 19 to 28 °C (Fig. S4).

### 3.4. Habitat suitability modelling

Habitat suitability model performance was high across all months, with mean monthly AUC values > 0.85 (Table S3). Training and test AUC values were similar, with mean monthly differences <0.05 (Table S3). Overall, high levels of habitat suitability matched well with areas used by tiger sharks (Fig. S5). Threshold Habitat suitability index (HSI) values ranged between 0.08–0.22 and 0.8–0.32, for the '10th percentile training presence' and 'maximum training sensitivity plus specificity' metrics, respectively. Tiger shark habitat suitability changed across months with consistently high HSI values at/between Norfolk Island and New Caledonia (Fig. 6). Habitat suitability index values were most restricted from December to March, with Norfolk Island having the highest values, coinciding when tiger sharks are most likely to be present (Fig. 6). Between April and July, the typical period tiger sharks departed Norfolk Island, HSI values were high across much of the study area, particularly around islands at lower latitudes such as New Caledonia, Chesterfield Islands, Vanuatu, Fiji, and the southeastern margin of the Great Barrier Reef, but also Norfolk Island (Fig. 6). These patterns continued into August and September except at Norfolk Island, which began to show low HSI values. From October to November, when tiger

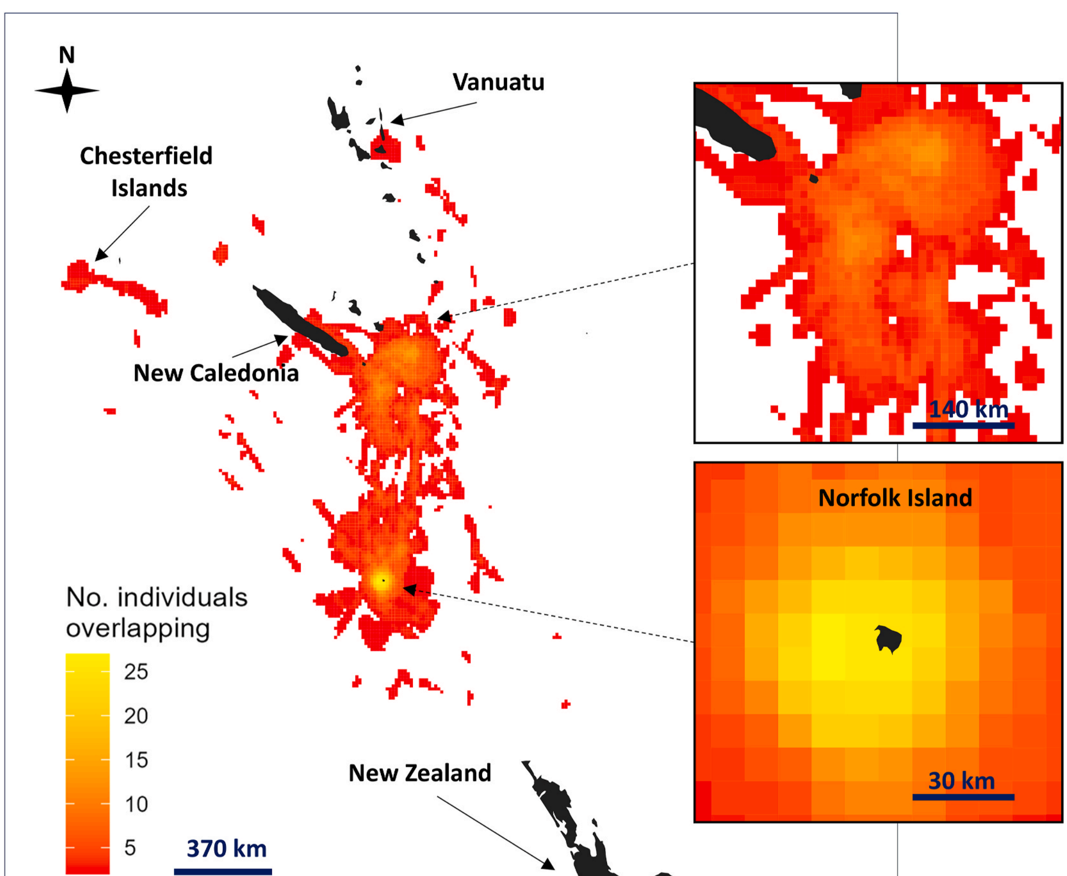


**Fig. 5.** Activity space overlap between tiger sharks based on 95 % utilisation distributions (using the Dynamic Brownian Bridge Movemement Model approach) across individuals. Grid resolution is 10 × 10 km. Only cells with more than one individual present, independent of temporal period, are shown.

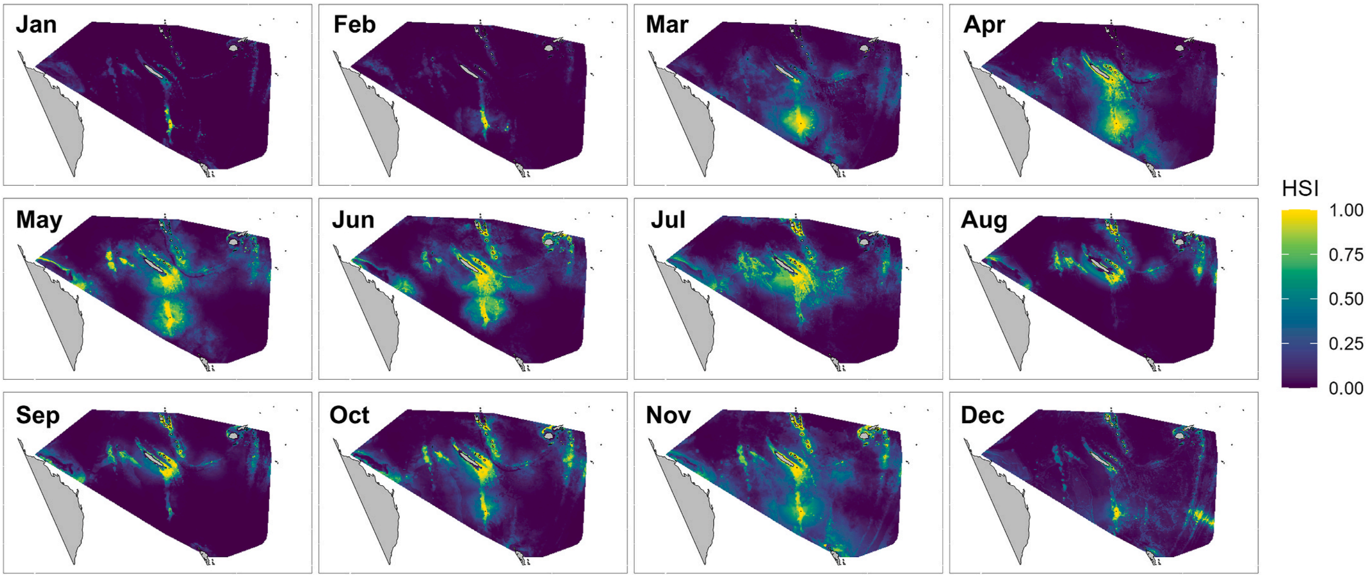


**Fig. 6.** Monthly habitat suitability maps for tiger sharks tagged at Norfolk Island predicted over 10 × 10 km grids. Input variables included depth, bathymetrical slope, distance to nearest land, sea surface temperature, and chlorophyll. Habitat Suitability Index (HSI) ranges from 0 (blue) to 1 (yellow), with values above 0.8 often considered highly suitable.

sharks began returning to Norfolk Island, HSI values at Norfolk Island increased again, while other habitats throughout their distribution appeared to remain suitable (Fig. 6). The variables contributing the most to permutation importance across monthly models were distance to nearest land (highest contribution across variables in Feb, May–Nov), SST (highest contribution across variables in Mar–Apr and Dec), and bathymetry (highest contribution across variables in Jan; Table 2). Chlorophyll and bathymetrical slope contributed the least to model output, with slope only marginally improving model performance in most months and hindering it in others (based on jackknife tests).

## 4. Discussion

Our findings represent a rare insight into an abundant female-dominated tiger shark aggregation that is seasonally persistent at a remote island hundreds of kilometres from any other land masses. The individuals making up this population were some of the largest ever tracked at oceanic scales and consisted exclusively of individuals that were mature, providing novel information on the movements of tiger sharks that are likely influenced by reproductive factors (e.g., mating, pregnancy, parturition), in addition to others (e.g., energy acquisition, physiological homeostasis). Following departure from Norfolk Island, tiger sharks showed extensive migrations throughout large parts of the western South Pacific Ocean, spending time in waters within 100 km of New Caledonia, the Great Barrier Reef, Papua New Guinea, Chesterfield Islands, Vanuatu, Fiji, and New Zealand. Coastal areas of these islands (and reefs) were the most suitable habitat and were associated with localized movement persistence across seasons. New Caledonia was the most frequently visited area (apart from Norfolk Island) with 63 % of all tracked sharks detected in its waters. There was also high fidelity to Norfolk Island, with 88 % of individuals detected for >300 days migrating back to Norfolk Island. Additionally, one individual (the smallest of all sharks tagged at 3.1 m TL) appeared to have never departed waters surrounding Norfolk Island, and was tracked beyond the typical seasonal residency period. Interestingly, this shark remained in water temperatures of ~18 °C during winter, which is below the suggested thermal optimum of tiger sharks (22°C; Payne et al., 2018).

### 4.1. *Importance of Norfolk Island*

The large number of individuals caught at Norfolk Island, in combination with their high seasonal residency and site fidelity — with individuals often making return migrations from >1000 km away, indicate that the island is a seasonal hotspot for mature female tiger sharks. While other hotspot or high-density areas have been identified, Norfolk Island is unique given its remoteness to other major island systems, and because all individuals were captured in a relatively small area (i.e., ~0.1 km$^2$) and both males and females were some of the largest ever tracked globally. Affinity to high-use areas has primarily been attributed to mating/reproduction/demography (Papastamatiou et al., 2013; Werry et al., 2014; Ajemian et al., 2020; Smukall et al., 2022), temperature (Holmes et al., 2014; Lipscombe et al., 2020; Hammerschlag et al., 2022; Niella et al., 2022), and foraging (Meyer et al., 2010; Lea et al., 2015), or a combination thereof. Below we investigate these three themes in relation to sharks consistently aggregating at Norfolk Island.

Tiger sharks were mainly present at Norfolk Island between December and May, but there was high variability in the timing of arrivals and departures. Reproductive factors or sexually dimorphic behaviors likely contribute to this seasonality, since it was primarily large

**Table 2**
Monthly variable importance (%) explaining habitat suitability based on permutation importance (all years combined). Grey highlighted cells indicate the variable with the highest importance each month.

| Variable | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Mean |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CHL | 4.1 | 11.7 | 4.3 | 7.6 | 17.6 | 16.3 | 16.9 | 17.7 | 16.4 | 15.5 | 23.3 | 7.9 | 13.3 |
| Distance to land | 29 | 38.8 | 34.3 | 28.5 | 52.2 | 59.9 | 44.1 | 67.7 | 55.7 | 49.8 | 44.4 | 16.3 | 43.4 |
| SST | 6.4 | 25.5 | 46.1 | 51.7 | 18.2 | 18.2 | 34.9 | 7.6 | 6.2 | 16.8 | 23.2 | 41.9 | 24.7 |
| Bathymetry | 60.4 | 23.9 | 11.8 | 8.3 | 11.9 | 5.0 | 1.9 | 6.0 | 20.2 | 16.7 | 8.6 | 17.2 | 16.0 |
| Slope | 0.2 | 0.0 | 3.5 | 3.9 | 0.0 | 0.6 | 2.3 | 0.9 | 1.5 | 1.2 | 0.5 | 16.8 | 2.6 |

females (median total length: 4.0 m) — all of which were presumably mature (i.e., > 3m total length; Simpfendorfer, 1992; Whitney and Crow, 2007; Castro, 2011) — caught during this study. Parturition in the Hawaiian population of tiger sharks occurs between September and October, likely on a triennial cycle, following gestation periods of 15 – 16 months (Whitney and Crow, 2007). Biennial reproductive cycling (i.e., 12-month gestation period) has also been suggested (Castro, 2009; Holland et al., 2019). Given that many individuals returned to Norfolk Island annually, parturition may not be the underlying driver. The reproductive biology of tiger sharks in the South Pacific Ocean is not readily documented, but embryo sizes from fisheries captures near Townsville, Australia suggested that pupping occurs in the Austral summer (Simpfendorfer, 1992), coinciding, at least in part, with the presence of tiger sharks at Norfolk Island. Female-dominated aggregations studied elsewhere have been associated with pupping, as well as avoidance of mating interaction with males (Simpfendorfer, 1992; Papastamatiou et al., 2013; Sulikowski et al., 2016). The males (all of which were above size-at-maturity estimates) that were tracked in this study for >14 days (n = 4) were otherwise only detected travelling to or at New Caledonia, suggesting that at least one of these locations may be important for mating. We never observed any mating scars on the female sharks caught at Norfolk Island, suggesting mating occurs elsewhere. The smallest female tagged (3.1 m total length) was never detected away from Norfolk Island over a period of 441 days — a pattern also observed for immature or smaller individuals of populations elsewhere (Werry et al., 2014; Lea et al., 2015). Whether long-term residency was associated with a lack of reproductive behavior compared to larger individuals or in response to something else (e.g., competition release leading to increased foraging capacity) is not known. Further work is needed to examine the reproductive status of females (e.g., pregnant, ovulating, resting stage), in this area to help distinguish whether large females are present due to reproductive drivers. It would also be valuable to identify whether immature females (and males) readily migrate to waters near Norfolk Island, and if so, whether they remain further offshore due to competition with or avoidance of larger females (e.g., Papastamatiou et al., 2013).

Although it is presently difficult to disentangle reproductive factors, additional drivers are also likely influencing the movement patterns observed here. For example, the peak period of arrivals at Norfolk Island was in December, a period in which habitat suitability was best explained by SST (presence peaking at ~22 °C at Norfolk Island). In this regard, movements (mainly south) to Norfolk Island during summer may have been related to affinity for cooler surface waters relative to lower latitudes, in line with optimal thermal regime predictions (Payne et al., 2018). Sea surface temperature was also the most important factor associated with habitat suitability when departures from Norfolk Island were common (i.e., March and April), and were demarcated by presence across different areas mainly between 23 – 26 °C. The co-occurrence of movements (primarily to lower latitudes) with the end of summer may act as a cue to migrate away from Norfolk Island to inhabit broad areas where winter temperatures are warmer. Following these periods, SST did not appear to strongly affect the distribution of individuals as they were found at a range of temperatures (18 – 28 °C) throughout the western South Pacific Ocean. Niella et al. (2022) also found that satellite-tracked adult female tiger sharks occupied a broad thermal range throughout the east coast of Australia, as did Payne et al. (2018) across multi-decadal catch data, although catch rates peaked at 22 °C (sex and size patterns not evaluated). Still, during the coldest months of the year (e.g., June to September), no shark was detected south of Norfolk Island, presumably due to cooler water temperatures. As such, Norfolk Island represented a southern boundary for this population during winter, in which coastal waters typically remained >18 °C. Future work on this population should incorporate depth-temperature sensors to further evaluate thermal preferences when not at the surface.

Foraging and prey availability may have also influenced movements of tiger sharks. Norfolk Island and surrounding seamounts within the Norfolk Island Seamounts Area host productive and diverse ecosystems, and the Norfolk Ridge is thought to be a key ecological feature connecting deep benthic species between New Caledonia and New Zealand (Williams et al., 2006; Director of National Parks, 2018). The oceanography in the area is influenced by the Eastern Australian Current, which brings warm waters from the Coral Sea south, enabling both temperate and tropical species to thrive (Director of National Parks, 2018). Prey at the water surface, such as seabirds, may provide a reliable food source supporting tiger sharks whilst at Norfolk Island. There is a coastal nesting/breeding colony of wedge-tailed shearwaters (*Ardenna pacifica*) resident on the island during the austral summer throughout the period of high tiger shark abundance. Seabirds are common prey of tiger sharks globally, particularly for large sharks (Rancurel and Intès, 1982; Lowe et al., 1996; Simpfendorfer et al., 2001; Meyer et al., 2010; Dicken et al., 2017), and are vulnerable when rafting in groups or if fledgelings fall from nests. Shearwaters have been documented in the stomachs (often regurgitated) of tiger sharks caught at Norfolk Island, including one report of ~40 individual birds in the stomach of one shark (Tofts, 2001). In addition to abundant natural prey sources, foraging may also be associated with human-derived food, namely livestock (e.g., offal, bones, and hides) that cannot be sold and are disposed of into Headstone Bay — the same area where the sharks were caught. Whether tiger sharks return to Norfolk Island each year because of a learnt associative behaviour with food availability or for other reasons (e.g., philopatry) is not known, but they evidently have the cognitive ability to reliably do so (Guttridge et al., 2009; Heinrich et al., 2021). The relationship between the presence of tiger sharks and natural prey or human-derived food, particularly at a local scale, is beyond the scope of this study, but is a line of research for future work.

### 4.2. Movements throughout the south Pacific ocean

Broad-scale movements are common in tiger sharks globally, with females often showing greater propensity to travel long distances between areas of high use, such as seamounts or oceanic islands (Papastamatiou et al., 2013; Werry et al., 2014; Meyer et al., 2018). Coastal areas were identified as strong predictors of habitat suitability across most monthly periods. These habitat suitability models had high levels of accuracy and predicted areas of high suitability matched areas where detections occurred, particularly Norfolk Island and New Caledonia, and the seamounts between. There was, however, relatively high positioning error away from islands because sharks tended to surface less frequently offshore than near coastal areas of islands or seamounts. Reduced satellite coverage may have also affected position accuracy or successful signal transmission. Consequently, much of our analysis is biased towards areas where sharks were spending time at the surface, potentially undervaluing the importance of deeper habitats. Light-based geolocating pop-up satellite tags are an alternate option that may assist fill gaps when not at the surface. Still, the propensity to surface near offshore islands or seamounts is a valuable finding and further highlights the importance of these areas for specific behaviors — one of the most probable is foraging for seabirds, sea turtles, and other prey at or near the surface, which has been found in New Caledonia (Rancurel and Intès, 1982), the Great Barrier Reef (Fitzpatrick et al., 2012; Hammerschlag et al., 2016), Western Australia (Simpfendorfer et al., 2001; Heithaus, 2001), and Hawaii (Lowe et al., 1996; Meyer et al., 2010), among other locations. Other studies that have tracked the broad-scale movements of large female sharks — mainly from the Hawaiian Islands — showed similar results to those reported here with high fidelity to core use oceanic islands and inter-island movements of mature females, as well as partial migration within a mature female cohort consisting of movements >1000 km away from tagging locations (Meyer et al. 2010, 2018; Papastamatiou et al., 2013) — although in our study a higher proportion of individuals undertook large-scale migrations.

The frequent movements between Norfolk Island and New Caledonia commonly overlapped with the Norfolk Ridge, which may act as a navigational tool with sharks moving along this underwater corridor. However, tiger sharks tend to stay in the upper 100 m of the water column with only periodic deep dives (Meyer et al., 2010; Vaudo et al., 2014; Afonso and Hazin, 2015), and the ridge lies at the upper margins of tiger shark depth use (i.e., ~1000 m; Werry et al., 2014; Afonso and Hazin, 2015; Lipscombe et al., 2020). Therefore, other cues may also explain the use of this movement corridor, such as geomagnetic fields, cognitive mapping, olfaction, or social learning (Keller et al., 2021; Brown and Schluessel, 2023), or cueing on thermal differences across latitudes (see section 4.1). Movements between Norfolk Island and New Caledonia were relatively quick; for example, the median travel time between islands was 15 (Norfolk Island to New Caledonia) and 13 (New Caledonia to Norfolk Island) days, equating to at least ~50 km $d^{-1}$ or 2 km $h^{-1}$. High rates of persistence were also associated with low bathymetrical slopes and movements away from Norfolk Island and other coastal areas. As such, movements between islands were likely migratory in nature with linear or directional trajectories and any foraging done so opportunistically along the way (e.g., Andrzejaczek et al., 2020), until the sharks reached coastal areas or seamounts, where persistence decreased and presumably foraging search patterns were initiated (e.g., Lea et al., 2015).

Females showed a high degree of variation in locations visited and distances travelled away from Norfolk Island, including entering waters adjacent to at least six different geopolitical areas in South Pacific Ocean. These high levels of dispersal highlight connectivity between jurisdictions and potential capture vulnerability due to different national and regional regulations and policies regarding fishing and shark control programs. For example, New Caledonia carried out a culling program during 2023 targeting tiger and bull (*Carcharhinus leucas*) sharks. Our activity space overlap across individuals highlighted the importance of seamounts and small islands away from the mainland of New Caledonia, perhaps signalling less likelihood of being targeted by culling efforts in 2023. Without genetic evidence, it is not possible to comment on the degree of relatedness of these tiger sharks to others found in the South Pacific Ocean, such as those along the east coast of Australia or across the Coral Sea (Werry et al., 2014; Lipscombe et al., 2020; Niella et al., 2022).

### 4.3. Conclusion

Norfolk Island hosts a seasonal aggregation of large female tiger sharks, almost all of which undertake long-distance migrations. Our findings document some of the longest tracks of tiger sharks ever studied, including movements of one individual between New Caledonia, the Great Barrier Reef, Norfolk Island, the Chesterfield Islands, and New Zealand, a minimum distance of ~17,000 km in under 500 days. It was evident that this population had high levels of connectivity between New Caledonia and Norfolk Island. This study contributes to a distinct knowledge gap in understanding the spatial ecology of mature tiger sharks from one of the largest (in morphological size) tagged populations in the world. Although adults are caught in coastal areas, our study, in conjunction with previous work (e.g., Lea et al., 2015; Meyer et al., 2018), suggests that offshore habitats, such as oceanic islands and seamounts, are important areas supporting mature females in the Coral Sea region likely serving as productive oases in otherwise depauperate waters.

The consistency of movements between Norfolk Island and New Caledonia was distinct enough to represent a regional population pattern. Indeed, no other study has tracked tiger sharks travelling to Norfolk Island from other areas, the nearest being one individual tagged in southern New Caledonia and detected ~200 km to the west of Norfolk Island prior to returning (to New Caledonia) 225 days after tagging (Werry et al., 2014). Arguably, this study represents one of the most unified migration strategies observed in tiger sharks, behaving as obligate migrators (i.e., mature females always migrating; Dingle and Drake, 2007). After leaving Norfolk Island, most individuals migrated to seamounts and islands in the Coral Sea regions south and east of New Caledonia, while some individuals showed nomadic behavior across the Coral Sea and western South Pacific Ocean. The specific characteristics of Norfolk Island that consistently attract large female sharks for several months every year is still to be elucidated. The high density and consistency of large females at Norfolk Island provides a unique opportunity for future work to disentangle the roles of environmental, foraging, and reproductive drivers influencing migration patterns, which is difficult to achieve with large mobile marine predators.

## CRediT authorship contribution statement

**Jordan K. Matley:** Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Data curation, Conceptualization. **Lauren Meyer:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Conceptualization. **Adam Barnett:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Mark Scott:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **Elizabeth A. Dinsdale:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Michael P. Doane:** Writing – review & editing, Resources, Investigation. **David Harasti:** Writing – review & editing, Resources, Investigation. **Lisa A. Hoopes:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Charlie Huveneers:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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## 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.

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## Appendix. A - Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107026.

## Data availability

Data will be made available on request.

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