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# Environmental correlates of relative abundance of potentially dangerous sharks in nearshore areas, southeastern Australia

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ABSTRACT: Human–shark encounters garner a disproportionate amount of public attention. Long-term datasets from shark mitigation programs can help determine the environmental conditions that influence abundance of potentially dangerous sharks. We used 25 yr (1992–2016) of shark catches from the New South Wales (NSW) Shark Meshing Program (SMP) to model the abundance of all potentially dangerous shark species (tiger *Galeocerdo cuvier*, white *Carcharodon carcharias* and whaler sharks [genus *Carcharhinus*]) and individual species/genus to determine: (1) the temporal/spatial variability in catches and (2) the oceanographic and physical variables that could influence abundance. Too few tiger sharks were caught to individually model their abundance. Generalised additive mixed models revealed seasonal and inter-annual abundance trends that differ between white and whaler sharks. Overall, sea surface temperatures (SSTs), years with SSTs colder or warmer than the long-term average, El Niño events, moon illumination, and beach length influenced the abundance of shark groups tested. White shark abundance was highest during water temperatures of ~17–18°C and declined when SST increased above 19°C. Whaler abundance increased with higher SSTs. Shark abundance was higher during El Niño events than during La Niña, although the number of whalers caught was highest during neutral phases. All groups showed a decrease in the number of catches with increasing moon illumination and higher abundance on longer beaches. These results may aid public safety methods aimed at reducing human–shark encounters by highlighting when higher numbers of sharks may occur.

KEY WORDS: *Carcharodon carcharias* · *Galeocerdo cuvier* · *Carcharhinus leucas* · Generalised additive mixed model · Shark mitigation · Whaler shark · White shark · Tiger shark · Zero-inflated



## INTRODUCTION

Management of potentially dangerous wildlife is a delicate balancing act between meeting conservation targets and ensuring public safety. As the human population grows, the potential for conflict between wildlife and humans will continue to increase (Dickman 2010), and this is exemplified by human–shark encounters. The increase in the number of people using the ocean has been correlated with an increase in the number of shark attacks (McPhee 2014, Chapman & McPhee 2016), resulting in a decrease in the individual attack risk for beach users (Ferretti et al. 2015). Although the probability of a shark attack is

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low, it garners a disproportionate amount of media (Muter et al. 2013) and political attention (Neff 2012) and can result in water users avoiding the beach for months following an attack (Engelbrecht et al. 2017). It is therefore unsurprising that the public overestimates the risk of a shark attack despite evidence of its low risk compared to risks from other beach activities (e.g. drowning; Crossley et al. 2014). This has led many governments to introduce shark mitigation strategies to increase public safety and awareness (Curtis et al. 2012).

Following a spate of shark attacks in the late 1930s, the government of New South Wales (NSW), Australia, pioneered a large-scale bather protection program using gill nets (shark nets) (Reid et al. 2011). Similar netting programs followed in the 1950s and 1960s in KwaZulu-Natal, South Africa, and Queensland, Australia (Dudley 1997). These nets do not exclude sharks, but decrease local shark populations to theoretically reduce the likelihood of an encounter with sharks (Dudley 1997, Reid et al. 2011). Recent implementation of shark culling programs has been met with public discord (Gibbs & Warren 2015). This, coupled with the importance of apex predators in ecosystem health (Ferretti et al. 2010) and declining global shark populations (Dulvy et al. 2014), has resulted in a greater focus on non-lethal mitigation strategies (e.g. Shark Spotters in South Africa: Kock et al. 2012; shark translocation in Brazil: Hazin & Afonso 2014; aerial surveillance in Australia: Robbins et al. 2014) and improved understanding of the ecology of large sharks to help minimise risk (Cardno Pty Ltd 2015).

The majority of unprovoked shark attacks have been attributed to 3 species: white *Carcharodon carcharias*, tiger *Galeocerdo cuvier* and bull shark *Carcharhinus leucas* (West 2011, McPhee 2014, Chapman & McPhee 2016). An increasing amount of research has been conducted on these species, detailing broad-scale movements (e.g. Block et al. 2011, Bruce & Bradford 2012, Holmes et al. 2014, Heupel et al. 2015, Skomal et al. 2017), habitat use (Kock et al. 2013, Papastamatiou et al. 2013), site fidelity (e.g. Espinoza et al. 2016) and how environmental variables correlate with presence or abundance (Wintner & Kerwath 2018). However, few studies have examined shark abundance and environmental/oceanographic variables incorporating local physical characteristics (e.g. bathymetry) in the same analyses (but see Sleeman et al. 2007). Understanding the physical characteristics of areas with high shark occurrence together with the oceanographic drivers may help inform where shark bite mitigation efforts can be targeted.

Western boundary currents (WBCs), such as the Gulf Stream, Agulhas Current and the East Australian Current (EAC), strongly influence the productivity of the adjacent coastal areas through upwellings of nutrient-rich water and generation of mesoscale eddies (Roughan & Middleton 2002). Off eastern Australia, the strength of the EAC, the WBC of the South Pacific sub-tropical gyre, varies seasonally (Ridgway & Godfrey 1997), inter-annually and with the El Niño/La Niña/Southern Oscillation (ENSO; Holbrook et al. 2011). In addition, the EAC system is dominated by mesoscale eddy shedding on 90–110 d cycles (Cetina Heredia et al. 2014) which have an impact on cross-shelf transport and upwelling (Schaeffer et al. 2014). This results in a spatially irregular and variable level of productivity and nutrient inflow that is dependent on the strength of the flow (Hallegraeff & Jeffrey 1993) as well as a complex combination of eddy activity and wind-, current- and topography-driven upwellings (Roughan & Middleton 2002, 2004).

High-resolution satellite-derived oceanographic measurements, such as sea surface temperature (SST) and SST anomalies, can indicate the presence of mesoscale (Everett et al. 2012) and frontal eddies (Roughan et al. 2017, Schaeffer et al. 2017) indicating areas of high primary productivity. However, it is unclear how these oceanographic variables affect the distribution and abundance of apex predators within the near coastal zone of eastern Australia.

Long-term fishing programs (e.g. the NSW Shark Meshing Program [SMP]), can provide fisheries-independent datasets that can be used to examine shark abundance and distribution in relation to environmental and physical variables. The SMP began in 1937, with nets deployed at beaches in the metropolitan areas of Sydney to target potentially dangerous shark species, namely tiger sharks, white sharks and whaler sharks (*Carcharhinus* spp.) (Reid et al. 2011). While the number of beaches netted and the seasonal deployments of the nets has subsequently undergone substantial changes (for detailed descriptions see Dudley 1997, Reid et al. 2011) since 1992, 51 beaches (Fig. 1), spanning over 200 km of coastline, have been netted from the austral spring (beginning of September) to mid-autumn (end of April) (Reid et al. 2011). This timing coincides with the availability of high-resolution satellite-derived oceanographic measurements.

The aim of this study was: (1) to determine the temporal and spatial variability of shark catches, (2) to determine the oceanographic, environmental and physical variables that correlate with the occurrence

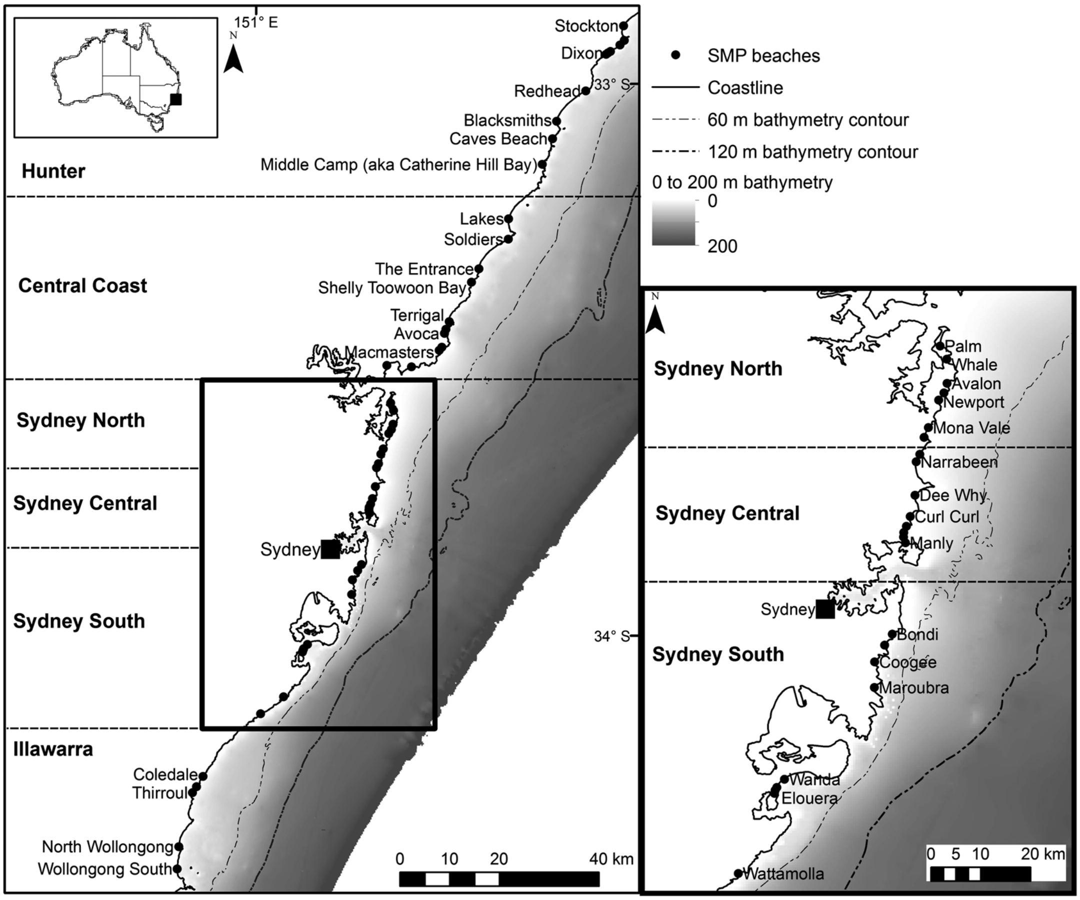



Fig. 1. Location of the beaches along the New South Wales (Australia) coast where shark nets are positioned as part of the NSW Shark Meshing (Bather Protection) Program, SMP

and abundance of 3 groups of potentially dangerous sharks caught in the SMP nets and (3) to assess whether models of these variables would be able to predict shark abundance in an independent dataset.

## MATERIALS AND METHODS

### Shark Meshing Program

The NSW SMP consists of bottom-set multifilament flat-braid polyethylene nets (160 kg breaking strength, stretched mesh size of 50–60 cm), 150 m long and 6 m high. These nets are set 500 m offshore in water 10–12 m deep on bare sand and positioned in the bottom half of the water column at each of the 51 SMP beaches (Fig. 1). Changes were made to the frequency and duration of net deployments in 2009; therefore, the temporal fishing effort during the timeframe of this study is represented by 2 distinct periods: from 1992 to 2009 (17 yr) and 2009 austral spring onwards (8 yr). Prior to 2009, nets were deployed at each beach for a minimum of 9 weekdays and every weekend per month. The maximum soak time was 4 d; however, operationally the nets remained in the water for 24 h and 3 d for weekday and weekend deployments, respectively (Reid et al. 2011). From 2009 onwards, nets were deployed continuously at each beach from the beginning of September to the end of April (inclusive) and had a maximum soak time of 72 h between checks. NSW Department of Primary Industries (DPI) Fisheries reported the catch as monthly returns.

### Catch records

Catch records from 20 March 1992 (when satellite environmental data were first available; Table 1) to 30 April 2017 were used. Only records when a target or non-target species were caught were available, i.e. there were no records identifying days when the

Table 1. Data sources and resolutions of oceanographic and physical characteristics

| Oceanographic and biophysical variables | Data source | Spatial resolution | Temporal resolution | Temporal coverage |
|---|---|---|---|---|
| Satellite-derived sea surface temperature (foundation) | SRS Satellite- Pathfinder AVHRR instruments on NOAA satellites 17, 18 and 19 (IMOS 2017a) | 0.02 decimal degrees | One day (day and night) composites | 20 March 1992 to present |
| Southern Oscillation Index (SOI) | Monthly SOI and SOI phase (see explanation in Materials and methods) data (https://www.longpaddock.qld.gov.au/soi/soi-data-files/) | | Monthly | 1876 to present |
| Estuary locations | Geoscience Australia (https://www.ozcoasts.gov.au/search_data/estuary_search.jsp) | | | |
| Moon illumination | Astronomical Applications Department of the U.S. Naval Observatory (http://aa.usno.navy.mil/data/docs/MoonFraction.php) | Sydney | Daily | 1992 to present |
| Bathymetry | Australian Bathymetry and Topography Grid, June 2009 (Geoscience Australia, www.ga.gov.au/metadata-gateway/metadata/record/gcat_67703) | 0.0025 decimal degrees | | |

nets were hauled/checked but nothing was caught. Prior to 1998, sharks of the genus *Carcharhinus* were recorded as 'whalers', which subsequent DNA analysis has shown are represented by 7 species (Reid et al. 2011): bignose *C. altimus*, bronze *C. brachyurus*, bull *C. leucas*, common blacktip *C. limbatus*, dusky *C. obscurus*, silky *C. falciformis* and spinner sharks *C. brevipinna*. All white sharks *Carcharodon carcharias* and tiger sharks *Galeocerdo cuvier* were identified to species level. From 2010, all sharks were identified to species level.

### Oceanographic and environmental data

Oceanographic, environmental and physical datasets were downloaded from various sources (Table 1). Specifically, we investigated SST, daily and annual SST anomalies, SST gradient, southern oscillation index (SOI) phase, moon illumination, distance to estuaries, beach length and orientation, and a bathymetry dataset to calculate the slope (gradient in depth; see descriptions for each variable below).

Differences between *in situ* and satellite-derived SST measurements are common in nearshore areas (Lathlean et al. 2011, Stobart et al. 2016). To overcome this, Stobart et al. (2016) averaged all satellite pixels within a 20 $km^2$ box. As the EAC typically flows anisotropically, meaning the flow dominates in one direction, in this case along-shore to the south (poleward), known across- and along-shelf de-correlation distances were used to choose the number of SST pixels over which to average. A distance of 8 km across-shelf and 30 km along-shelf was used to average the satellite SST values; these were within known de-correlation distances (Schaeffer et al. 2016). If no satellite SST data were available on a particular sampling day due to cloud cover, the SST from the same area was interpolated using a 3 d window centred on the sampling day. This is in line with the minimum de-correlation time found for sea temperature by Roughan et al. (2015).

We obtained an annual SST anomaly by calculating the mean SST for each calendar day for each beach over a period of 24 yr (1992–2016) and subtracted this from the daily SST measurements. The difference between consecutive (or nearest previous record within a 3 d period) daily SST measurements (daily SST anomaly) was used to detect the presence of mesoscale/frontal eddies or upwelling events. SST gradient, i.e. the difference between inshore and offshore SST, provides an indication of frontal zones which are ecologically important for mobile marine species (Scales et al. 2014). SST gradient was calculated as the difference between the SST at the beach and the maximum SST recorded within the same latitude, divided by the distance. Moon illumination was included, as it has been shown to influence the vertical distribution of sharks in pelagic areas (Lowry et al. 2007), the likelihood of sighting white sharks in coastal areas (Weltz et al. 2013) and how visible the nets are to sharks (Werry et al. 2012).

Satellite derived chlorophyll *a* (chl *a*), an indication of biological productivity, is commonly used to determine the distribution of marine apex predator species (e.g. Block et al. 2011, Hazen et al. 2013). However, it could not be included in this study, as satellite-derived chl *a* (MODIS OC3) measurements were only available from 2002 onwards, and SeaWiFS (available 1997–2010) measurements used different sensors, which would give different values to those provided by more recent MODIS OC3. During preliminary model testing, MODIS OC3 measurements were included from 2002 onwards with missing values included as random effects and indicator factors to prevent the model from excluding all the data when chl *a* was missing (Wood 2006). However, these models did not converge and thus chl *a* was excluded from subsequent analyses.

The Southern Oscillation Index (SOI) describes the intensity and phase of ENSO, which is a measure of the changing atmospheric pressure gradient between the central Pacific Ocean and the northeastern Indian Ocean. Changes in ENSO have been shown to shift suitable habitats for large pelagic teleost predators (Hill et al. 2016) and influence the nearshore abundance of white sharks off the coast of South Africa (Towner et al. 2013). Sustained SOI values of $<-7$ (using the Troup SOI calculations: Troup 1965) indicate El Niño events, while values of $>+7$ represent La Niña events. Short-term SOI values reflect daily weather patterns rather than overall ENSO changes (Australian Bureau of Meteorology 2017). In addition, absolute SOI values are unlikely to influence the behaviour of sharks, but rather large-scale changes in SST anomalies associated with ENSO phases would drive changes in nearshore abundance. Therefore, 5 SOI phases, which incorporated not only the month of interest but also the preceding month's values (Stone et al. 1996), were used as indicators of ENSO. The 5 phases represented: phase 1: consistently negative (El Niño - higher SSTs), phase 2: consistently positive (La Niña - lower SSTs), phase 3: rapid fall, phase 4: rapid rise and phase 5: consistently near zero (ENSO neutral).

### Physical factors

Estuaries are highly productive systems that are used by a range of fish (Beck et al. 2001) and shark species (Taylor & Bennett 2013). To determine if estuaries influenced the abundance of sharks caught in the SMP, the distance from each beach to the nearest estuary mouth was calculated. A shapefile of all coastal waterways in NSW that are open to the ocean was downloaded from Geoscience Australia (Table 1). This shapefile included the locations of rivers, lakes, harbours and embayments, hereafter referred to as estuaries. For simplicity, only estuaries with a continuous flow (i.e. open despite recent rainfall amounts) were included, as estuaries in this region only become stratified after heavy rainfall ($>50$ mm $d^{-1}$) (Lee et al. 2011) and salinity levels at the mouth of large estuaries remain close to the level of seawater even after extreme rainfall events. For example, on 25 April 2015, ~ 300 mm of rain fell within a 24 h period that led to flooding in the Hunter River, in the north of the SMP; however measurements from gliders deployed in the area showed that the salinity of the river plume was 33 psu, only 2 psu lower than normal (data available on the Australian Ocean Data Network Integrated Marine Observing System Ocean Portal; IMOS 2017b).

The distance from each beach to the nearest estuary was calculated using the 'Near' geoprocessing tool in ArcGIS 10.5 (ESRI). The slope value of each raster cell (resolution: 285 × 285 m) on the continental shelf (≤200 m depth) offshore of each beach was calculated using the 'Slope' in the surface tools of ArcGIS 10.5. This tool calculates the maximum rate of change in value from a particular cell to its neighbours. The average slope from each beach to the 60 m bathymetric isobath was calculated creating a polygon from the length of the beaches extending offshore to the 60 m isobath and then summarising the slope values across all raster cells within each polygon. Spearman's rank was used to test the correlation between the average slope and the distance to the 60 and 120 m bathymetry contours to ensure the results were comparable to Werry et al. (2012) and showed that the values were highly correlated (both Spearman's ranks: rho = –0.82).

## Data analysis

### Shark abundance modelling

The total number of days per month for which catch records were available varied throughout the study period. Between 23 and 85% of the 197 months that the catch at individual beaches was analysed had no catch records (i.e. no target [all potentially dangerous sharks, tiger sharks, white sharks and whaler sharks] or non-target species were caught). To ensure that the models included data points at the same frequency at which the nets were checked, we used a randomisation approach to impute the days where the nets were checked but nothing was caught. Prior to 2009, we included a record for every weekend during the SMP season and on 9 weekdays. After 2009, if a beach within a specific region had a catch record (i.e. a target or non-target species was caught), we assumed that the nets at all other beaches within that region were also checked, as per operational guidelines (NSW Fisheries SMP observer protocol). Other days were then randomly sampled to be within 1 to 3 d of a record (either a true record or randomly sampled day) to represent the frequency at which the nets were checked.

The occurrence and abundance of sharks was modelled: (1) for all potentially dangerous sharks and (2) at the species, genus or group level for each of the potentially dangerous species, where sufficient data were available. All potentially dangerous species were modelled together to determine the overall risk to beach users under certain environmental conditions, rather than attempting to discern the ecological drivers of abundance for each individual species. Given the uncertainty in species identification prior to 2009 (Green et al. 2009), all species in the genus *Carcharhinus* were modelled as 'whalers'. Whalers are potentially dangerous and have been identified as causing the fourth highest number of unprovoked shark attacks (West 2011). Although the frequency of such attacks by whalers may be inflated by bull sharks not identified to species level or by white sharks misidentified as whalers (West 2011), a variety of whaler species have been implicated in shark attacks (Chapman & McPhee 2016) and so were a target species for the SMP (Green et al. 2009). Sharks of all sizes were included in the models despite some protocols that consider only sharks >2 m as dangerous (West 2011). Firstly, the accuracy of length measurements prior to 2009 was unknown; secondly, some smaller whalers have been implicated in recorded shark bites; and thirdly, the abundance of sharks was too low to exclude potentially useful data.

The number of all potentially dangerous sharks (whalers, white and tiger) and species/group were calculated for each net deployment from the records and randomly sampled days. These were modelled against: (1) month, year (commencing in September; from 1992 to 2015) and SMP region (Fig. 1), and (2) oceanographic (SST, annual SST anomaly, daily SST anomaly, SST gradient, SOI and moon illumination) and physical variables (average slope, beach length and orientation) using generalised additive mixed effects models (GAMMs) in the 'mgcv' (Wood 2006, Wood 2011) package in R (R Core Development Team 2009). Year commencing in September was used instead of calendar year, as it better represented the 'meshing seasons', which occurred from September to April (inclusive). Preliminary data analysis showed non-linear relationships between the response and predictor variables, and GAMMs enabled the expected response to vary smoothly with continuous covariates. Month and year commencing in September were included in the models to test for seasonal and inter-annual differences in shark catches. A cyclic smoothing spline was used on month to account for the cyclic nature of the data. All models included a single random intercept term per beach, reflecting the individual idiosyncrasies of beaches not captured by the available predictor variables and to account for repeated observations from the same beaches. The number of days that each net had been deployed was used as an offset to account for the probability of higher catches with longer deployments. Generalised variance inflation factor tests were used to ensure no collinearity between variables. Smoothing terms were included for all the predictor variables included, and the number of knots for each predictor variable was set at a maximum of 10 estimated degrees of freedom. Model adequacy was checked using standard residual plots, as well as auto-correlation function plots and semi-variogram plots to check for unmodelled spatial and temporal correlation. Post hoc multiple comparison (Wald) tests were conducted for any multi-level factor variable (e.g. the SMP regions), using the *wald_gam_* function in the 'itsadug' package (Van Rij et al. 2017), to determine the pairwise significance of each level.

As the random sampling of days with no catch records would affect the short-term variables (annual SST anomaly and daily SST anomaly) included in the models, the random sampling and subsequent GAMM modelling was repeated over 25 randomly sampled iterations. To determine the number of iterations needed, 100 iterations of the random sampling and GAMM modelling were conducted. Parameter estimates and variance stabilised after 25 iterations, and thus 25 iterations were subsequently used. Model selection (accounting for the missing data and multiple imputation of data) was conducted using the framework proposed by Schomaker & Heumann (2014), whereby model selection is conducted on each data imputation iteration and estimated averaged over all iterations. Model and optimal degrees of freedom (degree of nonlinearity on splines) selection was automatically conducted on each iteration using the 'select' argument (with maximum likelihood methods) in the 'mgcv' *gam* function (Wood 2011). If a term was not selected in some of the iterations, it was defined as zero; thus less clear effects will be shrunk towards zero (Schomaker & Heumann 2014). The estimates and variance of all iterations were non-normally distributed, so the median of the parameter estimates and p-values of the 25 GAMM iterations were used.

Shark catch records included a high proportion of zeros and a maximum of 4 sharks caught per net deployment. Zero-inflated distributions are commonly used to describe the relationship between species abundance and environmental variables (Potts & Elith 2006, Dransfield et al. 2014) because of their ability to account for a high number of zeros in the data (Cunningham & Lindenmayer 2005, Martin et al. 2005). Warton (2005), however, found that using a negative binomial log-linear distribution could provide the best fitting model for data with a small means. The Tweedie exponential distribution can model zero-inflated data more accurately than the negative binomial distribution (Shono 2008). Therefore, to determine the best distribution to use, 25 iterations of both model structures (1: month, year and region; 2: oceanographic and physical variables) were fitted for all potentially dangerous sharks using (1) Poisson, (2) negative binomial, (3) Tweedie and (4) zero-inflated Poisson distributions. Models were compared using Akaike's information criterion (AIC), and the distribution that produced models with the lowest AIC values across all the iterations was chosen to model the full dataset.

When a zero-inflated distribution is appropriate, the high proportion of zeros can be accounted for by using a mixture model (Zuur et al. 2009). Mixture models assume that some of the zeros in the data arise from the abundance data (e.g. the habitat is suitable but the species does not saturate it; 'true' zeros; Martin et al. 2005) so are modelled with a discrete probability distribution (e.g. Poisson) and a binomial distribution is used to model the probability of false zeros (e.g. sharks occur at a beach, but are not present during the survey period or sharks occur at the beach but are not caught in the nets). If not modelled correctly, the false zeros will lead to uncertainty as to whether changes in the parameter estimates are due to a change in species abundance or detection probability (Martin et al. 2005). As sharks are unlikely to saturate nearshore habitats, even under favourable environmental conditions, a mixture model was used when a zero-inflated distribution was appropriate.

Deviance explained from the 'mgcv' *gam* function was used to determine the quality of the fit to quantify the relationship between the variables. The predictive ability of the models was assessed on an independent dataset collected 1 September 2016 to 30 April 2017. Pearson's correlation coefficient, r, was used to provide an indication of how closely the observed and predicted values from each model iteration agreed in relative terms (Potts & Elith 2006).

### Influence of specific whaler species

Sensitivity tests were used to determine how each of the species included in the whaler group influenced the relationships observed between the number of sharks and was modelled against (1) the month, year and region and (2) the environmental and physical variables. Using the data collected after 2010, when whalers were all identified to species level, the same models as described above were run with each of the whaler species dropped one at a time. Only species that comprised more than 5 percent of the overall catch from 2010 to 2016 were included (i.e. no sensitivity tests were conducted for bignose and silky sharks). Again, 25 iterations were run for each species and the results were compared to models when all whalers were included using paired Wilcoxon ranked tests.

## RESULTS

### Catch records

In total there were 5324 catch records of target and non-target shark species caught between 20 March 1992 and 30 April 2016; 34% of the animals were alive when the nets were checked and were subsequently released. Potentially dangerous sharks accounted for 18% of the total catch (82% were non-target species) and included 694 whalers, 185 white and 63 tiger sharks. From 2009, when stricter species identification was introduced, there was high annual variability in the abundance of each whaler species caught (Fig. 2). Catch per unit effort (CPUE; number of sharks caught per 100 net days) showed that the number of potentially dangerous sharks, whites and whalers varied seasonally (Fig. 3), inter-annually (Fig. 4) and at each of the beaches (Fig. 5). There was little seasonal (Fig. 3) or inter-annual variability (Fig. 4) for tiger sharks, but CPUE did vary by beach (Fig. 5). There were 373 target and non-target spe-

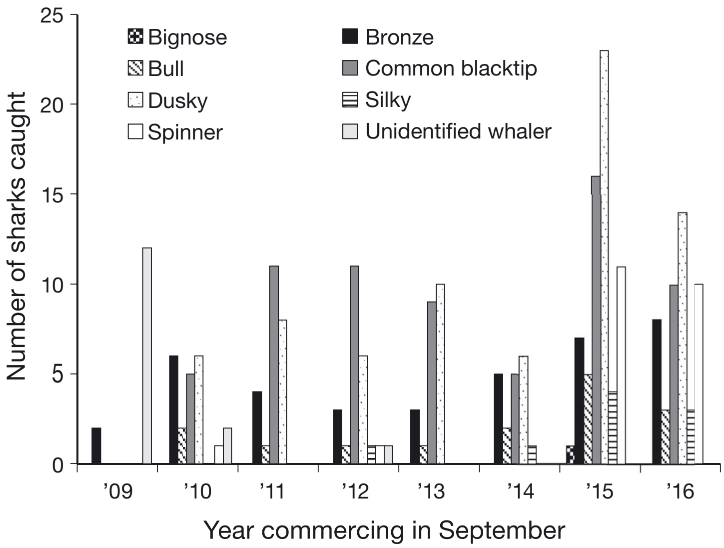



Fig. 2. Number of whaler sharks caught per year (commencing in September) since 2009 when stricter species identification measures were introduced. Effort was not included, as it was consistent from 2009 to 2016

cies caught from September 2016 to April 2017 (the independent dataset against which the trained models were tested) that included 48 whaler, 22 white and 3 tiger sharks.

## Shark abundance modelling

Inclusion of randomly sampled potential days when nets were checked but there was no catch increased the number of 'records' by an average of 3397% (range: 727 to 5763%) per year (commencing in September). The models with zero-inflated Poisson distributions had the lowest ΔAICs for both model structures (ΔAICs for month, year and region models: negative binomial: 12; Poisson and Tweedie: >100; ΔAICs for oceanographic and physical variables models: negative binomial: 15; Poisson and Tweedie: >100), thus the zero-inflated distribution was used for all subsequent analyses.

## Temporal and spatial patterns of shark abundance

We had insufficient data to model the abundance of tiger sharks against month, year (commencing in September) and region, with none of the models converging. Month, year (commencing in September) and 2 of the Sydney regions (central and north) were significant for all remaining groups (all

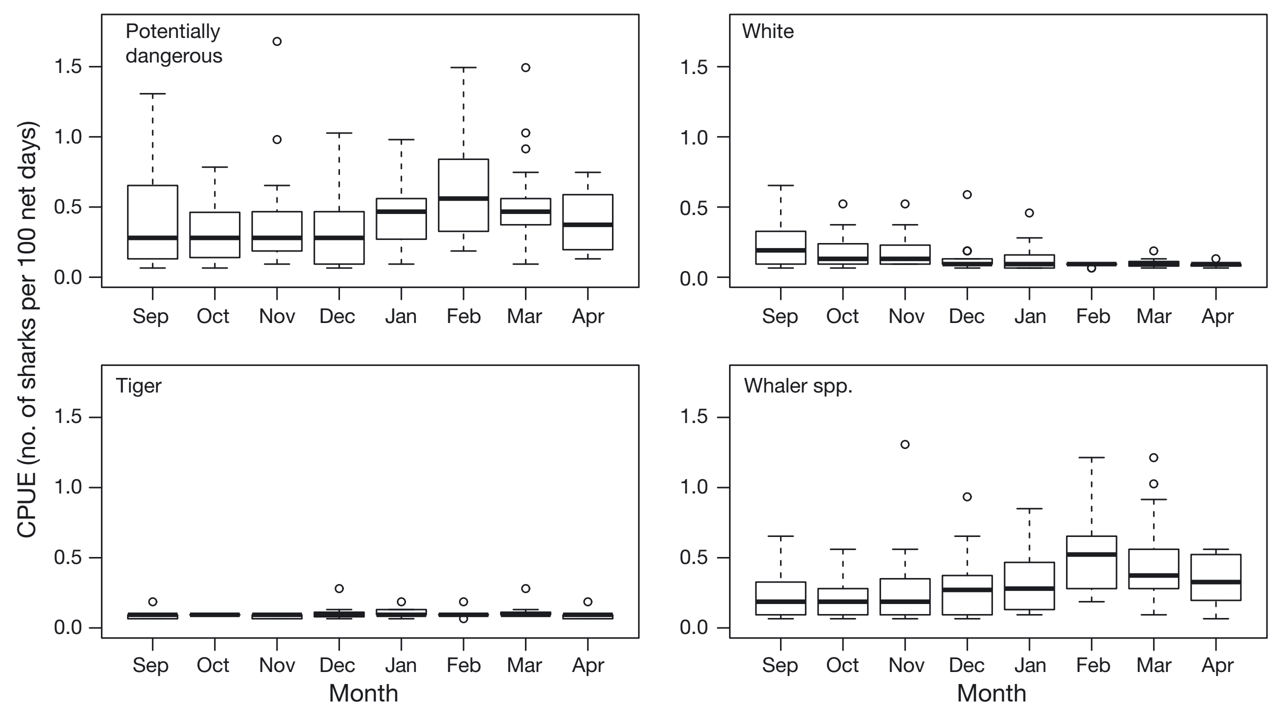



Fig. 3. Catch per unit effort of sharks (CPUE; number of sharks per 100 net days) by month per species. Boxes display the lower and upper quartile with the median shown as a line. The whiskers show the lower (upper) quartile minus (plus) one and a half times the interquartile range. Extreme values are displayed as circles

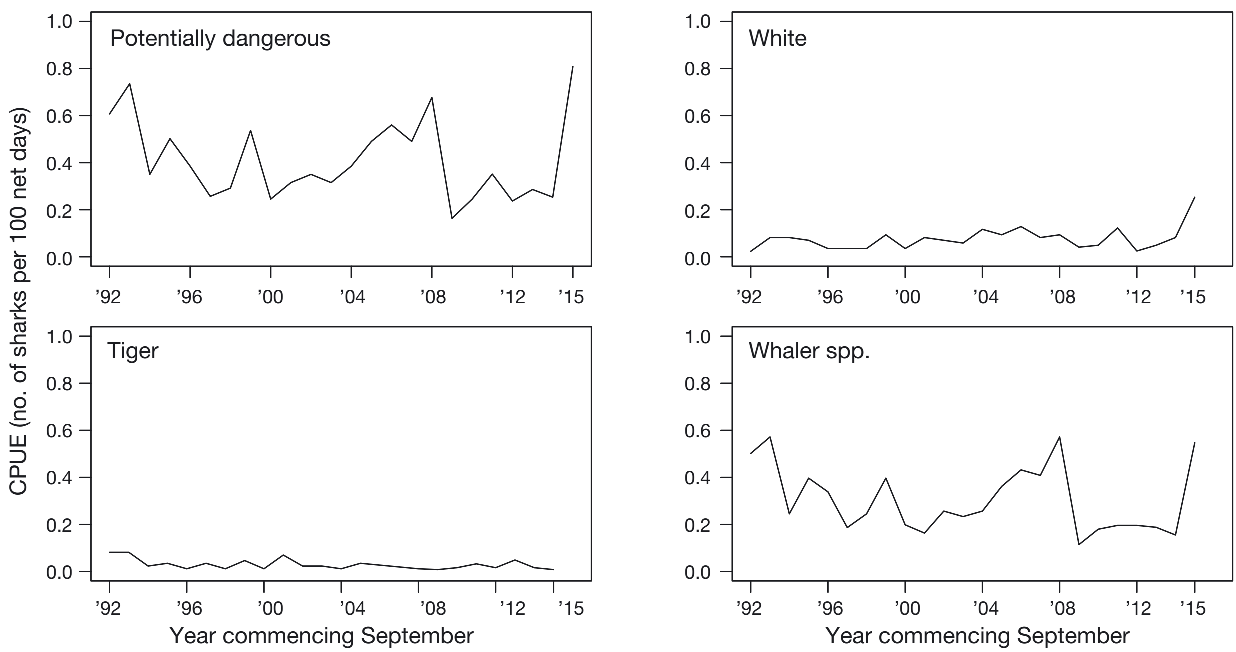



Fig. 4. Catch per unit effort of sharks (CPUE; number of sharks per 100 net days) by year commencing in September per species

potentially dangerous sharks, whites and whalers; Table 2). Despite being significant, the abundance of all potentially dangerous sharks only marginally increased in the summer months (December to March; Fig. 6a), while white sharks were caught in higher abundance from September to November with a decreasing catch from January to April (Fig. 6b). In contrast, whaler shark abundance increased from November, peaked in February and gradually decreased from February to October (Fig. 6c). Abundance of potentially dangerous and whaler sharks varied across years (Fig. 6a,c), while white sharks showed a steady increase (Fig. 6b). The northern- (Hunter) and southern-most regions (Sydney South and Illawarra) had the highest catches of all potentially dangerous sharks, whites and whalers (Fig. 6a–c), although the significance of the differences varied by region (Tables 2 & 3). There was little variance in the significance and model estimates/estimated degrees of freedom (degree of nonlinearity) of each variable across the different model iterations (Table 2) and deviance explained by the models (all potentially dangerous sharks: median 65% [range: 64–66%], white: 73% [72–75%] and whalers: 72% [71–73%]). However, the correlations between the predicted and actual catch values from September 2016 to April 2017 were low for all groups (Pearson's r values: all potentially dangerous sharks: median 0.050 [range: 0.047–0.054], whites: 0.116 [0.103–0.124], whalers: 0.031 [0.029–0.034]).

**Oceanographic and physical influence on shark abundance**

Again, insufficient data were available to model the abundance of tiger sharks. The significance of the predictor variables differed between the models of all potentially dangerous sharks, whites and whalers (Table 4). Overall, SST, SOI phase (phase 2 versus phase 1), moon illumination and distance to estuary were significant across all groups (Table 4). The abundance of all potentially dangerous sharks (modelled together) and whalers increased with increasing SST from 14 to 28°C (Fig. 7a,c). White shark catches increased when the SST increased from 14 to ~17–18°C and then decreased as SST increased above ~19°C (Fig. 7b). Annual SST anomaly was also significant for whites and whalers, and SOI phase 4 was lower (by a marginal but significant amount) than phase 1 for all potentially dangerous sharks (Table 4). Catches of all species decreased with increasing moon illumination and increased with increasing distances from the nearest estuary (Fig. 7, Table 4). The degree of nonlinearity and significance of the smoothers varied between species group and model iterations for the many remaining predictor variables (Table 4, Fig. 7). The probability of false zeros was low across all the models (0.01–0.02). The deviance explained by the models was, again, high across all the model iterations (all potentially dangerous: 64% [range: 64–65%]; whites: 72% [70–74%];

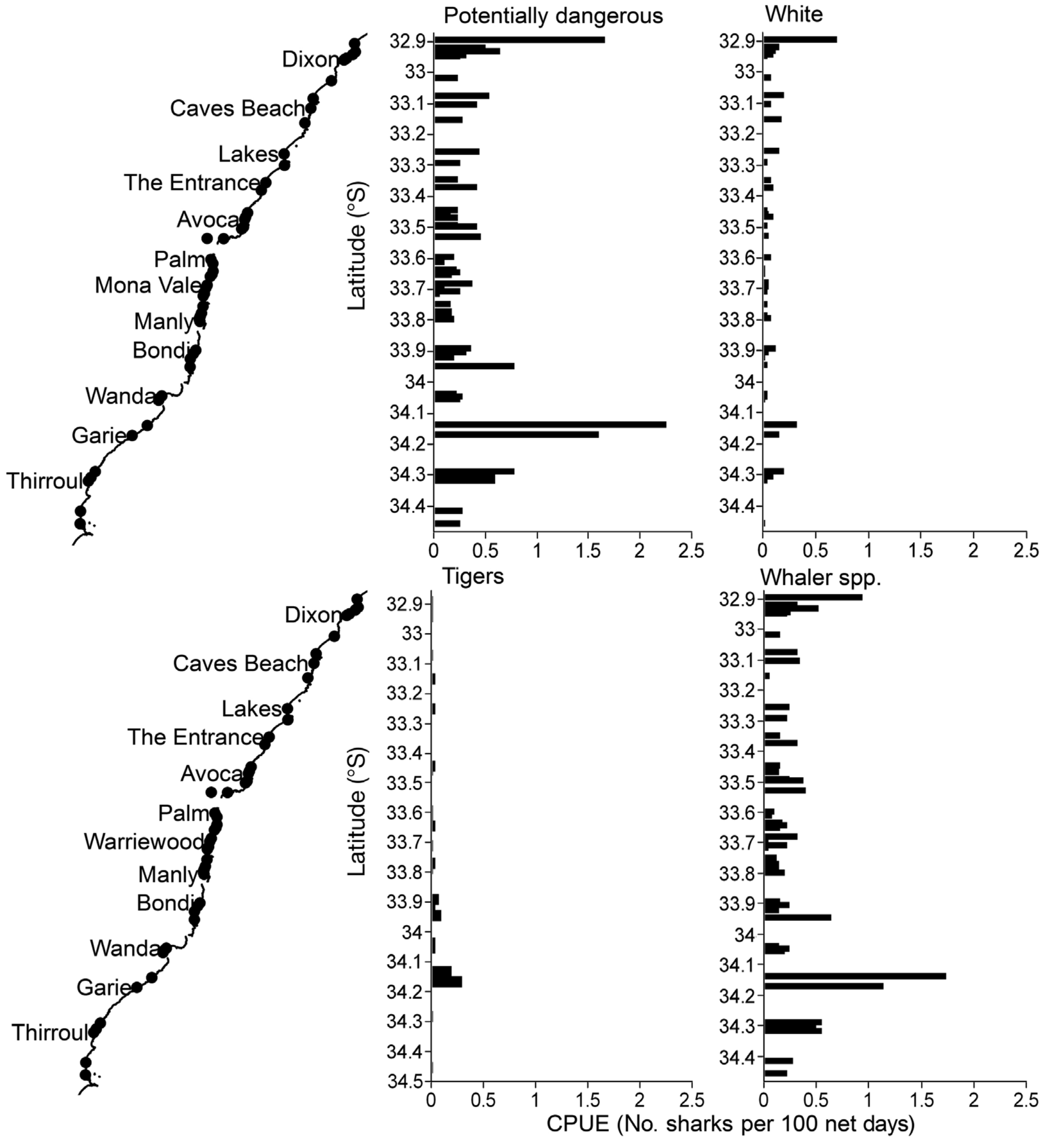



Fig. 5. Catch per unit effort (CPUE; number of sharks caught per 100 net days) for each net installation in the Shark Meshing Program (SMP). Black dots along the coastline show the location of SMP beaches

whalers: 71% [71–72%]). Despite this, the models again had poor predictive power with a median correlation of only 0.011 (0.001–0.042), 0.055 (0.001–0.088) and 0.001 (0.001–0.009) for all potentially dangerous sharks, whites and whalers, respectively.

### Influence of specific whaler species

GAMMs with common blacktips removed from the whaler catch failed to converge (when modelled against month, year and region or oceanographic and physical variables), as there were only 2 days when 2 or more of the remaining whaler species were caught (the maximum number caught) and 61 days when 1 shark was caught. The month and year smoother terms were significant in the GAMMs with all whaler species included and when bronze and dusky sharks were excluded (Table 5). The median p-value for the smoother term applied to month was significant for bull and spinner sharks, but the maximum p-value was not (Table 5). Only the intercept term was significant for all GAMMs (Table 5), and there was no significant difference between the different regions for any of the models (all Wald tests, $p > 0.05$). Models with spinner sharks excluded showed the greatest difference from the GAMMs with all whaler species included, with all terms

Table 2. Median estimates and p-values (with ranges) from generalised additive mixed models (GAMMs) of 'potentially dangerous' sharks, white sharks and whaler sharks against month, year (commencing in September) and region. **Bold** text shows significant variables (mean $p < 0.05$), and s() denotes a smoother term. β denotes the estimated degrees of freedom (degree of nonlinearity) for smoother terms and the variable estimate for parametric terms. The Hunter region is given as the reference level (intercept value), relative to which the other regions should be interpreted

| | All potentially dangerous | | White | | Whaler spp. | |
|---|---|---|---|---|---|---|
| | Median β | Median p | Median β | Median p | Median β | Median p |
| s(Year) | 5.04 (4.96–5.20) | **<0.001 (<0.001–<0.001)** | 0.96 (0.96–0.96) | **<0.001 (<0.001–<0.001)** | 4.79 (4.67–4.84) | **<0.001 (<0.001–<0.001)** |
| s(Month) | 2.18 (1.86–3.02) | **0.01 (0.00–0.02)** | 2.61 (2.56–2.64) | **<0.001 (<0.001–<0.001)** | 4.16 (4.13–4.24) | **<0.001 (<0.001–<0.001)** |
| (Intercept) | −3.64 (−3.67 to −3.61) | **<0.001 (<0.001–<0.001)** | −5.49 (−5.71 to −5.23) | **<0.001 (<0.001–<0.001)** | −4.5 (−4.54 to −4.45) | **<0.001 (<0.001–<0.001)** |
| Central Coast | −0.73 (−0.77 to −0.69) | 0.11 (0.10–0.12) | −1.74 (−1.84 to −1.57) | 0.10 (0.09–0.11) | −0.39 (−0.40 to −0.38) | 0.47 (0.45–0.49) |
| Sydney North | −1.66 (−1.72 to −1.60) | **<0.001 (<0.001–<0.001)** | −3.57 (−3.85 to −3.29) | **0.01 (0.01–0.01)** | −1.37 (−1.42 to −1.35) | **0.03 (0.03–0.04)** |
| Sydney Central | −1.87 (−1.94 to −1.81) | **<0.001 (<0.001–<0.001)** | −3.81 (−4.05 to −3.46) | **0.01 (<0.001–0.01)** | −1.51 (−1.57 to −1.49) | **0.01 (0.01–0.02)** |
| Sydney South | 0.18 (0.16–0.20) | **0.70 (0.65–0.72)** | −0.93 (−0.99 to −0.90) | 0.35 (0.32–0.40) | 0.44 (0.42–0.46) | 0.41 (0.39–0.43) |
| Illawarra | 0.24 (0.22–0.26) | 0.66 (0.63–0.68) | −1.26 (−1.32 to −1.21) | 0.33 (0.30–0.38) | 0.76 (0.71–0.80) | 0.24 (0.22–0.26) |

Table 3. Median estimates and p-values (with ranges) from Wald tests showing multiple comparisons between the different regions from generalised additive mixed models (GAMMs) of 'potentially dangerous' sharks, white sharks and whaler sharks against month, year (commencing in September) and region. **Bold** text shows significant variables (mean $p < 0.05$)

| Regions being compared | All potentially dangerous | | White | | Whaler spp. | |
|---|---|---|---|---|---|---|
| | Median β | Median p | Median β | Median p | Median β | Median p |
| Central Coast Sydney North | −0.93 (−0.98 to −0.89) | 0.09 (0.08–0.10) | −1.85 (−2.25 to −1.60) | 0.20 (0.19–0.21) | −0.97 (−1.02 to −0.92) | 0.13 (0.12–0.14) |
| Central Coast Sydney Central | −1.15 (−1.19 to −1.10) | **0.03 (0.03–0.04)** | −2.07 (−2.42 to −1.81) | 0.14 (0.14–0.15) | −1.11 (−1.19 to −1.09) | 0.07 (0.06–0.07) |
| Central Coast Sydney South | 0.91 (0.86–0.94) | 0.05 (0.04–0.06) | 0.78 (0.65–0.96) | 0.47 (0.46–0.53) | 0.83 (0.80–0.87) | 0.11 (0.11–0.13) |
| Central Coast Illawarra | 0.97 (0.91–1.02) | 0.08 (0.07–0.09) | 0.48 (0.35–0.68) | 0.72 (0.67–0.78) | 1.12 (1.10–1.22) | 0.08 (0.06–0.08) |
| Sydney North Sydney Central | −0.21 (−0.26 to −0.19) | 0.73 (0.68–0.76) | −0.2 (−0.26 – −0.15) | 0.9 (0.88–0.94) | −0.15 (−0.19 to −0.13) | 0.84 (0.78–0.86) |
| Sydney North Sydney South | 1.83 (1.77–1.90) | **<0.001 (<0.001–<0.001)** | 2.62 (2.29–3.22) | 0.07 (0.06–0.08) | 1.80 (1.74–1.86) | **<0.001 (<0.001–0.01)** |
| Sydney North Illawarra | 1.91 (1.83–1.97) | **<0.001 (<0.001–<0.001)** | 2.33 (1.97–2.93) | 0.16 (0.13–0.18) | 2.09 (2.02–2.20) | **<0.001 (<0.001–<0.001)** |
| Sydney Central Sydney South | 2.06 (1.97–2.11) | **<0.001 (<0.001–<0.001)** | 2.83 (2.51–3.38) | 0.04 (0.04–0.05) | 1.94 (1.92–2.02) | **<0.001 (<0.001–<0.001)** |
| Sydney Central Illawarra | 2.12 (2.04–2.19) | **<0.001 (<0.001–<0.001)** | 2.54 (2.17–3.10) | 0.11 (0.10–0.13) | 2.24 (2.2–2.36) | **<0.001 (<0.001–<0.001)** |
| Sydney South Illawarra | 0.07 (0.04–0.09) | 0.9 (0.88–0.95) | −0.29 (−0.36 to −0.18) | 0.83 (0.78–0.89) | 0.29 (0.28–0.35) | 0.65 (0.6–0.66) |

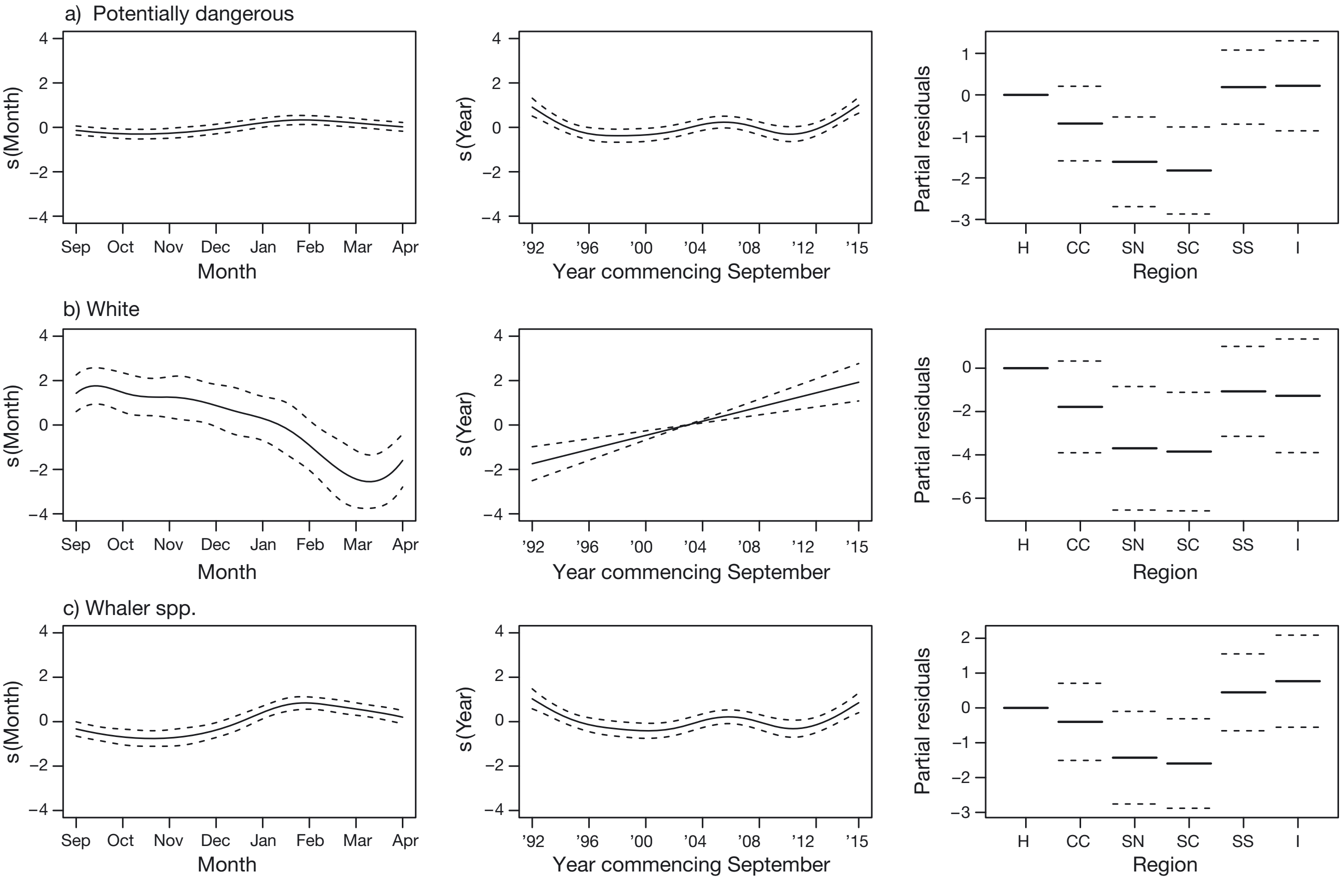



Fig. 6. Median generalised additive mixed model (GAMM) relationships for (a) all potentially dangerous shark species, (b) white sharks and (c) whaler sharks against month, year (commencing in September) and Shark Meshing Program region. Region is plotted as north to south (from left to right), with the Hunter region used as the reference. H: Hunter, CC: Central Coast, SN: Sydney North, SC: Sydney Central, SS: Sydney South and I: Illawarra. Solid lines represent the GAMM estimates, and the dashed lines show the 95% confidence interval

except the intercept significantly different (Table 5). There was a varying amount of significant difference in the GAMMs with the remaining whaler shark species excluded versus the models with all whaler species included (Table 5). Despite these significant differences, all models showed an increase in whaler abundance from January to March and from 2010 to 2016 (Fig. 8).

The significance of the smoother terms varied between GAMMs with the number of sharks modelled against the oceanographic and physical variables (Table 6). SOI phases 2 and 4 differed significantly from SOI phase 1 when bronze, bull and dusky sharks were excluded (Table 6). Five of the 9 smoother terms included in the GAMMs with dusky whalers excluded were significantly different from the GAMMs with all whaler species included (Table 6). While 3 smoother terms were significant when bronze whalers or spinner sharks were removed, only 1 smoother term was significantly different when bull sharks were not included (Table 6). The parametric terms (for SOI phase) were significantly different when spinner (SOI phases 3, 4 and 5), dusky (SOI phases 1 and 4) and bronze whalers (SOI phase 1 only) were removed compared to when all whaler species were included (Table 6).

When dusky whalers were excluded from the whaler catch there was a negative correlation with average slope compared to no relationship when all whaler species were included (Fig. 9a). Although there was a significant difference when each of the whaler species was excluded versus when all whalers were modelled for distance to estuary (Table 6), the abundance of sharks still increased with increasing distances, albeit at different rates (Fig. 9b). When bronze whalers were excluded, the remaining whalers were more abundant when the water was colder than the previous day (Fig. 9c). The relationship for the model with all whalers included showed a different relationship to the data modelled from 1992–2016

Table 4. Median estimates and p-values (with ranges) from generalised additive mixed models (GAMMs) of 'potentially dangerous' sharks, white sharks and whaler sharks against oceanographic and physical variables. **Bold** text shows significant variables (median and maximum p-values < 0.05), and *italicised* text indicates that the median p-value was significant (< 0.05) but the maximum was not. s() denotes a smoother term, β denotes the estimated degrees of freedom (degree of nonlinearity) for smoother terms and the variable estimate for parametric terms. SST: sea surface temperature, SOI: Southern Oscillation Index

| | All potentially dangerous | | White | | Whaler spp. | |
|---|---|---|---|---|---|---|
| | Median β | Median p | Median β | Median p | Median β | Median p |
| s(Average slope) | 0.00 (0.00–0.00) | 1.00 (0.89–1.00) | 0.00 (0.00–0.00) | 0.43 (0.40–0.46) | 0.00 (0.00–0.00) | 0.80 (0.78–0.84) |
| s(Beach length) | 0.75 (0.75–0.76) | 0.05 (0.05–0.05) | 0.78 (0.77–0.81) | *0.04 (0.03–0.05)* | 0.55 (0.54–0.56) | 0.15 (0.14–0.15) |
| s(Beach orientation) | 0.00 (0.00–0.01) | 0.37 (0.36–0.40) | 0.00 (0.00–0.00) | 1.00 (1.00–1.00) | 0.00 (0.00–0.01) | 0.36 (0.35–0.37) |
| s(Distance to estuary) | 0.92 (0.92–0.92) | **<0.001 (<0.001–<0.001)** | 1.22 (1.19–1.23) | **0.03 (0.03–0.03)** | 0.88 (0.88–0.89) | **<0.001 (<0.001–<0.001)** |
| s(Daily SST anomaly) | 0.00 (0.00–0.00) | 0.73 (0.54–1.00) | 1.49 (0.17–1.97) | 0.10 (0.02–0.35) | 0.00 (0.00 – 0.00) | 0.48 (0.31–1.00) |
| s(SST) | 0.93 (0.92–1.75) | **<0.001 (<0.001–<0.001)** | 2.15 (1.99–2.41) | **<0.001 (<0.001–<0.001)** | 2.34 (0.98–2.38) | **<0.001 (<0.001–<0.001)** |
| s(Moon illumination) | 0.95 (0.94–0.95) | **<0.001 (<0.001–<0.001)** | 1.13 (1.06–1.16) | *0.04 (0.03–0.06)* | 0.91 (0.9–0.93) | **<0.001 (<0.001–<0.001)** |
| s(Annual SST anomaly) | 0.57 (0.17–0.83) | 0.13 (0.08–0.26) | 0.93 (0.91–2.04) | **<0.001 (<0.001–<0.001)** | 3.17 (2.89–3.66) | **<0.001 (<0.001–<0.001)** |
| s(SST gradient) | 0.00 (0.00–0.00) | 0.76 (0.62–0.92) | 0.00 (0.00–0.00) | 1.00 (1.00–1.00) | 0.00 (0.00–0.00) | 0.60 (0.44–0.75) |
| (Intercept) | −4.04 (−4.09 to −4.00) | **<0.001 (<0.001–<0.001)** | −5.26 (−5.51 to −4.96) | **<0.001 (<0.001–<0.001)** | −4.70 (−4.79 to −4.64) | **<0.001 (<0.001–<0.001)** |
| SOI phase 2 | −0.79 (−0.85 to −0.74) | **<0.001 (<0.001–<0.001)** | −1.94 (−2.03 to −1.73) | **<0.001 (<0.001–0.01)** | −0.70 (−0.73 to −0.69) | **0.01 (0.01–0.01)** |
| SOI phase 3 | −0.10 (−0.12 to −0.06) | 0.65 (0.57–0.76) | −0.98 (−1.1 to −0.84) | 0.17 (0.13–0.20) | −0.04 (−0.07 to −0.01) | 0.88 (0.78–0.97) |
| SOI phase 4 | −0.48 (−0.52 to −0.47) | **0.04 (0.03–0.04)** | −0.91 (−1.05 to −0.73) | 0.11 (0.08–0.17) | −0.51 (−0.53 to −0.50) | 0.07 (0.06–0.08) |
| SOI phase 5 | −0.02 (−0.03 to 0.01) | 0.92 (0.86–0.98) | −1.01 (−1.14 to −0.84) | 0.05 (0.03–0.08) | 0.16 (0.14 to 0.20) | 0.50 (0.43–0.56) |

(Fig. 7c), showing a decrease in shark abundance from 14 to 18°C and an increase from ~18 to 26°C (Fig. 9d). When bronze whalers were excluded, the smoother showed the same abundance from 14 to 18°C and then increased to ~25°C before plateauing (Fig. 9d). When dusky whalers were excluded, more sharks were caught when SST was less than or greater than 18°C, and the models with no spinner sharks showed a steady increase in abundance from 14 to 26°C (Fig. 9d). Models without dusky sharks showed higher shark abundances around new moon and decreased more from new to full moon than the models with all whalers (Fig. 9e). Models without spinner sharks showed a higher shark abundance in years with lower or higher SST than 1°C, while models with no dusky sharks showed no relationship (Fig. 9f).

## DISCUSSION

### Temporal and spatial patterns of shark abundance

Seasonal, inter-annual and spatial variability in shark abundance between the SMP regions was evident for all species included in the models (potentially dangerous, white and whaler sharks). Although too few tiger sharks were caught to model abundance, there was seasonal and inter-annual variability in catches (Figs. 3 & 4), with tiger sharks primarily caught off 2 beaches (Wattamolla and Garie towards the south of the SMP; Fig. 5). Analysis of the (monthly) SMP from 1950 to 1982, along with data from the Queensland shark control program and tracking, show that tiger sharks inhabit waters of ~22°C (Payne et al. 2018). Stable isotope analysis of tissues from tiger sharks caught off NSW show that they rely on pelagic food-webs (Ferreira et al. 2017), and satellite tracking off eastern Australia shows that they predominately inhabit continental slope waters (Holmes et al. 2014). The 2 beaches with the highest tiger shark catches have a relatively narrow continental shelf with deep water closer to the shark nets compared to the other beaches. The low catches in the SMP, plus an apparent preference for pelagic habitats with only short sojourns into nearshore waters, suggest that tiger sharks may not pose as high a risk to humans compared to whites or whalers in NSW.

White shark abundance was highest in the austral spring months (September to November; Fig. 3), at the end of the study period (2015–2016) and in the northern-most part of the SMP region. This season-

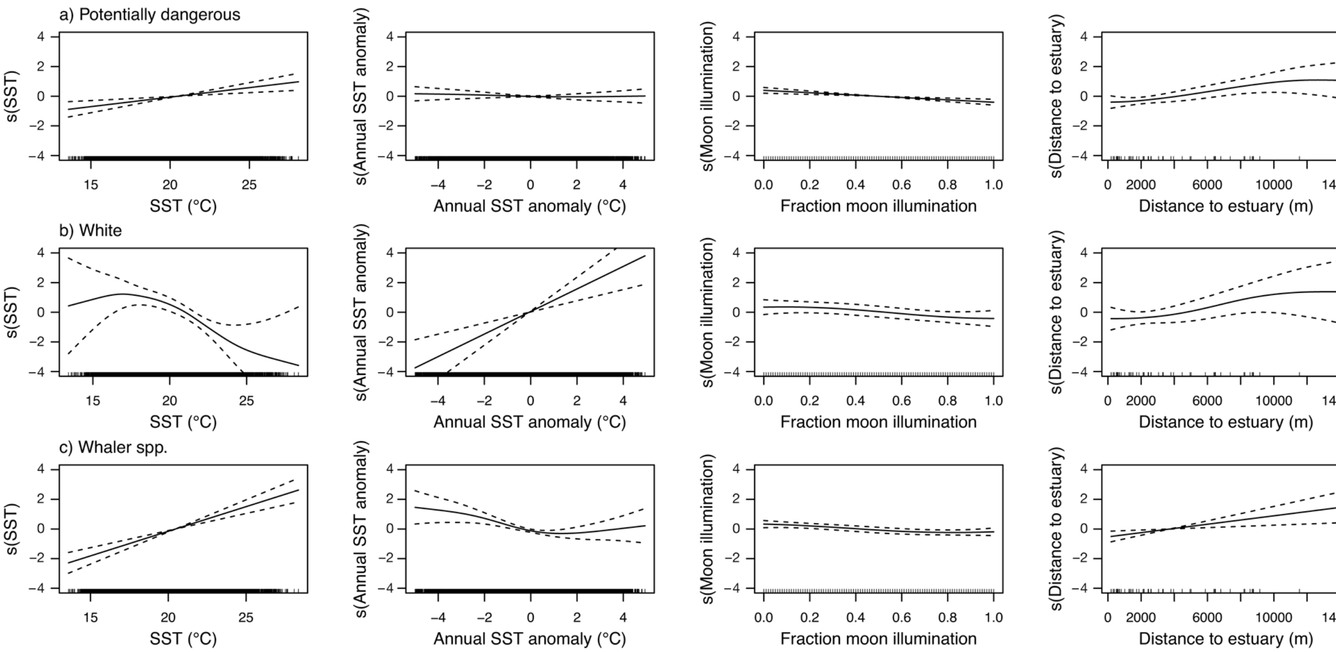



Fig. 7. Median generalised additive mixed model (GAMM) relationships between statistically significant oceanographic and physical model covariates for (a) all potentially dangerous sharks, (b) white and (c) whaler sharks. Solid lines represent the GAM estimates and the dashed lines show the 95% confidence interval. SST: sea surface temperature

ality is consistent with previous research reporting highest white shark catches from September to November between 1950 and 2010 in the SMP (Reid et al. 2011). Reid et al. (2011) reported that the majority of whites caught from 1990 to 2010 in the SMP were juveniles (<3 m). Satellite tagged juvenile white sharks travel through this section of coast during the austral spring and summer (Bruce & Bradford 2012). Inter-annual catches of white sharks showed a linear increase over the whole study period (Fig. 6b). Reid et al. (2011) reported that white shark catches in the NSW SMP decreased substantially from 1970 to the mid-1990s and then increased from the late 1990s to 2009. Here we show that the catch has continued to increase over the 23 yr period modelled (Fig. 6b: from −2 to +2). This is equivalent to an increase of 0.17 sharks or 4% $yr^{-1}$, which is within the 2–6% increase modelled for white sharks recovering from population depletion in Western Australia (Braccini et al. 2017). White sharks have been listed as a 'vulnerable' species in Australia since 1999, although recreational and commercial fishing remain ongoing

Table 5. Median estimates and p-values from generalised additive mixed models (GAMMs) of whaler sharks and models with one species removed at a time modelled against month, year and region from 2010 to 2016. Species names indicate which species were removed from the models. Models with common blacktip sharks excluded did not converge. **Bold** text shows significant variables (median and maximum p-values < 0.05), and *italicised* text indicates that the median p-value was significant (< 0.05) but the maximum was not. * denotes a significant difference between the model estimate from the GAMM with all whalers versus the GAMM with a species removed (Wilcoxon rank tests; α = 0.05)

| | All whaler spp. Median β | Bronze Median β | Bull Median β | Dusky Median β | Spinner Median β |
|---|---|---|---|---|---|
| s(Year) | **1.55 (1.07–1.86)** | **0.94 (0.92–0.95)*** | **1.61 (0.93–1.89)*** | **1.55 (0.85–1.89)** | **0.89 (0.88–1.29)*** |
| s(Month) | **1.62 (1.43–1.75)** | **2.28 (2.11–2.37)*** | *1.31 (1.12–1.42)* | **2.32 (2.12–2.62)*** | *1.48 (1.15–1.65)** |
| (Intercept) | **−6.09 (−7.17 to 5.30)** | **−5.78 (−6.48 to −5.38)*** | **−6.07 (−7.12 to −5.40)** | **−6.37 (−7.63 to −5.49)** | **−6.56 (−7.26 to −5.76)** |
| Central Coast | 0.92 (0.63–1.27) | 1.16 (1.03–1.38)* | 1 (0.78–1.40) | 0.19 (0.14–0.26)* | 0.43 (0.30–0.52)* |
| Sydney North | 0.55 (0.37–0.81) | 0.53 (0.40–0.66)* | 0.66 (0.45–0.89) | −0.27 (−0.42 to −0.13)* | 0.97 (0.71–1.26)* |
| Sydney Central | 0.16 (0.03–0.23) | 0.62 (0.50–0.74)* | 0.10 (0.04–0.23)* | −1.06 (−1.57 to −0.80)* | 0.23 (0.15–0.38)* |
| Sydney South | 1.36 (1.09–1.77) | 1.40 (1.23–1.75) | 1.31 (1.06–1.71) | 0.39 (0.29–0.55)* | 1.68 (1.36–1.98)* |
| Illawarra | 1.35 (1.01–1.72) | 1.08 (0.83–1.48)* | 1.24 (1 .00–1.60)* | 0.77 (0.55–1.02)* | 1.69 (1.30–2.03)* |

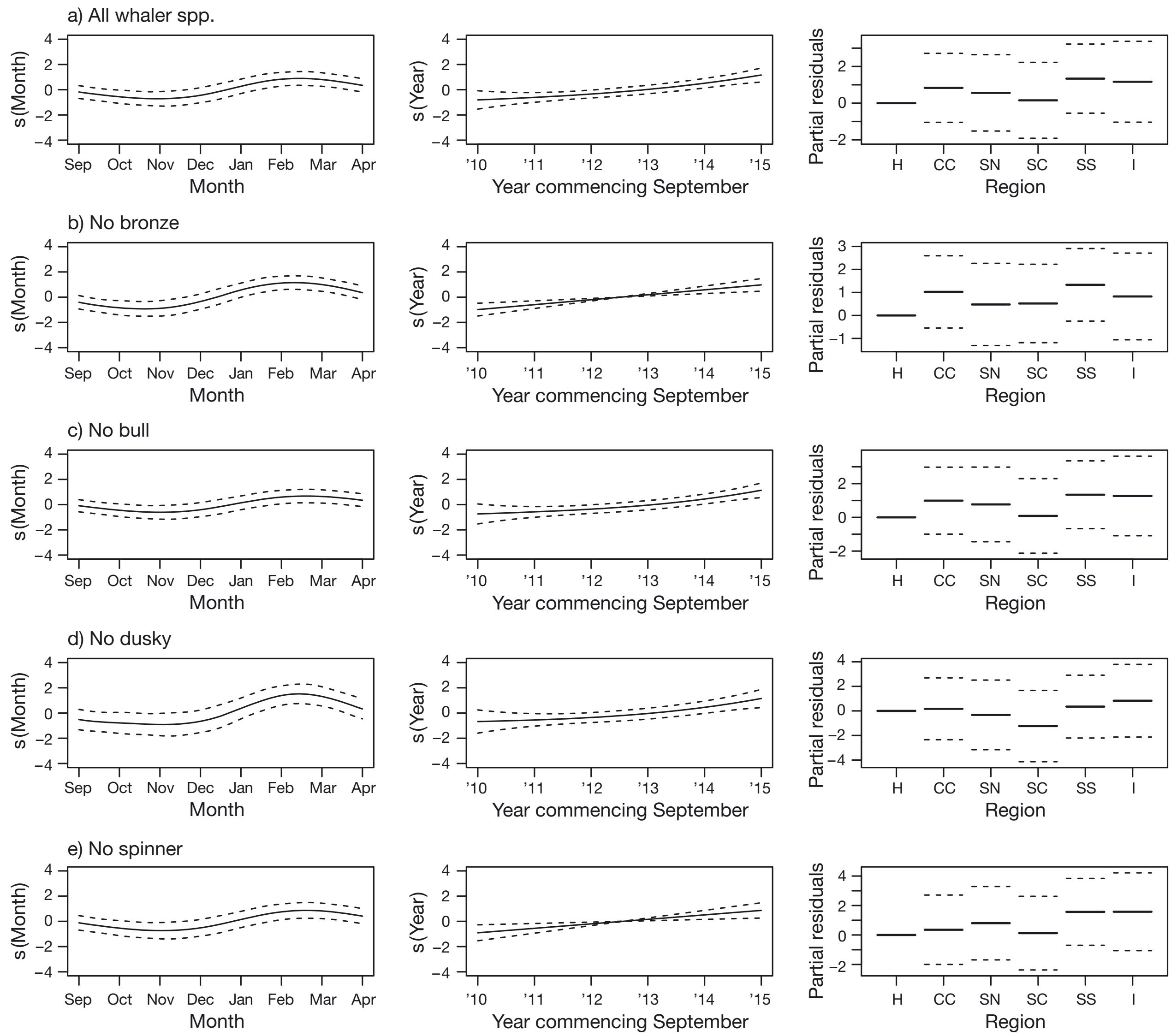



Fig. 8. Median generalised additive mixed model (GAMM) relationships for (a) all whaler shark species and (b–e) with 1 whaler species removed from the catch modelled against month, year (commencing in September; from 2010 to 2016) and Shark Meshing Program region. Region is plotted as north to south (from left to right) with the Hunter region used as the reference; abbreviations as in Fig. 6. Solid lines represent the GAM estimates, and the dashed lines show the 95% confidence interval

threats (DSEWPaC 2013). The increase in catches observed in this study could reflect the effectiveness of conservation efforts. However, further research, with larger sample sizes, would be needed to verify this, as uncertainty in life-history stages can greatly influence a population trajectory (Braccini et al. 2017).

White shark catches were not evenly distributed within the netted region of the NSW coastline, with the northern-most region (Hunter; Fig. 1) exhibiting the highest catches. This area is adjacent to Port Stephens, a recognised white shark nursery area where sharks reside during the austral spring and summer (Bruce & Bradford 2012). The central regions of the SMP (the Sydney North and Sydney Central regions; Fig. 1) had significantly lower catches than the Hunter region. This suggests that white sharks do not travel from offshore to the nearshore zone in this region of the NSW coastline. These catch characteristics corroborate previously described movements for juvenile white sharks where they travel offshore from the Port Stephens nursery area to other areas and do not display residence behaviour outside of the nursery areas (Bruce & Bradford 2012).

More whaler sharks were caught in the austral summer and early autumn (January to March) than in other months (Fig. 3), but with a varying inter-

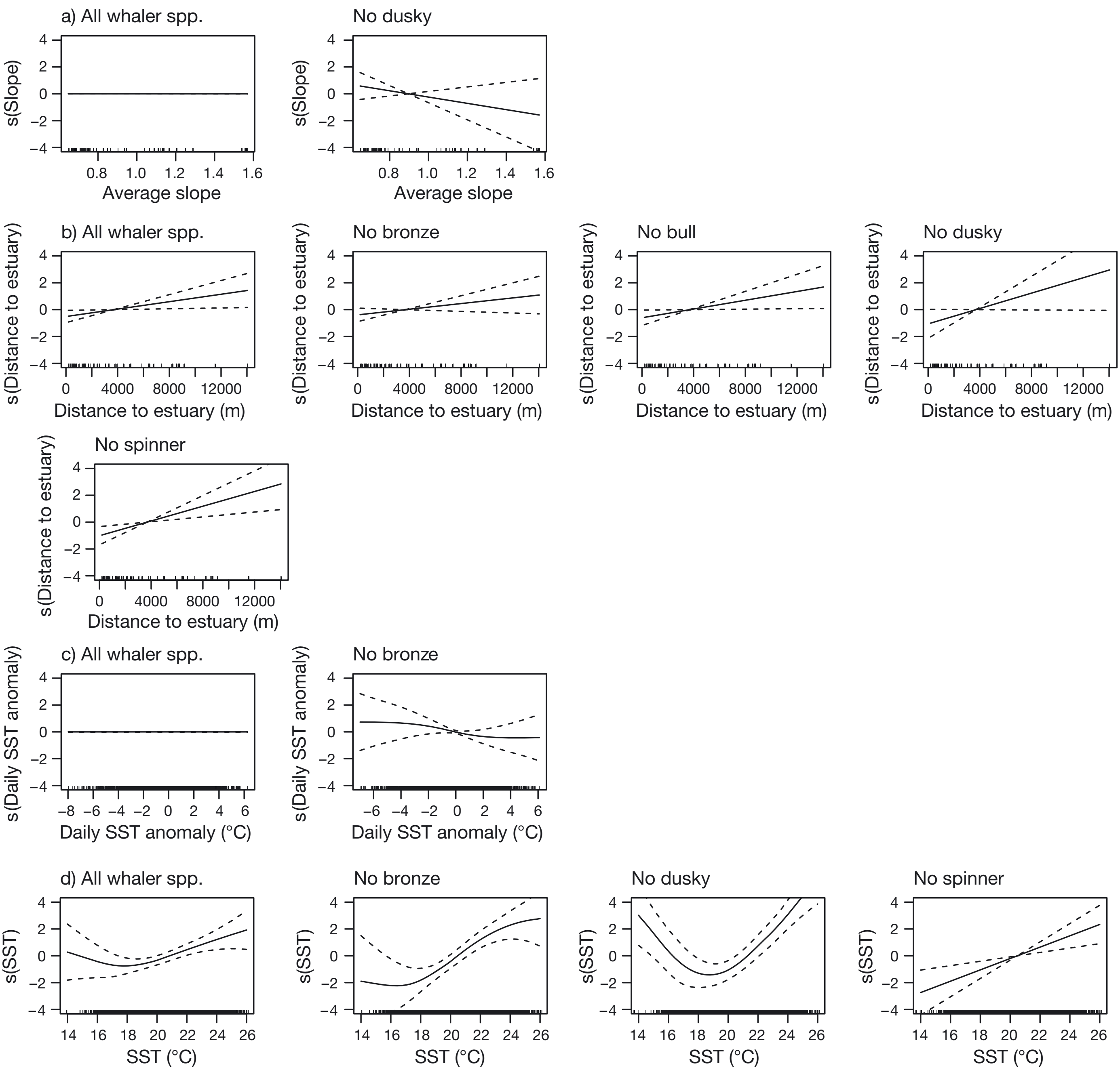
Table 6. Median estimates and p-values from generalised additive mixed models (GAMMs) of whaler sharks and models with 1 species removed at a time modelled against oceanographic and physical variables from 2010 to 2016. Species names indicate which species were removed from the models. Models with common blacktip sharks excluded did not converge. **Bold** text shows significant variables (median and maximum p-values < 0.05), and *italicised* text indicates that the median p-value was significant (< 0.05) but the maximum was not. * denotes a significant difference between the model estimate from the GAMM with all whalers versus the GAMM with a species removed (Wilcoxon rank tests; α = 0.05). SST: sea surface temperature, SOI: Southern Oscillation Index

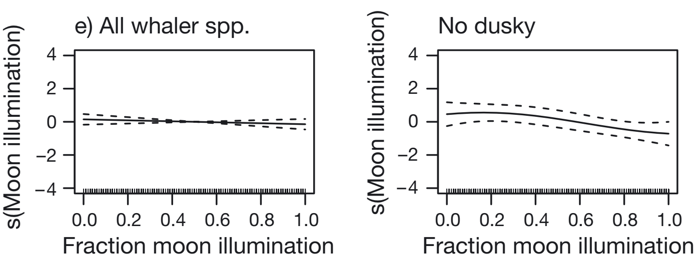
| | All whaler spp. Median β | Bronze Median β | Bull Median β | Dusky Median β | Spinner Median β |
|---|---|---|---|---|---|
| s(Average slope) | 0.00 (0.00–0.00) | 0.00 (0.00–0.00) | 0.00 (0.00–0.00) | 0.56 (0.51–1.04)* | 0.00 (0.00–0.00) |
| s(Beach length) | 0.00 (0.00–0.00) | 0.00 (0.00–0.00) | 0.00 (0.00–0.00) | 0.00 (0.00–0.00) | 0.00 (0.00–0.00) |
| s(Beach orientation) | 0.00 (0.00–0) .00 | 0.00 (0.00–0.00) | 0.00 (0.00–0.00) | 0.00 (0.00–0.00) | 0.00 (0.00–0.00) |
| s(Distance to estuary) | **0.85 (0.85–0.86)** | 0.74 (0.71–0.99)* | **0.84 (0.83–1.29)*** | **0.82 (0.78–0.83)*** | **0.91 (0.9–0.91)*** |
| s(Daily SST anomaly) | 0.00 (0.00–0.86) | **0.81 (0.00–2.31)*** | 0.00 (0.00–1.38) | 0.00 (0.00–1.05) | 0.00 (0.00 – 0.00) |
| s(SST) | **1.82 (0.92–1.98)** | **0.96 (0.96–2.08)*** | **1.59 (0.9–2.07)** | **2.48 (2.33–3.11)*** | **0.93 (0.89–1.78)*** |
| s(Moon illumination) | 0.72 (0.46–0.82) | 0.64 (0.31–0.90) | 0.62 (0.28–0.87) | *1.33 (1.10–2.67)** | *0.73 (0.56–0.83)* |
| s(Annual SST anomaly) | *1.90 (1.52–2.52)* | **1.99 (1.77–2.20)** | **1.95 (1.62–3.28)** | 0.00 (0.00–0.00)* | **2.11 (1.93–2.38)*** |
| s(SST gradient) | 0.00 (0.00–0.00) | 0.00 (0.00–0.00) | 0.00 (0.00–0.00) | 0.00 (0.00–0.00) | 0.00 (0.00–0.00) |
| (Intercept) | **−5.34 (−6.22 to −4.64)** | **−5.37 (−6.00 to −4.69)** | **−5.40 (−7.21 to −4.57)** | **−8.83 (−16.02 to −6.30)*** | **−6.06 (−7.43 to −5.01)** |
| SOI phase 2 | **−1.75 (−2.04 to −1.28)** | **−1.77 (−2.01 to −1.48)** | **−1.83 (−2.39 to −1.40)** | **−1.76 (−1.97 to −1.49)** | **−1.59 (−1.80 o −1.40)*** |
| SOI phase 3 | −0.55 (−0.87 to −0.36) | −0.44 (−0.69 to −0.31) | −0.54 (−0.90 to −0.29) | −0.60 (−1.03 to −0.16) | −0.77 (−1.29 to −0.51)* |
| SOI phase 4 | **−1.31 (−1.72 to −1.03)** | **−1.43 (−1.69 to −1.2)** | **−1.53 (−2.49 to −1.12)** | **−2.10 (−3.27 to −1.45)*** | −1.14 (−1.42 to −0.93)* |
| SOI phase 5 | −0.29 (−0.50 to −0.04) | 0.45 (0.21–0.75)* | −0.33 (−0.43 to −0.22) | −0.19 (−0.58 to +0.64) | −0.37 (−0.64 to −0.13)* |

annual catch rate (Fig. 4). Latitudinal catch rates were not consistent, with only a few beaches exhibiting higher catches (e.g. Wattamolla and Garie beaches in the south of the SMP, and Stockton beach in the northern Hunter region) (Fig. 5). Models that excluded common blacktip sharks from the whaler catch did not converge, showing the strong influence that this species had on the relationships observed across all whaler species. This is unsurprising given that it was the second most abundant whaler species caught overall from 2010 to 2016 and that catch varied inter-annually (Fig. 2). Inter-annual variability in the models with all whaler species could reflect varying environmental conditions across the years driving different shark abundances (Fig. 2). While size was not considered in this study, previous research has shown that the SMP catches a wide size range of whaler sharks (Reid et al. 2011). Thus, the catch modelled in this study likely comprises both juveniles and adults, and some might exhibit an ontogenetic shift in the ecological niches they inhabit and so produce different responses to varying environmental conditions. Nevertheless, the sensitivity analyses showed that when individual species were excluded from the whaler catch, all models showed an increase in shark abundance during January to March and from 2010 to 2016. Common blacktip sharks, the only species that when excluded from the whaler catch the models did not converge, are distributed through the tropics and warm temperate regions (Last & Stevens 2009) and would likely be present along the SMP region year-round.

Significantly lower catches of whalers in the central regions of the SMP (Sydney north and central SMP regions; Fig. 1) suggest that they could display similar behaviour to white sharks. Alternatively, whaler species that used to be resident in these regions may have been fished out so that the nets only harvest sharks migrating through the area (Dudley 1997). Removal of local populations could, however, lead to an edge effect with alongshore movements of sharks leading to higher catches in nets on the northern and southern portions of the netted area (Dudley & Cliff 1993). However, recurring seasonal long-distance migrations of bull sharks from tropical waters to Sydney Harbour (Heupel et al. 2015), in the centre of the SMP, with very few catches of this species in the SMP suggest that despite travelling along this coastline, these sharks are not regularly caught in the nets.

The diverging seasonal trends of white and whaler sharks led to low variability in the seasonal



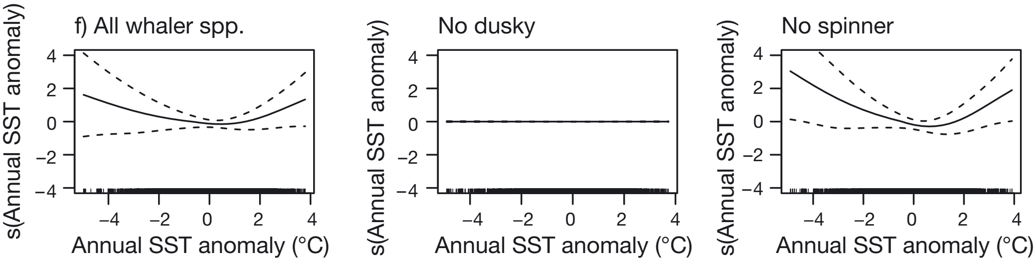




Fig. 9. Median generalised additive mixed model (GAMM) relationships for either all whaler shark species or with 1 whaler species removed from the catch modelled against significant oceanographic and physical model covariates. Solid lines represent the GAM estimates and the dashed lines show the 95% confidence interval. SST: sea surface temperature

trend for all potentially dangerous sharks versus month (Fig. 6a). However, the inter-annual trend was overall similar to that of whalers (Fig. 6c), suggesting that the higher catches of whalers dominate the model. Nevertheless, this model does show that potentially dangerous sharks occur along this portion of the NSW nearshore coastline from September to April, with an increase in abundance during the austral summer months when more people are likely to be using the ocean. Despite this, attacks on humans remain low (McPhee 2014).

### Oceanographic and physical influences on shark abundance

Overall, the abundance of all shark species/groups tested (all potentially dangerous sharks, whites and whalers) were influenced by mean SST, SOI phase, moon illumination and distance to estuary. Tracking of tagged juvenile white sharks off the east coast of Australia indicated that this species prefers water with SSTs between 18 and 20°C (Bruce & Bradford 2012). These findings concur with observations in South Africa, where the probability of encountering white sharks was highest in SSTs of 17–18°C (Wintner & Kerwath 2018) or 14–18°C (Weltz et al. 2013). White sharks in the eastern Pacific use SST niches of ~10–15°C and ~18–25°C (Block et al. 2011). Although the age class was not reported in any of these latter studies, the studies from South Africa likely reflect the SST preference of juveniles or subadults (as they are most commonly encountered at the study sites, Cliff et al. 1989 and Kock et al. 2013, respectively) while the results of Block et al. (2011) could possibly reflect the thermal preferences of larger sharks using broad ranges of temperatures as has been observed in the North Atlantic (Skomal et al. 2017). White sharks in this latter location inhabit temperature ranges of 1.6–30.4°C; however, this is largely driven by sharks >3 m using pelagic waters, as shelf-oriented white sharks occupied a consistent temperature range of between 13 and 23°C (Skomal et al. 2017).

SST may be a proxy for other environmental variables (Robbins & Booth 2012), such as productivity. Although chl *a*, a recognised indicator of productivity, could not be included in our analyses, phytoplankton biomass within the northern region of the SMP increases up to 107% annually each spring with little inter-annual variability (Everett et al. 2014). This area exhibits more frequent upwelling-favourable conditions during the period of peak catch (September to December; Rossi et al. 2014). These regular spring blooms, and subsequent increases in local fish stocks, provide a predictable seasonal cycle which may attract sharks (Bruce & Bradford, 2012).

Six of the 7 whaler species caught inhabit warm temperate to tropical waters (i.e. all species except bronze whalers; Last & Stevens 2009). Many whaler species caught in the SMP undertake long-distance, temperature-regulated migrations (e.g. common blacktip sharks: Heupel 2007; bull sharks: Heupel et al. 2015; dusky sharks: Barnes et al. 2016), with increases in abundance in temperate areas only during periods of warmer water. As whaler sharks are ectothermic, remaining within a thermal preference would decrease the energetic requirements of thermoregulation (Carlson et al. 2004). Therefore, it is unsurprising that their abundance increases with increasing water temperature in the later summer and autumn months when SST is highest in NSW. However, when all whaler species were included in the models, the data from 2010 to 2016 showed that there were 2 temperature niches (~14–18°C and >18°C). When bronze whalers were excluded from the models, the lower niche decreased, suggesting they are the predominant species caught when SST is <18°C. Bronze whalers inhabit bays in Argentina when water temperatures are ~16°C (Lucifora et al. 2005) and are distributed through southern Australia (Last & Stevens 2009), where water temperatures are lower. The 2 temperature niches were more pronounced when dusky whalers were excluded from the models, as they occupy broad thermal niches (Dudley et al. 2005, Barnes et al. 2016) and are caught throughout the year. Dudley et al. (2005) found that dusky whalers were caught in the shark meshing nets deployed off South Africa when water temperatures were 16 to 27°C, with seasonal peaks in the summer and winter, which they attributed to catching sharks of different age classes. Similarly, Wintner & Kerwath (2018) found higher catches when the water was <18°C and between 20 and 22°C, and Barnes et al. (2016) found that tagged dusky whalers occupied waters of 18–26°C. The results in our study when spinner sharks were excluded that suggest they were caught in low water temperatures (less than 18°C) is surprising given that their abundance increases with increasing water temperature in South Africa (Wintner & Kerwath 2018). However, Allen & Cliff (2000) found that larger spinner sharks were caught in the same shark nets in the summer and smaller sharks in the winter. Although size was not taken into account in our study, younger spinner sharks are predominately caught in the SMP (Dalton et al. 2017).

Extreme temperature events, such as ENSO, have been cited as possible causative factors influencing unprovoked shark attacks as they alter the natural habitat for sharks and their prey (Chapman & McPhee 2016). The results of this study show significantly lower shark abundance for all species/groups tested during La Niña episodes compared to El Niño (SOI phase 2: consistently positive; Table 4). Towner et al. (2013) found that white shark numbers increased during warmer (El Niño) events, which is surprising given their higher catch rates during lower SSTs in the SMP. However, significantly higher abundances of white sharks occurred during years with higher SSTs than the long-term average (i.e. positive annual SST anomalies as shown in Fig. 7b).

In contrast, higher abundances of whalers during El Niño versus La Niña events was not surprising given that the majority of the species caught in the NSW SMP are found in tropical waters (Last & Stevens 2009). Whaler abundance was highest during ENSO neutral phases (phase 5: consistently near zero; Table 4) and only higher in the sensitivity tests conducted for the whaler species when bronze whalers were excluded from the catch (Table 6). Whaler catch was higher in years with lower SST than the long-term mean (i.e. low SST anomaly in Fig. 7c), although no relationship was found when dusky whalers were excluded from the whaler catch. Pelagic fish species are known to extend their ranges poleward during periods of higher SSTs (Hobday 2010, Hill et al. 2016). Similarly, whaler sharks may extend their range poleward, occupying warmer waters to the south of the SMP regions during El Niño years with higher SSTs than ENSO neutral years.

Phases of the moon are known to influence the abundance and behaviour of white sharks around seal colonies, with an increase in the likelihood of successful prey (seal) capture during new moon (Fallows et al. 2016). Similarly, catch rates of large fish (e.g. black marlin) and sharks (e.g. shortfin makos) (Lowry et al. 2007) and vertical movements of juvenile white sharks (Weng et al. 2007) in pelagic waters are correlated with lunar phase, as the vertical distribution of their prey species changes with the levels of light from the moon (Benoit-Bird et al. 2009). In nearshore areas, lunar periodicity (and the associated changes in tidal range) affect the abundance of zooplankton (Marques et al. 2009) and movement (Henderson et al. 2014) and spawning (Taylor 1984) of teleost fish. In this study, there was a small, but significant, decrease in catch of all potentially dangerous sharks, whites and whalers as moon illumination increased. These results are similar to those of Weltz et al. (2013), who found an increased likelihood of white shark sightings around new moon. This could suggest that sharks occupy nearshore areas during new and quarter moon in sync with movement of prey distributions. Alternatively, the nets may be more visible with increasing moon illumination and sharks are less likely to be caught.

White and whaler abundance increased with increasing distance from the nearest estuary, with the highest abundance of whites 10 km from an estuary. White sharks occur in estuaries for only short periods of time compared to surrounding coastal areas (Harasti et al. 2017); thus estuaries are unlikely to be an important variable in their distribution. However, the influence of distance to estuary is surprising for whaler sharks, as bull sharks and dusky whalers are regularly found near or within Sydney Harbour (Smoothey et al. 2016), a large marine-dominated estuary. Even when each of the whaler species was excluded from the catch one at a time, shark abundance still increased with increasing distance from the nearest estuary. Beach length was significant for white sharks and almost significant for all potentially dangerous sharks and may therefore play a more important role in shark distribution than the distance to an estuary. The longest beach (Stockton beach) in the SMP region is within a recognised white shark nursery area (Bruce & Bradford 2012) and a highly productive area with frequent cyclonic eddies (Brassington et al. 2011). Surprisingly, daily SST anomalies or SST gradient were not significant for any of the species groups tested (Table 4), although the former was significant when bronze whalers were excluded from the whaler catch. Frontal zones are highly productive areas and are important for many marine vertebrates (reviewed by Scales et al. 2014); therefore, it is surprising there we found no relationship in this study.

## CONCLUSIONS

The results of this study highlight the seasonal variation in potentially dangerous shark species inhabiting the temperate coastal areas along south-eastern Australia. Due to the distribution and movements of these species occurring off NSW, potentially dangerous sharks are present along this coastline from September to April, and maybe all year-round, although different species present higher or lower risk to beach and ocean users at different times of the year. Nonetheless, shark attacks remain a relatively rare event despite the large human population using the ocean (West 2011, McPhee 2014). The relatively low catch of tiger sharks precluded modelling conditions of potential enhanced risk by this species; however, the overall low catch and it being caught only at beaches with a narrow continental shelf suggest that this species presents less potential danger to NSW beach-goers than white or bull sharks. Only 2 tiger shark attacks were recorded in NSW between 1993 and 2015, and both occurred along the far northern sub-tropical coastline (Australian Shark Attack File unpubl. data). The high number of tiger shark attacks reported by West (2011) were likely from tropical regions in Queensland, where the shark control program reports much higher catches of tiger sharks (data available from https://www.daf.qld.gov.au/fisheries/services/shark-control-program).

Our analysis highlights that white shark nearshore abundance increased during periods of SST between 17 and 18°C, and declined when SST increased above 19°C as well as during years that SST was higher than the long-term average (i.e. El Niño years). Whaler (and bull) shark abundance increased during periods of warmer water, but was highest during ENSO neutral phases and during periods of low SST anomaly. This provides a first indication of the oceanographic (changes in SST or ENSO) conditions under which increased shark mitigation measures need to be employed.

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