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Environmental drivers of abundance and residency of a large migratory shark, *Carcharhinus leucas*, inshore of a dynamic western boundary current

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ABSTRACT: Understanding the environmental drivers of movement of potentially dangerous shark species can help inform mitigation strategies. Bull sharks are known to undertake seasonal migrations from tropical to temperate waters along the east coast of Australia. However, the environmental drivers of their movements from sub-tropical to temperate waters are unknown. Using multi-year (2010–2016) acoustic telemetry data from 68 bull sharks and generalised additive models, we evaluate the (1) temporal and (2) environmental variables that drive shark abundance, presence/absence and residency along the south-eastern coast of Australia. Bull sharks were detected in sub-tropical waters (~28°S) almost year-round but were most abundant in the southern latitudes in the austral summer and autumn. Abundance, presence and residency were all highest around the latitudes that sharks were tagged, indicating a bias to tagging location, and at estuary mouths and mid-shelf (20–60 m water depth) habitats. Bull sharks were present when sea surface temperature (SST) was 20–26°C, with peak abundance at 24°C, and low chlorophyll *a* (chl *a*). There was a higher abundance of sharks in months when SST was higher than the long-term average. Residency duration was longest when SST was <22°C or >24°C, and in areas of low SST slope (<3°C) and chl *a* slope. Although no sex bias in residency time was detected, sharks <200 cm TL had the longest residency times. These results provide the power to predict when and where bull shark abundance may be higher, which can help management authorities deploy mitigation strategies for bull shark interactions along eastern Australia.

KEY WORDS: Bull shark · East Australian Current · Generalised additive modelling · IMOS ATF · Passive acoustic telemetry · Shark bite mitigation

1. INTRODUCTION

Mitigating interactions between humans and large, potentially dangerous sharks occurring in coastal and estuarine areas is a complex issue for management authorities. Shark bites attract a disproportionate amount of media attention and public concern (Neff 2012) despite their relative rarity (West 2011, Mcphee 2014). The majority of serious and fatal injuries on humans are attributed to white sharks *Carcharodon carcharias*, tiger sharks *Galeocerdo cuvier* and bull sharks *Carcharhinus leucas* (West 2011, Mcphee 2014). Historically, shark mitigation strategies have used relatively detrimental practices such as fishing nets to remove sharks from the vicinity of populated beaches (Dudley 1997, Reid et al. 2011).

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More recently, however, there has been a greater focus on non-lethal methods such as translocation of sharks caught near beaches (Hazin & Afonso 2014), aerial (Robbins et al. 2014) or land-based (Kock et al. 2012) surveillance, and ecological studies to predict drivers of local shark abundance in areas populated by swimmers and surfers (Weltz et al. 2013, Lee et al. 2018a, Werry et al. 2018, Wintner & Kerwath 2018). Understanding the drivers of local shark distribution and abundance will enhance the predictability of shark encounters and potentially reduce the risk of shark bites by informing water-users about areas and times of increased risk or through deployment of target-specific shark mitigation strategies such as increased drone surveillance.

Large sharks play an important role in the health of marine ecosystems, and their removal can cause major perturbations (Ruppert et al. 2013, Grubbs et al. 2016). Bull sharks and tiger sharks are primarily found in tropical and warm temperate waters (Last & Stevens 2009), either in coastal and estuarine areas (bull sharks; Carlson et al. 2010, Smoothey et al. 2016) or along the continental shelf and across open oceans (tiger sharks; Holmes et al. 2014, Lea et al. 2015, 2018), respectively. In contrast, white sharks inhabit waters of the continental shelf of temperate and subtropical regions, venturing to offshore areas for several months of the year (Jorgensen et al. 2009, Bruce & Bradford 2012, Skomal et al. 2017). Management of these species is often complicated due to their long-distance migrations (Bruce & Bradford 2012, Werry et al. 2014, Francis et al. 2015, Heupel et al. 2015) and cross-jurisdictional movements (Heupel et al. 2015). However, understanding the environmental variables that drive abundance and residency can help individual jurisdictions identify when those shark species are most likely to encounter humans and potentially pose a risk. Beach management authorities can potentially use this information to implement target-specific mitigation strategies during periods of increased presence of potentially dangerous sharks.

Bull sharks occur along the entire east coast of Australia, the most populous coastline in the country. Although they are known to travel over 1700 km annually from the tropical waters in north-eastern Australia (Queensland; see Fig. 1) to temperate estuaries in south-eastern Australia (Heupel et al. 2015), not all bull sharks undergo these movements (Espinoza et al. 2016). Southward movement during the warmer months enables bull sharks to occupy the estuarine waters of Sydney Harbour during summer and early autumn (Smoothey et al. 2016). This is the time when the East Australian Current (EAC), the dynamic western boundary current (WBC) of the south Pacific gyre, brings warmer waters (Wood et al. 2016) and tropical species (Booth et al. 2007) into this temperate environment. Current hypotheses therefore imply that temperature is a driving force regulating abundance and distribution of many tropical species, including bull sharks, in the temperate waters of south-eastern Australia.

The EAC also strongly influences the productivity of the continental shelf waters through upwelling of nutrient-rich water and generation of mesoscale eddies (Roughan & Middleton 2002). The strength of the EAC varies seasonally (Ridgway & Godfrey 1997, Archer et al. 2017), 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 upwelling (Roughan & Middleton 2002, 2004). Yet bull sharks return annually to Sydney Harbour, irrespective of EAC variability (Smoothey et al. 2016).

Extensive research has quantified that bull sharks exhibit high philopatry to pupping grounds (Karl et al. 2011, Tillett et al. 2012, Chapman et al. 2015), tropical coastal areas (Brunnschweiler et al. 2010, Brunnschweiler & Barnett 2013) and offshore reefs (Heupel et al. 2015, Espinoza et al. 2016). While recent studies have investigated movement patterns and/or drivers of bull sharks along the east coast of Australia, our study is the first to examine the timing, duration and environmental drivers of the movement patterns of bull sharks in sub-tropical and temperate coastal environments. For example, Heupel et al. (2015) showed that adult bull sharks are capable of undertaking long-range movements between temperate and tropical environments, yet little was revealed about the seasonal linkages between the 2 regions or the drivers responsible for their movement decisions. In tropical and sub-tropical environments, Espinoza et al. (2016) quantified patterns of movement and residency of adult bull sharks and identified biological and environmental drivers responsible for the observed patterns. Yet, little is known about how environmental variables relate to their movements into sub-tropical and temperate coastal waters. This paucity of knowledge exists despite these regions being the areas in which bull shark distributions are most likely to differ with the variability in boundary current characteristics and are also those which may exhibit marked changes under climate change as WBCs warm and strengthen.

We used multi-year (2010–2016) acoustic telemetry data from 68 bull sharks tagged in south-eastern Australia to determine (1) the seasonal and inter-annual variability in bull shark abundance, (2) the relative influence of biophysical conditions on broad-scale patterns of bull shark abundance and (3) the environmental drivers of residency behaviour by modelling individual-level residency times along the EAC. This information will help inform when and where it is appropriate to employ shark bite mitigation strategies to reduce the risk of human–bull shark interactions.

2. MATERIALS AND METHODS

2.1. Study site

The study area was in the western Tasman Sea (Fig. 1) and extended from 27.1°S (Moreton Bay) to 35.2°S (Sussex Inlet, New South Wales [NSW]; Fig. 1) spanning subtropical to temperate latitudes. This encompasses the latitudes where the EAC is most coherent in the north and extends southward beyond the known distribution of bull sharks along the east coast of Australia (Sydney Harbour, 33.8°S; Last & Stevens 2009). To determine the spatial patterns in bull shark abundance and residency, the study area was separated into 46 × 0.2° latitudinal bands and classified into 4 different habitat types: estuary mouth (<1 km upstream of an estuary); inner-shelf (0–20 m water depth); mid-shelf (20–60 m); and outer-shelf (60–200 m) habitats using the definitions given in Jordan et al. (2010) (Fig. 1). Latitudinal bands of 0.2° were chosen to match the along-shelf de-correlation length (i.e. the distance at which measurements become statistically dissimilar) of sea surface temperatures (SSTs; see Section 2.3), and this was the distance that resulted in the highest number of latitudinal bands having receivers deployed throughout the study period.

2.2. Tagging and acoustic tracking

Seventy-two bull sharks were caught using bottom-set longlines in Sydney Harbour (33.8°S, 151.2°E; n = 41) and Clarence River (29.4°S, 153.3°E; n = 31; Table 1) between March 2009 and January 2013 using methods described in Smoothey et al. (2016). Each shark had a Vemco V16 acoustic transmitter (16 mm; random transmission interval of 30 to 90 s [n = 2] or 40 to 80 s [n = 70]; for details see Table S1 in the Supplement at www.int-res.com/articles/suppl/m622p121_supp.pdf) inserted into its coelomic cavity via small insertion made along the ventral line approximately 30 cm above the anus. The sex and lengths

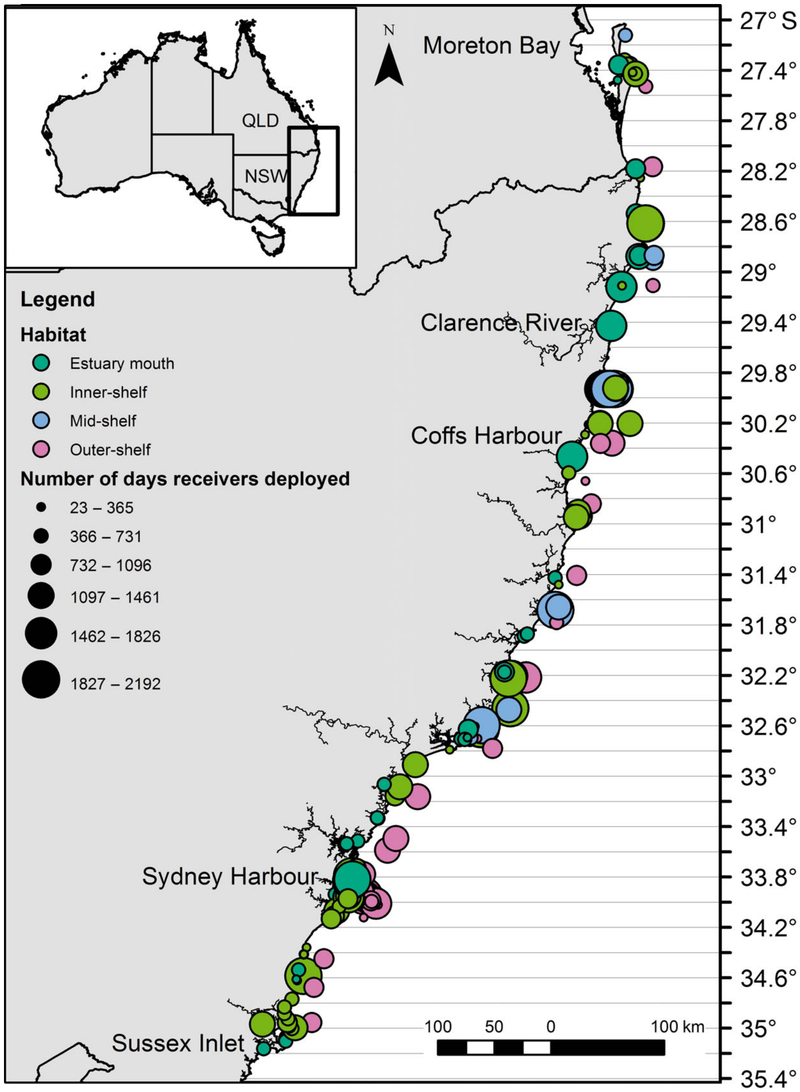

Fig. 1. Locations of the acoustic receivers deployed in the study area (27.1°S–35.2°S). Each receiver is colour coded by habitat type and the size indicates the number of days the receiver was deployed during the study period. Horizontal lines indicate the latitudinal bands used

Table 1. Number of sharks tagged summarised by tagging location (see Fig. 1), size-class and sex

Location tagged	Size class (total length, cm)	Sex	No. of sharks tagged (no. caught by fishers)
Clarence River	<200	Female	15 (4)
Clarence River	<200	Male	10 (2)
Clarence River	200–250	Female	2
Clarence River	>250	Female	4
Sydney Harbour	200–250	Female	2
Sydney Harbour	200–250	Male	5
Sydney Harbour	>250	Female	11
Sydney Harbour	>250	Male	23

(precaudal, fork and total) of each shark were recorded and the hook was removed prior to release. The entire handling process took less than 15 min per shark.

In total, 38 males (Sydney Harbour: n = 28; Clarence River: n =10) and 34 females (Sydney Harbour: n = 13; Clarence River: n = 21) were tagged (Table 1). Bull sharks move from estuarine to marine habitats at around ~130 cm total length (TL; Werry et al. 2011). To ensure only sharks that would be using marine coastal areas were included in the analyses, all sharks that were <130 cm TL at tagging were excluded until they reached that size. Shark lengths post tagging were estimated using von Bertalanffy equations (Fabens 1965) and growth parameters (asymptotic length and Brody's growth coefficient) from 3 studies (Wintner et al. 2002, Neer et al. 2005, Cruz-Martinez et al. 2005). All measurements were converted to TL from precaudal and fork length using equations given in Cliff & Dudley (1991) and Branstetter & Stiles (1987), respectively. The post-tagging date for these individual sharks attaining 130 cm TL was calculated using the mean TL from the 3 different growth models produced using the van Bertalanffy equation and the growth parameters from the above studies. Although analyses of historical shark bites (1900–2010) in Australia found no fatalities were recorded for sharks <200 cm TL, West (2011) established that 22% of bull shark bites were attributed to sharks <200 cm. Therefore, all sharks >130 cm TL were included in the analyses. Irrespective of whether a tagged shark was included in the data analyses from 2 days post-tagging or from the point at which they were estimated to attain >130 cm TL, all sharks included in the analyses were potentially tracked for >1 yr (Table S1). Number of days potentially tracked refers to the number of days from 2 days post-tagging or from the day on which individuals attained >130 cm TL, to the end of the study.

All the acoustic detections from receivers deployed within the study area between 1 September 2010 and 31 August 2016 were downloaded from the Integrated Marine Observing Systems (IMOS) Animal Tracking database (https://animaltracking.aodn.org.au/). In total, this included data from 316 acoustic receivers (Fig. 1). This data was supplemented by additional detections from 41 acoustic receivers deployed and provided by New South Wales Department of Primary Industries (NSW DPI) Fisheries along the coast. The total number of receivers from which data was available within the study extent varied over the course of the study, with the largest number deployed in 2012 (216 receivers) and smallest in 2016 (122). Only data from 2 or more days post-tagging were included in the analyses (see Section 2.4) to remove the influence of any short-term changes in shark behaviour arising from the tagging procedure.

2.3. Environmental data

Remotely sensed sea surface temperature (SST), SST daily climatology and chlorophyll *a* (chl *a*) were downloaded from the AODN IMOS Ocean Portal (https://portal.aodn.org.au) (IMOS 2017), along with physical and ENSO information from a suite of sources (Table 2). The spatial and temporal resolution for each of the remotely sensed variables are summarised in Table 2. These data were then spatially and temporally matched with the bull shark detection data. Derivatives of the remaining variables were calculated as described below.

Differences between *in situ* and satellite-derived SST measurements are common in coastal areas (Smale & Wernberg 2009, Lathlean et al. 2011, Stobart et al. 2016). Lee et al. (2018b) showed that an area- and time-averaged approach, based on known *in situ* de-correlation length and time scales, can be used to process satellite-derived data. The accuracy produced using this method leads to SST measurements with the same temperature differences from *in situ* data as using a single satellite pixel over the study location. This method subsequently increased the number of days that satellite data were available for a particular location by minimising the effect of missing pixels due to localised conditions (e.g. cloud cover) or contamination of coastal areas. A distance of 8 km across-shelf and 20 km along-shelf was used to average the satellite SST values, as these were within known de-correlation distances (Schaeffer et al. 2016) and had the highest correlations overall for this part of the coast (Lee et al. 2018b). A 3-day rolling mean centred on the day of interest was applied to the area-averaged SST data to interpolate the values for days when no satellite data was available (due to cloud cover).

Chl *a* was area-averaged using an across-shelf distance of 4 km and 6 km along-shelf, as these values are less than the de-correlation lengths estimated by Schaeffer et al. (2016). The geometric mean was used to calculate the monthly chl *a* for each latitudinal band and habitat type, as the chl *a* data was log-normally distributed, which is common in continental shelf waters (Mouw & Yoder 2005, Everett et al. 2014).

Monthly SST climatology was calculated as the monthly mean of the daily climatologies (Table 2) for each latitudinal band and habitat type. Monthly chl *a* climatology for each latitudinal band and habitat type were calculated for the study period (6 yr) by taking the geometric mean chl *a* for each month. Monthly SST and chl *a* anomalies were calculated by subtracting the monthly climatologies from the monthly mean for each latitudinal band and habitat type.

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 and north-eastern Indian Oceans. Changes in ENSO have been shown to shift suitable habitats for large pelagic teleost predators (Deary et al. 2015, Hill et al. 2016) and influence the nearshore abundance of white sharks off the coast of South Africa (Towner et al. 2013) and the number of white and whaler sharks caught in shark nets off the coast of NSW (Lee et al. 2018a). 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). Therefore, 5 SOI phases incorporating both the month of interest and the preceding month's values (Stone et al. 1996), were used as indicators of ENSO. The 5 phases used in our models were: Phase 1: consistently negative (El Niño — higher SSTs in equatorial regions); Phase 2: consistently positive (La Niña — lower SSTs in equatorial regions); Phase 3: rapid fall; Phase 4: rapid rise; and Phase 5: consistently near zero (ENSO neutral).

Daily satellite-derived measurements were used to calculate the weekly mean SST and (geometric mean) chl *a* using the same methods as described above.

Table 2. Sources and resolutions of oceanographic data and physical characteristics. AODN: remotely sensed data sourced from the AODN IMOS Ocean Portal (https://portal.aodn.org.au). NA: the metric is not applicable to this dataset

Oceanographic and biophysical variables	Model covariate	Derived variables (units) used as model covariates	Data source	Spatial resolution	Temporal resolution	
					Monthly models	Weekly models
Sea surface temperature (foundation)	SST	SST anomaly (°C) and SST slope	AODN - SST L3S	0.02°	1 month (day and night time) composite	Mean of daily (day and night time) composites
Sea surface temperature climatology	NA	SST anomaly (°C)	AODN - SST Atlas of Australian Regional Seas Daily Climatology Fit	0.02°	Mean of SST anomaly (°C)	NA
Chlorophyll *a* concentration	Chl *a*	Chl *a* anomaly and chl *a* slope	AODN - MODIS OC3 model)	0.01°	Geometric mean of daily values	Geometric mean of daily values
Southern Oscillation Index	SOI		Monthly SOI and SOI phase data (https://www.longpaddock.qld.gov.au/soi/soi-data-files/)		Monthly	NA
Estuary locations	Habitat type		Geoscience Australia (www.ozcoasts.gov.au/search_data/estuary_search.jsp)		NA	NA
Bathymetry	Habitat type		Australian Bathymetry and Topography Grid, June 2009 (Geoscience Australia, www.ga.gov.au/metadata-gateway/metadata/record/gcat_67703)	0.0025°	NA	NA

SST slope, an estimate of thermal fronts (Lea et al. 2018), and chl *a* slope, an approximation of productivity fronts, were calculated as the difference between the maximum and minimum values within the respective areas averaged.

2.4. Data analysis

2.4.1. Seasonal and inter-annual variability in abundance

The number of sharks 'present' in each latitudinal band and habitat type per month was calculated as the sum of all sharks present within that month, including months when no sharks were detected. A shark was considered to be present when there were 2 or more detections within a 24 h period, eliminating the possibility of false detections (Pincock 2011, Simpfendorfer et al. 2015). This was modelled against month (to assess seasonal variability), year (to determine inter-annual variability), latitudinal band and habitat type using a generalised additive mixed model (GAMM) in the 'mgcv' (Wood 2006, 2011) package in R (R Core Development Team 2009; v. 3.4.3). Interactions between month and latitudinal band, and between latitudinal band and habitat type, were also included to assess the abundance of the sharks in each month/habitat type for each latitudinal band. The latitude–month interaction was modelled with a tensor product as the 2 covariates are measured on different scales and this type of spline is invariant to the scale (unlike isotropic thin plate splines). A full tensor product smooth and a tensor product interaction (with main effects also present) were tested and the latter had the lowest Akaike information criterion for small sample sizes (AICc; 'MuMIn' package for R; Bartoń 2016). A cyclic smoothing spline was used on month to account for the cyclic nature of the data. The number of sharks that were tagged increased during the study period. Likewise, the number of receivers that were deployed within each latitudinal band and habitat type varied (Fig. 1). Therefore, the number of sharks that were detectable for the whole month (i.e. sharks were not included the month they were tagged) and the number of receivers deployed were (additively) combined and used as an offset in the model. The inclusion of each of the explanatory variables was assessed using AICc. Poisson, negative binomial and zero-inflated distributions were all tested with the negative binomial having the lowest AICc (ΔAICc $\geq$ 34). The concurvity function in the mgcv package was used to ensure that there was no concurvity (the GAMM equivalent of collinearity) between the explanatory variables. Model adequacy was checked using standard residual plots, as well as auto-correlation function plots and semi-variogram plots to check for un-modelled spatial and temporal correlation. Model predictive error was assessed using k-fold cross-validation, with the data split and randomly sampled into training (75% of total data) and testing (25%) data frames over each of the 5-folds, and calculating both the root mean square error (RMSE) and average error as the model diagnostics (Potts & Elith 2006).

2.4.2. Environmental drivers of abundance and residency

A multi-scale approach was taken to modelling the relative abundance and residency of tagged bull sharks along the EAC. First, broad-scale monthly models were used to determine the relative abundance. Second, finer temporal scale (weekly) models were used to investigate contemporaneous oceanographic and biological influences on individual shark's habitat use.

Broad-scale monthly abundance. Broad-scale monthly relative shark abundance models were used to identify the environmental conditions characterising areas of high abundance. The number of individual sharks present in each latitudinal band and habitat type per month was modelled against mean SST, mean chl *a*, SST anomaly, chl *a* anomaly, monthly SOI phase and an interaction between latitude and habitat type using a GAMM. Again, the total number of sharks tagged and number of receivers deployed within each latitudinal band and habitat type were used as an offset. The same distributions as the seasonal and inter-annual model were tested with the negative binomial having the lowest AICc (ΔAICc $\geq$ 26). Model adequacy and predictive error were checked as described in Section 2.4.1.

Influences on individual habitat use. A 2-stage hurdle model was used to determine the environmental conditions influencing habitat use of bull sharks. A hurdle model uses 2 processes to model the data. The first uses presence/absence of each shark within each latitudinal band and habitat type to determine the environmental variables influencing the areas that the sharks use or do not use. The second uses the zero-truncated residency times (the number of days in a week that a shark was present in each latitudinal band and habitat type) to determine how the environmental variables affect the length of time they occupy the areas that they use. Weekly presence/absence and residency times were modelled against sex of the shark, SST, TL (<200 cm, 200–250 cm, >250 cm TL), chl *a*, SST slope, chl *a* slope, latitudinal band and habitat type, with an individual-level random effect. There was not enough presence/residency time data available in each latitude–habitat combination to include a latitude–habitat interaction. Only weeks when data was available for the full 7 d were included. To account for a higher probability of detecting a shark when more receivers were deployed, the number of receivers deployed within each latitude/habitat type was again used as an offset. Complementary log-log and logit link functions were used to model the presence/absence data, and the model with a logit link function had the lowest AICc (ΔAICc = 1.64). Likewise, the zero-truncated residency data was modelled using Poisson, negative binomial, Poisson-Tweedie and Gamma distributions. The Gamma distribution produced the lowest AICc (ΔAICc ≥ 19.4). Inclusion of the explanatory variables and model checking were conducted as described above. K-fold cross validation was used to assess the predictive error of the presence/absence model and the mean area under the receiver-operating curve (AUC) was used as the model diagnostic. K-fold cross validation with RMSE and average error were used as diagnostics for the zero-truncated residency time model. Post hoc multiple comparison (Wald) tests were used to determine the pairwise significance between the different levels of any multilevel factor (i.e. habitat type and length-class), using the wald_gam_ function in the 'itsadug' package (van Rij et al. 2017).

3. RESULTS

Six of the bull sharks <200 cm TL that were tagged in the Clarence River were caught by fishers (Table 1). The exact date of capture was unknown and the sharks were excluded from all subsequent analyses. The remaining 66 sharks were detected for an average of 40 d (range: 0 to 228 d; Table S1) over the entire study period. These detections varied from 2 d post-tagging until the end of the study. The average period of tracking an individual shark was 1779 d (range: 404 to 2737 d). In total, 15 sharks were not detected on the receivers included in this study or during the timeframe examined (Fig. 2). Eleven of these were <200 cm TL (n = 7 females and 4 males; all tagged in the Clarence River), one was between 200 and 250 cm TL (male; tagged in Sydney Harbour) and 3 were >250 cm TL (n = 1 female tagged in the Clarence River; n = 2 males tagged in Sydney Harbour). One male shark, that was <130 cm TL at the time of tagging, was detected on receivers deployed upstream of the Clarence River entrance after the date it was included in the study. One juvenile female (82 cm TL) tagged in the Clarence River undertook a migration to Sydney 3 yr before reaching ~130 cm TL, but was not detected after the time it was estimated to have reached that length. Shark #51 (Fig. 2), a male that was 228 cm TL when tagged in Sydney Harbour, was only detected on receivers in tropical north-eastern Australia. Likewise, a large female (shark #28 in Fig. 2; 268 cm TL tagged in the Clarence River) was only detected on receivers deployed too far upstream of an estuary in northern NSW to be included in this study. The 51 remaining sharks were detected for varying lengths of time, with the majority inhabiting the study area on a seasonal basis (Fig. 2).

3.1. Seasonal and inter-annual variability in abundance

Abundance of tagged bull sharks was significantly influenced by month, year and latitude, depending on time of year or habitat type (i.e. both latitude-month and latitude–habitat interactions). These variables explained 66.6% of deviance observed in the data. Overall, abundance increased from November, peaked in January then decreased through May (Fig. 3a). However, the magnitude of this increase was strongly influenced by latitude, with the highest abundance of sharks at the same latitude as Sydney Harbour (~33.8°S; Figs. 3c–f & 4), where the majority of the sharks were tagged. Tagged bull sharks were detected at latitudes of ~27°S in varying abundance from August to May (Fig. 4). The number of tagged sharks detected off NSW decreased throughout the study period, with the largest decrease from 2010 to 2011 (Fig. 3b). Receivers in the estuary and mid-shelf habitats recorded more bull sharks compared to the inner- and outer habitats (Figs. 3c–f). K-fold cross-validation with 5 folds showed the number of sharks (per receiver deployed) predicted by the model compared to that observed had a RMSE of 0.95 ± 0.12 (0.25 of the maximum number of sharks detected per receiver deployed) and average error of 0.007 ± 0.02 (<0.01 of the maximum number of sharks detected per receiver deployed).

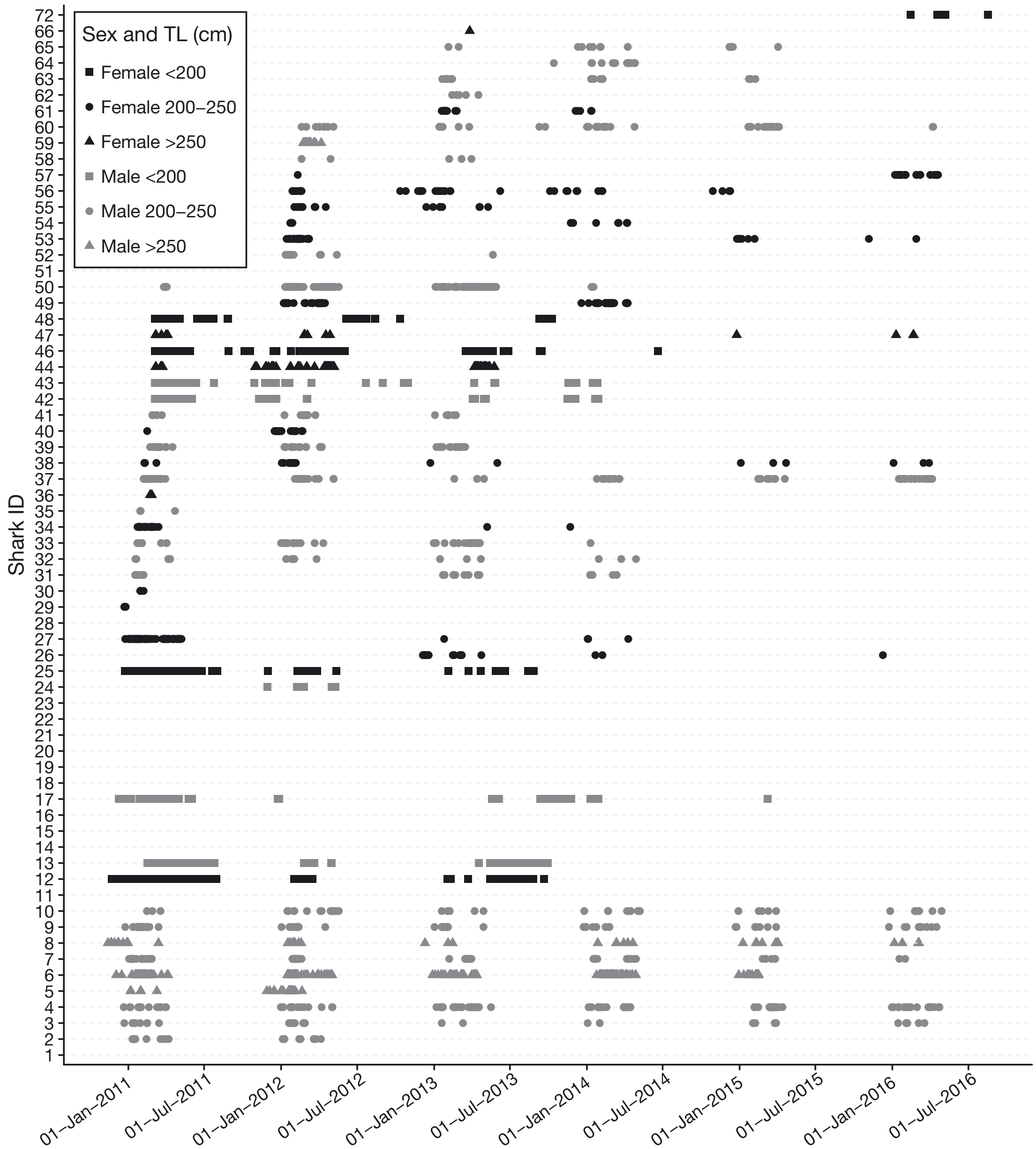

Fig. 2. Time series of detections for each shark across all acoustic receivers deployed in the study area

3.2. Environmental drivers of abundance and habitat use

3.2.1. Broad-scale monthly abundance

Broad-scale models showed that shark abundance was influenced by mean SST, SST anomaly, chl *a* anomaly, SOI phase, and latitude depending on habitat type (Fig. 5). This model explained 58.5% of the deviance observed in the data. Bull shark abundance increased as SST increased from 20°C, peaking at 24°C before decreasing to 28°C (Fig. 5a) and when the SST anomaly was higher than the long-term average (Fig. 5b). There was a slight decrease in bull shark abundance as the chl *a* anomaly increased from being lower to higher than the long-term average (Fig. 5c). Conversely, there were significantly more sharks in SOI Phase 2 (La Niña, lower SSTs) and 4 (rapid rise) than 1 (El Niño, higher SSTs; p-values <0.001); however, there were no significant differences in abundance between Phase 1 and Phases 3 or 5 (Fig. 5d). Like the seasonal and inter-annual model, the abundance of sharks was significantly higher over the estuary and mid-shelf habitats

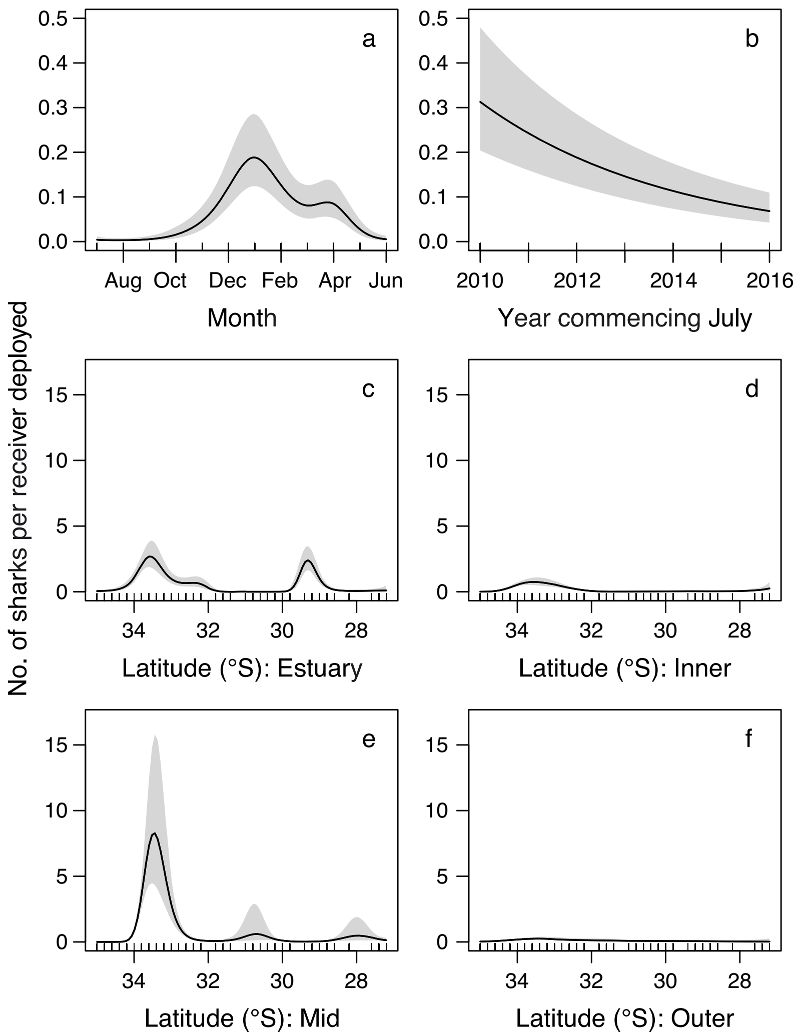

Fig. 3. Response curves of monthly abundance GAMM, showing the influence of (a) month, (b) year and (c–f) latitude by habitat type on bull shark abundance where inner, mid and outer refer to shelf habitat types as identified in Fig. 1. Note: (a) and (b) are on a different *y*-axis scale from (c–f). The grey shaded areas indicate the 95% confidence interval

than inner- or outer-shelf (Fig. 5e–h). RMSE showed that model-predicted abundance was 0.27 of the maximum observed number of sharks per receiver deployed (k-fold CV score, RMSE = 1.01 ± 0.08; max. observed = 3.77) and average error was 0.02 ± 0.08 (<0.01 of the maximum number of sharks detected per receiver deployed).

3.2.2. Influences on individual habitat use

The probability of an individual shark being present in the study area was influenced by latitude depending on habitat type, and to a lesser extent SST, SST slope, chl *a*, chl *a* slope, sex and TL (Fig. 6). However, this model only explained 15.8% of the deviance observed in the data despite the model having a good predictive ability, with a mean AUC of 0.88 ± 0.002. There was a higher probability of sharks being present in waters of ~20 to 26°C (peaking at ~24°C; Fig. 6a), high SST slope (>10°C; Fig. 6b), low levels of chl *a* (0.0 to 0.5 mg m^{-3}; Fig. 6c), high chl *a* slope (>1.5 mg m^{-3}; Fig. 6d) and in latitudes of ~29.5 and 33.8°S (Fig. 6e). The probability of being present was significantly different between each habitat type (all pairwise Wald test p-values <0.001), with the highest probability at estuary mouths, followed by mid-shelf (Fig. 6f). Males had a higher probability of presence than females (model estimate ± SE = 0.58 ± 0.06; Fig. 6g). Sharks <200 and >250 cm TL had a higher probability than sharks 200–250 cm TL (both Wald test p-values < 0.001), but there was no significant difference between the smallest (<200 cm TL) and largest size-classes (>250 cm TL; Wald test p-value = 0.68). Overall, the probability of shark presence was low across all sexes and length-classes (~0.001; Fig. 6g,h).

Once present, the length of time that sharks spent in areas was influenced by SST, SST slope, latitude, habitat type, length of the shark and, to a lesser extent, chl *a*, chls *a* slope, and sex. This model accounted for 62.3% of the deviance observed in the data. Sharks spent longer in areas with a mean SST of <22°C or >24°C (Fig. 7a), a SST slope of <3°C (Fig. 7b), high mean chl *a* (Fig. 7c), and a small chl *a* slope (Fig. 7d). Sharks spent the most time at ~33°S latitude, followed by secondary peaks at ~29° and ~31.5°S (Fig. 7e) and significantly longer in estuary and mid-shelf habitats (pairwise Wald test p-values < 0.001; Fig. 7f). Males spent less time in areas with acoustic detectability than females (model estimate ± SE = −0.17 ± 0.05; Fig. 7g), while sharks <200 cm TL had significantly longer residency times than sharks 200–250 or >250 cm TL (pairwise Wald test p-values ≤ 0.001; Fig. 7h). The individual-level random effect had a very low estimated degrees of freedom (0.001) and

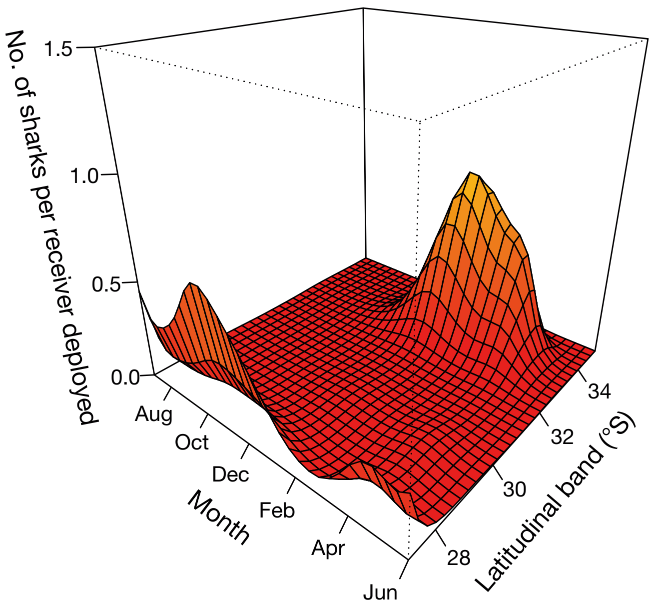

Fig. 4. Response curve of the monthly bull shark abundance GAMM showing the influence of month depending on latitudinal band modelled with a tensor product interaction

was not significant (p-value = 0.13), indicating low intraspecific variability in individual residency times. Predicted residency time was 0.23 of the maximum observed (k-fold CV score, RMSE = 1.6 ± 0.13 d per receiver deployed; maximum observed = 7) with an average error of −0.29 ± 0.06 d per receiver deployed.

4. DISCUSSION

Using 6 yr of passive acoustic telemetry tracking data, we highlight the variation in environmental variables driving bull shark abundance and habitat use along the sub-tropical and temperate coast of eastern Australia. Latitude and habitat type were the strongest predictor variables, as evident from the magnitude of their effect on the response variables versus the remaining predictors used. Bull sharks showed a bias to their tagging locations, with abundance, probability of presence, and residency times all highest around the latitudes where sharks were tagged (Clarence River: ~29.4°; Sydney region: ~33° to 33.8°S), as well as at estuary mouths and in mid-shelf habitats. Bull sharks are known to exhibit high levels of philopatry to natal sites (Karl et al. 2011, Tillett et al. 2012, Chapman et al. 2015). This explains the high abundance, probability of presence and residency times at the Clarence River where all the smaller sharks were tagged (Table 1) and neonates are known to occur (Smoothey et al. 2016). Genetic analyses from the western Atlantic have shown that females, but not males, exhibit natal philopatry (Karl et al. 2011). Only mature females (i.e. no mature males) were caught and tagged in the Clarence River (Table 1), further supporting the contention that this is a nursery ground for bull sharks. No neonates or juveniles were caught in Sydney Harbour (Smoothey et al. 2016), where only larger sharks (>200 cm TL) were tagged. Smoothey et al. (2016) suggested that adult bull sharks may inhabit this estuary due to the high seasonal abundance of prey species. Regardless of the underlying ecological mechanism, the present study has shown a very high site fidelity of adult bull sharks to the greater Sydney region. This region represents the most populated stretch of coastline in Australia, with over 5 million residents (https://www.businessinsider.com.au/this-map-shows-population-density-across-australia-2017-7). Sydney also has the highest number of visitors in Australia, with over 4 million visitors spending over $10 billion in 2017 (https://www.tra.gov.au/ArticleDocuments/242/IVS_one_pager_Dec2017_FINAL.pdf.aspx). Given that visiting beaches is an important component of Sydney tourism, this philopatry by large bull sharks has implications for the management of human–shark interactions. The environmental drivers identified here can be confidently used by beach management agencies to reduce potential risk of bull shark interactions through increased vigilance and/or deployment of other shark risk management strategies during times of increased likelihood of bull shark abundance.

The significance of estuaries is likely underrepresented in this study, as only estuaries that had acoustic receivers deployed at their mouths were included in the analysis. Surprisingly, however, our data show that bull sharks occur more frequently and in higher abundance at mid-shelf habitats compared to nearshore areas (<20 m water depth), where they potentially pose a higher risk to humans. This distribution is supported by the low numbers of bull sharks caught in the NSW Shark Meshing (Bather Protection) Program around the greater Sydney region (Lee et al. 2018a) despite large bull sharks repeatedly occurring within Sydney Harbour (Smoothey et al. 2016) and adjacent waters. Haig et al. (2018) found that mostly immature bull sharks were caught in the shark control program deployed near key beaches in Queensland (spanning both tropical and subtropical habitats) and hypothesized that larger sharks migrate in deeper waters. Our study provides empirical support for this hypothesis.

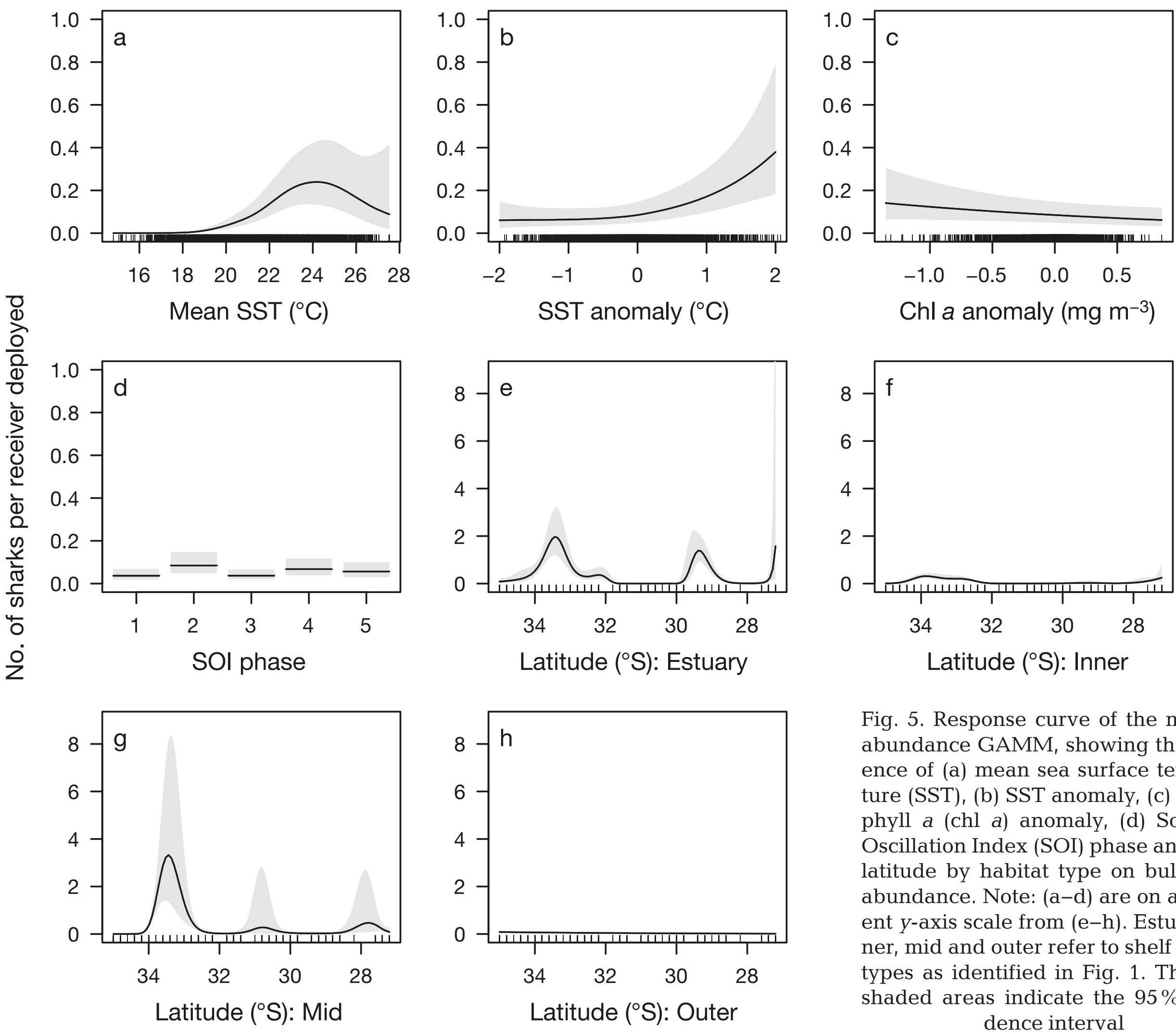

Fig. 5. Response curve of the monthly abundance GAMM, showing the influence of (a) mean sea surface temperature (SST), (b) SST anomaly, (c) chlorophyll *a* (chl *a*) anomaly, (d) Southern Oscillation Index (SOI) phase and (e–h) latitude by habitat type on bull shark abundance. Note: (a–d) are on a different *y*-axis scale from (e–h). Estuary, inner, mid and outer refer to shelf habitat types as identified in Fig. 1. The grey shaded areas indicate the 95% confidence interval

4.1. Seasonal and inter-annual variability in bull shark abundance

Bull sharks were most abundant around the greater Sydney region in the austral summer months (December to February) but occurred, albeit in lower abundance, until May. This is consistent with findings of previous studies which showed that bull sharks migrated from tropical to sub-tropical (Espinoza et al. 2016) and temperate (Heupel et al. 2015) waters of eastern Australia in the austral summer and were consistently present in Sydney Harbour in the austral summer and autumn (Smoothey et al. 2016). Tagged adult bull sharks in southern Africa have also been shown to migrate to higher latitudes (i.e. polewards) in the austral summer (Daly et al. 2014), with increased catches in shark nets during these months (Cliff & Dudley 1991). Similarly, bull shark distribution on the east coast of the USA appears to vary seasonally, with adult sharks only being caught in the more tropical waters of the Indian River Lagoon, Florida, in the late spring to early summer months (Curtis et al. 2011).

Bull sharks were detected in sub-tropical waters at the northern extreme of this study (>28°S) almost year-round but with a marginal peak in the austral late winter/early spring (August to September) and decrease from December to February, presumably due to emigration, when sharks were detected at higher latitudes. This is in contrast to Espinoza et al. (2016), who found that bull sharks tagged in tropical waters of the Great Barrier Reef (north-east Australia) were not present around Moreton Bay (~27.4°S, Fig. 1) in the winter or spring months. Haig et al. (2018) also found that fewer bull sharks were caught in the Queensland shark control program in the win-

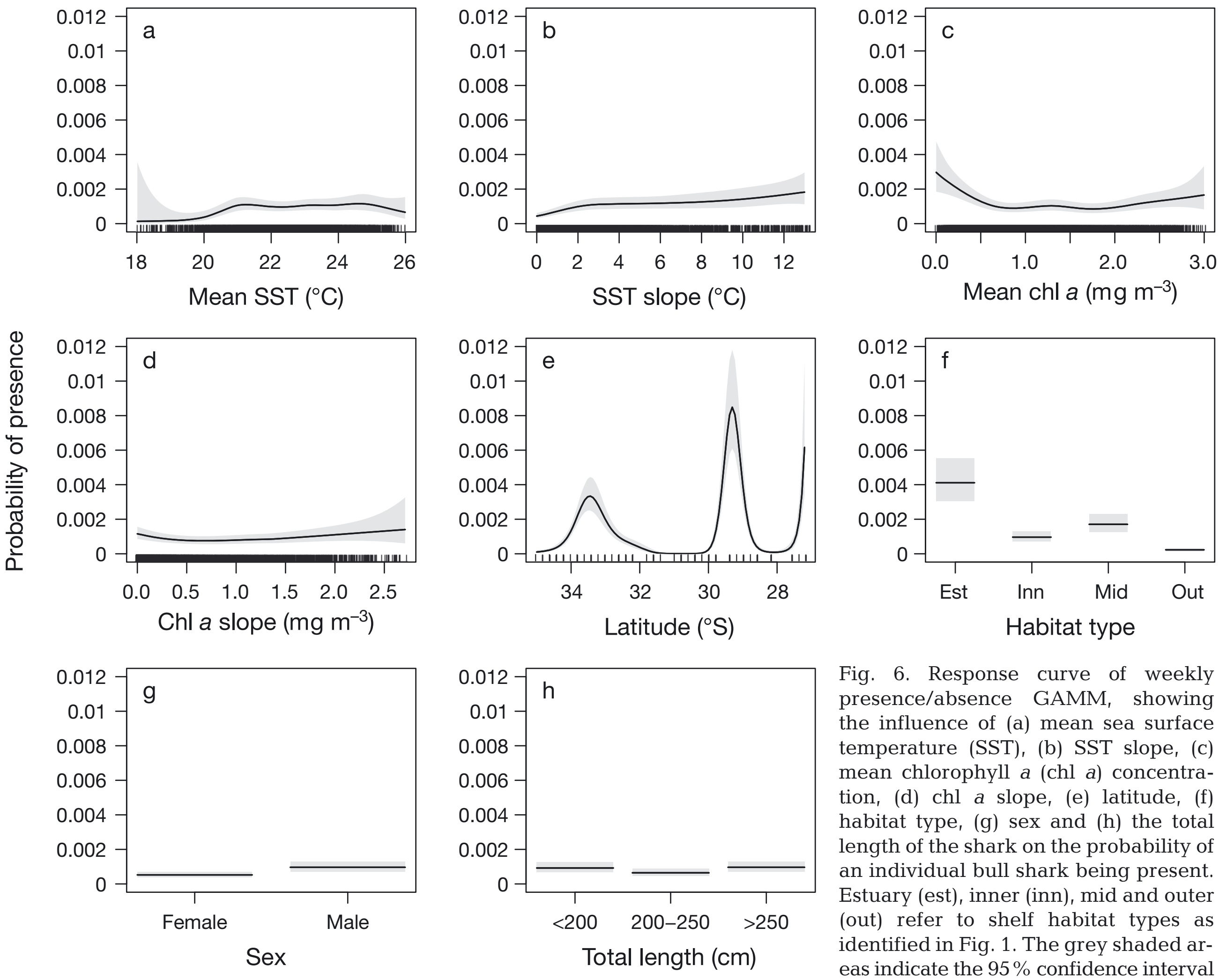

Fig. 6. Response curve of weekly presence/absence GAMM, showing the influence of (a) mean sea surface temperature (SST), (b) SST slope, (c) mean chlorophyll *a* (chl *a*) concentration, (d) chl *a* slope, (e) latitude, (f) habitat type, (g) sex and (h) the total length of the shark on the probability of an individual bull shark being present. Estuary (est), inner (inn), mid and outer (out) refer to shelf habitat types as identified in Fig. 1. The grey shaded areas indicate the 95% confidence interval

ter. The disparity in movements and distribution between bull sharks tagged in tropical waters with those tagged in temperate waters (Heupel et al. 2015) suggests that there are potentially different sub-populations within the Australian east coast bull shark population, with only some undertaking these discrete latitudinal movement patterns along the coast. Although recent genetic analyses of the population structuring and connectivity of bull sharks at a global scale revealed low genetic differentiation within the Western Pacific (i.e. NSW, Australia and New Caledonia; A. Pirog pers. comm.), further research is required to determine the level of genetic structuring and connectivity between tropical and temperate waters on the east coast of Australia.

The abundance of tagged bull sharks decreased across all locations as the study progressed, with the largest decline between 2010 and 2011. Nine of the 25 sharks <200 cm TL tagged in the Clarence River were not detected during this study. It is possible that a proportion of these sharks transitioned from the estuarine to marine environment and moved to areas without acoustic receivers, as evidenced by one shark's movements. More likely, however, is that these sharks were undetected due to mortality in commercial fishing gear. Commercial fishers target small sharks in this river system, and 6 tagged sharks were reported dead. Therefore, it is entirely possible that more sharks were caught and killed but not reported.

4.2. Environmental drivers of abundance and habitat use

Bull sharks were present when SST ranged between 20°C and 26°C, with peak abundance at 24°C. However, residency at a site is not constant within this temperature range and exhibits a bi-

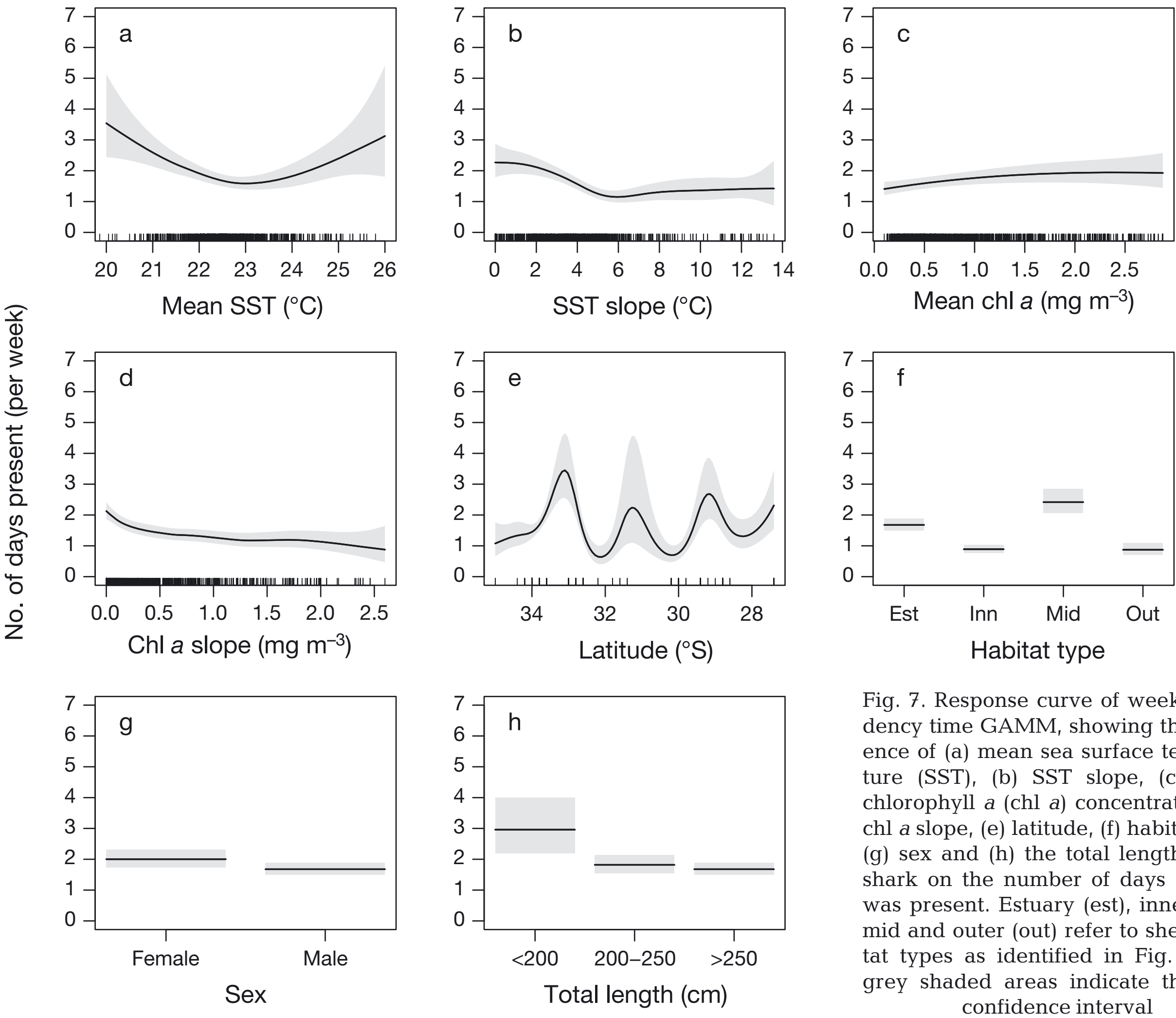

Fig. 7. Response curve of weekly residency time GAMM, showing the influence of (a) mean sea surface temperature (SST), (b) SST slope, (c) mean chlorophyll *a* (chl *a*) concentration, (d) chl *a* slope, (e) latitude, (f) habitat type, (g) sex and (h) the total length of the shark on the number of days a shark was present. Estuary (est), inner (inn), mid and outer (out) refer to shelf habitat types as identified in Fig. 1. The grey shaded areas indicate the 95% confidence interval

modal increase when SSTs are <22°C and >24°C. These results corroborate earlier findings for catch rates in Sydney Harbour (Smoothey et al. 2016) and South Africa (Cliff & Dudley 1991). In Florida, bull sharks were rarely found in waters <20°C but their preferred temperatures during tracking were higher (between 26 and 32°C) than those found elsewhere (Carlson et al. 2010). While temperature is an important predictor of the seasonal residency and migration of bull sharks within sub-tropical and temperate coastal areas, further research is required to understand if individuals gain physiological advantages from using seasonally warmer environments (e.g. Payne et al. 2018) and to determine whether biological drivers (e.g. foraging) act in combination to create the observed patterns of migration.

Bull sharks were found in higher abundance in NSW waters in months when SST was higher than the long-term average. Surface water temperatures in this part of the Tasman Sea have already increased by 0.2°C per year (over a ~60 year period; Thompson et al. 2009), with the EAC experiencing the second fastest warming trend of all WBCs (Wu et al. 2012). The strong correlation between SST and bull shark abundance and distribution suggests that, as surface waters warm due to climate change, the range of this species is likely to extend poleward. Such a change is already being detected on the east coast of the USA, where there appears to be a range extension of bull shark nursery areas into North Carolina due to higher summer temperatures attributed to climate change (Bangley et al. 2018).

The model of bull shark presence/absence only explained a small proportion of the variance observed in the data and produced very low probability of presence. As previously stated, the rates of fishing mortality are unknown; therefore, it is unclear if this is due to sharks being fished or if other factors are driving the likelihood of individual sharks returning to the study site despite conditions favourable for high bull shark abundance.

Once sharks were present, SST was the strongest predictor of residency time (after latitude and habitat), with sharks spending longer in areas at the cooler end (<22°C) of their thermal preference. The preference observed for areas of low SST slope (<3°C) is surprising given the importance of thermal gradients for many marine vertebrates (Scales et al. 2014). Encroachment of the EAC onto the continental shelf can result in large changes in temperature at distances of up to 35–40 km (at ~100 m water depth) from the EAC jet (~1500 m water depth at 30°–31°S; Archer et al. 2017) as nutrient-rich, cold water upwells from the continental slope. Further inshore, wind plays a more dominant role than the EAC (Schaeffer et al. 2013, Archer et al. 2017); however, the colder nutrient rich water is often restricted to bottom bathymetry (Roughan & Middleton 2004) and therefore not detected by remotely sensed SST.

Chl *a* concentration and its derivatives (chl *a* anomaly and slope) had less influence on the abundance (Fig. 5) and residency time (Fig. 7) of bull sharks than SST or SST anomaly. Conversely, chl *a* did, however, have a greater influence on the probability of an individual shark being present than SST or SST slope (Fig. 6) with a higher likelihood of a shark being present when chl *a* was low. As with the patterns observed for SST, the predominately EAC-driven cross-shelf circulation in the mid-shelf habitats (Schaeffer et al. 2013, Archer et al. 2017) would result in nutrients being restricted to the bottom of the water column (Roughan & Middleton 2002), meaning that resultant phytoplankton blooms (Armbrecht et al. 2014) may not be observed at the surface as remotely sensed chl *a*. In addition, remotely sensed chl *a* is unreliable in coastal areas due to water turbidity (Chen et al. 2013), and thus the relationship with bull shark abundance or residency and chl *a* near estuaries and the inner-shelf habitats must be interpreted with caution. The pattern observed in this study contrasts with previous research conducted in inshore habitats or estuaries where bull sharks have been shown to be more abundant in highly turbid waters (Cliff & Dudley 1991, Wintner & Kerwath 2018) and near tidal inlets (Froeschke et al. 2010). *In situ* measurements of turbidity would be needed to discern if chl *a* or turbidity are drivers of bull shark movement in these habitats.

4.3. Implications for management of human-shark interactions

The results from this study highlight that the greatest chance of encountering bull sharks in NSW waters is in or near estuaries, especially when SST is between 20 and 26°C. The higher abundance of bull sharks in the austral summer and autumn months coincides with greater (human) beach and water-use. This seasonal distribution is particularly evident for large, potentially dangerous bull sharks and especially so in the southernmost portion of their range (greater Sydney region) where the potential for interaction with humans is increased due to this area being the most populous in Australia. Yet bull shark bites are rare, despite the high numbers of people that use near-shore areas along Australia's coasts and beaches (West 2011, Mcphee 2014). Our findings suggest that this may be in part due to bull sharks not spending much time in shallow, coastal inshore waters where they are most likely to encounter people. Factors associated with bull shark attacks warrant further investigation.

Philopatry to natal areas has previously been shown in this species, especially for populations on large continental coastlines (Karl et al. 2011, Tillett et al. 2012, Chapman et al. 2015). However, our results are the first to indicate medium-term philopatry by adult bull sharks to non-natal areas along a continental coastline spanning sub-tropical and temperate environments. Although there are individual differences in residency times, overall residence was clearly related to latitude and water temperature, potentially increasing the likelihood of encountering sharks when the temperature is between 22 and 24°C. To account for any bias from tagging location and philopatry, future studies should incorporate tagging at multiple locations, preferably of individuals larger than 200 cm total length, to assist in developing suitable shark encounter mitigation strategies. At this stage, we can only provide broad advice for reducing potential shark bites by bull sharks: implement mitigation strategies during periods when water temperatures are between 20 and 26°C, particularly in waters adjacent to estuaries and during La Niña years and increase vigilance if sightings have occurred in an area when the SST is between 22 and 24°C.

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