



Dynamics of marine predators off an oceanic island and implications for management of a preventative shark fishing program

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Abstract

Oceanic islands are productive ecosystems, and so have higher densities of many marine predators. We investigated the dynamics of elasmobranch and teleost predators in coastal waters off Réunion Island, Indian Ocean, using fisheries-independent data from a preventative shark fishing program from January 2014 to December 2019. We developed a moonlight index that calculates exact moonlight through incorporating lunar azimuth, elevation angle and island topography. We quantified spatial–temporal and environmental drivers of occurrence using zero-inflated mixed models and assessed species-specific catchability in the program. A consistent segregated pattern was observed with higher occurrence of all species at dusk and after-dusk associated with lower luminosity. Scalloped hammerhead sharks (*Sphyrna lewini*) and giant trevally (*Caranx ignobilis*) were found to patrol coastal waters earlier in the day than the other species. Tiger (*Galeocerdo cuvier*) and bull (*Carcharhinus leucas*) sharks showed high spatial segregation, potentially reducing competition. Teleost predators were found more frequently inside the coral reef environment of the Marine Protected Area but there was no clear pattern for sharks. Seasonality was observed for giant trevally, stingrays, bull sharks, and giant guitarfish (*Rhynchobatus australiae*), with higher presence during early winter periods related to turbidity, photosynthetically available radiation, and temperature. Inter-annual variation in catch rates suggested that juvenile tiger sharks might be replacing bull sharks in nearshore habitats, and the consequences for mitigation of shark bite hazard are discussed. Operational alternatives are proposed to enhance reducing the impacts of preventative shark fishing upon critically endangered species, improve their conservation and ensure local ecosystem balance.

Introduction

Oceanic islands are discontinuities in the vast and rather homogeneous open ocean, and as such, they are responsible for atmospheric and oceanographic phenomena such

as island and ocean wakes, upwellings and internal waves (Wolanski and Delesalle 1995; Suthers et al. 2006; Sandulescu et al. 2008). These processes contribute to both enhance primary production (Doty and Oguri 1956) and aggregate biomass and diversity of organisms, including large marine predators (Friedlander and DeMartini 2002; Meyer et al. 2018; White and Samhouri 2011). Therefore they are dynamic environments (Heywood et al. 2008),

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compared to the surrounding oceanic environment, composed of a complex and diverse variety of habitats that host permanent and transient species.

Large-bodied predators are generally highly mobile and capable of exploring neighbouring communities for exogenous food sources, thereby heavily inflating the top-levels of trophic webs when present in large numbers (McCauley et al. 2018). These animals usually play an important role in structuring fish communities by regulating their composition and population dynamics, either directly through predation or indirectly via behaviour-mediated effects (Heithaus et al. 2008; Roff et al. 2016). Inverted biomass pyramids with elevated predator abundance are characteristic of ‘pristine’ oceanic islands, whereas regions with higher cumulated human impacts frequently have more bottom-heavy trends (Friedlander and DeMartini 2002; Sandin et al. 2008; Halpern et al. 2019). Understanding the dynamics of marine predators in these ecosystems is essential, as it provides information on its ecological functioning, health and management (Estes et al. 2016). A powerful approach is ecosystem modelling as it can reveal the complex influences of physical and environmental drivers upon the occurrence of marine predator species (Afonso et al. 2014; Niella et al. 2017b; Wintner and Kerwath 2018).

A common gap in marine spatial planning is the inclusion of life-threatening risk to humans into the decision-making process (Shabtay et al. 2020). Shark bite hazard is the most global example of human-wildlife conflict (Hardiman et al. 2019), to which practicable solutions with minimal impacts for both humans and sharks should focus on coexistence (Frank 2016). Réunion Island is a tropical oceanic island in the southwest Indian Ocean that represents a hotspot of biodiversity with remarkable assemblages of marine species, but, also where human activities (870,000 inhabitants), fuelled by European and French state funds, currently threaten ecosystem integrity and functioning (Myers et al. 2000). As with many small island states, the economic development of the island is based on tourism and marine-related activities. This has resulted in increasing anthropogenic pressure, and in 2007 a Marine Protected Area (MPA) was designated along the leeward west coast of the island to protect the fragile coral reef ecosystems (<http://www.reservemarinereunion.fr/>, Accessed on 13 November 2020). The west coast of Réunion Island is also where most nautical activities occur and where Réunion became renowned for surfing since the 1970s. There were 48 shark bite events (22 fatal) recorded (see method in Lagabrielle et al. 2018) around the island between 1980 and 2020, (fatality rate of 46% compared to a global average of 11%). These bites occurred mostly on surfers (i.e. wave-based activities), in the late afternoon/early evening between 5 and 7 pm. From 2011 the frequency of bites tripled (25 incidents, 11 fatal) particularly along the west coast (Lagabrielle et al. 2018;

Taglioni et al. 2019). In response to these widely reported bites, combined with other measures (swimming ban, non-meshing shark nets), local authorities implemented a preventative shark fishing program in 2014 designed to kill bull (*Carcharhinus leucas*) and tiger (*Galeocerdo cuvier*) sharks caught in proximity to the most popular beaches. The aim of this program is to reduce the likelihood of shark bites while simultaneously causing minimal impacts upon the marine ecosystem. As a part of the preventative shark fishing program, a drumline was developed by authorities: the Shark Management Alert in Real Time (SMART) drumline. This provides a means of reducing the mortality of bycatch by sending an alert when an animal is hooked, thereby increasing the likelihood of successfully releasing alive non-targeted species (Guyomard et al. 2019). In combination with SMART drumlines, bottom setlines are also used in this program as complementary fishing gear, particularly at deeper isobaths.

Once shark ‘control programs’ apply fisheries-independent standardized procedures over consistent periods of time, i.e. use the same gear deployed in the same areas for several consecutive years, they provide reliable long-term data for investigating the ecosystem dynamics of the regions in which they operate (Holmes et al. 2012). However, long-term, systematic removal of higher trophic level predators may have unforeseen impacts upon ecosystems and so there is a pressing need to understand the ecological impacts arising from such programs. A first step in mitigating generalised effects has been to improve selectivity. In contrast to mesh nets or conventional drumline gears, the combined use of SMART drumlines with a real-time alarm triggered when the bait is taken (Guyomard et al. 2019), and bottom setlines with short soaking times, allow the prompt release of non-target species. These fishing methods combined with thorough monitoring of this shark control program provides a unique opportunity to investigate the dynamics of the predatory fish caught as targeted or non-targeted species in relation to environmental and physical parameters in coastal ecosystems of the oceanic Réunion Island, and also assess the potential environmental impacts of this shark bite mitigation program.

The occurrence of marine predators is frequently tested against various environmental parameters in ecosystem approaches to determine which conditions influence species-specific distributions. These include water turbidity parameters, which are known to influence predator–prey relationships by affecting teleost abundance (Lutjeharms et al. 2000), predator-avoidance behaviour (Duncan and Holland 2006) and facilitating foraging success (Hueter et al. 2004). Water temperature is also a key variable influencing the occurrence of marine predators, with species-specific distributions closely related to particular seasonal gradients such as an influx of warm waters during the summer

(Smoothey et al. 2019; Niella et al. 2020), or preference of some species for cold-water (Wintner and Kerwath 2018). Indicators of biological productivity, such as concentrations of chlorophyll-*a*, are also good estimators of predator occurrence regulated through bottom-up processes (Block et al. 2011; Hazen et al. 2013).

The moon not only drives tidal rhythms, but influences catch in some pelagic fisheries suggesting they might be driven by biological influences. For example, alterations in animal vertical movements or their proximity to the coast during particular moon phases could induce changes in predator behaviour, thus leading to higher catch rates during such periods (Lowry et al. 2007; Wintner and Kerwath 2018). Moon phases directly influence the amounts of environmental luminosity and some species have adaptations to optimize foraging at low light levels, such as the enlarged retinas of swordfish (*Xiphias gladius*) and bigeye tuna (*Thunnus obesus*) (Poisson et al. 2010). Most studies investigating the effects of moon illumination upon species distribution have focused on daily temporal scales, whereas virtually nothing is yet known about their possible fine-scale effects.

This study focuses on the dynamics of marine predators off Réunion Island, using the catch data from the local preventative shark fishing program. By assessing the spatial, temporal, and environmental factors influencing sympatric elasmobranch and teleost predatory species with fine-scale resolution, we reveal the ecological patterns regulating their

nearshore distribution and habitat use in this region with particular reference to their use of the MPA. Understanding how top-level species make use of the productive coastal habitats of this oceanic island provides a means of quantifying ecosystem interactions of marine predators in these waters and the factors influencing catchability with SMART drumline fishing gear. This information will help improve the management and conservation of endangered species thereby reducing ecological impacts of this preventative shark fishing program without reducing the efficacy of the program for ocean users.

Materials and methods

Study area and fishing operations

Réunion Island (21.11°S, 55.54°E) is a small (~2500 km²) tropical island located ~800 km east of Madagascar (Fig. 1a). With only 250 km of coastline, the eastern coast is exposed to tropical trade winds and regular rains whereas the dryer south-western and western coasts are the only parts of the island's coastal ecosystems where coral reefs have established. These habitats are formed by discontinuous fringing reefs sometimes surrounded by a few, narrow shallow island shelves, like the Sec de Saint-Gilles on the north-western part of the island (Fig. 1a). Only a few permanent rivers exist

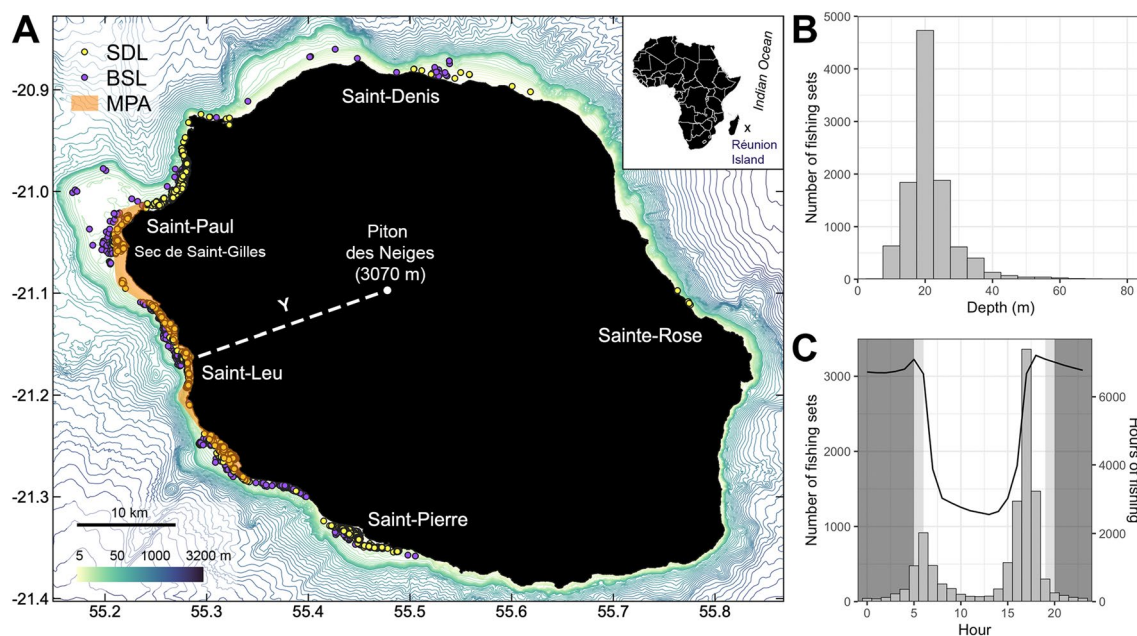


Fig. 1 **a** Locations of the fishing sets performed off Réunion Island by the respective gears used (SMART drumlines=SDL; bottom setlines=BSL) between January 2014 and December 2019. The highlighted area represents the Marine Protected Area (MPA). The dashed line corresponds to the distance ($Y=21,030$ m) between the highest

point of the island at Piton des Neiges and the beach. Histograms show distributions of number of fishing set deployments for both gears combined according to **(b)** depth and **(c)** hour of the day. Solid line and shaded areas **(c)** respectively depict the corresponding total fishing efforts and the pre-dawn, dawn, dusk and after-dusk periods

along the east coast. The coastal habitats of the island are thus very limited in size and exhibit very high depths close to the coastline, making the pelagic influence very strong (Trystram et al. 2015).

The shark bite mitigation fishing program uses two types of fishing gear, SMART drumlines set in water depths < 30 m, in combination with bottom setlines which are deployed in waters between 30 and 80 m depth (Fig. 1b). Bottom setlines were also used in areas where bull sharks had been previously seen (Soria et al. 2015), including off-shore island shelves or near river mouths. Sets were either late in the afternoon and early in the morning and more extensively along the south-western to north-western coast of the island (Fig. 1a), with most of the total fishing effort (i.e. > 6000 h of fishing from January 2014 to December 2019) occurring at night between 18:00 and 06:00 and hourly daytime efforts spanning around 3000 h (Fig. 1c). Fishing sets were performed year-round opportunistically by several fishing contractors, with the most effort between August and December and a lower number of sets in 2017 (Fig. S1) due to changes in program management.

The SMART drumlines were baited for 12-h periods, except when triggered and then serviced immediately by the fishermen with response times generally lower than 90 min from the alert (Guyomard et al. 2019). Drumlines were equipped with two 16/0 hooks in a snelled-hook configuration and set suspended approximately one meter from the bottom. Hooks, wires, and the general material and assembly of SMART drumlines were standardized from the outset in 2014. Bottom setlines were 1600 m long and set with 25 hooks and soak times of up to 2 h, to reduce the risk of mortality for bycatch species. Bait used on setlines mainly comprised wastes from pelagic fish such as tuna, swordfish and marlin. Bait used on SMART drumlines usually comprised whole fish with information on bait size (i.e. weight) and species precisely recorded for each fishing set, as well as the respective times and positions of deployment.

Because only a few SMART drumline sets were performed near Sainte-Rose on the eastern side of the island and most of the effort was distributed along the western part of Réunion Island between Saint-Denis and Saint-Pierre (Fig. 1a), sets near Sainte-Rose were excluded prior to analysis. Only the eight most frequently caught species were included in this study, as catches of the remainder were too low to yield any statistically significant results (Table S1). These included the elasmobranchs: bull, tiger, and scalloped hammerhead (*Sphyrna lewini*) sharks, the giant guitarfish (*Rhynchobatus australiae*), the round ribbontail ray (*Taeniura meyeni*) and the thorn-tail stingray (*Dasyatis thetidis*); and the teleosts: barracuda (*Sphyraena barracuda*) and giant trevally (*Caranx ignobilis*); representing 70.7% of the total catch (Table S1). During the early years of the program, stingrays were only identified to the family level, and so all

the Dasyatidae rays (Table S1) were pooled into a single group for analysis, i.e. stingrays. Consequently, catch of a total of seven species were analysed in this study. Statistical analyses were performed in the *R* software (version 4.0.2) and the significance level set at 0.05.

Seasonal and inter-annual variation in sex and maturation ratios

Size and sex information were available for two of the species caught during the study period, i.e. the tiger shark ($n = 222$) and the bull shark ($n = 116$). Size-at-maturity data were inspected for seasonal and interannual trends in occurrence. Local size-at-maturity of bull and tiger sharks from Réunion Island were obtained from Pirog et al. (2019a) and Pirog et al. (2020), respectively. Two-sample Mann–Whitney tests were used to assess for possible significant shifts in monthly and yearly sex and maturity stage ratios for each species.

Candidate predictor variables

Environmental variables

Since fine-scale field data is not yet available for Réunion Island, remote sensed environmental data was used. Daily Moderate Resolution Imaging Spectroradiometer (MODIS) images were obtained from Terra and Aqua satellites. The data was composed of Level-2 pre-processed and validated oceanographic images distributed by the Ocean Biology Processing Group (OBPG) from the National Aeronautics and Space Administration (NASA), obtained through the Ocean Color website (<http://oceancolor.gsfc.nasa.gov>, Accessed on 10 June 2019). Remote sensing environmental indices used for the analysis included: *i*) diffuse attenuation coefficient for downwelling irradiance at 490 nm (K_d_{490}): considered a direct proxy for water turbidity (Lee et al. 2005; Werdell and Bailey 2005); *iii*) night sea surface temperature (SST): temperature (°C) of the uppermost water layer during nighttime calculated with an altered version of the non-linear SST retrieval algorithm (Walton et al. 1998); *iv*) photosynthetically available radiation (PAR): estimated daily average photosynthetically available radiation at the ocean surface ($\text{Einstein m}^{-2} \text{ day}^{-1}$), defined as the amount of quantum energy flux from the sun in the 400–700 nm range (Behrenfeld et al. 2009) and negatively correlated with chlorophyll-*a* concentration (Rubio et al. 2003; Feng et al. 2015).

To factor in seasonal sea temperature changes, the derivative of the sea surface temperature (derSST) was calculated using night data SST, to remove any potential bias effect derived from solar radiation incidence during the day. The derivative was calculated using the following slope formula, where Δx is the change in time and Δy is the change in SST

(°C) and the derivative is the slope (m) of y with respect to x :

$$m = \frac{\Delta y}{\Delta x} = \frac{f(x + \Delta x) - f(x)}{\Delta x}$$

Spatial resolution was set to 0.02° latitude by 0.02° longitude for all environmental variables to prevent data loss or distortion in zones of maximum swath angles known as the *bow-tie* effect (Souri and Azizi 2013). Since there is frequently high daily cloud cover at Réunion Island, which may lead to missing data if daily satellite data is used, values for each variable were averaged over 8-day periods for the 6-year period from January 2014 to December 2019. Cloudy pixels (i.e. with no data) were interpolated using a 3-pixels (~6 km) radius mean kernel. Fishing set locations were matched to the 0.02° × 0.02° grids of environmental variables to obtain their corresponding values.

Fishing variables

The following variables were considered to test the catchability of marine predators with SMART drumline fishing gear: (i) bait type: 1 = locally fished including Scombridae (alive or just dead, fresh or defrosted fish caught by the fishermen; $n = 3369$ sets), 2 = non-Scombridae standardized (mainly defrosted milkfish *Chanos chanos* from aquaculture; $n = 3426$), 3 = Scombridae standardized (defrosted skipjack *Katsuwonus pelamis* or mackerel tuna *Euthynnus affinis*, purchased and imported from industrial tuna fisheries; $n = 2604$), and 4 = wastes (heads and carcasses; $n = 320$); (ii) bait size: 1 = less than 1 kg (A; $n = 1093$), 2 = between 1 and 2 kg (B; $n = 7696$), and 3 = more than 2 kg (C; $n = 930$); (iii) MPA (Marine Protected Area) location: 1 = inside ($n = 3980$) or 2 = outside ($n = 5739$); and the continuous variables (iv) depth of SMART drumline set in meters (between 5 and 30 m); and (v) hour of catch: time when the device was triggered for the positive captures, or time of gear retrieval for sets without a catch.

Fine-scale moonlight index

SMART drumline gear provides the exact time at which a capture occurs, enabling us to investigate the potential influence of environmental luminosity on the likelihood of a predator interacting with the baited hooks from SMART drumlines with fine-scale resolution. Moonlight is simply sunlight reflected from the surface of the moon. The amount of moon illumination that reaches the surface of the Earth at a given time is influenced by the relative position of moon, earth and sun, the cloud coverage, and the local relief (Austin et al. 1976). Only the true night-time periods fishing sets were considered for this analysis, the sets performed during

exclusively daytime were identified and excluded. True night-time was considered in relation to the daily times of nautical twilight and dawn, i.e. when the sun angle below the horizon exceeds 12°, as this is the period when the moon illumination is capable of exceeding that of the sun (Austin et al. 1976). In addition, the sets that encompassed multiple night-time periods, i.e. either those setting before the nautical dawn and retrieved after the nautical twilight on the same day, or with soak times longer than 24 h, were also removed prior to analysis.

For identifying the moments of maximum moon angle during each set, true night-time periods were divided into 30-min intervals to which the corresponding angles of the moon in relation to the horizon were obtained using the *suncalc* package (Thieurmél and Elmarhraoui 2019). The fractions of the moon illuminated by the sun (i.e. from 0 at new moon to 1 at full moon) for the times of maximum angle were obtained with the same package. Piton des Neiges in Réunion Island is the highest point of the Indian Ocean at 3,070 m of altitude (Villeneuve et al. 2014). As this mountain partially shades the moon on the leeward side of the island, we were required to estimate the angle above which the moon was sufficiently high to light the leeward sea surface. To estimate this angle, a straight-line distance was found between the highest point on the island (− 21.09°S, 55.48°W) and the nearest point on the beach opposite moon rise. This distance ($Y = 21,030$ m; Fig. 1a) and the altitude of Piton des Neiges (altitude) were considered as the sides of a right triangle thereby obtaining the approximate angle of the moon above the horizon (α) where it would illuminate the leeward side of Réunion Island according to the equation:

$$\alpha = \tan^{-1} \frac{\text{altitude}}{Y}$$

Cloud data (presence/absence) was retrieved from Level-2 Ocean Color product tiles with a resolution of 0.02° latitude by 0.02° longitude. It is not possible to estimate exclusively night-time cloud cover, since cloud cover is identified with passive visible light sensing which depends on the sunlight. The daily cloud cover was then calculated as the daily proportion of cloud presence for each fishing site using the available Terra and Aqua MODIS tiles for each day (maximum of 4 tiles per day, mean = 1.6, standard deviation = 0.6). A moonlight index was then calculated for each SMART drumline set using:

$$\text{Moonlight index} = x \cdot \sin \cdot \frac{(100 - z)}{100}$$

In which x represents the moon illumination at the time of maximum angle, β is the maximum angle of the moon in the sky during gear deployment, and z is the percentage of daily cloud cover. For those sets in which β was lower than α , the

moonlight index was automatically set to zero. The code for obtaining the moon variables and calculating this standardized moonlight index is available online together with a tutorial for use with other similar fishing data (Niella 2020).

Modelling approach

Spatial–temporal and environmental patterns of occurrence

Due to the large number of zero observations, characteristic of fishing datasets for sets without a capture, zero-inflated models were applied. Zero-inflated Generalized Additive Models (ZIGAM) with the *mgcv* R package (Wood 2017) were used to model the spatial–temporal and environmental patterns in species occurrence. These models were run separately for each species and included the corresponding total number of specimens caught per fishing set as the response variables, and so Poisson families of error distribution were used.

The times of capture/gear retrieval were grouped according to the circadian period using the *suncalc* R package (Thieurmél and Elmarhraoui 2019) into one of the following categories: (i) pre-dawn: between midnight and the time of nautical dawn (i.e. solar depression below the horizon is lower than 12°), (ii) dawn: between nautical dawn and time of sunrise, (iii) day: between sunrise and time of sunset, (iv) dusk: between sunset and time of nautical dusk (i.e. solar depression below the horizon is greater than 12°), and (v) after-dusk: from the time of true night start, when it is dark enough to enable astronomical observations (Austin et al. 1976). Catches at night-time were considered as those occurring during either pre-dawn or after-dusk periods.

The species-specific occurrence patterns were further investigated combining catch-and-effort data from SMART drumline (9717 sets) and bottom setline fishing (709 sets) gears (Fig. 1a), to investigate the influences of spatial–temporal and environmental variables. Since the island is approximately circular, a trigonometric approach was performed to obtain the corresponding sectoral angles of each fishing position, included as a continuous geographical variable in the analysis. For this purpose, the southernmost fishing set was used as the reference point to which the angles of each fishing position were compared according to an anti-clockwise direction (Fig. S2). Candidate spatial–temporal variables included: (i) an interacting effect between sectoral angle and depth (highly correlated with the distance from the shore due to the cone shape of the island), (ii) year and (iii) month. The environmental models included all the aforementioned satellite-derived variables as candidate predictor effects.

Catchability of marine predators with SMART drumlines

An additional approach was conducted to model predator catchability with SMART drumlines. Most fishing variables were categorical and there were expected linear relationships between marine predator catchability with SMART drumline gear and the continuous variables depth of fishing set (i.e. either increasing or decreasing towards higher isobaths), hour of catch (i.e. either increasing or decreasing over the circadian cycle), and moonlight index (i.e. either increasing or decreasing in relation to periods with more illumination). Therefore, Zero-inflated Generalized Linear Mixed Models (ZIGLMM) were applied with the *glmmTMB* R package (Brooks et al. 2017). These models were run separately for each species and included the respective presence/absence as the response variables, and so binomial families of error distribution were used. In addition, the year was included as a random effect in all ZIGLMM to account for the inter-annual variation in sampling. To standardize catch data between the two fishing gears, the logarithm of nominal fishing effort (number of fishing hours multiplied by number of hooks) was included as an offset covariate in all models.

Two independent ZIGLMM were used to model marine predator catchability with SMART drumline gear. The first model included all the fishing variables as candidate predictors and data on all sets performed during the study period. The second model included only the moonlight index as a candidate predictor and only the data on those sets that fished at least for some period during the night-time.

Variable selection

Pearson's correlation tests were used to assess for possible collinearity among continuous predictors, in which candidate variables significantly correlated were not simultaneously included in a model. A stepwise variable selection procedure was performed for both ZIGAM and ZIGLMM to select only the best variables responsible for influencing species-specific occurrence patterns and catchability with SMART drumline gear for each predator species. For this purpose, starting from the null models, significant new variables were gradually included in a nested model according to lower Akaike Information Criterion (AIC) values, and confirmed after an analysis of variance (ANOVA) indicated the more complex model with a new variable was significantly different from the previous simpler one (Tables S2–S5). Final models were selected based on higher AIC weights (AICw) using the *qpcR* R package (Spiess 2018) and visually inspected for a normal residual distribution.

Results

A total of 850 individuals (SMART drumlines = 429; bottom setlines = 421) were caught during the study period, of which 85.8% were from the seven species analysed in this study (SMART drumlines = 377; bottom setlines = 352) (Table S1). The mean total length of measured sharks was 268.4 (standard deviation = ± 69.5) cm, 202.5 ± 49.8 cm for the giant guitarfish, 124.7 ± 34.3 cm for stingrays, and 119.4 ± 17.4 cm for teleost. All species occurred mostly during dusk and after-dusk periods (Fig. 2). Tiger sharks were the dominant species at pre-dawn periods, and their occurrence together with scalloped hammerhead sharks and giant trevally was higher than the other species at dusk (Fig. 2). While most species were more frequently caught during after-dusk periods, the occurrence of scalloped hammerheads and giant trevally peaked earlier, at dusk (Fig. 2).

Seasonal and inter-annual variation in biological ratios

For both tiger (female:male = 1.4) and bull (female:male = 1.2) sharks, more females were caught. Females were also larger for both species (Fig. 3). Within years, male and juvenile tiger sharks were more commonly caught after March (Fig. 4a), and over multiple years there was a steady increase in the proportion of juvenile tiger sharks caught (Fig. 5a). Within years there was a peak in the proportion of juvenile bull sharks caught in November (Fig. 4b), but over multiple years the proportion of male bull sharks at first increased in the catches until 2016 following which there was a steady decline (Fig. 5b).

Spatial-temporal and environmental occurrence patterns

The interaction between sectoral angle and depth was the most important spatial variable influencing the occurrence of most species (Table 1). Tiger sharks were consistently more frequently caught when the fishing gears were set at deeper isobaths, particularly below 40 m between the south and west portion of the Island but tended to occur in shallower waters elsewhere (Fig. 6a). In contrast, bull sharks generally occurred in waters shallower than 20 m between the south and west part of the island but in deeper isobaths from the mid-west-to-north region to the east side (Fig. 6b). Giant guitarfish showed similar trends to bull sharks, occurring more frequently at depths up to 55 m within the south-to-west region but shallower than 20 m in the west-to-north area (Fig. 6c). Giant trevally were less common on the south-to-west portion of Réunion and occurred mostly in deeper waters from the north-to-east part of the island (Fig. 6d).

Interannual variation was the second most important variable affecting the occurrence patterns of tiger and bull sharks and stingrays, and a significant seasonal effect was only observed for giant guitarfish (Table 1). The capture of tiger sharks increased over the study period and became significantly higher after 2017 (Fig. 7a). Bull shark and stingray catch initially steadily decreased, but bull shark catch decreased further after 2017, while there was a slight recovery of stingray catches in the same period (Fig. 7a). Giant guitarfish were seasonally more frequent with a peak between April to June (Fig. 7b).

The occurrence of bull shark, giant guitarfish, stingrays, and giant trevally were significantly influenced by the environmental variables Kd₄₉₀, PAR, and derSST

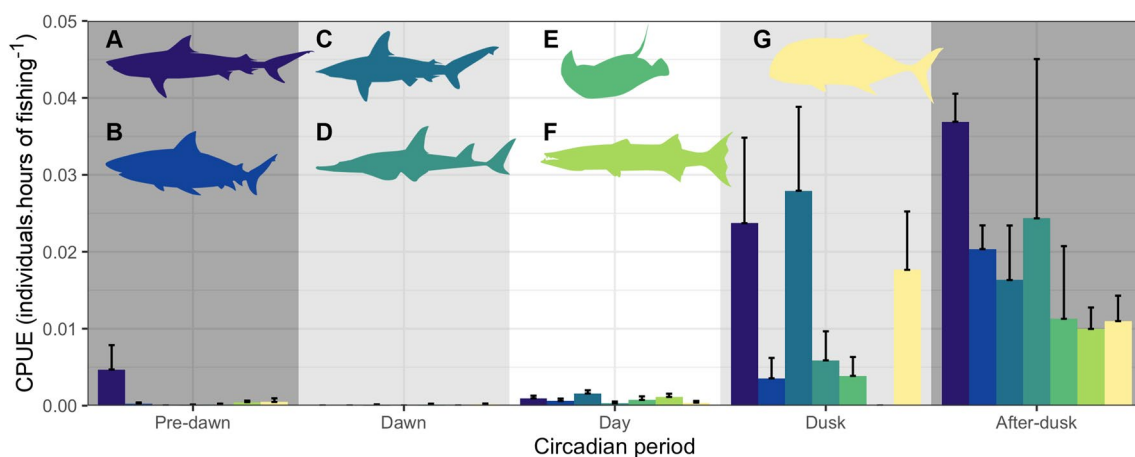


Fig. 2 Mean capture-per-unit-of-effort (CPUE) in SMART drumlines of (a) tiger sharks, (b) bull sharks, (c) scalloped hammerhead sharks, (d) giant guitarfish, (e) stingrays, (f) barracuda and (g) giant trevally, per each circadian period category considering the respective hours

of capture. Lines represent the corresponding standard errors. The CPUE was calculated as the number of individuals caught in each set divided by the number of hooks in the water multiplied by the number of fishing hours

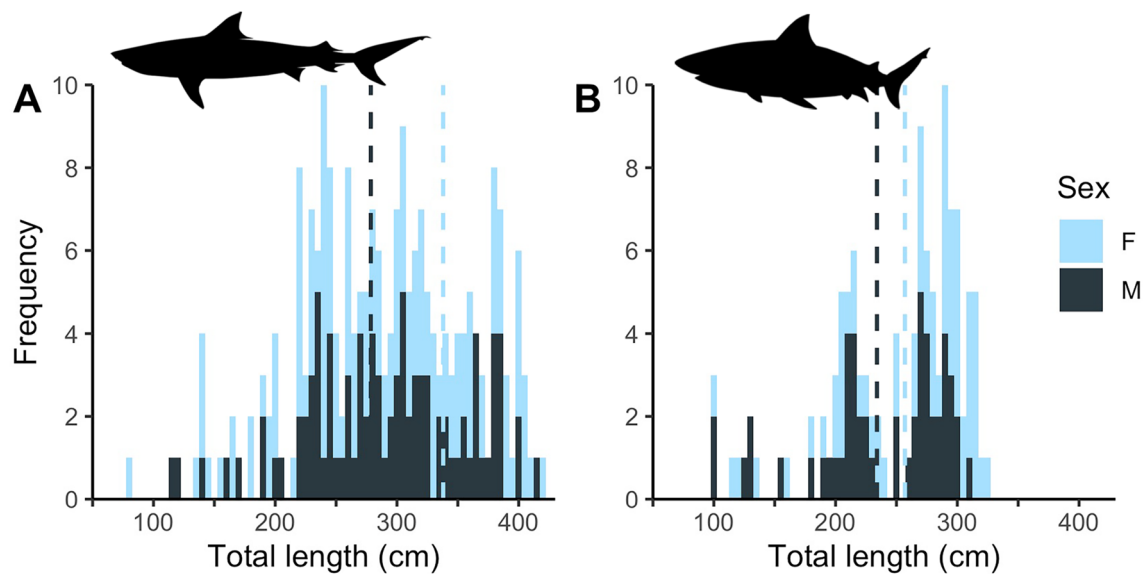


Fig. 3 Size frequency histograms by sex of (a) tiger shark and (b) bull shark. Dashed lines represent the corresponding maturation sizes for each species and sex for Réunion Island retained from the literature (Pirog et al. 2019a, 2020)

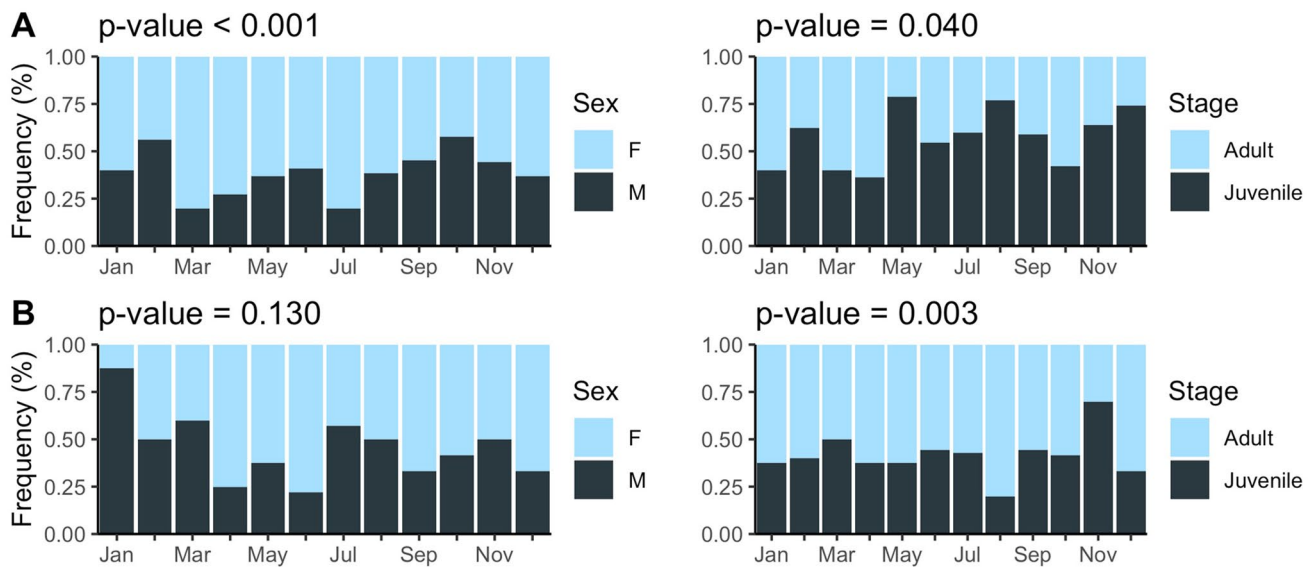


Fig. 4 Seasonal variations of sex (left panels) and maturity (right panels) ratios for (a) tiger shark and (b) bull shark off Réunion Island, including the significance levels of the respective Mann–Whitney tests

(Table 2). Both bull shark and giant trevally were more frequent with higher turbidity levels of $Kd_{490} > 0.03$ m (Fig. 8a). The higher presence of giant guitarfish was mostly influenced by lower PAR levels below $52 \text{ m}^2 \text{ day}^{-1}$ i.e. with reduced available light periods over the sea surface (Fig. 8b), and stingrays were more commonly caught in periods of cooling SSTs (Fig. 8c).

Catchability of marine predators with SMART drumline gear

A significantly varied likelihood of capturing marine predators was observed over the circadian period for tiger, bull, and scalloped hammerhead sharks, giant guitarfish, stingrays, and giant trevally (Table 3), with a more pronounced

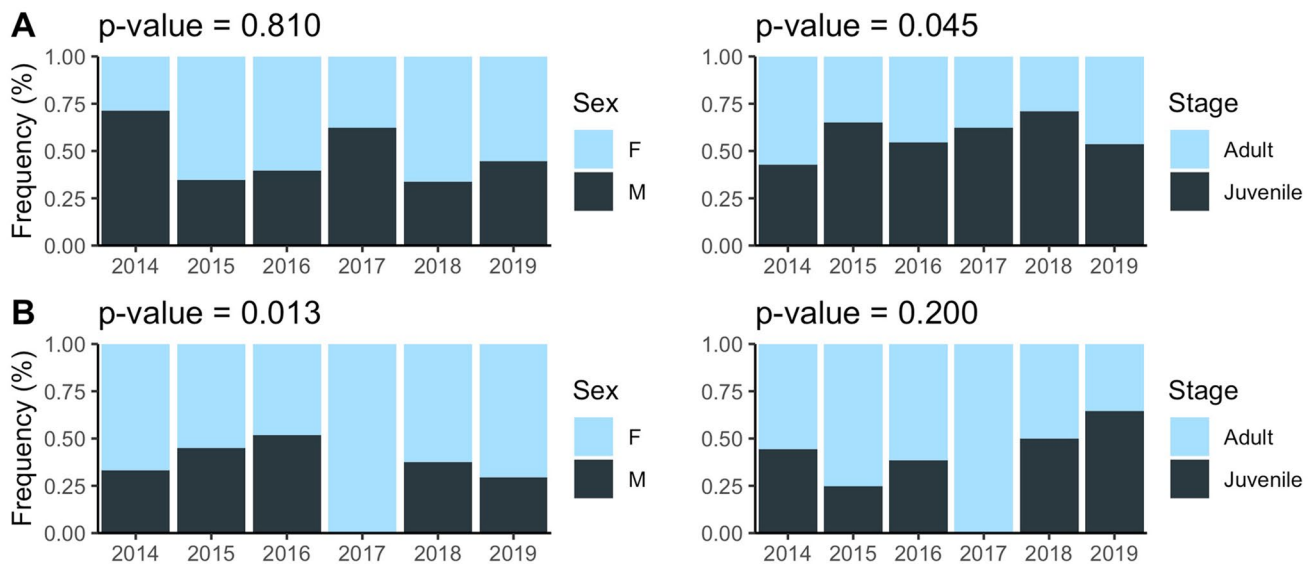


Fig. 5 Yearly variations of sex (left panels) and maturity (right panels) ratios for (a) tiger shark and (b) bull shark off Réunion Island, including the significance levels of the respective Mann–Whitney tests

Table 1 Species-specific Zero-Inflated Generalized Additive Models for the influence of spatial–temporal predictors, including the corresponding selected significant effects of month, year and the interacting effect between sectoral angle (SectAngle) and depth

Species	Variable	Edf	Ref.df	Chi.sq	p
Tiger shark	SectAngle x Depth	11.20	12.73	139.35	<0.001
	Year	2.63	3.09	17.27	<0.001
Bull shark	SectAngle x Depth	9.58	11.52	55.53	<0.001
	Year	1.84	2.25	13.09	0.002
Giant guitarfish	SectAngle x Depth	10.86	12.68	37.76	<0.001
	Month	2.72	3.25	11.74	0.010
Stingrays	Year	2.56	3.08	32.11	<0.001
Giant Trevally	SectAngle x Depth	7.95	9.95	125.20	<0.001

trend for scalloped hammerheads (Fig. 9a–f). Tiger sharks were also more likely to be caught when SMART drumlines were set at deeper waters (Fig. 9g). Only the teleost predators were significantly more frequent inside the MPA (Table 3). Both the type and size of the baits used were found to influence the catch of the shark species. Tiger sharks occurred more frequently when wastes were used, whereas bull sharks had a similar chance of being caught either with locally provided bait or wastes (Table 3). Scalloped hammerhead sharks were more likely to be caught when larger baits > 2 kg were used (Table 3).

The moonlight index was found to influence the catchability of five species with SMART drumline gear. All these species exhibited negative relationships with moonlight index (Table 4), suggesting that they were more likely to interact with the baited hooks during dark night periods (Fig. 10). Giant guitarfish exhibited the most pronounced trend with moonlight index, and while the giant trevally showed the least pronounced trend, it was still significant (Fig. 10).

Discussion

This study examined the spatial, temporal, and environmental factors influencing the distribution of sympatric elasmobranch and teleost predatory species in coastal waters of an oceanic island, using standardized catch data and a combination of statistical approaches. The moon is known to affect the behaviour of marine organisms at all trophic levels (Benoit-Bird and Au 2006; Lowry et al. 2007; Hammerschlag et al. 2017). Here a standardized moonlight index was developed and showed that all the marine predators exhibited similar daily patterns, being more frequent during periods of lower ambient light. At longer temporal scales (i.e. seasons and years), different species-specific patterns emerged in relation to particular spatial and environmental conditions. In the dynamic and narrow coastal ecosystems off Réunion Island, marine predator nearshore occurrence might be adapted to inter-specific avoidance, possibly to reduce resource competition (Trystram et al. 2017).

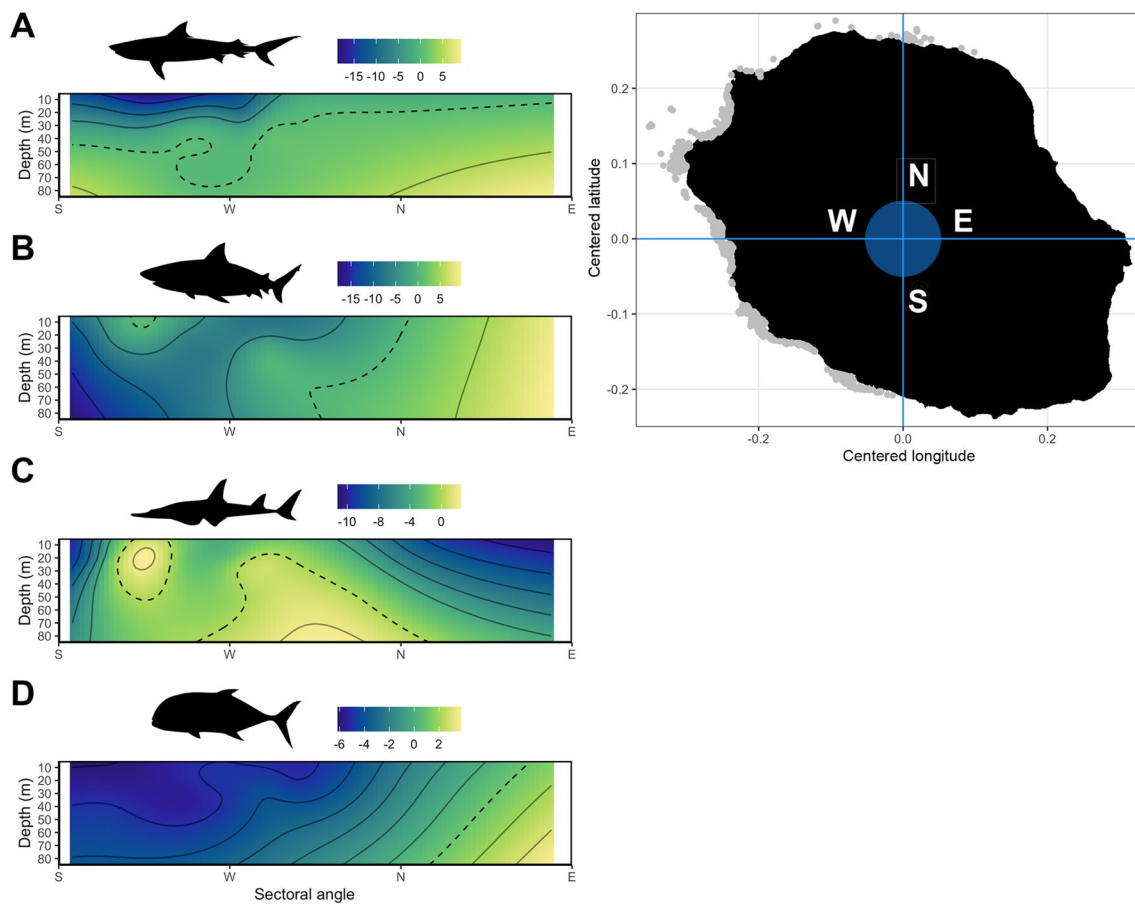


Fig. 6 Species-specific Zero-inflated Generalized Additive Models including the significant interacting effects of geographic sectoral angle and depth of gear deployment upon the occurrences of (a) tiger

shark, (b) bull shark, (c) giant guitarfish and (d) giant trevally. The colour scales and dashed lines respectively represent the corresponding standardized residuals and null effects

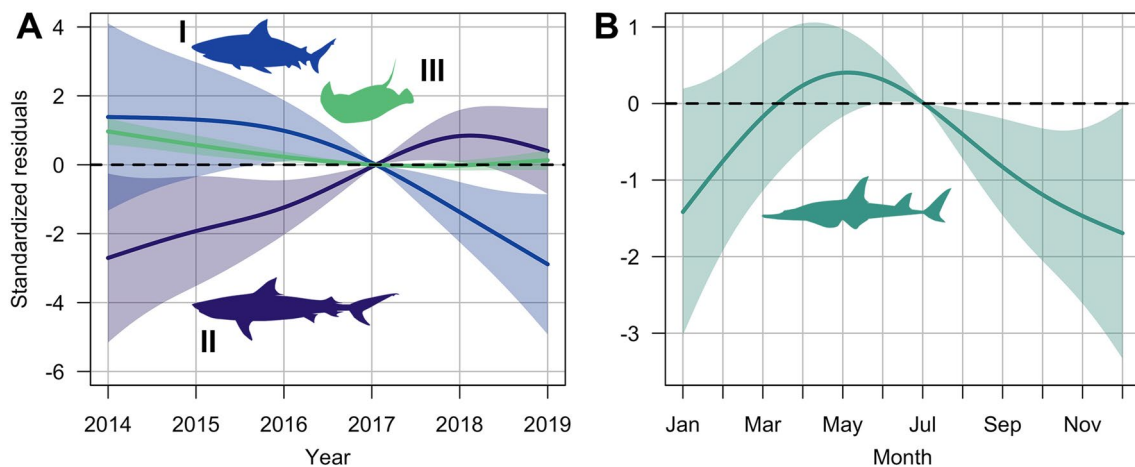


Fig. 7 Species-specific Zero-inflated Generalized Additive Models including the significant temporal effects of (a) year and (b) month upon the occurrences of (a) bull sharks (I), tiger sharks (II) and sting-

rays (III); and (b) giant guitarfish. Dashed lines and shaded areas respectively represent the null effects and the 95% confidence intervals

Table 2 Species-specific Zero-Inflated Generalized Additive Models for the influence of environmental predictors, including the corresponding selected significant effects of diffuse attenuation coefficient at 490 nm (Kd₄₉₀), photosynthetically available radiation (PAR) and derivative sea surface temperature (derSST)

Species	Variable	Edf	Ref.df	Chi.sq	<i>p</i>
Bull shark	Kd ₄₉₀	2.44	2.96	5.12	0.001
Giant guitarfish	PAR	1.18	1.35	15.75	<0.001
Stingrays	derSST	2.08	2.56	8.29	0.037
Giant trevally	Kd ₄₉₀	1.91	2.35	9.53	0.013

Species-specific ecological patterns

We suggest that as a response to the removal of bull sharks from coastal waters off Réunion, juvenile tiger sharks might be migrating into this region and starting to frequent these vacated habitats. Even though tiger sharks are targeted by the preventative shark fishing program, yearly occurrence increased off Réunion Island during the study period, especially for juveniles. The Hawaiian program observed similar trends, attributed to the immigration of smaller individuals following selective removal of larger sharks rather than to a population increase (Wetherbee et al. 1994; Dudley and Simpfendorfer 2006). These sharks are highly mobile, moving great distances across latitudes (Ferreira et al. 2015) and between different ocean basins (Afonso et al. 2017a). Tiger

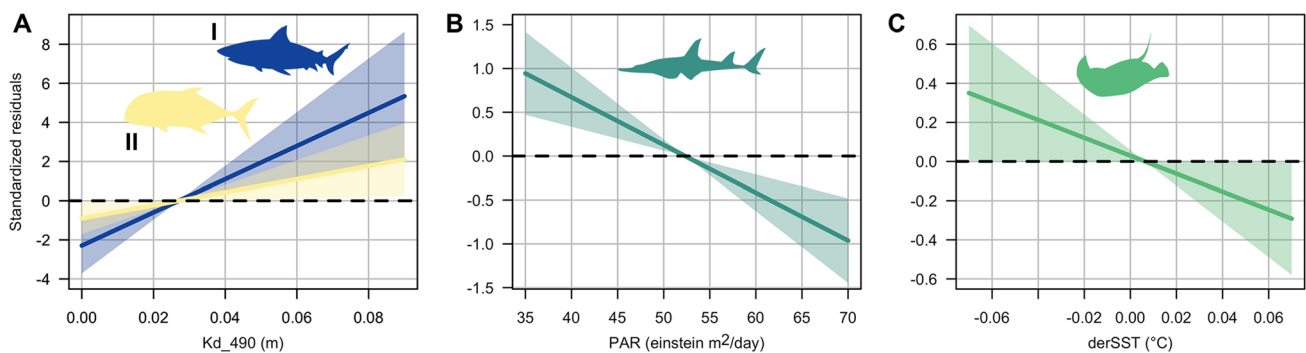


Fig. 8 Species-specific Zero-inflated Generalized Additive Models including the significant environmental effects of (a) diffuse attenuation coefficient at 490 nm (Kd₄₉₀), (b) photosynthetically available radiation (PAR) and (c) derivative sea surface temperature (derSST)

upon the occurrences of (a) bull shark (I) and giant trevally (II), (b) giant guitarfish, and (c) stingrays. Dashed lines and shaded areas respectively represent the null effects and the 95% confidence intervals

Table 3 Species-specific Zero-inflated Generalized Linear Mixed Models for the catchability of SMART drumlines, including the corresponding selected significant effects of hour of catch (Hour catch), bait type, bait size, depth of gear deployment (Depth) and MPA location

Species	Variable	Est	SE	<i>z</i>	<i>p</i>
Tiger shark	Bait type (Non-Scombridae)	− 1.16	0.23	− 5.14	<0.001
	Bait type (Scombridae)	− 1.04	0.24	− 4.26	<0.001
	Bait type (Wastes)	1.08	0.27	4.02	<0.001
	Hour catch	0.07	0.01	5.29	<0.001
	Depth	0.06	0.01	4.28	<0.001
Bull shark	Hour catch	0.15	0.02	6.93	<0.001
	Bait type (Non-Scombridae)	− 1.66	0.34	− 4.89	<0.001
	Bait type (Scombridae)	− 2.59	0.75	− 3.47	<0.001
	Bait type (Wastes)	− 0.84	0.61	− 1.37	0.172
Hammerhead shark	Hour catch	0.27	0.05	5.61	<0.001
	Bait size (B)	0.37	0.66	0.57	0.570
	Bait size (C)	1.69	0.81	2.08	0.038
Giant guitarfish	Hour catch	0.20	0.05	4.25	<0.001
Stingrays	Hour catch	0.17	0.03	5.407	<0.001
Barracuda	MPA (Outside)	− 1.39	0.52	− 2.67	0.008
Giant trevally	Hour catch	0.14	0.03	5.26	<0.001
	MPA (Outside)	− 1.64	0.36	− 4.53	<0.001

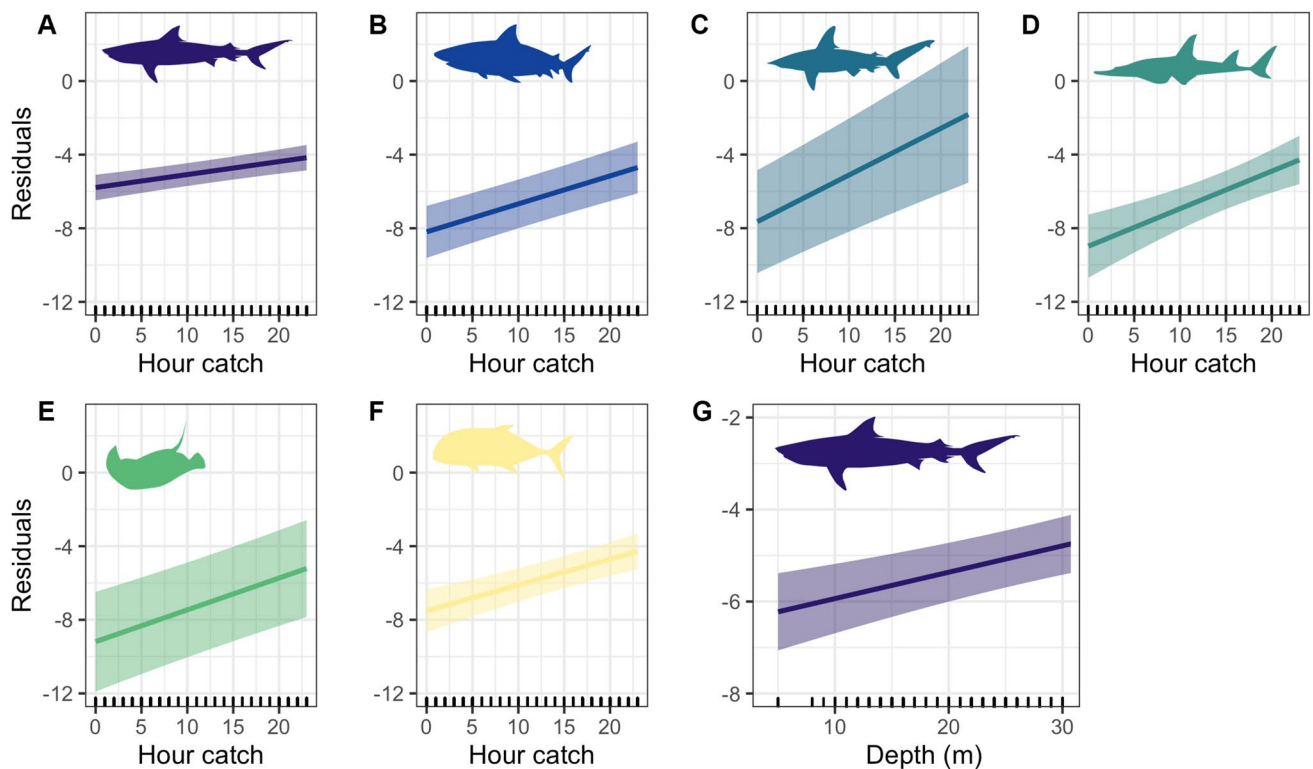


Fig. 9 Species-specific Zero-inflated Generalized Linear Mixed Models of SMART drumline catchability including the significant effects of hour of catch upon the likelihood of capturing (a) tiger, (b) bull and (c) hammerhead sharks, and (d) the giant guitarfish, (e) sting-

rays and (f) giant trevally; and (g) depth of gear deployment for tiger sharks. Shaded areas represent the corresponding 95% confidence intervals

sharks have been shown to be a single Indo-Pacific population (Pirog et al. 2019b) suggesting that the removal of this species from a single coastal location, such as Réunion Island, will provide minimal enhanced bather protection as other individuals may occupy vacated niches. This increased presence in nearshore habitats may, in fact, strengthen if potential competitors such as the more philopatric bull sharks (Pirog et al. 2019c) have been removed from the ecosystem following fishing pressure. These sort of reductions in bull shark nearshore presence have been observed elsewhere following long-term capture in shark bite mitigation programs (De Bruyn et al. 2005; Reid et al. 2011).

Table 4 Species-specific Zero Inflated Generalized Linear Mixed Models including the corresponding selected significant effects of moonlight index

Species	Est	SE	<i>z</i>	<i>p</i>
Tiger shark	− 2.36	0.40	− 5.92	< 0.001
Bull shark	− 2.29	0.63	− 3.62	< 0.001
Giant guitarfish	− 3.77	1.65	− 2.28	0.022
Stingrays	− 2.86	1.01	− 2.84	0.004
Giant trevally	− 1.71	0.80	− 2.13	0.034

In South Africa, this removal of other potential competitor species was postulated to contribute to increased tiger shark catch (Dicken et al. 2016). Similarly, in the isolated marine park of Coco Island, in Costa Rica, a significant increase in tiger shark occurrence was attributed to a local decrease of other predatory species (White et al. 2015). White et al. (2015) hypothesised that some individuals had moved to Coco Island and established long-term residency there, with the local increase being more likely due to these movements than population trends. Long-term residency has not been shown to occur in any other locations for tiger sharks, although some philopatry has been identified but not linked to reproductive strategies (Pirog et al. 2019b).

A consistent pattern was observed with most species being more frequently caught during dark periods, i.e. after-dusk and in low moonlight. Similarly, white sharks (*Carcharodon carcharias*) make the most use of nearshore areas in eastern Australia during new moon periods (Lee et al. 2018) and rely on low-light conditions to increase predation success in South Africa (Hammerschlag et al. 2006). Nevertheless, feeding chronology has been observed to vary among carcharhinid sharks in the North Atlantic Ocean, indicating different periods of feeding intensity among species (Driggers III et al. 2012). This variability in lunar-linked

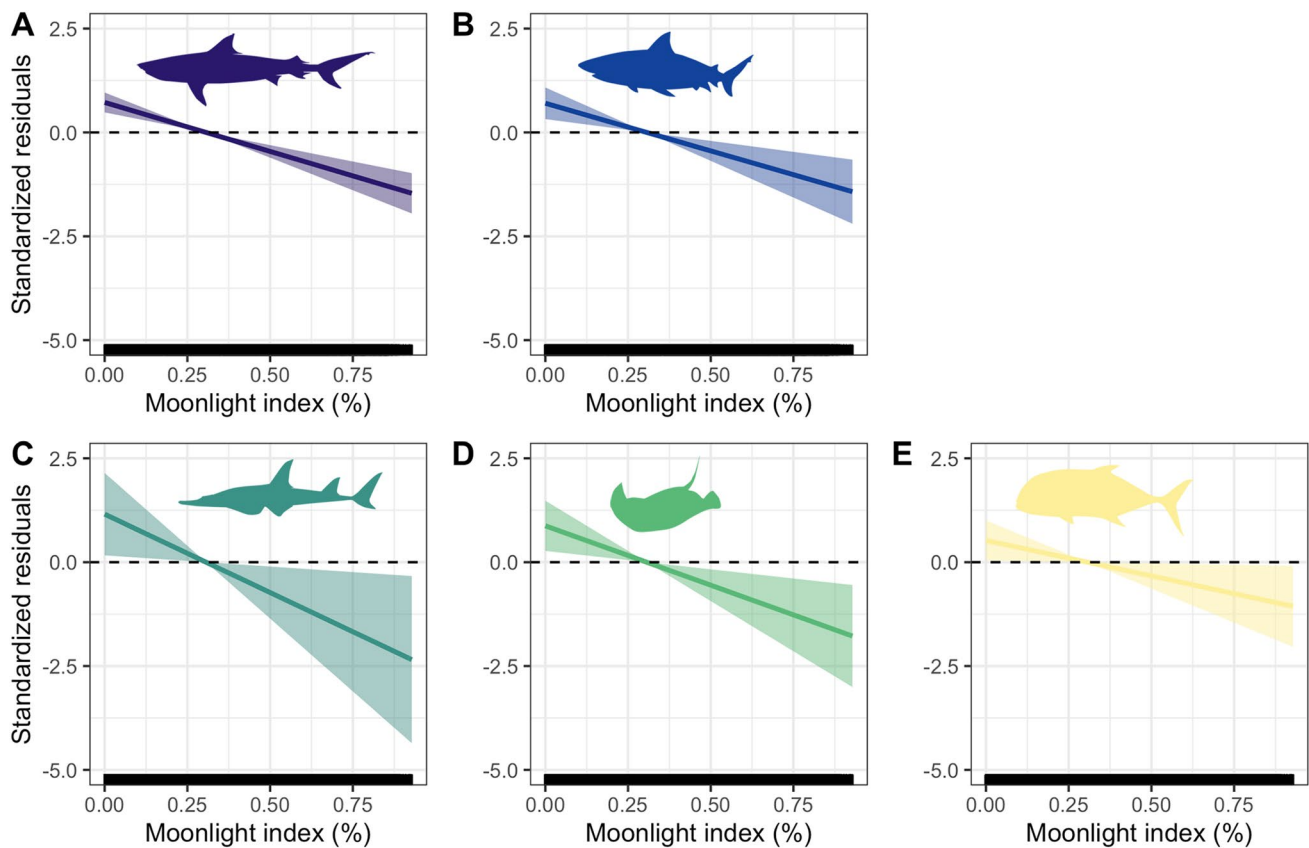


Fig. 10 Species-specific Zero-inflated Generalized Linear Mixed Models of SMART drumline catchability including the significant effects of moonlight index upon the likelihood of capturing (a) tiger

and (b) bull sharks, (c) giant guitarfish, (d) stingrays and (e) giant trevally. Shaded areas represent the corresponding 95% confidence intervals

predatory activity may be driven by whether preferred prey species follow nocturnal movements of the deep scattering layer. Off the tropical oceanic island of Oahu, in Hawaii, an environment very similar to Réunion Island, a more pronounced movement of the scattering layer closer to the surface has been observed during dark nights than during well-lit ones (Benoit-Bird et al. 2009). Hawaiian land-associated mesopelagic micronekton also undertakes long, nocturnal, horizontal migrations of up to 11 km towards the shore (Benoit-Bird and Au 2006). Although the species analysed in our study do not directly rely on micronekton, Trystram (2016) showed that many fish off Réunion Island were obligate nocturnal micronekton feeders. An associated nocturnal increase in fish biomass could therefore provide feeding opportunities for top predators that forage upon these mesopredators. Our data suggest that the higher coastal occurrences of apex predators during low moonlight may be driven by these foraging-related linkages. On brighter nights, top predators could either (1) be less actively foraging in response to lower biomass of micronekton in coastal ecosystems or (2) able to detect the fishing gear more easily and so avoiding the bait. Scalloped hammerhead sharks

and giant trevally generally patrolled nearshore waters earlier than the other species, i.e. during dusk periods. Larger baits were also an important factor influencing catchability of scalloped hammerheads in SMART drumlines, but hammerheads were not influenced by the moonlight. This corroborates suggestions that scalloped hammerhead sharks might have a higher dependence on visual cues for foraging (Broadhurst et al. 2014), i.e. preferring pre-dark periods and more likely to interact with larger baits.

Since 2007 a great part of the fringing reefs on the western coast of Réunion Island has been protected by an MPA. Our results did not point to any greater use of the MPA by any of the sharks or the other elasmobranch species, corroborating previous telemetry research that indicated bull sharks actually spent more time outside the MPA than within it (Soria et al. 2019). Conversely, both barracuda and giant trevally made greater use of the MPA, even though they share dietary habits with bull and tiger sharks (Trystram et al. 2015) and would therefore be expected to exhibit similar distribution patterns. We subsequently propose that sharks probably have broader foraging habitats than the two teleost predators, and this may reduce competition for the

resources (i.e. food and space) in the narrow coastal ecosystems of Réunion Island. This also suggests that this small coastal MPA, dedicated to protecting the coral reef ecosystem, has limited effects upon large transient apex predatory sharks that frequent multiple coastal and pelagic ecosystems (Roff et al. 2016).

Along the south-west part of the island, the continental shelf is narrow with deep canyons (Fig. 1a). Bull sharks show site fidelity to this region (Soria et al. 2019) and here we identified significant overlap in distribution with giant guitarfish in these shallower waters. In contrast, tiger sharks occurred mostly over deeper isobaths corroborating previous studies in this region and elsewhere (Afonso et al. 2014; Blaison et al. 2015). Off Réunion Island, bull sharks rely more on coastal food sources than tiger sharks which feed on more coastal-pelagic and deep-water prey (Trystram et al. 2017; Le Croizier et al. 2020), thus supporting our results and implying local spatial segregation between the two species. By contrast, from the mid-western-to-east part of the island, an inverted pattern in the distributions of bull and tiger sharks was observed with tiger sharks caught in shallower waters and bull sharks in deeper isobaths. This region is characterized by the presence of open bays and permanent larger river mouths, as well as deep canyons (Fig. 1a) that might be used by tiger sharks to move from deeper oceanic waters towards coastal waters. In New South Wales, Australia, tiger shark catch in the bather protection program was correlated to the presence of steep drop-offs to deep water in the vicinity of the nets (Lee et al. 2018). Bull sharks are known to move into deeper isobaths when exhibiting transient behaviour (Carlson et al. 2010; Niella et al. 2017a). In the mid-western-to-east part of Réunion Island the shelf is slightly larger than in the leeward region (Fig. 1a), thus possibly explaining bull shark movements into deeper isobaths similarly to that observed in the southwestern Atlantic (Niella et al. 2017a). Overall, in the coastal ecosystems of Réunion Island, these two shark species seem to limit co-occurrence potentially to reduce competition.

Virtually nothing is known about nearshore occurrence patterns of giant guitarfish, which are among the most threatened of all elasmobranchs (Kyne et al. 2020). These animals were seasonally more frequent off Réunion between April and May, during the transition between summer and winter, and this pattern accords with the negative relationships with PAR values (i.e. higher abundance during periods of lower sunlight availability periods). Since lower PAR values are indicative of higher photosynthetic activity (Rubio et al. 2003), it is plausible to assume that the giant guitarfish move closer inshore during these periods of increased biological productivity to optimize foraging success. Giant trevally shared a similar distribution pattern to bull sharks, showing an affinity to higher turbidity and deeper waters of the east coast. Since this is the rainy coast of the island, this

suggests an indirect effect of rainfall levels and freshwater runoff on their distribution (Cliff and Dudley 1991; Ortega et al. 2009). It also suggests a possible indirect effect of higher water turbidity influencing the abundance of teleost prey, which giant trevally and bull sharks could be relying on to improve foraging success (Lutjeharms et al. 2000; Hueter et al. 2004; Trystram et al. 2015). Stingrays were more frequently caught when water temperatures decreased in autumn, a period characterized by an increase of the trade winds and the end of the rainy season (Conand et al. 2007). Coastal ecosystem dynamics highly shift during this transition period between summer and winter in Réunion Island, due to fluctuations in primary production and subsequent distribution of mesopredators which in turn affects the nearshore occurrence and behaviour of top-order predator species.

Implications for management of the preventative shark fishery

Seasonality in local abundances of potentially dangerous species has been previously related to the increased risk of shark bites (Cliff and Dudley 1991; Afonso et al. 2017b; Ryan et al. 2019). Off Réunion Island, a higher risk of bites was observed during winter possibly due to the increased presence of bull sharks in nearshore waters (Lagabrielle et al. 2018). Although the increased catch of tiger sharks primarily over 200 cm TL (Fig. 2a), a size considered as potentially dangerous to humans (Dudley 1995), is concerning and warrants future consideration, it must be noted that few bites have been attributed to tiger sharks in Réunion (Ballas et al. 2017) and no bite has been attributed to tiger sharks < 300 cm TL (Lagabrielle et al. 2018).

Managing human-wildlife conflicts such as shark bite risk is challenging, with resolutions to the problem often leading to adverse consequences for both humans and the animals involved (Game et al. 2014). Effective marine spatial planning should combine the ecological impacts of management with information on the spatial overlaps between people and animals while consulting sea-users towards shark risk policy and possible actions (Shabtay et al. 2020). Modern public changes in attitudes towards the killing of sharks to reduce interactions with bathers have led to substantial international condemnation of governments enacting shark culling programs (Gibbs and Warren 2014; Ferretti et al. 2015; Powell 2017). Our data indicate that both bull and tiger sharks are predominantly caught after dusk. This correlates with the probability of a shark bite in La Réunion, which increases in the afternoon independently from the abundance of water users (Lagabrielle et al. 2018). As bull sharks have been identified as the species most regularly involved in shark bites in Réunion, fishing for this species during times that they are most susceptible to capture may assist in reducing

shark encounters. This has been suggested for South Africa where a significant reduction in shark attacks of 88% (Dudley 1997) was attributed to fishing down the portion of the bull shark population that seasonally occupy small home ranges off beaches where nets are deployed (Dudley and Simpfendorfer 2006). However, similar reductions in shark interactions were not evident for regions like Hawaii where tiger sharks were the primary species biting humans, even after the eradication of 4,668 sharks around the island of Oahu (Wetherbee et al. 1994). This implies that the ongoing killing of tiger sharks may not enhance bather protection for La Réunion.

This research has identified potential ways of reducing the impacts of the preventative shark fishing program of Réunion Island upon the marine ecosystem. The type of bait used was a significant factor influencing the catchability of the two targeted species with fish carcasses being highly selective for tiger sharks but not for the bull shark, which showed a preference for fresher local baits. Setting the SMART drumlines later in the day, i.e. during after-dusk periods, and secondarily using smaller baits might contribute to reducing captures of the critically endangered scalloped hammerhead sharks, a highly vulnerable bycatch species (Gallagher et al. 2014). The co-occurrence between targeted bull sharks and the giant guitarfish suggests that it might be more complicated to reduce the impact of the program upon the endangered giant guitarfish. Nevertheless, the mortality of bycatch species in this program is minimal due to the SMART drumline gear (Guyomard et al. 2019). Since 2014, 53 large guitarfish have been fished and 52 were released alive as part of this program, including 33 externally tagged individuals. Frequent recaptures and observations of these individuals on Baited Remove Underwater Videos (Guyomard pers obs), possibly indicate a good post-release survival of this species from SMART drumlines. However, further research is recommended to assess the survivorship of released giant guitarfish. Catches of stingrays decreased over the first years of the fishing program probably as a consequence of hooks being suspended from the sea bottom in 2014, as observed in other pelagic fisheries in the southwestern Atlantic (Afonso et al. 2011). Better understanding the influences of gear configurations on species-specific bycatch catchability will help benefit conservation of endangered species in fisheries.

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Author contributions YN, AW, UA, SJ, EL, RH, VP, and DG conceived the ideas and designed the methodology; DG collected the data; YN analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability The data used in the present research was collected by the Shark Security Centre (collected from the field from 2018 to 2019, and from the Fisheries Committee for the data previously collected). Datasets used in the publication are available on the SIMM website (link to be provided).

Compliance with ethical standards

Conflicts of interest The authors declare no conflicts of interest.

Code availability (software application or custom code) The moonlight index code (<https://doi.org/https://doi.org/10.5281/zenodo.3971062>) is publicly available together with a manual from <https://github.com/YuriNiella/Moonlight-index>.

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