Vol. 631: 165–179, 2019
https://doi.org/10.3354/meps13138

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published November 21

Environmental predictive models for shark attacks in Australian waters

Laura A. Ryan[1,*], Samantha K. Lynch[1,*], Robert Harcourt[1], David J. Slip[1,2], Vic Peddemors[3], Jason D. Everett[4], Lisa-Marie Harrison[1], Nathan S. Hart[1,]**

[1]Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia
[2]Taronga Conservation Society Australia, Mosman, NSW 2088, Australia
[3]New South Wales Department of Primary Industries, Fisheries, Sydney Institute of Marine Science, Mosman, NSW 2088, Australia
[4]School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia

ABSTRACT: Shark attacks are rare but traumatic events that generate social and economic costs and often lead to calls for enhanced attack mitigation strategies that are detrimental to sharks and other wildlife. Improved understanding of the influence of environmental conditions on shark attack risk may help to inform shark management strategies. Here, we developed predictive models for the risk of attack by white *Carcharodon carcharias*, tiger *Galeocerdo cuvier*, and bull/whaler *Carcharhinus* spp. sharks in Australian waters based on location, sea surface temperature (SST), rainfall, and distance to river mouth. A generalised additive model analysis was performed using shark attack data and randomly generated pseudo-absence non-attack data. White shark attack risk was significantly higher in warmer SSTs, increased closer to a river mouth (<10 km), and peaked at a mean monthly rainfall of 100 mm. Whaler shark attack risk increased significantly within 1 km of a river mouth and peaked in the summer months. Tiger shark attack risk increased significantly with rainfall. We performed additional temporal and spatio-temporal analyses to test the hypothesis that SST anomaly (SST_{anom}) influences white shark attack risk, and found that attacks tend to occur at locations where there is a lower SST_{anom} (i.e. the water is relatively cooler) compared to surrounding areas. On the far north coast of eastern Australia — an attack hotspot — a strengthening of the East Australian Current may cause white sharks to move into cooler upwelling waters close to this stretch of the coast and increase the risk of an attack.

KEY WORDS: Shark attack · Attack risk · Pseudo-absence data · White shark · Tiger shark · Bull shark

1. INTRODUCTION

Worldwide, the number of shark attacks on humans has increased over the past 3 decades (West 2011, Curtis et al. 2012). This trend is also evident in Australia, where between 1990 and 2000 there was an average of 6.5 bites yr^{-1}, but between 2000 and 2010 this had more than doubled to an average of 15 bites yr^{-1} (West 2011). One in every 8.5 incidents (12%) over the period 1990–2010 in Australia resulted in a fatality (West 2011).

Statistically, the risk of dying from a shark attack is very low; in Australia, many more people die each year from incidents with farm animals and dogs than with sharks, which kill about as many people as bee stings (National Coronial Information System 2011). Nevertheless, shark attacks are traumatic and emotive events that generate disproportionate media scrutiny, and in doing so create a level of fear that arguably does not reflect the actual risk. As a result, clusters of attacks in an area may have economic ramifications for the local community, for example

*These authors contributed equally to this work
**Corresponding author: nathan.hart@mq.edu.au

through loss of tourism income (Curtis et al. 2012), and can lead to calls for policy makers to implement more intensive attack mitigation strategies (Neff 2012, Gibbs & Warren 2015). Traditionally, such strategies have involved targeted culls of sharks or deployment of nets or baited drumlines to reduce the abundance of large, potentially dangerous sharks close to popular bathing beaches (Dudley 1997, Curtis et al. 2012). However, these methods are relatively indiscriminate, killing not only target shark species, but also non-target and harmless species, including protected and/or endangered sharks, sea turtles, and marine mammals (Cliff & Dudley 2011, Reid et al. 2011, Sumpton et al. 2011). Moreover, the effectiveness of such large-scale shark control programs in reducing the likelihood of shark attacks is still strongly debated (Wetherbee et al. 1994, Dudley 1997).

Australia records one of the highest annual incidences of shark attack in the world and most attack-related fatalities are attributed to just 3 species: white sharks *Carcharodon carcharias*, tiger sharks *Galeocerdo cuvier*, and bull sharks *Carcharhinus leucas* (West 2011). The rise in shark attacks in Australia and elsewhere over recent years has been attributed to the growth in human population and participation in ocean-based recreational activities such as surfing and SCUBA diving, especially in more isolated coastal areas where shark-control measures are not deployed (West 2011). However, these factors alone cannot explain the more than doubling of attacks per capita since the 1990s (Curtis et al. 2012), and so other biotic and abiotic factors have also been implicated, including habitat degradation, weather patterns, and the distribution/abundance of prey (Chapman & McPhee 2016). As shark attacks on humans are relatively rare events (Ferretti et al. 2015), the lack of attack data complicates analysis of the related circumstances that might have explanatory and predictive value.

A shark attack may be classified as provoked — where the victim has attempted to approach, hurt, catch, or otherwise handle a shark or was engaged in activities known to attract sharks, e.g. spear-fishing; or unprovoked — where the victim has had no deliberate interaction with the shark, or even knowledge of its presence, prior to the attack (Schultz 1963). The proximate causes of these unprovoked attacks are likely varied and may include defensive or offensive territorial aggression (Johnson & Nelson 1973), curiosity/exploratory behaviour (Hammerschlag et al. 2012), or the shark mistaking a human and/or any equipment they might be using for potential prey (Tricas & McCosker 1984, McCosker & Lea 2006).

In addressing patterns of shark attacks on humans, it may be instructive to look at how environmental factors influence shark foraging behaviour. For example, the frequency and success of white shark predation on pinnipeds is known to be affected by swell height and upwelling events (Pyle et al. 1996), time of year, water depth, tide height, wind direction (Klimley et al. 1992, Hammerschlag et al. 2006, Brown et al. 2010), and lunar phase (Fallows et al. 2016). White sharks also change their angle of approach to an artificial prey item at the surface depending on the position of the sun such that they keep the sun behind them (Huveneers et al. 2015). This apparent relationship between diverse environmental factors and predation behaviour suggests that shark attacks on humans may be similarly linked. For example, the frequency of shark attacks on surfers has been linked to lunar phase, presumably in relation to its effect on tide height/swell (Hazin et al. 2008).

Attempts have been made previously to correlate attacks with patterns of human behaviour and/or environmental parameters. The earliest attempts found weak relationships between a number of environmental factors, most noticeably water temperature, and the likelihood of shark attack, but that correlation was explained by the number of people in the water (Baldridge 1974). The increased popularity of water sports, such as surfing, along with the increased human population, has been suggested as the reason for the steady increase in the number of shark attacks over recent years (Wetherbee et al. 1994, West 2011, Curtis et al. 2012). However, there was a decline in white shark attacks in Australia from 1876–1992, a time of continually increasing human population. This may have been the result of a declining white shark population (West 1996). In Australia, an increase in white shark attacks has only occurred over the last 3 decades (West 2011, Chapman & McPhee 2016). Although Reid et al. (2011) and Lee et al. (2018) reported a slight increase in catch rate for this species in the New South Wales (NSW) Shark Meshing Program over the last 20 yr, recent genetic research suggests that the white shark population over this period has not increased substantially (Hillary et al. 2018). This suggests that the changing trends in shark attacks may be due, at least in part, to other factors such as environmental cues, anomalous environmental conditions (e.g. unusually warm or cool sea surface temperatures [SSTs]), a reduction in prey availability, and/or potential changes in the distribution of sharks (Wetherbee et al. 1994, McCosker & Lea 2006).

More recent understanding of shark movements and populations suggests that shark attacks may not be purely random events, but are more likely to occur under specific conditions (Chapman & McPhee 2016). The movements of sharks can be influenced by their environment, which suggests a level of predictability regarding their movement and presence (Heupel et al. 2015, Espinoza et al. 2016, Lee et al. 2018). Geographical location, such as proximity to river mouths (Pillans & Franklin 2004), or specific environmental conditions, such as clear waters that are less than 20°C (Burgess & Callahan 1996), or time of year (West 2011) might increase the risk of shark attack. However, the relationship between environmental factors and the likelihood of a shark attack remain poorly understood.

In recent years, concerns about the environmental impacts of shark nets and drum lines have led to the development of alternative, non-lethal shark-attack mitigation strategies, including aerial surveillance by helicopters or drones, smart drumlines, eco-barriers, and a range of personal shark deterrent technologies (Gibbs & Warren 2015, Hart & Collin 2015). However, the ability to assess relative shark attack risk is lacking. An evidence-based risk assessment would complement a suite of other educational programs and allow the public to make more informed decisions before entering the ocean, as well as improving the effectiveness of shark management strategies by concentrating efforts and resources to where and when they might reduce the risk of attack (Gibbs & Warren 2015, Chapman & McPhee 2016). In this study, we evaluated how environmental conditions influence the likelihood of attacks by white, tiger, and whaler (including bull) sharks in Australian waters. We used this to generate predictive models of attack risk based on a retrospective analysis of the circumstances of shark attacks recorded from 1915–2015. We also investigated the influence of SST anomaly (SST_{anom}) on white shark attacks using separate temporal and spatio-temporal analyses, to provide insights into the occurrence of attack 'clusters' that sometimes occur in Australia, particularly along the far north coast of NSW.

2. MATERIALS AND METHODS

2.1. Theoretical approach

Species distribution models are often used in ecology and conservation management as tools to identify key habitat and to describe the niche environmental requirements of a species. This modelling approach has been used to predict distribution patterns of sharks, and to determine the probability of shark presence based on environmental conditions (Dicken & Booth 2013, Sequeira et al. 2014). For this type of distribution modelling, the spatio-temporal occurrence or 'presence' of a species has been recorded, but there are often no corresponding 'absence' data where the species was not found; consequently, these are known as 'presence-only' data sets (Elith et al. 2006, Barbet-Massin et al. 2012). Shark attack data are also considered a presence-only data set because while attacks are typically well documented there are no comparable absence data for circumstances where a shark and a human were present simultaneously at a time and/or location when an attack did not occur. Therefore, absences are not true absences. One approach for analysing a presence-only data set is to use randomly generated pseudo-absences or 'background data points' (Elith et al. 2006, Chefaoui & Lobo 2008, Barbet-Massin et al. 2012).

The most common practice for predictive modelling is to use generalised additive models (GAMs), an appropriate model choice when working with binary data such as presence/absence data (Venables & Dichmont 2004, Barbet-Massin et al. 2012). GAMs accommodate assumptions such as non-normal data and non-heterogeneity by fitting a range of distributional types (Venables & Dichmont 2004), such as those likely to exist between something as complex as shark behaviour and environmental variables. Smoothing functions defined by the data are used to fit non-linear functions (Elith et al. 2006, Chefaoui & Lobo 2008). This is the approach we use in the present study.

2.2. Shark attack data

We obtained shark attack presence-only data from the Australian Shark Attack File (ASAF), which is curated by the Taronga Conservation Society Australia and is affiliated with the International Shark Attack File (West 2011). We restricted the analysis to shark species that have caused the most fatalities: white sharks, tiger sharks, and whaler sharks, but included both fatal and non-fatal attacks by these species between 1915 and 2015 that were within the Australian Exclusive Economic Zone (Fig. 1). Given the circumstances of an attack, shark identification can be problematic and often the identification of the species responsible in the ASAF is inferred or generic (West 2011). For example, attacks have often been attributed to 'whaler' sharks as not all attacks thought to be made by bull sharks (which are usually

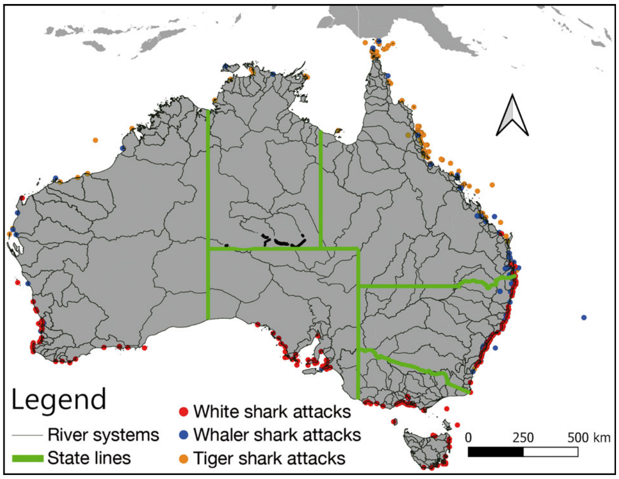


Fig. 1. Spatial distribution of shark attacks by white, tiger, and whaler sharks in Australian waters between 1915 and 2015. Spatial patterns in attack distribution for the different species reflect their natural distribution

responsible) were definitively identified as such, and might have been made by similar carcharhinids, such as dusky *Carcharhinus obscurus*, bronze whaler *C. brachyurus*, or pigeye *C. amboinensis* sharks. Moreover, whaler shark attacks are combined because in early ASAF records these sharks were not identified to species level and were combined in the 'whaler shark' category of the database. Accordingly, we categorised all attacks originally attributed in the ASAF to either bull sharks or 'whalers' as whaler shark attacks. Any other attacks where the species was unknown were excluded from the analysis. We did not separate attacks based on the activity of the victim.

To compare against the presence–attack data for each species, we generated twice the number of pseudo-absence–non-attack data points (Chefaoui & Lobo 2008, Barbet-Massin et al. 2012). For each species, we restricted the pseudo-absence data to the typical distribution of the species by limiting the latitude to ±1° (approximately 111 km) of where an attack occurred. As most shark attacks occur close to shore, we reduced bias by ensuring that the pseudo-absence data had the same statistical distribution in terms of distance from shore as the attack data (mean ± SD: white sharks, attack: 1.3 ± 3.9 km, pseudo-absence: 1.5 ± 1.7 km; whaler sharks, attack: 2.8 ± 4.4 km, pseudo-absence: 3.7 ± 5.3 km; tiger sharks, attack: 3.6 ± 10.5, pseudo-absence: 3.2 ± 4.2 km). The pseudo-absence data also had the same statistical distribution in terms of the proportion of attacks per year, to account for changes in human population, ocean usage, or other factors that may have influenced changes in attack frequency over time (Phillips et al. 2009). To account for population location biases, we also performed models using population statistics from major cities and centres (Australian Bureau of Statistics 2016). However, comparison of models showed that latitude and longitude already take population location biases into account and so population metrics were not used in the final models.

2.3. Environmental variables

Environmental data for both attack and pseudo-absence points were (1) the distance of the attack location from the nearest river mouth ($River_{dist}$, in km) calculated as a straight line. River mouth coordinates were based on the Geoscience Australia base layer using ArcGIS version 10.2 (Environmental Systems Research Institute 2014); (2) HadISST 1.1 SST (°C; 1° latitude and longitude, spatial resolution) (Rayner et al. 2003), as monthly SST, long-term mean monthly SST (SST_{mean}; 1915–2015), monthly SST_{anom} (i.e. monthly SST $-SST_{mean}$), and (3) rainfall, measured at the closest weather station (Bureau of Meteorology 2016) as monthly rainfall (Rainfall, in mm), long-term mean monthly rainfall ($Rainfall_{mean}$), and monthly rainfall anomaly ($Rainfall_{anom}$).

2.4. Generating explanatory/predictive models

To identify environmental factors affecting the likelihood of a shark attack and predict the probability of a shark attack occurring under certain conditions, we fitted a series of GAMs to the presence (attack) and pseudo-absence (non-attack) data using 'mgcv' package (Wood 2006) in R v.3.1.3 (R Core Team 2018; RStudio v.1.1.143). To fit the models, we randomly selected 80% of the presence data and used these along with approximately twice that amount of randomly generated pseudo-absence data (see above).

We fitted the binominal GAMs to attacks by each individual species (white, tiger, and whaler sharks) for the period 1915–2015 with month treated as a continuous variable and smoothed with a cyclic cubic regression spline and $River_{dist}$ $\log_{10}$ transformed. To account for location, we smoothed for the interaction between latitude and longitude. Terms were smoothed using the restricted maximum likelihood (REML) method. To avoid over-fitting in the modelling process, co-variates were retained in the model if they (1) were significant ($p < 0.05$); (2) increased the deviance explained; and (3) lowered the Akaike information criterion (AIC) (Chefaoui & Lobo 2008, Zuur et al. 2009). For the final model, *Q–Q* plots and residual histograms were used to inspect residuals and variance to ensure that model assumptions were not violated.

2.5. Model evaluation

We assessed the predictive performance of the model for each species through cross-validation (Hijmans 2012) on the remaining 20% of the attack data and the same amount (i.e. an approximately 1:1 ratio) of pseudo-absence (non-attack) data. Each model was assessed by predicting the probability of an attack on the cross-validation data (predicted values closer to 1 represent a high probability of an attack and values closer to 0 as a low probability). We assessed predictions in 2 ways. Firstly, we compared the mean predicted value between the attack data and pseudo-absence data from the cross-validation data set. Secondly, using the function 'evaluate' in the R package 'dismo' (v.1.0-15) (Hijmans & Elith 2013), we calculated the model's area under the receiver-operating curve (AUC) for the cross-validation data set (Hijmans 2012). The AUC has been used extensively in presence and absence modelling to evaluate the ability of a model to correctly predict true positives and false positive predictions (Elith et al. 2006), i.e. predicting an attack when an attack actually happened or incorrectly predicting an attack when an attack did not occur. An AUC score of 0.5 from a possible range of 0–1 indicates a prediction as good as random chance, whereas an AUC score >0.75 is considered to have good predictive power (Elith et al. 2006).

2.6. Investigation of the role of SST_{anom} in attacks by white sharks

The effect of SST in the white shark model did not appear to reflect the known distribution of white sharks, which tend to inhabit relatively cooler waters. Because SST is highly dependent on location (especially latitude) and varies seasonally, we also explored the monthly SST_{anom} on shark attacks independent of spatial and temporal variation, as follows.

To determine whether the monthly SST_{anom} on an attack day was consistent or abnormal for the attack location, we compared the monthly SST_{anom} at each white shark attack location in the month of the attack with the monthly SST_{anom} recorded in the same month both the year before and the year after the attack, using the mixed model package 'lme4' (v.1.1-10), and compared model terms using ANOVA (chi-squared test) in R (Bates et al. 2015). The attack ID was set as a random factor, and we assessed the differences between monthly SST_{anom} in the year before, the year after, and the attack year through a multiple comparison using the R package 'multcomp' (v.1.4-1) (Hothorn et al. 2008). Standardising month and location in this way reduced the effect of seasonal and/or spatial variation in SST on the comparison.

As 16% of all white shark attacks in Australia between 1915 and 2015 occurred along the far north coast of NSW, we selected this region (latitude ~28.00°–28.99° S) for a spatio-temporal comparison of SST_{anom}. We compared the monthly SST_{anom} for each attack location in the month of the attack to the monthly SST_{anom} (1) 111 km (+1° latitude) north of the attack location, (2) 111 km south (–1° latitude) of the attack location, (3) same month and location as the attack, but the year before, and (4) same month and location as the attack, but the year after. Comparisons were made using linear-mixed effects models, as described above.

3. RESULTS

3.1. Shark attack trends in Australian waters

Over the 101 yr period from 1915–2015 there were 835 shark bites in Australian waters, attributed to 12 different shark species. One in every 4 of these attacks were fatal. Three species of shark were responsible for those fatal attacks: white sharks, tiger sharks, and bull/whaler sharks. Of the 835 bites, 630 (75%) were attributed to the same 3 species, and after curation of the ASAF data, 531 of these were retained for further analysis, with 237 caused by white sharks, 160 by tiger sharks and 134 by bull/whaler sharks.

3.2. Environmental predictive models for shark attacks

Over the 101 year period from 1915–2015, the final white shark model explained 40.8% of the deviance. The risk of attack by a white shark increased close to river mouths within 10 km, peaked at a $Rainfall_{mean}$ of ~100 mm, increased with SST, and was greater at lower latitudes. White shark attack sites exhibited noticeable 'hot spots' along the south west coast of Western Australia and the far north coast of NSW, with fewer occurrences in the Great Australian Bight (Table 1, Fig. 2).

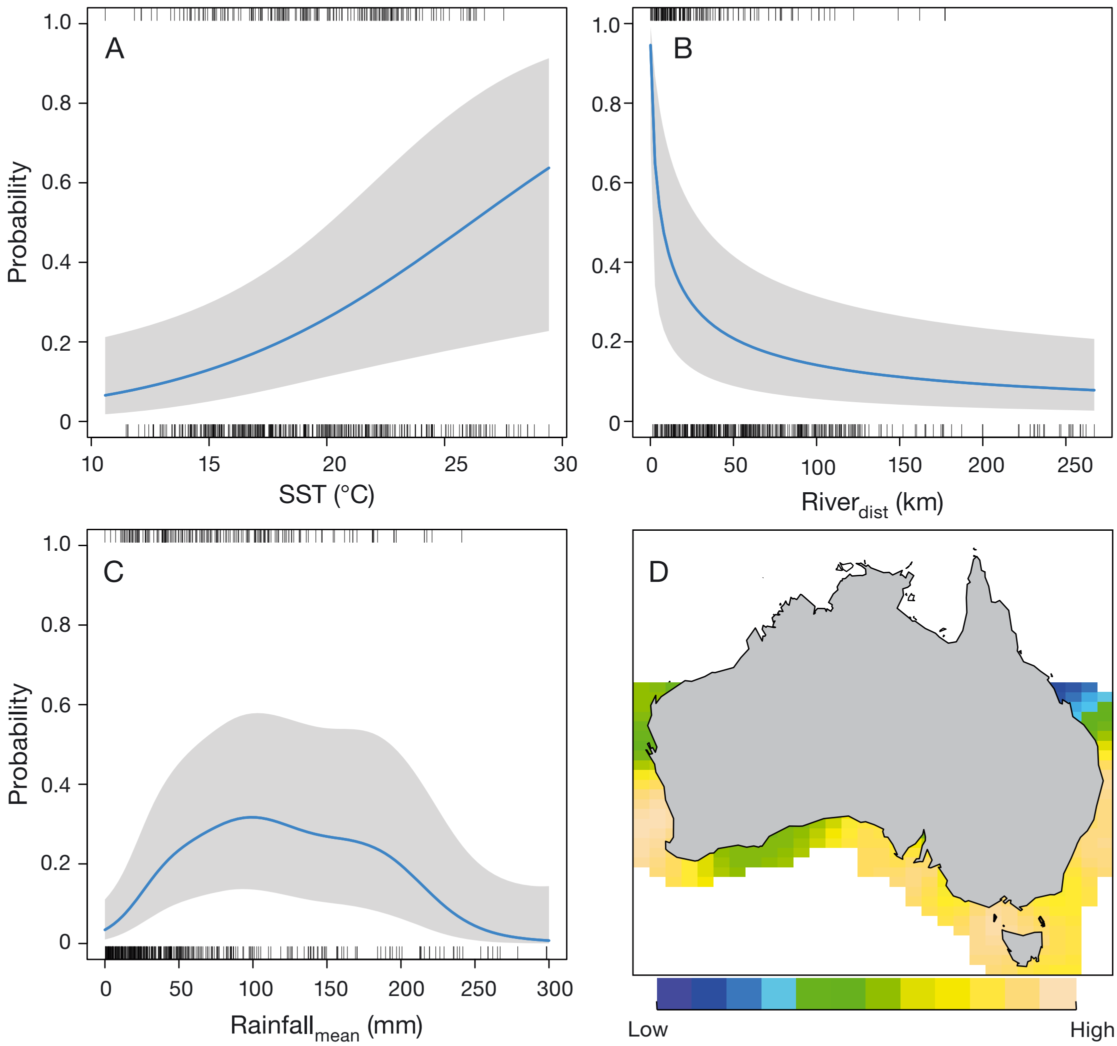


Fig. 2. (A–C) Covariate smoothing relationships for generalised additive models (GAMs) of white shark attacks and (A) sea surface temperature (SST), (B) attack distance from the nearest river mouth (River$_{dist}$), and (C) mean monthly rainfall (Rainfall$_{mean}$). Solid blue lines: GAM estimates; shaded areas: 95% CI. Markers along the lower and upper *x*-axes: distribution of pseudo-absence data and attack data, respectively. (D) Relative attack risk based on geographic location for the mean (±SD) attack SST (19.7 ± 3.6°C), River$_{dist}$ (31.9 ± 36.4 km) and Rainfall$_{mean}$ (82.1 ± 56.1 mm)

The whaler shark model explained 62.6% of the deviance in the data and showed that whaler attacks were more likely within 1 km of rivers and in summer months. Attacks by whaler sharks were more likely to occur at higher latitudes along the north of Western Australia and east coast of Queensland, with few occurrences in the Gulf of Carpentaria. (Table 1, Fig. 3).

The GAM model for tiger sharks explained 57.2% of the deviance. Tiger shark attacks increased with Rainfall$_{mean}$. Attacks by tiger sharks had the highest occurrence in the northern parts of Australia, close to tropical reef locations, as well as around Sydney, NSW (Table 1, Fig. 4).

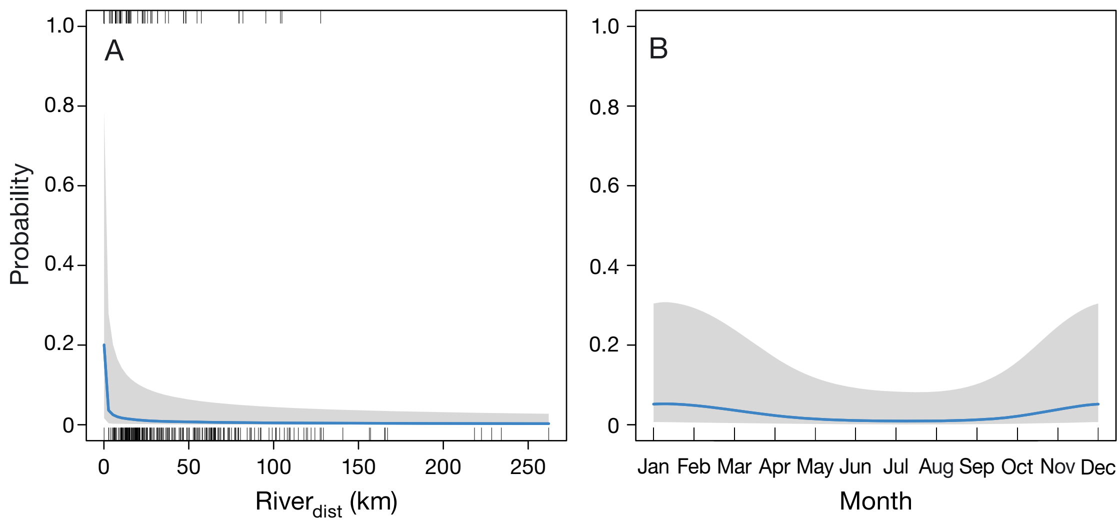
3.3. Attack risk model evaluation

The ability of the models to predict attacks based on the cross-validation data was assessed based on AUC values and the mean predicted values (between 0 = no attack, and 1 = attack) (Table 1). The ability of the white shark model to predict an attack was considered 'excellent' based on AUC values of 0.89 (Table 1). The mean (±SD) prediction for attacks was 0.63 ± 0.24 and non-attack pseudo-absence points as 0.22 ± 0.22. Only 1 of the 47 cross-validation attack data points was rated below 0.1, i.e. <10% chance of an attack occurring.

The whaler shark model also had an 'excellent' predictive power, with an AUC of 0.95. The mean

Table 1. Generalised additive model analysis for attacks by dangerous sharks (white sharks, whaler sharks, and tiger sharks). Significant environmental co-variates are given for the final model, along with the number (Fit model N) of attack data and randomly generated pseudo-absence data points (in parentheses) used to fit the models. The chi-squared statistics and estimated degrees of freedom (edf) of the models are shown, along with p-values. For the intercept, the *z*- and p-values are presented. (*) indicates significance ($p < 0.05$). The number (Predictive model N) of attack and pseudo-absence (in parentheses) data points used to make predictions using the final models is shown, along with the mean area under the receiver-operating curve (AUC) statistic, mean predicted attack probability for attack, and pseudo-absence data (in parentheses). SST: mean monthly sea surface temperature; $River_{dist}$: attack distance from the nearest river mouth; $Rainfall_{mean}$: long-term mean monthly rainfall

Model	Fit model N	Model co-variates	χ^2 (edf)	p-value	Predictive model N	AUC	Attack probability
White sharks	190 (380)	Intercept	−7.75	<0.001*	47 (47)	0.89	0.63 (0.22)
		s(Lon, Lat)	58.57 (18.1)	<0.001*			
		s(SST)	6.83 (1.00)	0.008*			
		$Log_{10}(River_{dist})$	20.69 (1.00)	<0.001*			
		$s(Rainfall_{mean})$	33.78 (5.53)	<0.001*			
Whaler sharks	107 (214)	Intercept	−5.05	<0.001*	27 (27)	0.95	0.77 (0.15)
		s(Lon, Lat)	60.41 (8.79)	<0.001*			
		$Log_{10}(River_{dist})$	15.78 (1.91)	0.001*			
		s(Month)	9.95 (2.24)	0.004*			
Tiger sharks	128 (256)	Intercept	−2.79	0.005*	32 (32)	0.86	0.64 (0.16)
		s(Lon, Lat)	92.86 (16.84)	<0.001*			
		$s(Rainfall_{mean})$	8.77 (1.00)	0.003*			



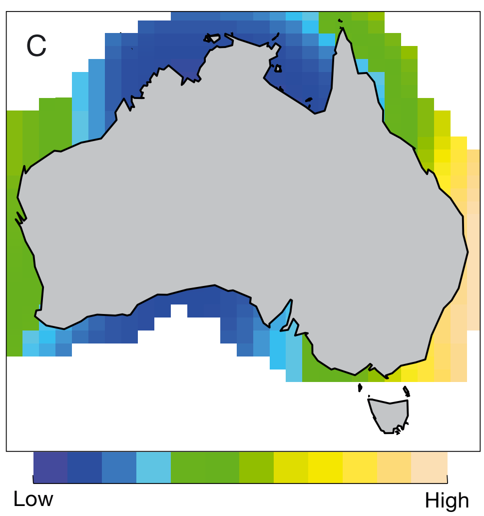


Fig. 3. Covariate smoothing relationships for generalised additive models of whaler shark attacks and (A) river distance and (B) month. See Fig. 2 legend for further information. (C) Relative attack risk based on geographical location for the mean (±SD) attack distance from the nearest river mouth ($River_{dist}$) (15.8 ± 25.7 km) and the month of February

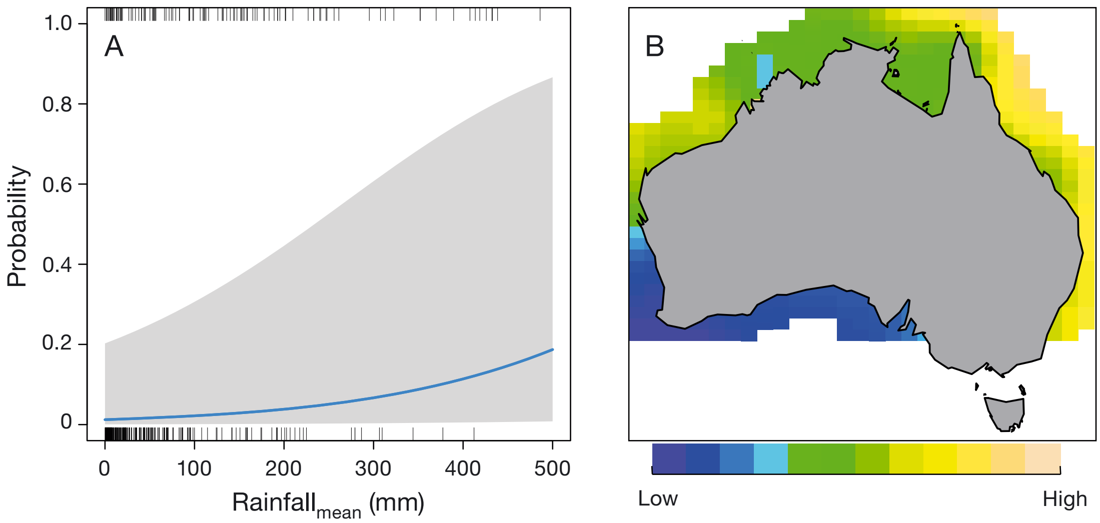


Fig. 4. (A) Covariate smoothing relationships for generalised additive models of tiger shark attacks and mean monthly rainfall. See Fig. 2 legend for further information. (B) Relative attack risk based on geographic location and long-term mean monthly rainfall (136.2 ± 127.2 mm)

predicted value of attacks was 0.77 ± 0.26 and non-attack pseudo-absence points was 0.15 ± 0.22. None of the 27 (~4%) cross-validation attack data points were rated below 0.1.

The tiger shark model had an AUC of 0.86, which is considered 'good' predictive power. The mean predicted value of attacks was 0.64 ± 0.33 and non-attack pseudo-absence points as 0.16 ± 0.20. However, 4 of the 32 (~16%) cross-validation attack data points were rated below 0.1 and substantially underestimated attack risk.

3.4. White shark attacks and SST$_{anom}$

3.4.1. Temporal analysis of SST$_{anom}$

White shark attacks across all locations occurred at a significantly lower SST$_{anom}$ (mixed model; mean = +0.33 ± 0.55°C; $\chi^2 = 10.5$, df = 2, $p = 0.005$) compared to the SST$_{anom}$ at the same location in both the year before (+0.49 ± 0.56°C) and the year after (+0.49 ± 0.57°C). There was no difference in the SST$_{anom}$ between the year before and the year after an attack (Table 2). This suggests that white shark attacks occurred in areas where the ocean was relatively cooler than average.

Table 2. Multiple comparisons of the sea surface temperature anomalies for all white shark attack locations between the attack year, the year before the attack and the year after the attack. (*) indicates significance ($p < 0.05$)

Comparison	*z*-value	p-value
Year before = attack year	2.83	0.005*
Year after = attack year	2.81	0.005*
Year after = year before	−0.023	0.98

3.4.2. Spatio-temporal analysis of SST$_{anom}$ on the far north coast of NSW

The spatio-temporal analysis of white shark attacks on the far north coast showed a significant difference (mixed model; $\chi^2 = 18.54$, df = 4, $p < 0.001$) in the SST$_{anom}$ between the attack locations and surrounding waters at the time of the attack. Attacks were more likely to occur in areas that were unusually cool compared to surrounding areas, because a lower (i.e. less positive) SST$_{anom}$ occurred at the attack location (mean = +0.13 ± 0.43°C) compared to the SST$_{anom}$ 100 km north in waters around North Stradbroke Island, Queensland (+0.58 ± 0.75°C) or 100 km south in waters around Yamba, NSW (+0.53 ± 0.53°C) (Table 3). There was no significant difference in SST$_{anom}$ between the attack year, the year after, and year before an attack (Table 3). The mean SST$_{anom}$ the year before an attack was +0.28 ± 0.45°C and the year after an attack was +0.25 ± 0.38°C.

4. DISCUSSION

In this study, the relationship between selected environmental variables and the likelihood of a shark

Table 3. Multiple comparisons of the spatio-temporal sea surface temperature anomalies analysis for white shark attack locations on the far north coast of NSW between the attack location, and locations either 100 km to the north or 100 km to the south at the same time as the attack, and the same location as attacks either the year before or the year after an attack. (*) indicates significance ($p < 0.05$)

Comparison	z-value	p-value
Attack = north	3.63	<0.001*
Attack = south	3.22	0.001*
North = south	−0.41	0.68
Attack = year before	1.21	0.22
Attack = year after	−0.96	0.34
Year after = year before	0.26	0.80
North = year before	2.42	0.02*
North = year after	2.68	0.007*
South = year before	2.01	0.04*
South = year after	2.27	0.02*

attack in Australian waters was evaluated over a 101 yr period from 1915–2015. Results suggest that such relationships do exist, but that the environmental predictors differ depending on the species of shark responsible for the attack. Our analyses highlight locational differences in what species are most likely to be involved in an interaction with humans, which may assist coastal communities and beach authorities in using our predictive models to determine relative risk of a shark encounter off Australia. The general approach and predictive models generated through this analysis may form a useful framework for analysing shark attack trends in other geographic regions and be useful as management tools for predicting the relative risk of shark attack based on forecast climatic and oceanographic conditions.

4.1. White shark attacks

The risk of attack by a white shark increased closer to a river mouth (28% occurred within 10 km), peaked at a $\text{Rainfall}_{\text{mean}}$ of ~100 mm, increased with SST, and occurred within noticeable hot spots off the southwest of the continent and the far north coast of NSW. Attacks by white sharks may occur close to rivers as a result of prey abundance; reef habitat around river mouths and associated nearshore environments may provide white sharks with a high abundance of prey and successful foraging opportunities (Jewell et al. 2013, Harasti et al. 2017). Juvenile white sharks are known to enter estuarine environments; however, they tend to stay only for short periods of time (Harasti et al. 2017). Our results suggest that white shark attacks decrease away from river mouths, yet in a finer-scale study using catch rates of sharks in the NSW shark nets, Lee et al. (2018) found that white shark catches increased away from river mouths. Our study examined environmental variables over a larger area of Australia and we believe this difference in spatial sampling resolution is a likely reason for our apparently conflicting findings.

The effect of rainfall and river distance may be inter-related. Locations close to river mouths will be affected most following periods of high rainfall, which will increase nutrient runoff and primary and secondary production from rivers. This may increase the presence of prey and subsequently attract predators to the area, as has been suggested for white shark distribution in Algoa Bay, South Africa (Dicken & Booth 2013). However, the peak in attack risk at around 100 mm of rain suggests that other ecophysiological factors may also influence attack risk close to rivers. White sharks rely heavily on vision for predation (Strong 1996, Yopak & Lisney 2012) and utilise a 'stealth' approach to capture their prey (Martin et al. 2005, Huveneers et al. 2015). In general, sharks appear to have high visual contrast sensitivity (Ryan et al. 2016, 2017), which would aid prey detection in turbid waters where scatter of light by suspended particles degrades visual contrast, although in very turbid waters vision may be seriously impeded. In South Africa, higher catches of white sharks in bather protection nets were associated with lower rainfall but higher turbidity (Cliff et al. 1996), which may reflect difficulties for white sharks in detecting the nets. Conversely, hunting in very clear waters might be less successful as the prey may be better able to detect an approaching shark at a greater distance than in turbid water. The fact that the median river distance from attack sites was 19 km suggests that attacks are often outside of the main river run-off plumes and that white sharks may avoid extremely turbid water, whilst still taking advantage of potential spill-over of increased prey in relation to higher productivity surrounding river mouths. Thus, it seems possible that there is an optimal water turbidity range that is exploited by white sharks when foraging, and that the effect of rainfall on attack risk in Australia may relate to increased water turbidity — which often accompanies heavy rainfall — as well as prey abundance and geographic location.

SST had a significant effect on the probability of a white shark attack and likely reflects an increase in the number of people using the warmer water for recreational use. The increased attack risk with warmer SST does not reflect the physiological requirements or known distribution of white sharks (Carey et al. 1982, Goldman 1997). However, ocean recreation along the coast of Australia is highest during the warmer months (Surf Life Saving Australia 2011), and this coincides with an increased frequency of white shark attacks (West 2011). Thus, in order to better understand the effects of SST on white shark attacks, the regional analysis was necessary to remove spatio-temporal biases.

Our analysis of SST_{anom} comparing attack locations to (1) the pseudo-absence data; (2) the same location the year before and the year after the attack (temporal analysis); and (3) locations to the north or south of the attack (spatio-temporal analysis on the far north coast of NSW) supports the hypothesis that cooler inshore SSTs increase the incidence of attacks by white sharks. We show that attacks by white sharks in Australia occurred more frequently in locations that were cooler relative to surrounding waters and/or were cooler relative to other years, potentially due to the effects of mesoscale and frontal eddies that occur regularly around the coast of Australia (Everett et al. 2012, Schaeffer et al. 2017). This finding mirrors the pattern of white shark attacks on humans observed in the eastern North Pacific (McCosker & Lea 2006), white sharks caught in shark mitigation nets around NSW, Australia (Lee et al. 2018), as well as migration patterns (Jorgensen et al. 2010) and predation success on pinnipeds (Pyle et al. 1996, Jorgensen et al. 2010).

Moreover, the locations of white shark attack hot spots correspond to Australia's major boundary currents, i.e. the western boundary current or East Australian Current (EAC), the poleward moving current off the west coast (Leeuwin Current), and their eddy effects (Waite et al. 2007, Suthers et al. 2011). The east coast of Australia experiences warm outer shelf waters driven by strengthening of the EAC boundary currents, and cooler inshore SSTs caused by upwelling (Roughan & Middleton 2002). The strength and eddy-shedding time scale of the EAC (Archer et al. 2017) may be a possible environmental cue used by white sharks to move closer to shore, and the resultant compression of white sharks into a smaller inshore area may heighten the risk of an attack on a human (Fig. 5). Future studies should take into account the eddy shedding time scale of the EAC (Archer et al. 2017) to further confirm the results of the current

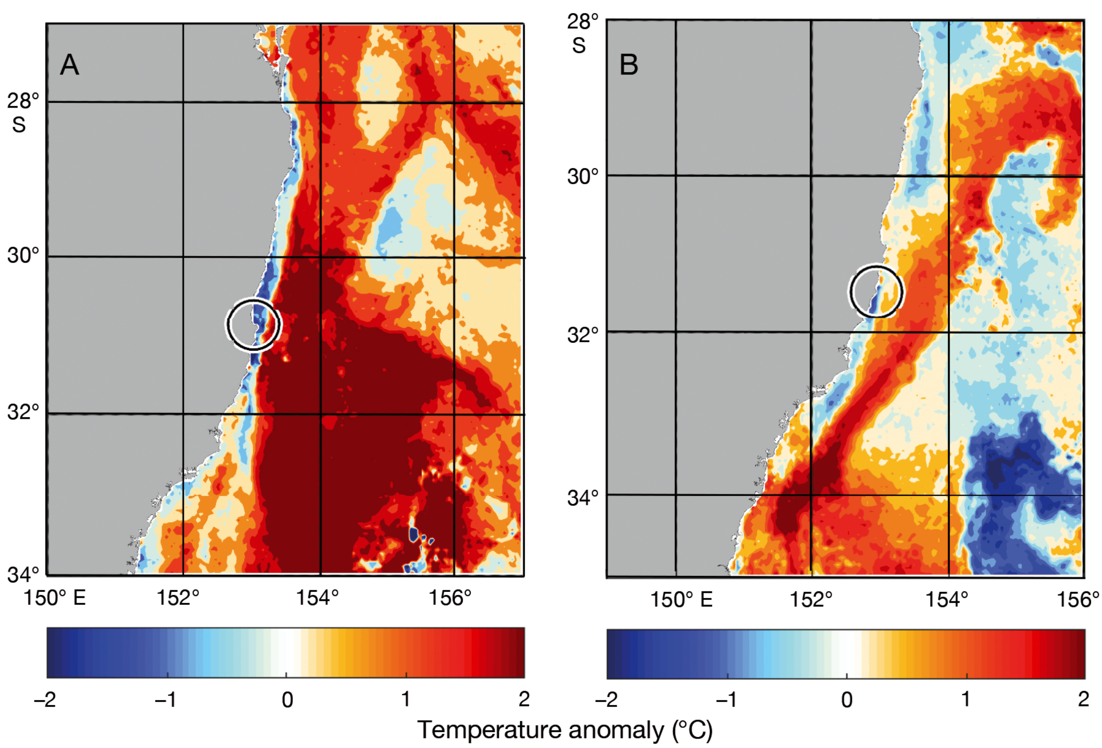


Fig. 5. Daily sea surface temperature anomaly maps generated (Kilpatrick et al. 2001) for the shark attacks that occurred in New South Wales on (A) 2 December 2012 and (B) 22 August 2015. Circle is centered on the attack location. These maps show a cooler pocket of water occurring along the coastline closer to shore at the attack location and the temperature difference compared to locations north, south, and offshore, suggesting that attacks are occurring when sharks are attracted into relatively cooler inshore locations

paper and potentially improve predictive capabilities of shark attacks off the east coast of Australia.

SST_{anom} and current boundaries in Australia are also affected year-to-year by the El Niño Southern Oscillation (ENSO), which generates either cooler (La Niña) or warmer (EL Niño) SSTs (Rasmusson & Carpenter 1982). Previous studies have found a correlation with El Niño events and shark attacks, with more shark attacks on humans occurring during periods of warmer oceanic waters characterised by an El Niño event (McCosker & Lea 2006, Burgess 2015, Chapman & McPhee 2016). World-wide, 2015 was one of the strongest El Niños recorded and was also the highest attack year on record (Burgess 2015). Australia also recorded the highest number of attacks in 2015, with white shark attacks occurring in waters with a 0.3°C lower SST_{anom} than attacks in the 10 yr prior (SST_{anom} 0.2 vs. 0.5°C, data not shown), suggesting that more attacks occur in areas that are cooler than the surrounding water. White shark catches increased in shark attack mitigation nets in NSW, Australia, during El Niño events but in waters with lower SST_{anom} (Lee et al. 2018). This supports the theory that during the warm currents of El Niño, white sharks seek cool upwelling waters close to the coast. However, ENSO affects coastlines around the world differently. For example, in 1974, California experienced one of its highest number of white shark attacks per year within a 'cold water' La Niña event. Similarly, fewer attacks occurred during the 1997–1998 El Niño oceanographic warming event (McCosker & Lea 2006). However, the influence of ENSO differs between the east coast of Australia and the California coast, which experiences reduced cold-water upwelling during El Niño (Philander 1983, Chavez et al. 2002).

4.2. Whaler shark attacks

Whaler shark attacks were found to increase closer to a river, with 47% of attacks occurring within 100 m of a river mouth. This coincides with the preferred habitat zone for bull sharks, i.e. coastal zones with high freshwater inflow (Carlson et al. 2010), as they can osmoregulate in both salt and fresh water (Pillans & Franklin 2004, Hammerschlag 2006). Acoustically tagged young bull sharks spend most of their time within 11 km of the river mouth (Heupel & Simpfendorfer 2008), and bull sharks breed and feed in nearshore coastal areas and rivers (Carlson et al. 2010, Werry et al. 2011). The pattern of Australian whaler shark attacks is consistent with that of whaler attacks internationally, in that most have been recorded near estuaries and river mouths (Chapman & McPhee 2016).

Attack risk by whalers is higher in summer months, which corresponds to the migration patterns seen in bull sharks. Large juvenile and adult bull sharks make lengthy migrations and, on the east coast of Australia, some individuals move south to the Sydney region in the warmer months (February–April) (Heupel et al. 2015, Espinoza et al. 2016). Month may also relate to temperature preferences, and the preference of bull sharks for warmer waters has been well documented (Reid et al. 2011, Heupel et al. 2015, Lee et al. 2019). These trends may also reflect whaler shark physiology because they are ectothermic, and staying within warmer waters may reduce the energy required to maintain body temperature (Carlson et al. 2004). The significance of month may also relate to rainfall, as monthly mean rainfall is highest in Australia in summer months (Bureau of Meteorology 2016). Rainfall has been identified as a major driver of the catch rate of bull sharks in nets in Queensland, Australia, probably due to the associated increased turbidity and/or movement of sharks from estuaries to nearshore environments (Werry et al. 2018). Similar to white sharks, high rainfall likely increases primary production and the abundance of prey on which bull sharks/whalers feed (Matich 2014, Werry et al. 2018).

4.3. Tiger shark attacks

Identified environmental predictors for tiger shark attacks indicated a strong influence of geographical location on the probability of attack by this species. Tiger shark attack risk increased further north and at reef locations. Tiger sharks occupy mainly tropical warm water environments around the world (Randall 1992). In Australian waters, they occur throughout tropical and subtropical waters and also enter temperate waters in summer (Stevens & McLoughlin 1991). Tiger shark attacks also occurred more often at higher mean monthly rainfall, which likely reflects both the geographical tropical locations and seasonal migration trends. More tiger sharks are caught on drum lines in Shark Bay, Western Australia, during warmer (wetter) months (September–May) than during cooler months (June–August) (Wirsing et al. 2006). Similarly, tiger shark catch in the Australian east coast shark bite mitigation programs, plus telemetry data, indicate they inhabit waters of ~22°C (Lee et al. 2018, Payne et al. 2018).

4.4. Modelling shark attack risk

This study was the first of its kind to predict the probability of a shark attack based on environmental conditions. However, the results must be interpreted with caution due to the small sample size, changes in human and shark populations, changing patterns of recreational ocean use over the study period, complexities of the models, and the particular environmental parameters used.

In order to maximise sample size, attack data going back as far as 1915 were analysed. However, because of the limited availability of environmental data over this entire period, SST data were restricted to monthly 1° grid samples. The mean monthly SSTs recorded at this scale limited the resolution of temperature for smaller bodies of water, e.g. areas of cooler water arising from upwelling events, and for shorter time scales. Future studies may be able to utilise SST data at a finer temporal and spatial resolution, e.g. daily/weekly records at 1 × 1 km grid, which are available from 1994 onwards.

Shark attacks where the species responsible has likely been misidentified or implied based on circumstantial evidence (e.g. a white shark recorded as a whaler) may have confounded the models. It has been reported that juvenile white shark attacks are often confused with bull shark attacks (Bruce 1992). Additionally, the whaler shark model potentially incorporates attacks by a range of whaler and other species, not necessarily just bull sharks, which may have affected the relationship with environmental conditions given their differing ecologies and life histories. Curating the data in the ASAF to remove records where species identification was uncertain reduced these types of errors in the modelling but may not have been perfect.

The ability of the fitted models to predict shark attacks were considered good–excellent based on the AUC (0.85–0.95). However, many of the models are based on predominantly seasonal and geographical factors which, although aligned to the sharks' biology and ecology, is likely to still result in a high number of false positives and limit the applicability of the present models as attack mitigation tools. For example, the model for tiger sharks would indicate a high probability of an attack on most summer days in tropical reef locations, yet such attacks are relatively rare. To further improve the accuracy and predictability of the model, future research could include other environmental or biotic factors, such as oceanographic processes, chlorophyll *a* levels, predator–prey interactions, energetic requirements in cooler waters, breeding periods, water turbidity, and salinity levels (Froeschke et al. 2010). Nevertheless, we suggest that the approach used here to understand the environmental drivers of shark attacks is a useful foundation on which to build more accurate models.

5. CONCLUSIONS

Complex relationships appear to exist between shark attacks and environmental conditions. Importantly, given some of the differing environmental predictors identified for the 3 species of shark investigated here, each species should be considered on its own rather than lumping all shark species together. Based on our models, public and private stakeholders could use the identified environmental predictors (location, rainfall, time of year, and especially SST_{anom}) to increase awareness of the relative risk of shark attack under current or predicted future conditions. For example, a 'higher risk day' warning system could be employed to allow water users to make more informed decisions before entering the water. Ultimately, we hope that ecological modelling approaches might be used to augment current shark attack mitigation strategies and further reduce the need for destructive population control-based shark attack mitigation methods.

Acknowledgements. This study was supported by ARC Linkage Grant (LP160100333). We acknowledge the numerous personnel who have investigated shark attacks in Australia over the years, especially Mr. John West, who established and curated the Australian Shark Attack File for the period under consideration in our study. We acknowledge the time and effort of the reviewers and appreciate their contributions and support.

LITERATURE CITED

Archer MR, Roughan M, Keating SR, Schaeffer A (2017) On the variability of the East Australian Current: jet structure, meandering, and influence on shelf circulation. J Geophys Res C Oceans 122:8464–8481

Australian Bureau of Statistics (2016) Australian historical population statistics 2016. https:www.abs.gov.au/AUSSTATS/abs@.nsf/DetailsPage/3105.0.65.0012016?OpenDocument

Baldridge HD (1974) Shark attack: a program of data reduction and analysis. Contributions from the Mote Marine Laboratory, Vol 1, No. 2. Mote Marine Laboratory, Sarasota, FL

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Selecting pseudo-absences for species distribution models: How, where and how many? Methods Ecol Evol 3:327–338

Bates DM, Mächler M, Bolker BM, Walker S (2015) Fitting linear mixed-effect models using lme4. J Stat Softw 67: 1–48
Brown AC, Lee DE, Bradley RW, Anderson S (2010) Dynamics of white shark predation on pinnipeds in California: effects of prey abundance. Copeia 2010:232–238
Bruce BD (1992) Preliminary observations on the biology of the white shark, *Carcharodon carcharias*, in south Australian waters. Mar Freshw Res 43:1–11
Bureau of Meteorology (2016) Average annual, seasonal and monthly rainfall. www.bom.gov.au/jsp/ncc/climate_averages/rainfall/index.jsp
Burgess GH (2015) Yearly worldwide shark attack summary. www.flmnh.ufl.edu/fish/isaf/worldwide-summary/
Burgess GH, Callahan M (1996) Worldwide patterns of white shark attacks on humans. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, CA, p 457–469
Carey FG, Kanwisher JW, Brazier O, Gabrielson G, Casey JG, Pratt HL Jr (1982) Temperature and activities of a white shark, *Carcharodon carcharias.* Copeia 1982:254–260
Carlson JK, Goldman KJ, Lowe CG (2004) Metabolism, energetic demand, and endothermy. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, FL, p 203–224
Carlson JK, Ribera MM, Conrath CL, Heupel MR, Burgess GH (2010) Habitat use and movement patterns of bull sharks *Carcharhinus leucas* determined using pop-up satellite archival tags. J Fish Biol 77:661–675
Chapman BK, McPhee D (2016) Global shark attack hotspots: identifying underlying factors behind increased unprovoked shark bite incidence. Ocean Coast Manage 133:72–84
Chavez FP, Pennington JT, Castro CG, Ryan JP and others (2002) Biological and chemical consequences of the 1997–1998 El Niño in central California waters. Prog Oceanogr 54:205–232
Chefaoui RM, Lobo JM (2008) Assessing the effects of pseudo-absences on predictive distribution model performance. Ecol Modell 210:478–486
Cliff G, Dudley SFJ (2011) Reducing the environmental impact of shark-control programs: a case study from KwaZulu-Natal, South Africa. Mar Freshw Res 62: 700–709
Cliff G, Dudley SFJ, Jury MR (1996) Catches of white sharks in KwaZulu-Natal, South Africa and environmental influences. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, CA, p 351–362
Curtis TH, Bruce BD, Cliff G, Dudley SF and others (2012) Responding to the risk of white shark attack: updated statistics prevention and recommendations. In: Domeier ML (ed) Global perspectives on the biology and life history of the white shark. CRC Press, Boca Raton, FL, p 477–510
Dicken M, Booth A (2013) Surveys of white sharks (*Carcharodon carcharias*) off bathing beaches in Algoa Bay, South Africa. Mar Freshw Res 64:530–539
Dudley S (1997) A comparison of the shark control programs of New South Wales and Queensland (Australia) and KwaZulu-Natal (South Africa). Ocean Coast Manage 34: 1–27
Elith J, Graham CH, Anderson RP, Dudík M and others (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151
Environmental Systems Research Institute (2014) ArcGIS version 10.2. Environmental Systems Research Institute, Redlands, CA
Espinoza M, Heupel MR, Tobin AJ, Simpfendorfer CA (2016) Evidence of partial migration in a large coastal predator: opportunistic foraging and reproduction as key drivers? PLOS ONE 11:e0147608
Everett JD, Baird ME, Oke PR, Suthers IM (2012) An avenue of eddies: quantifying the biophysical properties of mesoscale eddies in the Tasman Sea. Geophys Res Lett 39:L16608
Fallows C, Fallows M, Hammerschlag N (2016) Effects of lunar phase on predator-prey interactions between white shark (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*). Environ Biol Fishes 99: 805–812
Ferretti F, Jorgensen S, Chapple TK, De Leo G, Micheli F (2015) Reconciling predator conservation with public safety. Front Ecol Environ 13:412–417
Froeschke J, Stunz GW, Wildhaber ML (2010) Environmental influences on the occurrence of coastal sharks in estuarine waters. Mar Ecol Prog Ser 407:279–292
Gibbs L, Warren A (2015) Transforming shark hazard policy: learning from ocean-users and shark encounter in Western Australia. Mar Policy 58:116–124
Goldman KJ (1997) Regulation of body temperature in the white shark, *Carcharodon carcharias.* J Comp Physiol B 167:423–429
Hammerschlag N (2006) Osmoregulation in elasmobranchs: a review for fish biologists, behaviourists and ecologists. Mar Freshwat Behav Physiol 39:209–228
Hammerschlag N, Martin RA, Fallows C (2006) Effects of environmental conditions on predator–prey interactions between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*) at Seal Island, South Africa. Environ Biol Fishes 76:341–350
Hammerschlag N, Martin RA, Fallows C, Collier RS, Lawrence R (2012) Investigatory behavior toward surface objects and nonconsumptive strikes on seabirds by white sharks, *Carcharodon carcharias*, at Seal Island, South Africa (1997–2010). In: Domeier ML (ed) Global perspectives on the biology and life history of the white shark. CRC Press, Boca Raton, FL, p 91–103
Harasti D, Lee K, Bruce B, Gallen C, Bradford R (2017) Juvenile white sharks *Carcharodon carcharias* use estuarine environments in south-eastern Australia. Mar Biol 164:58
Hart NS, Collin SP (2015) Sharks senses and shark repellents. Integr Zool 10:38–64
Hazin FH, Burgess GH, Carvalho FC (2008) A shark attack outbreak off Recife, Pernambuco, Brazil: 1992–2006. Bull Mar Sci 82:199–212
Heupel MR, Simpfendorfer CA (2008) Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. Aquat Biol 1:277–289
Heupel MR, Simpfendorfer CA, Espinoza M, Smoothey AF, Tobin A, Peddemors V (2015) Conservation challenges of sharks with continental scale migrations. Front Mar Sci 2:12
Hijmans RJ (2012) Cross validation of species distribution models: removing spatial sorting bias and calibration with a null model. Ecology 93:679–688
Hijmans RJ, Elith J (2013) Species distribution modeling with R. R package 'dismo' version 1.0-15. https://rspatial.org/sdm/
Hillary RM, Bravington MV, Patterson TA, Grewe PR and

others (2018) Genetic relatedness reveals total population size of white sharks in eastern Australia and New Zealand. Sci Rep 8:2661

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biom J 50:346–363

Huveneers C, Holman D, Robbins R, Fox A, Endler JA, Taylor AH (2015) White sharks exploit the sun during predatory approaches. Am Nat 185:562–570

Jewell OJD, Johnson RL, Gennari E, Bester MN (2013) Fine scale movements and activity areas of white sharks (*Carcharodon carcharias*) in Mossel Bay, South Africa. Environ Biol Fishes 96:881–894

Johnson RH, Nelson DR (1973) Agonistic display in the gray reef shark, *Carcharhinus menisorrah*, and its relationship to attacks on man. Copeia 1973:76–84

Jorgensen SJ, Reeb CA, Chapple TK, Anderson S and others (2010) Philopatry and migration of Pacific white sharks. Proc R Soc B 277:679–688

Kilpatrick K, Podestá GP, Evans R (2001) Overview of the NOAA/NASA advanced very high resolution radiometer Pathfinder algorithm for sea surface temperature and associated matchup database. J Geophys Res C Oceans 106:9179–9197

Klimley AP, Anderson SD, Pyle P, Henderson RP (1992) Spatiotemporal patterns of white shark (*Carcharodon carcharias*) predation at the South Farallon Islands, California. Copeia 1992:680–690

Lee KA, Roughan M, Harcourt RG, Peddemors VM (2018) Environmental correlates of relative abundance of potentially dangerous sharks in nearshore areas, southeastern Australia. Mar Ecol Prog Ser 599:157–179

Lee KA, Smoothey AF, Harcourt RG, Roughan M, Butcher PA, Peddemors VM (2019) Environmental drivers of abundance and residency of a large migratory shark, *Carcharhinus leucas*, inshore of a dynamic western boundary current. Mar Ecol Prog Ser 622:121–137

Martin RA, Hammerschlag N, Collier RS, Fallows C (2005) Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. J Mar Biol Assoc UK 85:1121–1136

Matich P (2014) Environmental and individual factors shaping the habitat use and trophic interactions of juvenile bull sharks (*Carcharhinus leucas*) in a subtropical estuary. PhD dissertation, Florida International University, Miami, FL

McCosker JE, Lea RN (2006) White shark attacks upon humans in California and Oregon, 1993–2003. Proc Calif Acad Sci 57:479–501

National Coronial Information System (2011) Animal-related deaths. www.ncis.org.au/wp-content/uploads/2017/11/Animal-Related-Deaths.pdf

Neff C (2012) Australian beach safety and the politics of shark attacks. Coast Manage 40:88–106

Payne NL, Meyer CG, Smith JA, Houghton JDR and others (2018) Combining abundance and performance data reveals how temperature regulates coastal occurrences and activity of a roaming apex predator. Glob Change Biol 24:1884–1893

Philander SGH (1983) El Niño Southern Oscillation phenomena. Nature 302:295–301

Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol Appl 19:181–197

Pillans RD, Franklin CE (2004) Plasma osmolyte concentrations and rectal gland mass of bull sharks *Carcharhinus leucas*, captured along a salinity gradient. Comp Biochem Physiol A Mol Integr Physiol 138:363–371

Pyle P, Klimley AP, Anderson DS, Henderson RP (1996) Environmental factors affecting the occurrence and behavior of white sharks at the Farallon Islands, California. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, CA, p 281–291

R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.r-project.org

Randall JE (1992) Review of the biology of the tiger shark (*Galeocerdo cuvier*). Mar Freshw Res 43:21–31

Rasmusson EM, Carpenter TH (1982) Variations in tropical sea surface temperature and surface wind fields associated with the Southern Oscillation/El Niño. Mon Weather Rev 110:354–384

Rayner NA, Parker DE, Horton EB, Folland CK and others (2003) Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. J Geophys Res D Atmospheres 108:4407

Reid DD, Robbins WD, Peddemors VM (2011) Decadal trends in shark catches and effort from the New South Wales, Australia, Shark Meshing Program 1950–2010. Mar Freshw Res 62:676–693

Roughan M, Middleton JH (2002) A comparison of observed upwelling mechanisms off the east coast of Australia. Cont Shelf Res 22:2551–2572

Ryan LA, Hart NS, Collin SP, Hemmi JM (2016) Visual resolution and contrast sensitivity in two benthic sharks. J Exp Biol 219:3971–3980

Ryan LA, Hemmi JM, Collin SP, Hart NS (2017) Electrophysiological measures of temporal resolution, contrast sensitivity and spatial resolving power in sharks. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 203: 197–210

Schaeffer A, Gramoulle A, Roughan M, Mantovanelli A (2017) Characterizing frontal eddies along the East Australian Current from HF radar observations. J Geophys Res C Oceans 122:3964–3980

Schultz LP (1963) Attacks by sharks as related to the activities of man. In: Gilbert PW (ed) Sharks and survival. DC Heath and Company, Lexington, MA, p 425–452

Sequeira AMM, Mellin C, Floch L, Williams PG, Bradshaw CJA (2014) Inter-ocean asynchrony in whale shark occurrence patterns. J Exp Mar Biol Ecol 450:21–29

Stevens JD, McLoughlin KJ (1991) Distribution, size and sex composition, reproductive biology and diet of sharks from northern Australia. Mar Freshw Res 42:151–199

Strong WR Jr (1996) Shape discrimination and visual predatory tactics in white sharks. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, CA, p 229–240

Sumpton WD, Taylor SM, Gribble NA, McPherson G, Ham T (2011) Gear selectivity of large-mesh nets and drumlines used to catch sharks in the Queensland Shark Control Program. Afr J Mar Sci 33:37–43

Surf Life Saving Australia (2018) National coastal safety report 2018. https://issuu.com/surflifesavingaustralia/docs/ncrs-2018

Suthers IM, Young JW, Baird ME, Roughan M and others (2011) The strengthening East Australian Current, its eddies and biological effects — an introduction and overview. Deep Sea Res II 58:538–546

Tricas TC, McCosker JE (1984) Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. Proc Calif Acad Sci 43:221–238

Venables WN, Dichmont CM (2004) GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. Fish Res 70:319–337

Waite AM, Thompson PA, Pesant S, Feng M and others (2007) The Leeuwin Current and its eddies: an introductory overview. Deep Sea Res II 54:789–796

Werry JM, Lee SY, Otway NM, Hu Y, Sumpton W (2011) A multi-faceted approach for quantifying the estuarine–nearshore transition in the life cycle of the bull shark, *Carcharhinus leucas.* Mar Freshw Res 62:1421–1431

Werry JM, Sumpton W, Otway NM, Lee SY, Haig JA, Mayer DG (2018) Rainfall and sea surface temperature: key drivers for occurrence of bull shark, *Carcharhinus leucas,* in beach areas. Glob Ecol Conserv 15:e00430

West JG (1996) White shark attacks in Australian waters. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias.* Academic Press, San Diego, CA, p 449–455

West JG (2011) Changing patterns of shark attacks in Australian waters. Mar Freshw Res 62:744–754

Wetherbee BM, Lowe CG, Crow GL (1994) A review of shark control in Hawaii with recommendations for future research. Pac Sci 48:95–115

Wirsing AJ, Heithaus MR, Dill LM (2006) Tiger shark (*Galeocerdo cuvier*) abundance and growth in a subtropical embayment: evidence from 7 years of standardized fishing effort. Mar Biol 149:961–968

Wood SN (2006) Generalized additive models: an introduction with R. Chapman & Hall, New York, NY

Yopak KE, Lisney TJ (2012) Allometric scaling of the optic tectum in cartilaginous fishes. Brain Behav Evol 80: 108–126

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) GLM and GAM for count data. In: Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (eds) Mixed effects models and extensions in ecology with R. Springer, New York, NY, p 209–243

Editorial responsibility: Alistair Hobday, Hobart, Tasmania, Australia

Submitted: May 23, 2019; Accepted: September 13, 2019
Proofs received from author(s): October 28, 2019