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Inferring trends and linkages between shark abundance and shark bites on humans for shark-hazard mitigation

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Abstract. The present study aims at inferring linkages between the abundance of potentially dangerous sharks (PDSs) and shark hazard, so as to derive information about the underlying processes of shark peril off Recife, Brazil. Fishery-independent longline and drumline data collected from May 2004 through December 2014 for *Carcharhinus leucas* and *Galeocerdo cuvier* measuring ≥109 cm were considered for analysis. Generalised additive models showed that the frequency of shark bites was directly proportional to and followed the same seasonal trends as PDS abundance, meeting the hypothesis that higher shark abundance may result in an increased chance of a shark bite. However, the species-specific seasonality of bull and tiger sharks seemed to follow distinct patterns. This method was helpful in comparing the abundance dynamics of the PDSs caught by the local shark hazard-mitigation program with the distribution of shark bites, so as to infer whether the species involved in the incidents were being effectively captured. Also, it provided some information about each species' contribution to the overall dynamics in local shark hazard. However, despite being a potentially useful risk-management tool, its predictive efficacy for shark-peril mitigation may depend on the availability of abundant data spanning across wide temporal ranges.

Additional keywords: bull shark, drumline, longline, preventive fishing gear, shark attack, tiger shark.

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Introduction

The number of shark–human interactions has increased worldwide during the past few decades. However, in most circumstances, rather than sharks having become more abundant or aggressive towards humans, the development of coastal areas and the subsequent increase in beach usage has resulted in more frequent encounters between sharks and humans (Burgess 1990). In fact, nearshore habitats provide ideal foraging grounds where juvenile sharks may optimise growth (Simpfendorfer and Milward 1993) and shelter from predators (Heupel and Simpfendorfer 2011). Adults may also use these areas to give birth (Snelson *et al.* 1984), to mate (Carrier and Pratt 1998) or to target high-quality prey that are unavailable in oceanic waters (Heithaus *et al.* 2002). Among ~540 living shark species (Naylor *et al.* 2012), only ~30 have been implicated in incidents with humans and ~12 are considered particularly hazardous (International shark attack file, see https://www.flmnh.ufl.edu/fish/isaf/home/, accessed 25 March 2015). Further, three species are responsible for the majority of these incidents, namely the white (*Carcharodon carcharias*), tiger (*Galeocerdo cuvier*) and bull (*Carcharhinus leucas*) sharks (https://www.flmnh.ufl.edu/fish/isaf/home/). In the western equatorial Atlantic Ocean, examples of potentially aggressive species commonly found in coastal waters include carcharhinids such as the bull, blacktip (*Carcharhinus limbatus*) and tiger sharks, and sphyrnids such as the scalloped (*Sphyrna lewini*) and great (*S. mokarran*) hammerheads (Hazin and Afonso 2014). The simultaneous presence of humans and potentially hazardous sharks in coastal areas mediates the occurrence of shark–human interactions; thus, both human demography and shark abundance and behaviour should directly influence the occurrence of these events.

The term 'shark attack' (Schultz 1963) has been frequently used by scientists and the media to describe incidents with sharks (Burgess and Callahan 1996; Caldicott *et al.* 2001; Ritter and Levine 2004; West 2011). However, some authors have proposed a more prescriptive system for classifying such events, aiming at augmenting its informative content and curbing the use of the potentially sensationalist nomenclature 'shark attack'

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[1] Both authors contributed equally to this study.

in scientific communications (Lentz *et al.* 2010; Neff and Hueter 2013). This system is divided into the following four categories: (1) shark sightings, i.e. sightings of sharks in the water in proximity to people, with no physical contact; (2) shark encounters, i.e. interactions involving physical contact between a shark and a person, with no injuries taking place; (3) shark bites, i.e. incidents in which sharks bite people, leading to non-fatal injuries of lower to higher severity; and (4) fatal shark bites, i.e. incidents in which serious injuries are caused by a shark as a result of one or more bites, leading to a fatal outcome (Neff and Hueter 2013). It is noteworthy that, in spite of the great socioeconomic impacts resulting from shark hazard (Cliff and Dudley 2011; McPhee 2012; O'Connell *et al.* 2014), the frequency of these events is very low, averaging 64 per year worldwide (Burgess *et al.* 2010). However, local cluster of fatal and non-fatal shark bites has persistently occurred in some regions, prompting the implementation of shark hazard-mitigation programs that usually operate across large temporal scales (Cliff and Dudley 2011).

Since 1992, the Metropolitan Region of Recife (MRR) has experienced an abnormally high rate of shark incidents' that resulted in a significant socioeconomic loss (Hazin *et al.* 2008). Most incidents were reported off a ~20-km stretch of coastline, resulting in one of the highest shark-bite rates per unit of area in the world. In 2004, the State Government of Pernambuco implemented the Shark Monitoring Program of Recife (SMPR) to gather information about the ecosystem off the MRR and to develop an efficient strategy for reducing the occurrence of shark–human interactions, with minimum ecological impact. A thorough description of the SMPR and the results achieved can be found in Hazin and Afonso (2014).

Shark hazard-mitigation strategies have generally relied on culling programs aiming at reducing the local abundance of hazardous species, which has typically been accomplished by deploying gill-nets, drumlines and longlines (Wetherbee *et al.* 1994; Dudley and Cliff 2010). These programs contrast with the non-lethal strategy conducted by the SMPR, which aims at translocating such species from the hazardous coastal area to offshore waters, by using a standardised procedure. The SMPR strategy was able not only to reduce the shark-bite rate by one order of magnitude (Hazin and Afonso 2014) but also to collect valuable bioecological data pertaining to the species involved in the incidents (e.g. Afonso *et al.* 2012, 2014; Afonso and Hazin 2014, 2015). The ability to further mitigate shark hazard largely depends on the understanding of the dynamics in shark abundance at coastal waters and the linkages between shark abundance and the frequency of shark-inflicted injuries. Addressing the patterns in shark abundance and shark bites within the same framework could thus contribute to an increased knowledge about the biotic and abiotic processes underlying the dynamics of shark hazard.

The objective of the present study was to assess patterns in the abundance of potentially dangerous sharks off the MRR and to relate them with the distribution of shark bites, so as to understand the possible linkages between these two processes. Additionally, this approach will be used to examine the hypothesis that the SMPR removed the sharks that would otherwise be responsible for biting people, which is relevant for determining the suitability of the local shark-hazard mitigation strategy. Finally, the applicability of using the relative abundance of potentially hazardous species as a proxy of the likelihood of a shark bite is appraised.

Materials and methods

Ethics statement

The present study has been approved by the Instituto Chico Mendes de Conservação da Biodiversidade of the Brazilian Ministry of the Environment (Permit number 15083-8). Shark capture and handling was approved and performed in full compliance with the recommendations of the Regiment of the Commission of Ethics on the Usage of Animals from the Universidade Federal Rural de Pernambuco (Licence number 041/2009; Protocol number 23082.009679/2009 D18).

Study area and fishing protocol

The study area comprised nearshore waters off a ~20-km stretch of coastline from the MRR (8°10′S, 34°53′W), north-eastern Brazil. This area accounts for 78% of all shark bites in this region since 1992. Each fishing module consisted of longline and drumline gear that were deployed overnight at two contiguous nearshore sites, i.e. off the beaches of Paiva (PA) and Boa Viagem–Piedade (BV) (Fig. 1). The two areas essentially comprise soft-bottom habitats with some estuarine influence and differ mostly in the degree of urban development and beach usage, with PA being little urbanised and used by fewer people than is the heavily populated BV. The fishing gear was deployed on four consecutive days in each fishing trip, corresponding to an overall sampling effort of 246 hooks per day and 984 hooks per trip. Fishing trips were scheduled on a weekly basis from Friday to Tuesday, so as to reflect the distribution of beach usage (Silva *et al.* 2008) and shark-bite frequency (Hazin *et al.* 2008). Longlines (BV = 100 hooks; PA = 100 hooks) were deployed along the shore, ~2–3 km away from the coastline, in waters averaging 14 m (s.d. 4 m) in depth, whereas drumlines (BV = 26 hooks; PA = 20 hooks) were deployed <1 km from shore at the 8-m mean isobath (s.d. 3 m) (Fig. 1). Circle (17/0) hooks baited mostly with *Gymnothorax* moray eel were set to operate in the middle of the water column by attaching a styrofoam float to the leader. The shark survey spanned from May 2004 through December 2014, but the operations were interrupted in several occasions because of funding discontinuity. This resulted in shark abundance not being sampled for a total of 20.3% of the whole survey period. A thorough description of the fishing gear and procedures can be found in Afonso *et al.* (2011) and Hazin and Afonso (2014). On capture, all sharks were brought onboard of the R/V *Sinuelo*, identified and measured for stretched total length (TL) to the nearest centimetre, before being translocated and released.

Characterisation of sharks and shark bites

The composition of the shark catch was first divided into non-aggressive species and potentially aggressive species (PAS), i.e. species that have been previously implicated in unprovoked shark–human interactions (https://www.flmnh.ufl.edu/fish/isaf/home/). Given that the accurate identification of the species that inflicted a shark bite is usually difficult to assess, we opted for pooling the different PAS that were more likely to be

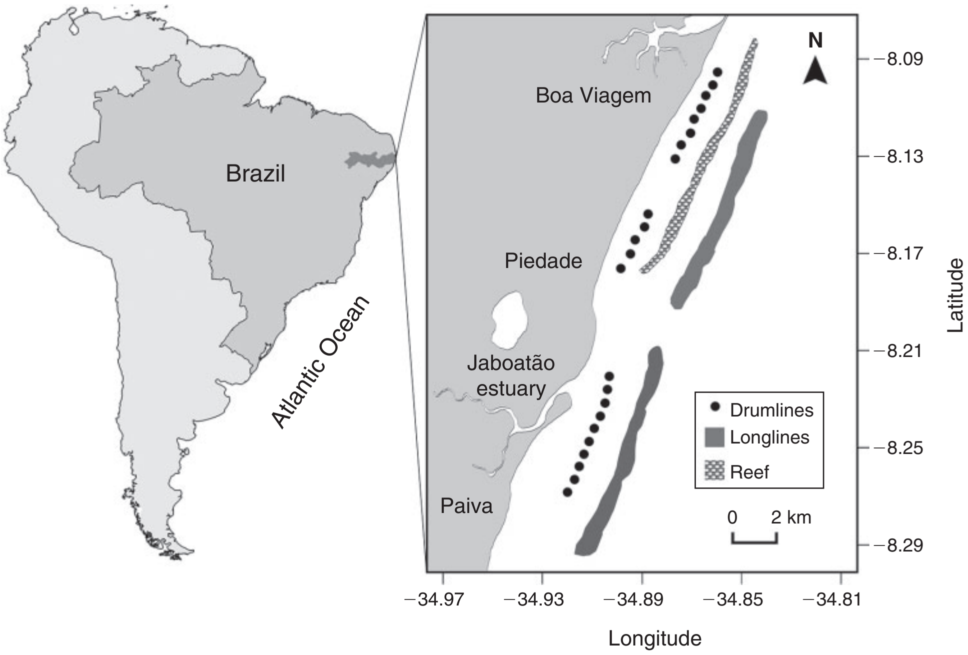

Fig. 1. Map of the study area off the Metropolitan Region of Recife, north-eastern Brazil, depicting the two fishing sites, i.e. Boa Viagem–Piedade and Paiva, and the general locations of longline and drumline gear deployments.

Table 1. Overall shark catch by the Shark Monitoring Program of Recife between May 2004 and December 2014 and the respective size distribution
Included are the species and number of sharks captured (*N*), the respective category, i.e. non-aggressive (NAS) and potentially agressive (PAS) species, the relative frequency in percentage, and the minimum ($\mathrm{TL}_{\mathrm{MIN}}$), maximum ($\mathrm{TL}_{\mathrm{MAX}}$) and median ($\mathrm{TL}_{\mathrm{MED}}$) total lengths are given in centimetres, as well as the mean total length ($\mathrm{TL}_{\mathrm{MN}}$) and its standard deviation ($\mathrm{TL}_{\mathrm{s.d.}}$)

Species	*N*	Category	Frequency	$\mathrm{TL}_{\mathrm{MIN}}$	$\mathrm{TL}_{\mathrm{MAX}}$	$\mathrm{TL}_{\mathrm{MED}}$	$\mathrm{TL}_{\mathrm{MN}}$	$\mathrm{TL}_{\mathrm{s.d.}}$
Ginglymostoma cirratum	211	NAS	46.9	43	300	183.0	183.8	47.9
Carcharhinus acronotus	125	NAS	27.8	67	177	120.0	118.9	19.4
Galeocerdo cuvier	78	PAS	17.3	87	426	151.5	168.6	67.6
Carcharhinus leucas	18	PAS	4.0	144	266	210.0	206.4	34.8
Carcharhinus limbatus	9	PAS	2.1	65	176	91.0	97.1	30.7
Carcharhinus brevipinna	2	PAS	0.5	64	190	127.0	127.0	63.0
Carcharhinus falciformis	2	PAS	0.5	118	123	120.5	120.5	2.5
Sphyrna mokarran	2	PAS	0.5	278	346	312.0	312.0	34.0
Carcharhinus perezi	1	PAS	0.2	107	107			
Sphyrna lewini	1	PAS	0.2	222	222			

responsible for the shark bites off the MRR, so as to identify the overall trends in the relative abundance of these *taxa* that could be associated with the shark bites. To accomplish this, we conducted a preliminary correlation-based procedure, in which different hypothetical combinations of PAS were considered to assess which PAS combination would render the highest correlation with the local distribution of shark bites. More explicitly, several hypothetical datasets were built so that the first would aggregate all possible PAS and the remainder would progressively discard the least abundant species from the analyses, except for the most abundant ones, i.e. tiger and bull sharks. The silky shark (*Carcharhinus falciformis*) and Caribbean reef shark (*C. perezi*) were not included in the analyses because of the small size of the few individuals captured (Table 1). Additional hypothetical datasets were also built, so as to progressively discard the smaller tiger sharks from the analyses (i.e. by removing the smallest tiger shark available in each new hypothetical dataset) because small juveniles were widely represented in the tiger-shark catch. We made the assumption that small tiger sharks would be less prone to interact with humans because the size of these sharks might prevent them from preying on human-sized prey, as suggested by the succession of ontogenetic dietary shifts exhibited by this species (Lowe *et al.* 1996). Bull sharks were all included in the analysis because of their generally large sizes. We then generated correlations between the aggregated monthly frequency of shark bites and the shark monthly abundance informed by each of the different hypothetical datasets, by using Pearson product moment correlation coefficients (*r*). The PAS combination included in the hypothetical dataset that rendered the highest correlation coefficient (hereafter referred to as potentially dangerous sharks, i.e. PDSs) was interpreted as the best proxy of the biological component regulating the dynamics in the shark-bite distribution and it was used in the subsequent analyses. Simultaneously, we examined the effect of discarding PAS abundance data collected from May 2004 through August 2005 on Pearson's correlation output, because half of the hooks were operating on the seafloor during this period as a selectivity assessment (Afonso *et al.* 2011). Similarly, although we interpreted PAS catch rate as the total number of specimens caught in longlines and drumlines normalised by the total number of hooks in both fishing gears, we also examined the effect of discarding drumline data on the correlation output. Albeit longlines and drumlines were deployed at different depths and comprised distinct amounts of hooks, there was no variation in the fishing module through time (Hazin and Afonso 2014). Therefore, the cumulative catch and effort of both fishing gears can be consistently used as the sampling unit of PAS relative abundance off the MRR. Nonetheless, we assessed whether longline data alone would yield a higher correlation with shark bites, so as to ascertain the best sampling approach for the purpose of the analysis.

Data on shark bites on humans were obtained from a comprehensive list of incidents recorded off the MRR since 1992 that has been maintained by the State Committee for the Monitoring of Incidents with Sharks (CEMIT 2015). The anatomical regions bitten included body extremities (i.e. hands, forearms, feet, calf, knees and thighs) and torso (i.e. trunk, shoulders and buttocks). Shark bites were categorised as non-fatal (NSB) and fatal (FSB). In the context of the present study, a shark bite is interpreted as an unprovoked shark-inflicted injury, regardless of the number of bites inflicted. In addition, shark bites were classified as (1) single bites to the body extremities (SBE), (2) single bites to the torso (SBT), (3) multiple bites to the body extremities (MBE), (4) multiple bites to the torso (MBT), and (5) multiple bites to both body parts (MBB), i.e. incidents simultaneously involving bites to the body extremities and torso. This classification scheme was used because it enabled the incorporation of a measure of severity in the distribution of shark hazard that could be associated with biological and human parameters, such as shark size or the activity of the victim at the time of the incident. For example, bite force in carcharhinid sharks correlates positively with body length (Huber *et al.* 2006; Habegger *et al.* 2012) and, expectedly, has an effect on wound severity. With this approach, we make the assumption that injuries resulting from FSB are more severe than the ones resulting from NSB, thus being probably inflicted by larger sharks, so as to verify whether there would be a positive relation between shark size and the likelihood of a fatal outcome.

Analytical methods

Several different approaches were used to detect patterns in PDS relative abundance and to infer their relationship with the distribution of shark bites. The significance level was set at 0.05 and all the analyses were conducted in R, ver. 3.0.2 (R Foundation for Statistical Computing, Vienna, Austria, see http://www.r-project.org/). First, we calculated PDS catch-per-unit-of-effort (CPUE), as the number of sharks caught during each fishing trip in both fishing gears at each site per 1000 hooks, to assess any conspicuous differences among years, months and fishing sites. Because the fishing gear and procedures were rigorously standardised, PDS CPUE is likely to be proportional to PDS relative abundance. We then assessed the significance of the spatiotemporal variability in PDS CPUE by using zero-inflated generalised additive models (ZIGAM) with a Poisson distribution and logarithmic link function. The response variable was the number of PDSs caught in each fishing trip, whereas candidate predictor variables were year, month and fishing site. The logarithm of fishing effort (i.e. the number of hooks deployed per site in each fishing trip) was included in the model as an offset covariate. A comprehensive description of the modelling procedure can be found in a dedicated section further below. Additionally, species-specific analysis of the two most abundant species, i.e. tiger and bull sharks, were also conducted with ZIGAM in a similar fashion, but using presence or absence as a binomial response variable with a logit link function instead.

In parallel, we used ZIGAM models with Poisson distributions and logarithmic link functions to examine trends in shark bites following distinct approaches. Given that only 13 (22.4%) shark–human interactions occurred between May 2004 and December 2014, we used data from June 1992 to December 2015 to model shark bites. To determine the overall distribution of shark-bite episodes, we used the total number of shark bites (TSB), i.e. both fatal and non-fatal incidents, per week as the response variable, whereas month and the state of the SMPR (i.e. active or inactive) were used as candidate explanatory variables. The effect of year was not assessed because the shark-bite rate was significantly reduced following the implementation of the SMPR in 2004 (Hazin and Afonso 2014). We also refrained from addressing spatial effects on the shark-bite rate because the variability in beach usage across different areas could not be quantitatively tracked and the number of people in the water expectedly has an influence on the shark-attack rate. However, we do not expect beach usage to have had a chronological effect on the shark-bite rate because (1) the shark-bite rate did not increase proportionally to the local population increase during the past few decades (Fig. S1, available as Supplementary material to this paper), and (2) the most hazardous season corresponded to the austral winter, when beach usage is substantially reduced (Silva *et al.* 2008). Furthermore, addressing TSB on a weekly basis precluded any possible influence of short-term periodicity in beach usage, e.g. resulting from weekend peaks. Besides, variability in PDS total length was assessed by months to verify whether months represented by sharks with larger mean sizes would match those exhibiting higher frequencies of fatal shark bites. We reason that such an approach could allow us to infer possible influences of biological factors (e.g. shark size or species) underlying the distribution of shark bites off the MRR. The monthly distributions of bites to bathers and surfers were also plotted separately to inspect any similarities with the trends in PDS size or species.

The several model outputs of PDS relative abundance and shark bites assessed independently were then inspected for any common trends. Next, the correlation between the monthly aggregated frequency of shark bites and the monthly mean PDS abundance was evaluated with both Pearson's r and Spearman's s correlation tests, as an update of Hazin and Afonso (2014). A significant correlation was considered only if the lowest absolute value in the confidence interval for r was greater than or equal to 0.3, because this value is generally ascribed to low correlations (Cohen 1988). Finally, the relationship between PDS abundance and shark-bite frequency was quantitatively assessed with a generalised linear model (GLM). We set the aggregated monthly frequency of TSB as the response variable, the mean monthly PDS CPUE as the predictor variable, and used a Gaussian distribution with identity link function.

Modelling procedure

Modelling was conducted with COZIGAM (Liu and Chan 2010), STATS (R Foundation for Statistical Computing) and qpcR (A. N. Spiess, ver. 1.4-0, see http://CRAN.R-project.org/package=qpcR) R-libraries. Because zero-inflation could be present in PDS abundance and shark-bite frequency data, an exploratory model-selection procedure was conducted using GAM and ZIGAM for each predictive variable independently. The best-fit model was selected on the basis of the approximated logarithmic marginal likelihood by LaPlace method, logE (Liu and Chan 2010), the Akaike's information criterion (AIC), the difference between the AIC of each model and the AIC of the best candidate model (i.e. the one with the lowest AIC; ΔAIC) and Akaike weights (AICw) (Wagenmakers and Farrel 2004). The thin-plate regression spline was used as a penalised smoothing basis, and the k dimensions of the smooth function were optimised for each continuous predictor variable by running several models, with k-values varying between 1 and 10. The families of error distribution and the respective link functions were selected on the basis of the smallest logE value and residual analysis. A forward stepwise model-selection procedure starting with the null model was conducted to incorporate new predictor variables in the model and to identify the most suitable model among all possible candidate models. A more complex, better model, incorporating a new predictor variable, was considered when the following three criteria were met: (1) the number of effective degrees of freedom of the new predictor was >1; (2) the model had both smallest logE and higher AICw values than did other candidate models; and (3) the ANOVA using the chi-square test indicated the new model to be significantly different from the previous, simpler model. Model diagnosis to all final models was performed to ensure that they would conform to their statistical assumptions.

Results

Fishing effort and catch composition

In total, 6940 longline and 6907 drumline sets distributed in 413 fishing trips were conducted. The global fishing effort totalled 505 861 hooks. The shark catch was composed of 113 specimens belonging to 8 potentially aggressive carcharhinid and sphyrnid species and 336 specimens belonging to other non-aggressive species; however, only 6 PAS were considered because both the Caribbean reef and the silky sharks were small-sized and rare in the catch (Table 1). The most frequent species were the nurse (*Ginglymostoma cirratum*), blacknose (*Carcharhinus acronotus*) and the tiger sharks. The preliminary correlation-based procedure for selecting the most adequate PDS combination showed that bull sharks grouped with tiger sharks measuring ≥109 cm TL rendered the highest correlation with the occurrence of shark bites. Therefore, all the remaining species were excluded, together with tiger sharks of <109 cm TL. Furthermore, we observed that a PDS abundance sampling unit based on longline data combined with drumline data for the period between May 2004 and December 2014 rendered the highest correlation with shark bites. Therefore, a total of 79 PDSs was included in the analyses, 77.2% of which were tiger sharks (hereafter referred to as potentially dangerous tiger sharks, i.e. tiger sharks measuring ≥109 cm TL). Among PDSs, tiger shark CPUE (mean = 0.148 sharks per 1000 hooks, s.d. = 1.29) was approximately three-fold higher than bull shark CPUE (mean = 0.045 sharks per 1000 hooks, s.d. = 0.63). The largest PDS caught was a 426 cm TL tiger shark; however, most PDSs measured <300 cm TL (Fig. 2), with bull shark mean length (Table 1) being greater than potentially dangerous tiger shark

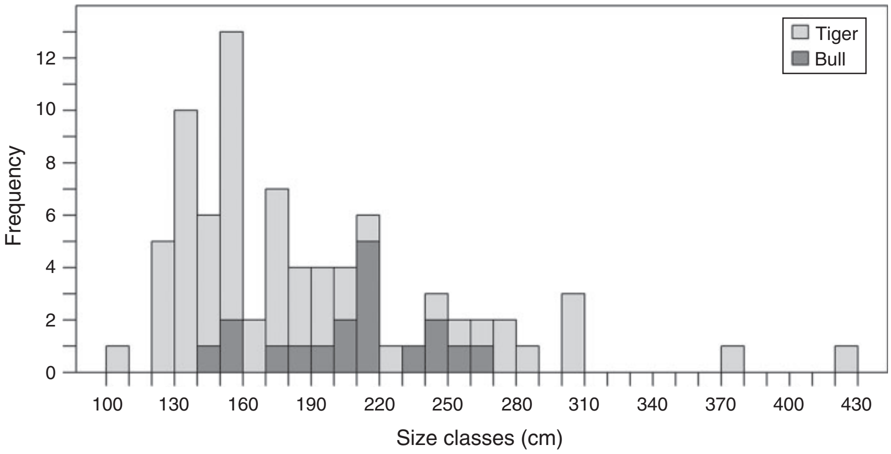

Fig. 2. Length–frequency distribution of potentially dangerous sharks captured off the metropolitan region of Recife from May 2004 to December 2014, in 10-cm total-length classes.

Table 2. Zero-inflated Poisson generalised additive model of the effect of spatiotemporal variables on the abundance of potentially dangerous sharks

Included are the predictor variables month (continuous; 1–12), site (categorical; Paiva, PA, and Boa Viagem–Piedade, BV) and year (continuous; 2004–2014), and the coefficient estimate (Est.), standard errors (s.e.) and *z*-statistics of the intercept and of the categorical variable, the effective (E. d.f.) and reference degrees of freedom (Ref. d.f.) and χ^2-statistics of the continuous variables, and the corresponding *P*-values

Model	Variable	Est.	s.e.	*z*	E. d.f.	Ref. d.f.	χ^2	*P*
Month + Site + Year	Intercept	−3.68	0.13	−26.84				<0.001
	Month				3.70	3.94	18.59	<0.001
	(Site) BV	0.61	0.23	2.57				0.010
	Year				3.51	3.86	36.81	<0.001

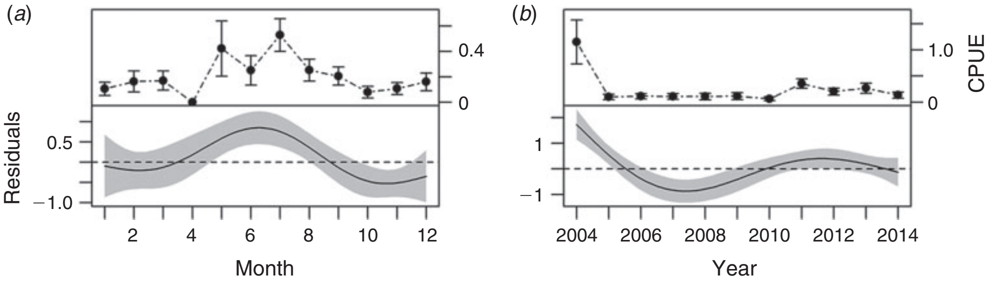

Fig. 3. Zero-inflated Poisson generalised additive model of the abundance of potentially dangerous sharks off Recife, depicting the effects of (*a*) month and (*b*) year. In the upper panels, solid points represent the catch-per-unit-of-effort (CPUE), as the number of sharks caught per 1000 hooks, and error bars depict the standard deviations of the mean. In the bottom panels, the horizontal dashed lines and shaded areas depict the null effects and 95% confidence intervals for the estimates respectively.

mean length (mean TL = 181.5 cm, s.d. = 65.5). Drumlines caught only four PDSs (i.e. one tiger and three bull sharks).

Patterns and dynamics in shark abundance

The comparison of GAM and ZIGAM types of model revealed that ZIGAM consistently yielded smaller logE and higher AICw (Table S1, available as Supplementary material to this paper), thus indicating the presence of zero-inflation in PDS abundance data (and in shark-bite data as well). Hence, ZIGAM models were used in the analyses. Stepwise model-selection procedures are described in supplementary tables.

The ZIGAM model of PDS abundance included month, fishing site and year as significant predictor variables (Tables 2, S2, available as Supplementary material to this paper). In relation to seasonality, PDSs tended to be more abundant during the austral winter, from May through August, with PDS mean CPUE peaking at 0.527 sharks per 1000 hooks (s.d. 0.12) in July (Fig. 3*a*). Such a trend was mostly shaped by potentially dangerous tiger sharks, which were most abundant and significantly more likely to occur off the MRR between March and September, whereas bull sharks were more likely to be caught between November and February in spite of a peak in bull shark CPUE being noticed in July (Fig. 4, Tables 3, 4, S3, S4, available as Supplementary material to this paper). Annual trends showed that PDS abundance fluctuated significantly across the survey period. It was greatest in 2004 but decreased to 0.063 sharks per 1000 hooks (s.d. 0.09) in the following years, before increasing in 2011 (Fig. 3*b*). Both species followed similar trends in abundance across the study span, although tiger-shark abundance fluctuated more prominently (Fig. 4, Tables 3, 4). Regarding spatial effects, PDSs were significantly more abundant in BV (Table 2), where 65.8% of the PDSs were caught, corresponding to a mean CPUE of 0.238 sharks per 1000 hooks (s.d. 1.69). In PA, PDS CPUE was 0.145 sharks per 1000 hooks (s.d. 1.16). However, only tiger sharks proved to be significantly more likely to occur in BV than in PA (Tables 3, 4).

Patterns in shark bites on humans

The first reported shark bite off the MRR dates back to the early 1970s (https://www.flmnh.ufl.edu/fish/isaf/home/) but these incidents were rare until 1992, after which the shark-bite rate suddenly increased (Fig. S1). A total of 60 shark bites occurred off the MRR within a 25-year period, the first of which was in June 1992 and the last in March 2015. Shark bites were most frequent off BV (71.6% of all incidents), especially among bathers. In contrast, only 6.6% of the incidents occurred off PA, where surfers were exclusively involved.

The frequency of shark bites increased during the first half of the year, peaking in July and then decreasing until December (Fig. 5). Cases of NSB corresponded to 60.0% of the incidents and were most frequent (61.1%) from March to August, i.e. during the austral winter. Similarly, FSB were also most frequent (70.8%) during the austral winter. This FSB pattern contrasts with the monthly variation of PDS mean total length, which tended to be greatest in the summer, between September and December (Fig. 6), a trend that could partially relate to the

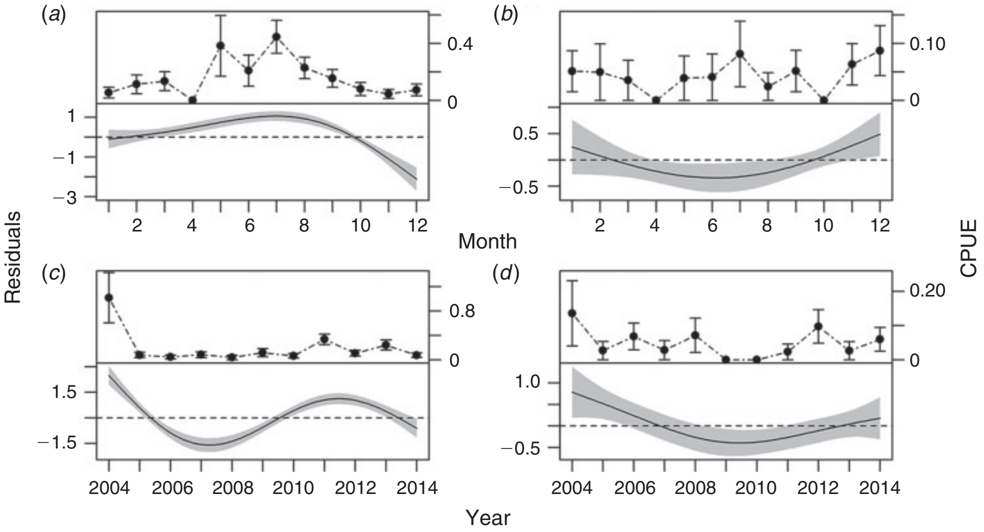

Fig. 4. Zero-inflated binomial generalised additive model comprising the effects of (*a*, *b*) month and (*c*, *d*) year on the occurrence of (*a*, *c*) tiger and (*b*, *d*) bull sharks off Recife. In the upper panels, solid points represent the mean catch-per-unit-of-effort (CPUE), as the number of sharks caught per 1000 hooks, and error bars depict the standard deviations of the mean. In the bottom panels, the horizontal dashed lines and shaded areas depict the null effect and 95% confidence intervals for the estimates respectively.

Table 3. Zero-inflated binomial generalised additive model of the effect of spatiotemporal variables on the occurrence of bull sharks
Included are the predictor continuous variables year (2004–2014) and month (1–12), and the coefficient estimate (Est.), standard errors (s.e.) and *z*-statistics of the intercept, the effective (E. d.f.) and reference degrees of freedom (Ref. d.f.) and χ^2-statistics of the continuous variables, and the corresponding *P*-values

Model	Variable	Est.	s.e.	*z*-value	E. d.f.	Ref. d.f.	χ^2	*P*
Year + Month	Intercept	−5.39	0.12	−43.78				<0.001
	Year				2.43	2.93	9.81	0.019
	Month				1.85	1.98	7.07	0.028

Table 4. Zero-inflated binomial generalised additive model of the effect of spatiotemporal variables on the occurrence of tiger sharks
Included are the predictor variables month (continuous; 1–12), year (continuous; 2004–2014) and site (categorical; Paiva, PA, and Boa Viagem–Piedade, BV), the coefficient estimate (Est.), standard errors (s.e.) and *z*-statistics of the intercept and of the categorical variable, the effective (E. d.f.) and reference degrees of freedom (Ref. d.f.) and χ^2-statistics of the continuous variables, and the corresponding *P*-values

Model	Variable	Est.	s.e.	*z*-value	E. d.f.	Ref. d.f.	χ^2	*P*
Month + Year + Site	Intercept	−4.39	0.11	−39.40				<0.001
	Month				2.91	2.99	77.52	<0.001
	Year				2.98	3.00	101.94	<0.001
	(Site) PA	−0.65	0.13	−4.84				<0.001

seasonality in bull shark occurrence, because they were larger, on average, than were tiger sharks. In addition, a higher proportion (43.3%) of shark-inflicted injuries resulted from SBE, which tended to be mostly non-fatal (Fig. 7). Incidents involving injuries to the torso (i.e. SBT and MBB) exhibited considerably higher fatality rates, whereas multiple bites exclusively to the torso were not observed. In relation to the activity of the victims, 52.5% were surfers and 47.5% were bathers. Surfers were exclusively injured on the body extremities, mostly as a result of single shark bites (71.8%). Only 12.5% of these incidents were fatal. In contrast, the fatality rate among bathers was 71.4%. This group was most prone to be injured by multiple shark bites (75.0%) to both the body extremities and torso (66.6%) or to the body extremities alone (33.4%). The monthly distribution of shark bites to surfers and bathers tended to follow similar trends (Fig. 6), with higher proportions of the incidents being recorded during the austral winter (56.2 and 64.3% respectively).

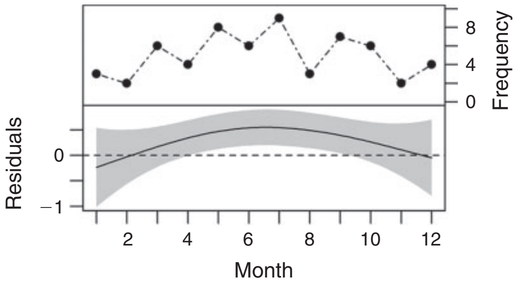

Fig. 5. Zero-inflated Poisson generalised additive model of the effect of month on the frequency of shark bites occurred off the metropolitan region of Recife. In the upper panel, solid points represent the absolute monthly frequency of shark bites. In the bottom panel, the horizontal dashed line and shaded area depict the null effect and 95% confidence intervals for the estimate respectively. (Effective degrees of freedom = 1.91; reference degrees of freedom = 2.39; χ^2-statistics = 3.45; $P = 0.002$).

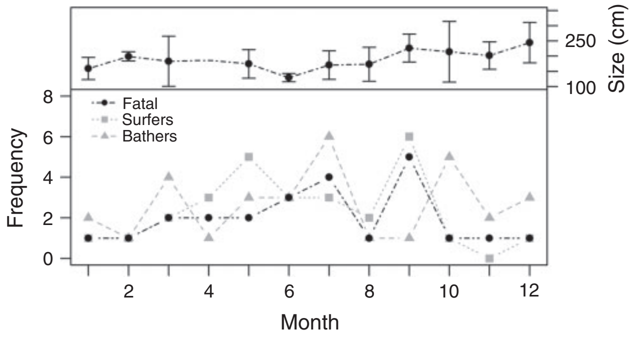

Fig. 6. Monthly aggregated frequencies of overall fatal shark bites and of total shark bites (i.e. both fatal and non-fatal) according to the activity of the victim at the moment of the incident, i.e. surfer or bather. In the upper panel, solid points represent the monthly mean length of potentially dangerous sharks and error bars depict the standard deviations of the mean.

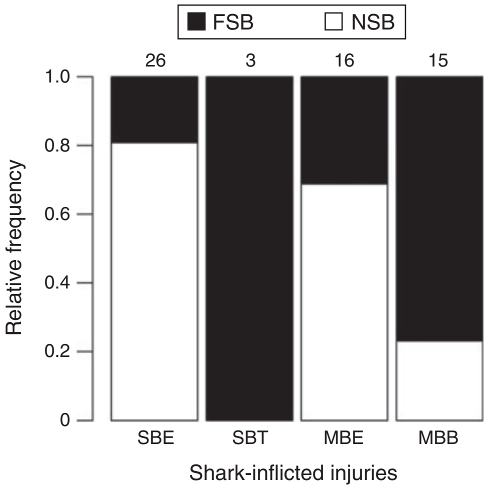

Fig. 7. Relative frequencies of fatal and non-fatal shark bites occurred off the metropolitan region of Recife from June 1992 to March 2015 in relation to the type of bite inflicted. MBB, multiple bites to both the body extremities and the torso; MBE, multiple bites to the body extremities; SBE, single bite to the body extremities; and SBT, single bite to the torso.

The ZIGAM of TSB included the variables month and state of SMPR as significant predictors (Tables 5, S5, available as Supplementary material to this paper). A significantly greater frequency of shark bites was predicted between April and September (Fig. 5) and also during the periods when the SMPR was inactive (Table 5). Concerning the effect of PDS abundance on the shark-bite rate, it was verified that the aggregated monthly frequencies of TSB were directly correlated with the mean monthly PDS abundance (Pearson $r = 0.57$; P-value = 0.008). Indeed, a GLM predicted a statistically significant approximately two-fold increment in the shark-bite rate when PDS CPUE shifts from 0.1 to 0.5 sharks per 1000 hooks (Fig. 8).

Discussion

The processes underlying shark hazard in coastal regions are usually obscured by the inability to identify which species were responsible for inflicting injuries to humans and how these species distribute along spatiotemporal gradients. However, the increasing utilisation of coastal areas by beach goers and water-sports practitioners warrants these processes to be understood, so that an effective mitigation of shark hazard can be achieved. The present study aimed to detect matching patterns between PDS CPUE and shark bites off Recife, Brazil, to examine the possible influence of shark abundance on the likelihood of shark-inflicted injuries. As the linkages between the anthropogenic and biological components of shark hazard become clear, more effective measures for shark-hazard mitigation will be available. Such an approach is also valuable to evaluate the adequacy of shark hazard-mitigation strategies based on the capture of potentially aggressive species. By comparing the patterns exhibited by the local distribution of shark-bite frequency and the abundance of PDS specimens captured within the scope of these programs, it can be inferred whether the species they catch correspond to the ones responsible for inflicting injuries to humans. Off the MRR, a substantial reduction in the shark-bite rate after the implementation of the SMPR in May 2004 resulted in only two shark bites being reported at the monitoring area, while the SMPR was operating (Hazin and Afonso 2014). This implies that the shark-bite and PDS sampling using the SMPR were, in general, mutually exclusive through time, explaining why it was possible to infer the relationship only between these two variables. In dealing with scenarios whose priority is mitigating shark hazard, the simultaneous collection of data on shark abundance and shark bites is widely unfeasible because this would generally require the suspension of the mitigation measures implemented. Even so, valuable information can be derived from this approach and incorporated into shark-hazard management, particularly if the shark bite and PDS abundance sampling procedures are consistent through a long time period, as was the case in the present study.

The SMPR captured eight potentially aggressive species including carcharhinids and sphyrnids, but the preliminary correlation-based procedure suggested that bull sharks and tiger sharks of $\geq$109 cm TL were most likely to be responsible for the shark bites off the MRR. Both these species may attain large sizes of $\geq$400 cm TL (McCord and Lamberth 2009; Holmes

Table 5. Zero-inflated Poisson generalised additive model of the shark-bite frequency

Included are the predictor variables month (continuous; 1–12) and state of the Shark Monitoring Program of Recife (SMPR) (categorical; active and inactive), the coefficient estimate (Est.), standard errors (s.e.) and *z*-statistics of the intercept and of the categorical variable, the effective (E. d.f.) and reference degrees of freedom (Ref. d.f.) and χ^2-statistics of the continuous variable, and the corresponding *P*-values

Model	Variable	Est.	s.e.	*z*-value	E. d.f.	Ref. d.f.	χ^2	*P*
Month + SMPR	Intercept	−1.53	0.26	−5.87				<0.001
	Month				1.73	2.17	4.56	0.007
	(SMPR) Inactive	2.79	0.72	3.87				<0.001

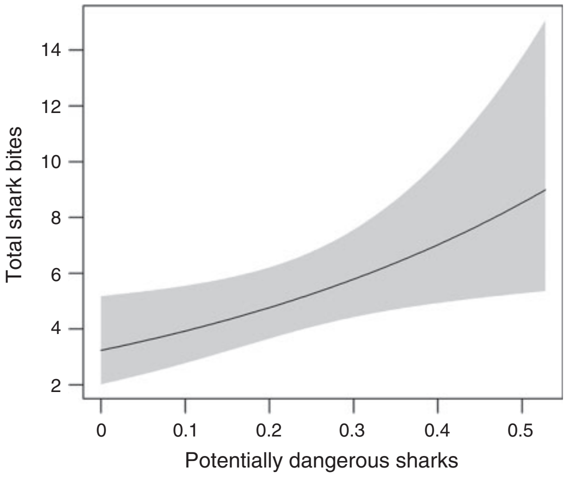

Fig. 8. Gaussian generalised linear model depicting the effect of the mean monthly abundance of potentially dangerous sharks, as the number of sharks caught per 1000 hooks, on the aggregated monthly frequency of total shark bites (i.e. both fatal and non-fatal incidents). The shaded area depicts 95% confidence interval for the estimate. (Estimate = 1.93; standard error = 0.81; *z*-statistic = 2.36; *P* = 0.018).

et al. 2012) and have previously been implicated in shark bites off the MRR (Gadig and Sazima 2003; Hazin *et al.* 2008) and elsewhere (https://www.flmnh.ufl.edu/fish/isaf/home/). Even though the 109-cm cut-off for potentially dangerous tiger sharks may seem low, Hazin *et al.* (2008) estimated the size of the sharks involved in some incidents to range between 1 and 3 m in total length, and there was at least one non-fatal incident in which the shark was described as being small. Therefore, the cut-off length proposed by the aforementioned procedure seems to be in accordance with previous estimates. There were four times as many potentially dangerous tiger sharks as there were bull sharks in the catch. Higher catches of tiger sharks compared with bull sharks have also been reported in other shark hazard-mitigation programs using drumline gear, with tiger-to-bull shark CPUE ratios equalling 34 : 1 off KwaZulu–Natal, South Africa (Cliff and Dudley 2011) and 6 : 1 off Queensland, Australia (Sumpton *et al.* 2011). The concurrent analysis of multispecies and species-specific PDS abundance patterns may thus provide valuable information on the spatiotemporal dynamics of shark hazard and on the contribution of the multiple biological components that regulate it. In scenarios involving multiple aggressor species, the likelihood of shark hazard at a particular site should be expressed by a composite probability density function that is regulated by the trends inherent to each of those species. However, the general inability to positively identify the aggressor species and its size usually precludes a direct biological interpretation of shark-bite episodes. By lumping all potentially dangerous sharks together, we aim at explicitly addressing the composite, multispecific response to the variables analysed, which can be most useful for shark-hazard management. Further, our method also scrutinised the species and lengths at which each species would be likely to become an active contributor to shark hazard, in an attempt to provide a potentially more realistic scenario of the biological component involved in the incidents off the MRR. Yet, and in spite of a substantial sampling effort (>500 000 hooks across ~10 years), a low number of PDSs were captured, which might be related to the fact that the fishing gear operated always in the same shallow, restricted area as part of a shark hazard-mitigation strategy, rather than operating in core habitats where shark abundance would be expectedly greater. An increased accuracy of the results obtained should, thus, be expected when considering larger sample sizes. Even though the robustness of this method may depend on the availability of sizeable datasets, it could endow researchers and managers with a simple, effective tool for examining some of the drivers underlying shark peril at persistently hazardous locations.

Seasonality in PDS abundance off the MRR suggests that the period from May to August, i.e. the austral winter, is the most hazardous. Such a trend coincides with the seasonality of shark bites, which tended to be most frequent between April and September. In agreement, July was the month with most shark bites and one of the greatest catch rates of both tiger and bull sharks. The frequency of beach use during the summer season seems to triple compared with the winter season in this region (Silva *et al.* 2008), thus beach-usage seasonality does not explain the seasonal variability in the shark-bite rate. Instead, seasonal environmental features could be shaping this pattern. For example, the increased estuarine discharge during the winter coupled with a decrease in water clarity due to increased siltation could respectively promote the attraction of PDSs to the hazardous area and the subsequent misidentification of humans as regular prey (Burgess 1990; Hazin *et al.* 2008). However, abundance seasonality of bull and tiger sharks differed, suggesting that the temporal distribution of shark hazard may be regulated by two distinct processes inherent to each of these species. PDS abundance seasonality was mostly shaped by the far more numerous tiger sharks. Although several pre-adult and adult tiger sharks were caught, this species makes extensive use of neritic habitats off north-eastern Brazil during the early juvenile phase (Afonso *et al.* 2014), exhibiting rapid growth, as great as ~100 cm year^{-1}, while young-of-the-year (Afonso *et al.* 2012). Because neonates measuring 90–100 cm TL occurred mostly from January through March (Afonso *et al.* 2014), they would likely have attained considerable sizes, >150 cm TL, at the end of their first year. Despite tiger sharks being particularly hazardous at sizes of ≥230 cm TL (Lowe *et al.* 1996), similarities between the seasonal trends in the shark-bite frequency and potentially dangerous tiger shark abundance suggest that this species might be responsible for a higher number of incidents than is the bull shark. Previous expectations that the bull shark could play a major role in the spate of shark bites off the MRR were based on six incidents that allowed for the species to be identified as a bull shark (Hazin *et al.* 2008), against only one incident positively ascribed to the tiger shark (Gadig and Sazima 2003). Yet, a large bull shark mean body size coupled with specific behavioural features, such as site-fidelity to some coastal habitats (Brunnschweiler *et al.* 2010; Carlson *et al.* 2010), require the hazard imposed by this species not to be neglected. Concerning spatial effects, a higher abundance of PDSs in BV was probably shaped by tiger sharks because bull sharks were as much likely to occur in PA as in BV. Nonetheless, such a trend in PDS spatial distribution is worrisome, given the high density of beach goers in BV. Site-specific features such as those related to the location of the Jaboatão Estuary and to an increased habitat complexity in BV shaped by a nearshore calcareous reef (Hazin and Afonso 2014) could perhaps explain the observed PDS spatial distribution.

In the present study, surfers had a considerably lower fatality rate than did bathers, because they were mostly bitten on the body extremities, which resulted in a reduced chance of death. Such a trend was expected because of the distinct position of a bather's and surfer's body to the water. However, no similarities between the monthly variability in the mean body length of PDSs and the monthly frequency of fatal shark bites could be detected to support the hypothesis that an increased shark size might lead to increased fatality rates; however, but this could be due to a relatively low number of fatal incidents in the data. Likewise, none of the species exhibited trends matching the seasonal distribution of shark bites to bathers and surfers, which could be indicative of a species-specific behavioural trait regulating the distribution of shark bites in relation to the activity of the victim. Interestingly, fatal incidents tended to be least common during the season in which bull shark abundance was higher, i.e. the austral summer. Yet, further research with larger sample sizes is required to statistically assess the possible existence of all these linkages. Features such as the activity of the victim (Gibbs and Warren 2015) and the body region bitten (Lentz *et al.* 2010), not to mention other important, uncontrolled factors such as the readiness and quality of medical assistance, might, nonetheless, play a more deterministic role in the outcome of shark bites off the MRR, rather than do shark species or size.

All the matching patterns between the dynamics in both PDS abundance and shark-bite frequency detected off the MRR, coupled with a substantial reduction of the shark-bite rate during periods in which the preventive strategy was operational (Hazin and Afonso 2014), seem to sustain the hypothesis that the SMPR was reasonably successful in capturing the species involved in the local spate of shark bites verified since 1992. A significant, positive correspondence between the shark-bite monthly frequency and PDS monthly CPUE indicated that the sharks sampled in the present study followed trends that were generally aligned with the seasonal dynamics in shark bites. Ascertaining whether the species being targeted by shark hazard-mitigation programs are the same as the ones responsible for the shark bites is necessary to evaluate the suitability of the mitigation strategies implemented and to sustain any positive results that such strategies may potentially exhibit regarding shark-hazard mitigation. Furthermore, this information might be also useful to improve the selectivity of the preventive fishing gear for the species of greatest concern, thus contributing to reduce potentially deleterious impacts on other species less likely to be involved in the incidents.

The method herein introduced may provide a useful framework for detecting linkages between shark abundance and shark-inflicted injuries in persistently hazardous regions, particularly if adequate amounts of sharks and shark bites have been sampled. Also, it enabled the proportionality between the likelihood of a shark bite and the abundance of potentially dangerous sharks to be examined for the first time, indisputably while assuming that beach usage is not altogether related to the likelihood of a shark bite off the MRR, as proposed by the frequencies in shark bite and beach usage (Silva *et al.* 2008) being seasonally out of phase. Although the results reported might be subject to quantitative variations if a larger sample size were used, they, nonetheless, support the hypothesis that the likelihood of a shark bite occurring off the MRR is directly proportional to the local abundance of potentially dangerous sharks. However, although such a relation could be present off the MRR, it should not, by any means, be expected that shark abundance and shark hazard would be necessarily linked in every other region or circumstance. On the contrary, there are numerous locations where potentially aggressive species are acknowledged to be far more abundant than they are off the MRR and where virtually no incidents have been recorded. Ultimately, site-specific features might be more important in shaping the geographic distribution of shark-hazard scenarios rather than is shark abundance itself. Despite this, the information derived from the present study may be potentially useful to assist local managers and stakeholders with shark-hazard mitigation. The SMPR has been discontinued due to funding constraints, thus compromising the mitigation efforts in a long-term perspective, and the local abundance of all potentially dangerous sharks combined appears also to have increased in recent years. Should this trend persist, a rise in the local shark-bite rate might be expected if adequate preventive measures are not put in place. In addition to shark hazard-mitigation programs, continued research on the spatial and behavioural ecology of potentially aggressive species in conjugation with efficient public outreach platforms may be indispensable to provide ocean users with essential information that could allow them to adapt their practices so as to reduce their own personal risk.

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