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Oceanographic conditions associated with white shark (*Carcharodon carcharias*) habitat use along eastern Australia

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ABSTRACT: Management of species with wide-ranging migrations is a complex issue, made more challenging when the species is both protected and poses a risk to humans. Understanding the oceanic conditions associated with shark habitat use can help develop mitigation strategies or warning systems that meet both conservation and human safety objectives. Using satellite tracks from 77 juvenile and sub-adult white sharks tagged over 10 yr, we modelled individual movement patterns using hidden Markov models and applied generalised additive (mixed) models to explore correlations between movement patterns (presence–absence, habitat selection and behavioural state) and oceanographic and bathymetric variables. White sharks used the whole of the continental shelf, down to depths of 350 m on the continental slope. Sharks were present over a wide range of sea surface temperatures (SSTs; 10–27°C), with the highest probability of occurring at ~20°C. However, the number of average daily tag positions was greatest when SST was between 14 and 18°C, and sharks were more likely to exhibit area-restricted movement when SST was between ~19 and 23°C. Sharks were more likely to be present and selected habitats in productive areas with moderate to high surface chl *a* concentrations as well as thermal and productivity fronts. Although mesoscale eddies did not influence the likelihood of individuals being present in an area, there was a higher density of sharks in cold-core eddies compared to warm-core eddies. This study indicates that white shark presence and dispersal may be linked, perhaps via prey distribution, to oceanic conditions, potentially assisting development of suitable shark bite mitigation strategies.

KEY WORDS: *Carcharodon carcharias* · Chl *a* · Generalised additive mixed models · Habitat use · Satellite tracking · Sea surface temperature

1. INTRODUCTION

Apex predators are vital to the health of the marine environment, and their removal can result in top-down effects that cascade through the trophic levels (Heithaus et al. 2008, Baum & Worm 2009, Ferretti et al. 2010). However, managing wide-ranging species, especially those that span several national or international jurisdictions, is a complex issue. This is made even more challenging for species that may pose a risk to humans, such as sharks, where the risk has to be mitigated while still achieving management and/or conservation targets (Ferretti et al. 2015). Understanding the ecology of these species, in particular the environmental variables associated with their movement and habitat selection, is essential to

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developing effective management practices that can meet both purposes (Ryan et al. 2019, White et al. 2019).

In Australia, 3 species of sharks (white shark *Carcharodon carcharias*, tiger shark *Galeocerdo cuvier* and bull shark *Carcharhinus leucas*) account for the majority of serious or fatal shark attacks on humans (West 2011, Mcphee 2014). Of the 3 species, white sharks have the widest distribution, ranging from Papua New Guinea to sub-Antarctic Islands (Bradford et al. 2020, Spaet et al. 2020), and have been responsible for the largest number of human deaths and injuries. The abundance of adult white sharks has remained relatively stable up to 2018 following protection (classified as Vulnerable, IUCN; Rigby et al. 2019) that was put in place in the 1990s (Hillary et al. 2018). Effective conservation efforts, however, should see an increase in white shark abundance over time. It remains to be seen how increases in human water usage, variation in shark behaviour and any change to the density of sharks in areas heavily utilised during human water activities lead to more or fewer human–shark interactions. Either way, to establish a baseline picture of shark movements from which we may judge the degree of future change requires interrogation of data from long-term tracking studies. These have already given us unprecedented insights into the range of movements displayed by white sharks, from repeated returns to specific locations (Bruce & Bradford 2012, Kock et al. 2013, Curtis et al. 2018) to continental- (McAuley et al. 2017) and transoceanic-scale migrations (Bonfil et al. 2005, Weng et al. 2007a, Domeier & Nasby-Lucas 2008, Duffy et al. 2012).

While characterised by these large-scale individual movements, several discrete populations exist throughout their global distribution (Pardini et al. 2001, Jorgensen et al. 2010, Gubili et al. 2012). In the Australasian region, genetic analyses have revealed that there are 2 white shark populations, south-western and eastern coastal populations (Blower et al. 2012). There is an approximate demarcation between the south-western and eastern populations from around Wilsons Promontory in Bass Strait (Fig. 1) to approximately 142° E (see Spaet et al. 2020). Both of these populations are genetically distinct from the South African population (Pardini et al. 2001). This divergence within the Australasian region has been corroborated using satellite tracking, which has revealed sharks moving between the east coast of Australia and New Zealand, New Caledonia and Papua New Guinea (Bruce & Bradford 2012, Duffy et al. 2012, Francis et al. 2015) but only limited movement between eastern and western Australia (McAuley et al. 2017, Bruce et al. 2019).

Traditional mark–recapture methods have been unable to provide an accurate estimate of white shark population trajectories (Braccini et al. 2017) or demonstrate the efficacy of existing conservation measures. However, using a new mark–recapture framework, based on genetic relatedness (close-kin mark–recapture), Hillary et al. (2018) provided the first estimate of abundance for the eastern Australasian white shark population (~2500–6750), inclu-

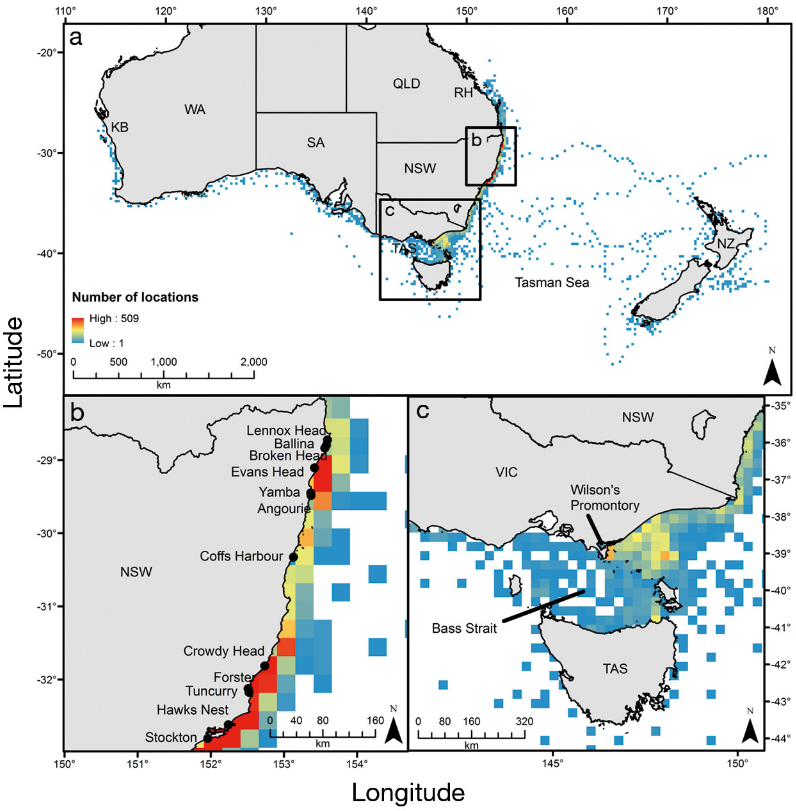

Fig. 1. Number of locations from 77 satellite-tagged white sharks tracked from 2007 to 2017 (a) in Australia and New Zealand (NZ), (b) along the New South Wales (NSW) coast where sharks were tagged and (c) in Bass Strait, showing limited movement west of the strait. QLD: Queensland; SA: South Australia; WA: Western Australia; VIC: Victoria; TAS: Tasmania. The northernmost extent of white shark distribution on the east and west coasts as shown with local town names: RH = Rockhampton and KB = Kalbarri. Maps were generated in ArcGIS 10.5

ding survival rates for both adults (>90%) and juveniles (73%). Despite the relatively high survival rates and having been protected in Australian waters since the mid-1990s, the abundance of the eastern Australasian white shark population has remained stable (Hillary et al. 2018, Davenport et al. 2020). Accidental and illegal by-catch by commercial and recreational fishers continues to threaten white sharks throughout Australian waters, with the eastern Australasian population further subjected to a range of lethal and non-lethal shark control activities in New South Wales (NSW; first implemented in 1937) (Lee et al. 2018a, Tate et al. 2020) and Queensland (Department of Sustainability 2013). Juvenile (<3 m) white sharks predominately use continental shelf waters (Bruce & Bradford 2012, Curtis et al. 2018, Bruce et al. 2019), shifting to pelagic habitats as they grow (Skomal et al. 2017). This makes juveniles and sub-adults more vulnerable to human-based activities than adults, as evidenced by their lower (albeit relatively high for an apex predator) survival rates (Hillary et al. 2018) and prevalence in the NSW Shark Meshing Program (Reid et al. 2011).

Predicting the distribution of top predators that are able to span a large range of oceanic conditions (Spaet et al. 2020) is challenging, as sharks most likely rely on evolved migration strategies and distribute at fine scales according to local distribution of prey resources. However, there has been little examination of the regional distribution of white sharks in eastern Australian waters in relation to ocean conditions (e.g. surface temperature and chlorophyll concentration), which, by being a proxy for influences on lower trophic levels, may predict distribution of white sharks (Huveneers et al. 2018). Improved understanding of the correlations between oceanographic conditions associated with juvenile white shark occurrence, habitat selection and movement patterns may help inform the framing of policy regarding non-lethal shark bite mitigation strategies (e.g. drones, shark management alert in real-time [SMART] drumline deployments, shark spotters, aerial surveillance). Effective mitigation strategies, in turn, could lead to a reduction in human-induced mortalities and improved conservation outcomes for white sharks.

Accordingly, using a 10 yr (2007–2017) satellite tracking dataset from 77 juvenile and sub-adult white sharks tagged in eastern Australian waters, we (1) show the relative influence of oceanographic and physical variables on shark occurrence and relative density and (2) identify environmental drivers of individual shark behaviour along eastern Australia.

2. MATERIALS AND METHODS

2.1. Tagging and track processing

White sharks were tagged at 10 locations in eastern Australia (Fig. 1b) between October 2007 and November 2017 (see Table 2). Capture and tagging followed methods described in Bruce & Bradford (2012) and Harasti et al. (2017), wherein sharks were either (1) visually located from a vessel or helicopter before being presented with a baited hook from a vessel or (2) caught on monitored surface-buoyed setlines. Once captured, the sharks were restrained alongside the vessel or held in an in-water stretcher for tagging. Satellite-linked radio tags (hereafter referred to as tags) were attached to their first dorsal fin. Two models of tags were used: Wildlife Computers© SPOT and SPLASH tags. Transmissions from the tags were extracted from the ARGOS collection and location system (www.argos-system.org/). The location accuracy of both tag models is determined by the timing and number of transmissions received by ARGOS satellites during a single pass (Hays et al. 2001, Hazel 2009). Accuracy of the location estimate is presented as location class (LC) 3, 2, 1, 0, A, B and Z, with LC3 providing the lowest error (predicted RMS ≤ 250 m), LCB the highest (predicted RMS > 1500 m) and LCZ indicating invalid positions. All LCZ locations were removed from subsequent analyses.

Accepted positions used for the analyses were obtained using the methods described in Bruce et al. (2006), whereby all positions with LC3, 2 and 1 were accepted, and LC0, A and B were only accepted if their location relative to a reliable previous location was within a feasible swimming distance (based on a swimming speed of 4 km h^{-1}) in the time period between transmissions. To ensure statistical power, all sharks that were tracked for less than or equal to the 5th percentile (9 d) were removed from subsequent analyses (4 sharks). There was also a natural cut-off at 9 d, with the remaining sharks being tracked from 12+ d.

Locations can only be calculated when a shark is at the surface, allowing communication with the ARGOS satellite constellation. Track reconstructions used all available data; however, temporal gaps occur where light-based data are unavailable, and SPOT and SPLASH tags do not collect light-based data to inform periods when the tag has not transmitted. Therefore, there is high variability in the number of location estimates due to each shark's surfacing behaviour (Lea et al. 2015, 2018). To avoid bias in the amount of time a shark spent in a given area, we followed the methods of Bruce et al. (2019), calculating an average daily position for each shark and using linear interpolation to normalise the frequency of locations by generating points at 24 h intervals along tracks with gaps of ≤5 d. Tracks with gaps of >5 d were split into separate sections.

Average daily positions (ADPs) were weighted by track duration, thereby reducing bias from high coverage closer to tagging locations. Following the methods outlined in Block et al. (2011), each ADP was weighted by the inverse number of sharks with locations on the same relative tracking day, up to the 85th percentile of all track lengths (382 d), beyond which the weights were set equal to that obtained on the 382nd day (the threshold day).

Table 1. Sources and resolutions of oceanographic data and physical characteristics. NA: temporal resolution is not applicable for static values

Oceanographic and biophysical variable	Model covariate	Derived variable (s) (unit [s]) used as model covariate	Data source	Spatial resolution (°)	Temporal resolution: Weekly model	Temporal resolution: Daily movement model
Sea surface temperature (SST) (foundation)	SST	SST anomaly (°C) and SST gradient	IMOS AODN Portal — SST L3S	0.02	Mean of daily (daytime and nighttime) composites	Daily (daytime and nighttime) composites
Chl *a* concentration	Chl *a*	Chl *a* anomaly (mg m^{-3}) and chl *a* gradient	IMOS AODN Portal — MODIS OC3 model	0.01	Geometric mean of daily values	Daily values
Bathymetry	Water depth		Australian Bathymetry and Topography Grid, June 2009 (Geoscience Australia)	0.0025	NA	NA
Sea surface height	Eddy type	Eddy type (cyclonic or anticyclonic)	Mesoscale Eddy Trajectory Atlas products produced by SSALTO/DUACS and distributed by AVISO+	Point locations derived from 0.25° grids	No. of eddies passing through each week	Presence or absence of eddies

2.2. Oceanographic and physical data

The spatial and temporal resolutions of each remotely sensed variable are described below and summarised in Table 1. Daily remotely sensed sea surface temperature (SST) and chl *a* data were downloaded from the Integrated Marine Observing System (IMOS) ocean data portal (AODN; https://portal.aodn.org.au) (IMOS 2017).

Cloud cover or opacity of coastal waters due to turbulence in nearshore areas can cause gaps in remotely sensed data at fine spatial and temporal scales. Lee et al. (2018b) showed that by using known de-correlation length and time scales of SST, the number of days that satellite data were usable for a particular location could be increased, while still obtaining similar accuracy to values extracted from a single pixel. Therefore, to obtain finer-scale SST values, we used the average SST from all pixels within distances of 8 km across-shelf and 20 km along-shelf to average the satellite SST values. These distances are 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 d 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 were available (due to cloud cover). Similarly, distances of 4 km across-shelf and 6 km along-shelf were used to average the chl *a*, as again these values are less than known de-correlation lengths (Schaeffer et al. 2016).

Bathymetry was obtained from the Australian Bathymetry and Topography Grid (www.ga.gov.au/metadata-gateway/metadata/record/gcat_67703) at a spatial resolution of 0.0025°. This was used to indicate water depth at the animal's position and hence identify location across the continental shelf and slope.

A global dataset tracking mesoscale eddies (called the Mesoscale Eddy Trajectory Atlas) was downloaded from Archiving, Validation and Interpretation of Satellite Oceanographic data (AVISO+; www.aviso.altimetry.fr/es/data/products/value-added-products/global-mesoscale-eddy-trajectory-product.html). The Mesoscale Eddy Trajectory Atlas uses a modified version of the algorithm used by Chelton et al. (2011) to identify and track eddies (Schlax & Chelton 2016) from global sea surface height data (Pujol et al. 2016). We classified the core of each eddy within our study (spatial and temporal) using definitions given in Gaube et al. (2018).

Weekly means of each environmental variable were calculated for 0.25° × 0.25° grids. The geometric mean was used for chl *a* due to its log-normal distribution, which is common in continental shelf waters (Mouw & Yoder 2005, Everett et al. 2014). Chl *a* was included as a measure of primary productivity in the absence of prey distribution data. Eddy type was summarised by calculating the total number of anticyclonic eddies, cyclonic eddies, both or neither that had passed through a grid cell in that week. Mesoscale eddy data were only available until 5 January 2017; therefore, all dates after 6 January 2017 were categorised as 'unknown' eddy type. Rapid changes in SST or chl *a* indicative of frontal features will be reflected in steep gradients in the underlying fields (i.e. thermal or primary productivity fronts). Both SST and chl *a* fronts can be associated with different water masses and are important for wide-ranging marine predators (reviewed by Scales et al. 2014 and Polovina et al. 2017) We therefore included gradient of SST and chl *a* calculated as the absolute difference between maximum and minimum values within each 0.25° × 0.25° grid cell (Lea et al. 2018).

2.3. Population-level habitat use

Weighted locations were summed with 0.25° × 0.25° grid cells to provide the relative habitat selection of white sharks along the east coast of Australia. A 0.25° × 0.25° grid was used, as it was the resolution of the coarsest oceanographic variable (sea surface height used to derive eddies; Table 1) and greater than the location error associated with the least accurate location class (LCB ~10 km; Hays et al. 2001, Costa et al. 2010). A 2-model approach, using generalised additive models (GAMs), was used to determine if white shark habitat selection was influenced by oceanographic and physical variables. First, a binary presence–absence model was used to determine the occurrence of white sharks across the study region. Second, all grid cells where the weighted number of (summed) locations was greater than zero were used to assess the biophysical correlates of relative habitat selection.

2.3.1. Occurrence (presence–absence) models

All cells with a relative density >0 were coded as 'presence' locations. Barbet-Massin et al. (2012) showed that GAM models with 10 000 randomly sampled pseudo-absence points and modelled with an equal weight for presences and absences produced the most accurate results. Likewise, pseudo-absence sampling from too restrictive or too broad geographic ranges (in relation to the presence points) can produce spurious models (VanDerWal et al. 2009). Ninety-five percent of shark ADPs were east of 142° E (see Section 3 and Fig. 2) and at locations with water depths ≤350 m. Therefore, to ensure that pseudo-absences were sampled from a geographic range encompassing the movement of the majority of sharks, we generated a grid matching the resolution of the weighted locations (0.25° × 0.25°), with 142° E as the westerly extent, the ≤350 m isobath as the easterly and the northern and southern extents defined by the weighted locations (Fig. 2). All cells on land were then removed. From this grid, 10 000 pseudo-absences were randomly sampled with weeks and years that matched the temporal extent of the presence data but did not include any non-zero density cells.

These were modelled against weekly mean bathymetry, SD of bathymetry (as a measure of bathymetric rugosity; Scales et al. 2017), SST, SST gradient, chl *a*, chl *a* gradient and eddy type using the 'mgcv' package (Wood 2006, 2011) in R (v3.5.0, R Core Team 2018) using a complementary log–log link function. Year and week were treated as a random effect, with each unique combination of year and week corresponding to a separate intercept. The inclusion of each of the explanatory variables was assessed using Akaike's information criterion for small sample sizes (AICc; 'MuMIn' package for R; Bartoń 2016). The 'concurvity' function in the 'mgcv' package was used to ensure that there was no concurvity (the GAM 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-

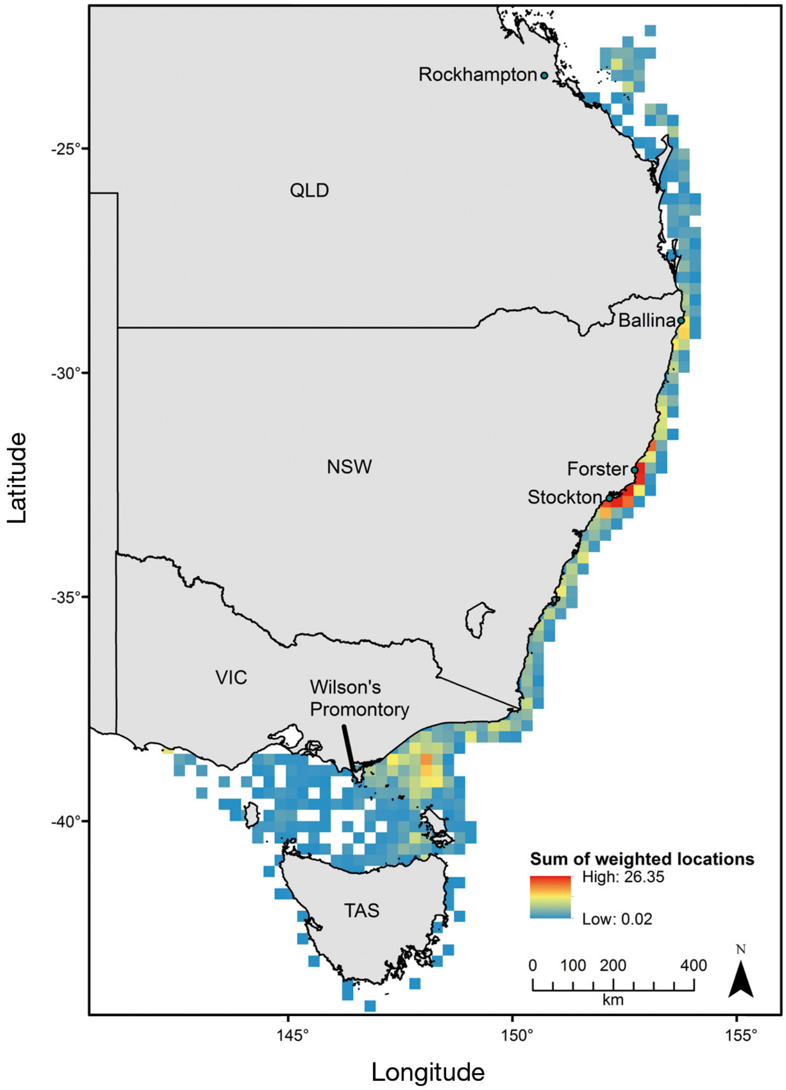

Fig. 2. Weighted locations summed in each 0.25° × 0.25° grid cell to show the overall occupancy across the study extent from 2007 to 2017. Locations were weighted to remove bias towards the tagging locations and tracking duration of each shark. QLD: Queensland; NSW: New South Wales; VIC: Victoria; TAS: Tasmania. Map was generated in ArcGIS 10.5

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 the mean area under the receiver operating characteristic curve (AUC) used as the model diagnostic. Post hoc multiple comparison (Wald) tests were conducted for any multi-level factor variable (e.g. eddy type), using the 'wald_gam' function in the 'itsadug' package (Van Rij et al. 2017), to determine the pairwise significance of each level.

2.3.2. Habitat selection (sum of weighted locations) model

All grids cells with a sum of (weighted) locations greater than zero were modelled against the same environmental variables and with the same random effects as the presence–absence data using a Poisson-Tweedie link function. *k*-fold cross-validation was used to assess the predictive error, with RMSE and average error as the model diagnostics (Potts & Elith 2006). The same methods as described above were used to assess model adequacy and inclusion of explanatory variables.

2.4. Individual-level movement patterns

Each ADP was categorised into either travelling or area-restricted behaviour using the methods described in Bruce et al. (2019). Briefly, hidden Markov models (HMMs) implemented using the 'moveHMM' (Michelot et al. 2015) R package used the turning angle and distance between successive locations to categorise the behaviour. Area-restricted movement was characterised by high turning angles and short distances between successive locations, while travelling was defined by low turning angles and larger distances between locations. The behavioural state was coded as a binary variable (0 is travelling; 1 is area restricted) and matched to the corresponding bathymetry and daily environmental variables. This was modelled against bathymetry, SST, SST gradient, chl *a*, chl *a* gradient, eddy type, sex and total length (TL) using a generalised additive mixed model with a logit link and the unique shark identity number as a random effect. The weights of each location (the inverse of the number of sharks also detected on that relative tracking day, as calculated above) were used as an offset in the model to account for the spatial bias towards tagging locations. The same model adequacy, variable selection and assessment of predictive accuracy were conducted as described above.

3. RESULTS

Seventy-seven sharks (mean ± SD: 250 ± 41 cm TL, range: 170–367 cm TL) were tagged between 2007 and 2017 and tracked for ≥10 d (Table 2, Fig. 1a). Of those sharks, 4% were young of the year (≤1.75 m; Bruce & Bradford 2012), 86% were juveniles (>1.75 and <3 m TL) and the remaining 10% were sub-adult (>3 m TL; Table 2); 57% were female (Table 2). Sharks were tracked for an average of 71 d (range: 11–401 d; Table 2). Six sharks travelled across the Tasman Sea to New Zealand, and 4 sharks moved west of Bass Strait, with 1 shark moving as far as Kalbarri in Western Australia before returning to the east coast of Australia (Fig. 1a). Overall occupancy was highest between Port Macquarie and Stockton on the mid-north NSW coast, with secondary areas in northern NSW (near Ballina) and south-eastern Victoria (east of Wilsons Promontory; Fig. 2). Occupancy was higher on the continental shelf than in areas further offshore (Fig. 2). For more in-depth information about the tracking of these sharks, refer to Bruce & Bradford 2012, Bruce et al. 2019 or Spaet et al. 2020, and refer to Table 2 for which sharks were included in these previous publications.

3.1. Population-level habitat use

3.1.1. Occurrence (presence–absence) models

Presence of white sharks was influenced by water depth, SST, chl *a* concentration and chl *a* gradient (Fig. 3, Table 3). SST explained the largest amount of deviance observed, followed by water depth (Table 3). The probability of a shark being present was highest in waters of ~50 to 130 m depth (Fig. 3a; 66% of presence locations were within this range) and when SSTs were between 17 and 23°C (71% of presence data points were within this range), with peak presence at ~20°C (Fig. 3b). Chl *a* concentration and gradient had less of an influence on the probability of a shark being present than depth or SST, with this reflected in its smaller contribution to the deviance explained (Table 3). Shark presence was highest at intermediate concentrations of chl *a* (Fig. 3c) and high chl *a* gradients (Fig. 3d). Although eddy type was included in the model, there was no statistical difference in the probability of presence between anticyclonic and cyclonic eddies or areas that had both eddy types in the same week (all Wald tests p-values > 0.05; Fig. 3e). The model had a high predictive ability (*k*-fold cross-validation, mean AUC ± SE = 0.86 ± 0.002) despite only explaining 33.6% of the variation observed in the data.

3.1.2. Habitat selection (sum of weighted locations) model

Habitat selection by white sharks was influenced by water depth and to a lesser extent SD bathymetry, SST, SST gradient, chl *a* concentration, chl *a* gradient and eddy type (Fig. 4, Table 3). Conversely, eddy type explained the largest amount of deviance, followed by SST and SD bathymetry (Table 3). The highest number of shark locations was in waters on the continental gradient with depths of ~250 to 300 m (Fig. 4a) and in areas of bathymetric rugosity (Fig. 4b). White sharks occurred in a wide range of water temperatures but preferentially used areas with SST <18 or >24°C (Fig. 4c) and in areas where SST gradient was ~1 or >4°C (Fig. 4d), where (logged) chl *a* concentration was ~1 mg m^{-3} (Fig. 4e) and along productivity fronts (Fig. 4f). However, there were few data points at the extreme ranges of each of the variables, which produced larger CIs at the data extremes. The highest number of shark locations was recorded when the presence of mesoscale eddies was unknown (after 6 January 2017; Fig. 4g). During the time when mesoscale eddies were tracked, sharks used cyclonic eddies significantly more than anticyclonic eddies (Wald test p-value: 0.044) or areas with both eddy types in 1 wk (Wald test p-value: 0.002) but no more than areas where no eddies occurred (Wald test p-value: 0.050). There was no significant difference in shark habitat selection between anticyclonic eddies and areas where neither (Wald test p-value: 0.359) or both (Wald test p-value: 0.059) occurred. RMSE showed that model-predicted density was 0.07 of the maximum observed (*k*-fold cross-validation, RMSE = 0.19 ± 0.03; max. observed = 2.67) and average error was 0.002 ± 0.001 (<0.01 of the maximum density), despite the model only explaining 26.7% of the variation observed in the data.

3.2. Individual-level movement patterns

HMMs showed that white sharks exhibited area-restricted movement (smaller distances between locations and higher turning angles) along the continental shelf from south-eastern Queensland to southern NSW, south-eastern Victoria and northern Tasmania, but this was limited west of Bass Strait

Table 2. Details of tag deployments for 77 white sharks tagged along the New South Wales coast between 2007 and 2017 (Fig. 1b). All sharks were previously reported in Spaet et al. (2020) as well as in reports shown in footnotes. Date format is d/mo/yr. Any discrepancies in the last date of detection between this study and previous studies were because no Z class locations were included in this study but were included where appropriate in previous publications

Shark no.	Date tagged	Tagging location	Total length (cm)	Sex	No. of days shark detected	Last date detected
1	11/10/07[a]	Stockton	240	Female	11	22/11/07
2	11/10/07[a]	Stockton	190	Male	11	31/3/08
3	30/10/09[a,b]	Hawks Nest	220	Female	13	26/1/10
4	10/10/12[b]	Hawks Nest	280	Female	16	27/11/12
5	27/10/10[b]	Hawks Nest	220	Female	16	8/12/10
6	11/10/07[a]	Stockton	200	Female	17	4/11/07
7	28/10/08[a,b]	Hawks Nest	229	Female	15	10/11/08
8	29/10/09[a]	Hawks Nest	230	Male	25	17/1/10
9	10/10/07[a]	Stockton	240	Female	15	21/11/07
10	28/10/09[a]	Hawks Nest	240	Female	19	9/2/10
11	08/10/07[a]	Stockton	210	Male	37	1/12/07
12	25/10/11[b]	Hawks Nest	240	Female	29	10/12/11
13	10/10/07[a]	Stockton	260	Male	53	20/1/08
14	8/10/07[a]	Stockton	190	Female	47	12/1/08
15	25/10/11[b]	Hawks Nest	220	Female	57	28/2/12
16	20/12/12[b]	Hawks Nest	320	Female	48	16/2/13
17	27/10/10[b]	Hawks Nest	190	Male	58	4/2/11
18	28/10/08[a,b]	Hawks Nest	175	Female	57	26/5/09
19	25/10/11[b]	Hawks Nest	170	Male	59	16/1/12
20	11/10/07[a]	Stockton	250	Female	63	30/12/07
21	19/12/12[b]	Hawks Nest	218	Female	58	15/3/13
22	28/10/09[a]	Hawks Nest	210	Male	67	10/2/10
23	10/10/12[b]	Hawks Nest	230	Male	99	4/2/13
24	14/12/10[b]	Hawks Nest	280	Female	168	31/5/12
25	24/11/14[b]	Hawks Nest	190	Female	122	15/5/15
26	19/12/12[b]	Hawks Nest	260	Female	176	19/1/14
27	24/11/14[b]	Hawks Nest	270	Female	158	10/6/15
28	04/07/16	Ballina	268	Female	35	20/11/17
29	28/08/15	Ballina	300	Female	14	18/4/16
30	02/6/16	Evans Head	280	Female	22	14/8/16
31	02/8/16	Coffs Harbour	264	Male	19	1/9/16
32	12/09/17	Yamba	242	Female	16	12/10/17
33	22/07/16	Tuncurry	290	Female	29	20/11/16
34	28/10/17	Ballina	306	Male	34	31/5/18
35	31/05/16	Evans Head	265	Male	42	9/12/16
36	08/10/16	Ballina	250	Female	24	19/11/16
37	31/05/16	Evans Head	245	Male	32	15/9/17
38	12/09/15	Broken Head	295	Female	25	11/11/15
39	13/10/15	Ballina	290	Female	67	23/4/16
40	1/8/16	Coffs Harbour	293	Male	68	30/9/17
41	30/5/17	Coffs Harbour	270	Male	42	15/10/17
42	7/9/16	Tuncurry	262	Male	51	13/4/17
43	6/9/16	Tuncurry	220	Female	76	21/2/17
44	15/11/17	Crowdy Head	250	Male	38	1/1/18
45	21/7/16	Tuncurry	220	Female	60	9/5/17
46	9/8/16	Ballina	259	Female	50	24/5/18
47	1/10/16	Ballina	213	Male	99	30/4/17
48	5/7/16	Ballina	360	Female	51	17/1/17
49	4/10/16	Ballina	367	Female	63	16/1/17
50	17/8/17	Forster	252	Male	65	2/12/17
51	26/8/15	Ballina	220	Female	38	6/11/15
52	13/9/15	Ballina	225	Female	58	9/1/16
53	2/10/16	Ballina	256	Male	63	29/9/17
54	14/10/15	Ballina	245	Male	59	18/2/16
55	8/10/16	Ballina	222	Female	44	28/12/16

Table 2. (continued)

Shark no.	Date tagged	Tagging location	Total length (cm)	Sex	No. of days shark detected	Last date detected
56	17/10/15	Ballina	282	Female	104	19/7/16
57	26/8/15	Ballina	220	Female	49	4/11/15
58	12/9/17	Yamba	282	Male	136	30/6/18
59	6/10/16	Ballina	281	Male	78	16/3/17
60	21/7/16	Tuncurry	267	Male	64	14/10/16
61	30/8/15	Ballina	243	Male	107	30/7/16
62	28/9/16	Ballina	172	Male	134	2/5/17
63	27/9/16	Ballina	291	Male	103	3/6/17
64	25/10/17	Ballina	252	Male	100	25/3/18
65	2/10/16	Ballina	300	Male	90	13/4/18
66	2/10/16	Ballina	232	Male	80	31/3/17
67	8/10/16	Ballina	213	Female	92	8/4/17
68	9/8/16	Ballina	305	Female	103	23/4/17
69	24/10/17	Forster	303	Male	80	21/3/18
70	6/6/17	Tuncurry	251	Female	92	9/3/18
71	6/6/17	Tuncurry	259	Female	103	26/2/18
72	4/10/16	Ballina	223	Female	125	26/5/18
73	7/9/16	Tuncurry	214	Male	153	17/7/17
74	8/9/16	Tuncurry	197	Male	151	10/10/17
75	10/8/16	Ballina	350	Female	163	28/6/18
76	1/8/16	Coffs Harbour	214	Female	156	28/1/18
77	5/7/16	Ballina	306	Male	401	30/6/18

[a]Bruce & Bradford (2012); [b]Bruce et al. (2019)

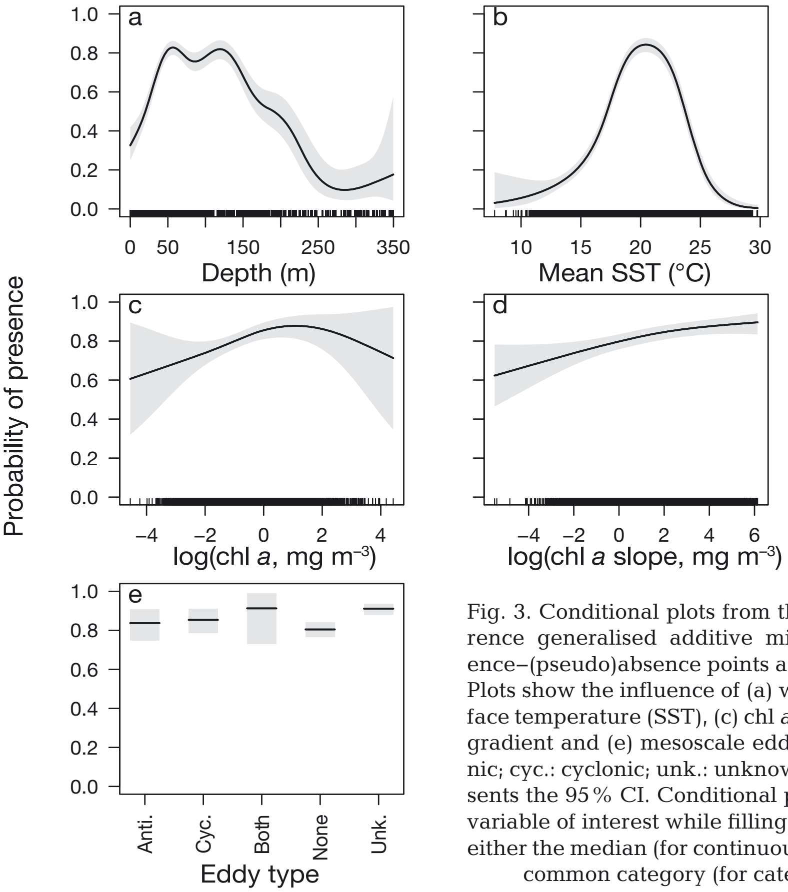

Fig. 3. Conditional plots from the weekly shark occurrence generalised additive mixed model with presence−(pseudo)absence points as the response variable. Plots show the influence of (a) water depth, (b) sea surface temperature (SST), (c) chl *a* concentration, (d) chl *a* gradient and (e) mesoscale eddy type (anti.: anticyclonic; cyc.: cyclonic; unk.: unknown). Shaded area represents the 95% CI. Conditional plots show the trend for variable of interest while filling all other variables with either the median (for continuous variables) or the most common category (for categorical variables)

Table 3. Details showing the change in Akaike's information criterion for small sample sizes (ΔAICc) and deviance explained for each model variable. ΔAICc values show the difference between the reduced model (i.e. the variable was not included) and the full model (all variables included). Variables with negative ΔAICc were dropped from the final model. SST: sea surface temperature; TL: total length; – denotes where the metric is not applicable for that variable, either as it was not included in the initial models or was dropped from the final model due to a negative ΔAICc

Variable	Weekly presence−absence		Weekly relative habitat selection		Individual-level movement patterns	
	ΔAICc	Deviance explained (%)	ΔAICc	Deviance explained (%)	ΔAICc	Deviance explained (%)
Depth	148.1	6.5	25.7	1.6	195.9	6.7
SD bathymetry	−0.5	–	52.0	2.0	–	–
SST	690.4	21.2	92.5	2.8	259.4	6.2
SST gradient	−0.6	–	31.3	1.5	12.4	0.3
Chl *a*	1.7	1.6	15.9	1.5	44.4	4.3
Chl *a* gradient	5.2	2.3	71.3	1.5	−1.4	–
Eddy type	17.6	1.4	374.5	11.0	99.6	3.3
TL	–	–	–	–	82.7	2.2
Sex	–	–	–	–	2.1	0.1
Random effects	17.2	0.6	56.8	4.7	15.4	1.7

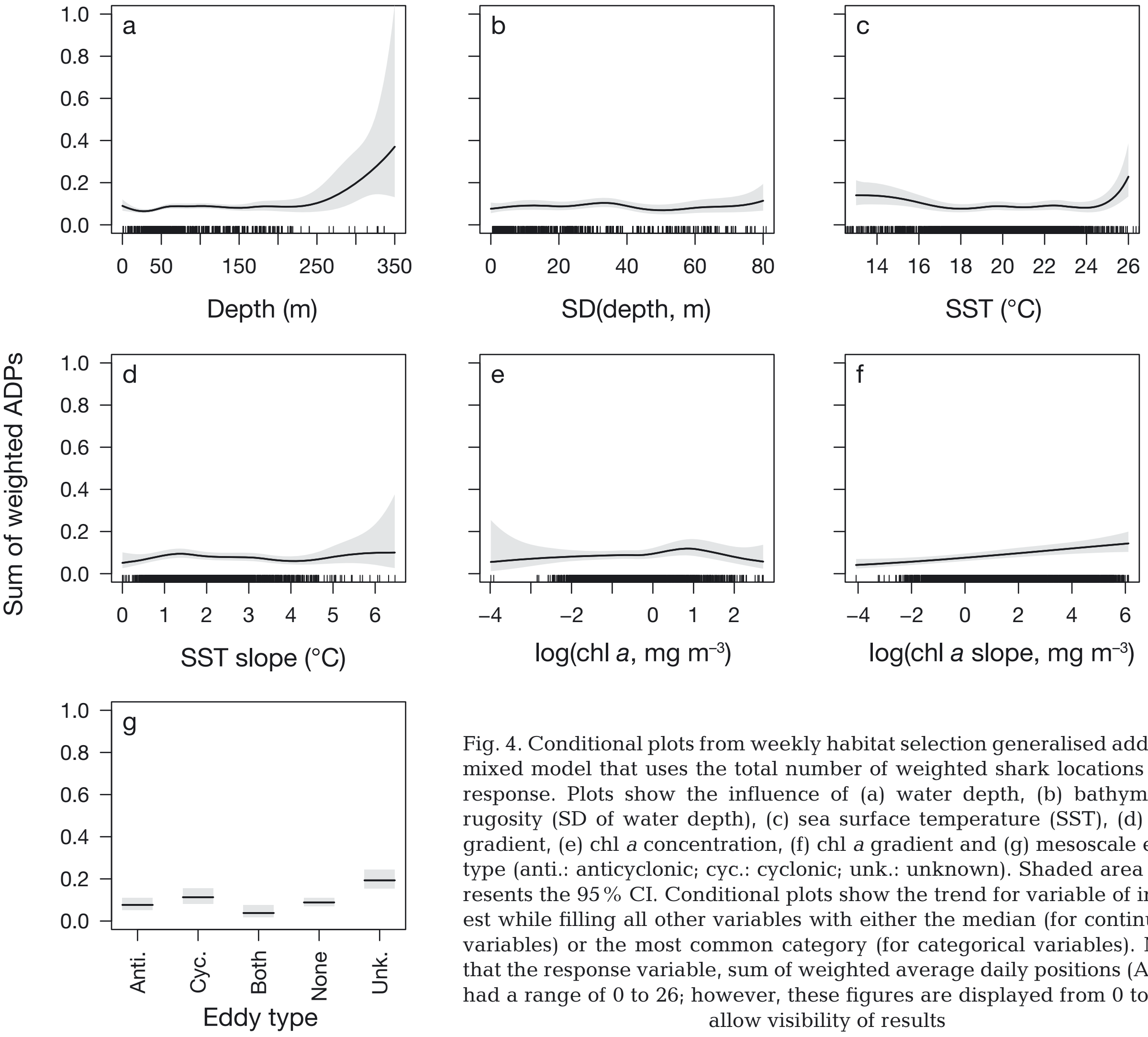

Fig. 4. Conditional plots from weekly habitat selection generalised additive mixed model that uses the total number of weighted shark locations as a response. Plots show the influence of (a) water depth, (b) bathymetric rugosity (SD of water depth), (c) sea surface temperature (SST), (d) SST gradient, (e) chl *a* concentration, (f) chl *a* gradient and (g) mesoscale eddy type (anti.: anticyclonic; cyc.: cyclonic; unk.: unknown). Shaded area represents the 95% CI. Conditional plots show the trend for variable of interest while filling all other variables with either the median (for continuous variables) or the most common category (for categorical variables). Note that the response variable, sum of weighted average daily positions (ADP), had a range of 0 to 26; however, these figures are displayed from 0 to 1 to allow visibility of results

(Fig. 5). Sharks, however, displayed travelling behaviour (longer distances between consecutive locations and low turning angles) throughout the study area (Fig. 5). Movement was classified as area restricted when step lengths were an average of 8.8 ± 8.5 km and as travelling when the step length was 63.7 ± 59.8 km. Sharks spent a median of 8 consecutive days displaying area-restricted movements (inter-quartile range: 4–16 d). One shark spent 116 d exhibiting area-restricted movement off the coast of Port Stephens, well in excess of the 90th percentile (26 d). Sharks spent a median of 4 consecutive days travelling (inter-quartile range: 2–8 d). As with area-restricted movements, number of days travelling was highly variable. For example, 1 shark spent 66 consecutive days travelling from Port Stephens to northern Tasmania (90th percentile = 13 d).

The probability of a shark displaying area-restricted movement was influenced by water depth, SST, SST gradient, chl *a* concentration and eddy type (Fig. 6, Table 3). Sharks showed more area-restricted movement in shallow waters (<60 m water depth) and on the continental slope at ~300 m (Fig. 6a), when SST was between ~19 and 23°C (Fig. 6b), at thermal fronts with an SST gradient of >3°C (Fig. 6c) and at high chl *a* concentrations (Fig. 6d). There was no statistical difference between anticyclonic and cyclonic eddies or areas with no eddies (all Wald test p-values > 0.05; Fig. 6e), but there was a lower probability of a shark displaying area-restricted movement in a cyclonic eddy versus no eddy (Wald test p-value = 0.04; Fig. 6e). Sharks between <200 and ~250 cm TL had the highest probabilities of showing area-restricted movement (Fig. 6f), and males had a significantly higher probability than females (Wald test p-value = 0.04; Fig. 6g). The model had an AUC of 0.71 ± 0.003 and explained 24.9% of the variation observed in the data with each variable individually contributing less than 7% (Table 3).

4. DISCUSSION

Using satellite tracks from 77 white sharks, we have shown the influence that oceanographic and physical factors have on the occurrence and habitat use of juvenile and sub-adult white sharks along the east coast of Australia. The spatial extent of their movement matches previous estimates by Bruce & Bradford (2012) and Bruce et al. (2019), which were based on a subset of the data presented here (22 and 27 sharks, respectively). However, like Spaet et al. (2020), we have quantified more extensive movement across Bass Strait than previously documented (Bruce & Bradford 2012, 2018). Nevertheless, only 3 sharks moved into South Australian waters, and so overall their movements support the 2-population model proposed by Blower et al. (2012).

Overall occupancy was highest in 3 areas on the east coast of Australia: 2 are known nursery areas (Stockton to Forster in NSW and south-eastern Victoria) previously reported by Bruce & Bradford (2012) and Bruce et al. (2019), while a new region of high occupancy in the far north coast of NSW was identified. Corroborating this third region was the capture and tagging of 36% of sharks around Ballina. Juvenile white sharks are known to return to the 2 nursery areas, with sharks visiting the Stockton to Forster region for at least 5 consecutive years following tagging (Bruce et al. 2019). One shark included in this study displayed area-restricted movement between Stockton and Forster for 116 consecutive days. Seasonal philopatry is common in white sharks with juveniles making annual migrations to the same areas in the North Atlantic (Curtis et al. 2018), while juveniles and adults in the eastern Pacific return to the same coastal sites (Jorgensen et al.

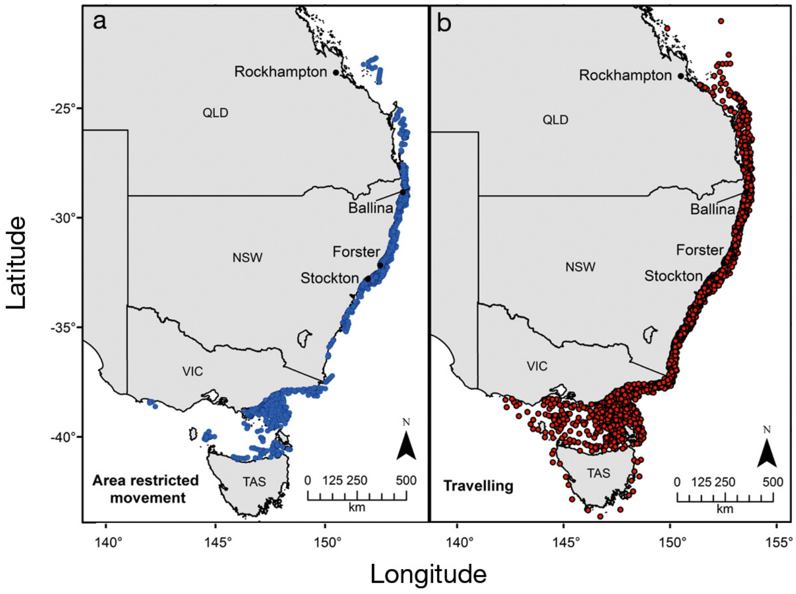

Fig. 5. (a) Area-restricted movement and (b) travelling locations estimated from hidden Markov models. QLD: Queensland; NSW: New South Wales; VIC: Victoria; TAS: Tasmania. Map was generated in ArcGIS 10.5

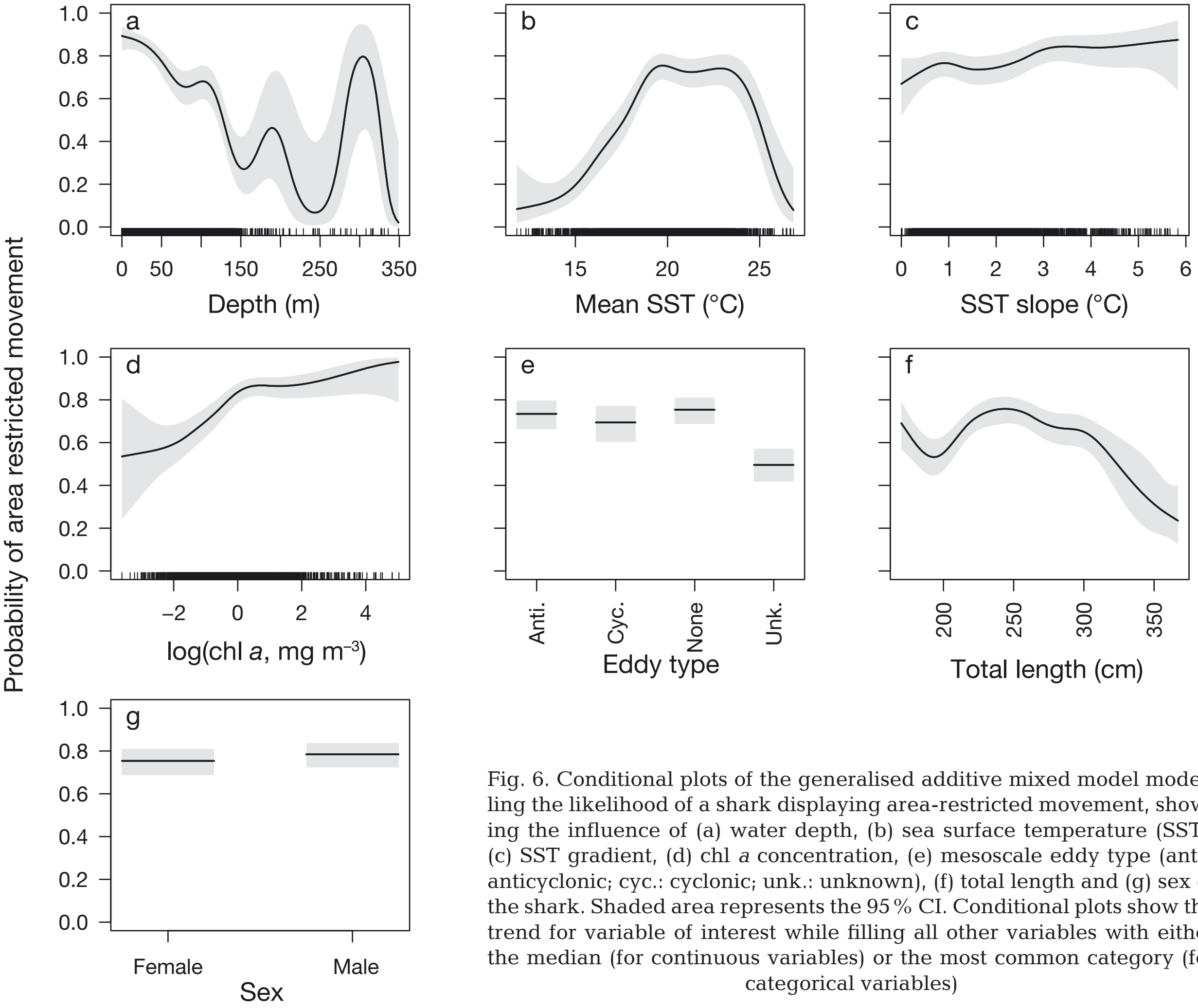

Fig. 6. Conditional plots of the generalised additive mixed model modelling the likelihood of a shark displaying area-restricted movement, showing the influence of (a) water depth, (b) sea surface temperature (SST), (c) SST gradient, (d) chl *a* concentration, (e) mesoscale eddy type (anti.: anticyclonic; cyc.: cyclonic; unk.: unknown), (f) total length and (g) sex of the shark. Shaded area represents the 95% CI. Conditional plots show the trend for variable of interest while filling all other variables with either the median (for continuous variables) or the most common category (for categorical variables)

2010, Domeier & Domeier 2012) and islands (Domeier & Nasby-Lucas 2007, Weng et al. 2007a).

We found 95% of daily satellite locations were in areas of ≤350 m water depth, corroborating previous findings that juvenile and sub-adult white sharks are largely shelf based (Weng et al. 2007b, Domeier & Nasby-Lucas 2008, Bruce & Bradford 2012, Domeier & Domeier 2012, Duffy et al. 2012, Skomal et al. 2017). Our modelling indicated that sharks had the highest probability of occurring in waters of ~50 to 130 m depth (Fig. 3a), a slightly wider range than that reported by Bruce & Bradford (2012) but within the margin of error in position estimates. Bruce & Bradford (2012) hypothesised that sharks were using relic coastline structures to navigate or enhance foraging. In south-eastern Australia, such relic structures are low gradient and only have a relief of up to ~5 m (Brooke et al. 2017), consistent with our findings that suggested bathymetric rugosity is a poor predictor of the presence of white sharks. Once present, sharks preferentially selected habitats in continental slope waters (>250 m water depth) compared to other depths (Fig. 4a). However, water depths of >250 m were at the upper extreme of those observed and had few data points. Therefore, the increase in habitat selection may be an artefact from the underlying data distribution and must be interpreted with caution. High use of waters over the continental slope could indicate sharks forage in the nutrient-rich slope waters. Juvenile white sharks have previously been recorded making regular slope excursions and diving to 984 m (Bruce & Bradford 2012).

4.1. Oceanographic conditions associated with white shark occurrence, habitat selection and movement patterns

White sharks had a wide thermal niche (10–27°C), with the highest probability of presence at 20°C

(Fig. 3b). This estimate suggests a wider thermal range than those previously reported for populations in south-eastern Australia (14–22°C; Bruce & Bradford 2012), New Zealand (10–16°C; Francis et al. 2012), the North Atlantic (13–23°C; Skomal et al. 2017) or South Africa (11–22°C; Weltz et al. 2013) but similar to adults tracked in the eastern Pacific (bimodal distribution between 10 and 26°C; Block et al. 2011). Within this broad range, we found that the relative habitat selection of white sharks was slightly higher when SST was less than 18°C or higher than 24°C (Fig. 4c) and had a much smaller influence than in the occurrence model. This suggests that while SST is associated with the presence of white sharks, it does not strongly influence shark habitat selection. However, these SST values were at the extremes of those observed, and this pattern may be an artefact from the underlying data distribution. Nevertheless, the cooler range is consistent with catches in shark control programs in NSW and South Africa, which both showed higher white shark catches when SSTs were ~17 to 18°C (NSW: Lee et al. 2018a, South Africa: Wintner & Kerwath 2018). Likewise, sightings of white sharks in South Africa increased when water temperature was higher than 14°C with a maximum at 18°C (Weltz et al. 2013). In contrast to the population-level habitat use patterns, we found that white sharks were more likely to show area-restricted movement patterns in areas with SSTs of 19 to 23°C (Fig. 6b). The wide thermal niche and variability in how SST influences a shark's behaviour suggests that SST may be a proxy for other environmental variables affecting white sharks (Robbins & Booth 2012), such as productivity.

White shark occurrence and movement patterns were influenced by chl *a* concentration, while there was a weaker relationship between chl *a* and habitat selection. Although the highest probability of presence and habitat selection occurred at intermediate chl *a* concentrations (logged chl *a* concentrations of ~1 mg m^{-3}; Figs. 3c & 4e), the likelihood of a shark showing area-restricted movement patterns increased as chl *a* increased (Fig. 6d). The East Australian Current (EAC), the western boundary current of the South Pacific sub-tropical gyre that flows poleward along the south-eastern continental slope, strongly influences the dynamics of chl *a* along the east coast of Australia (Everett et al. 2014). In the northern extent of our study area (north of 31° S), the EAC meanders on and off the narrow continental shelf (Archer et al. 2017), and as it encroaches on the coast, current-driven upwellings move the nutrient-rich slope water into the euphotic zone (Roughan & Middleton 2002, 2004), resulting in higher primary productivity (Armbrecht et al. 2014, Everett et al. 2014, Rossi et al. 2014). Downstream, the EAC separates from the coast, typically at ~31° to 32° S (Cetina-Heredia et al. 2014), where the current bifurcates into the eastward-flowing Tasman Front and a southward EAC extension (Hill et al. 2011). At the separation zone, both wind- and current-driven upwellings (Roughan & Middleton 2002, 2004, Rossi et al. 2014) result in high chl *a* concentrations (Everett et al. 2014). Immediately south of the separation zone, the reduced velocity of the EAC and wide shelf results in retention of enriched waters around the Stockton area (Everett et al. 2014). This region is dominated by eddies, both cyclonic and anticyclonic, that have the potential to drive onshore transport (Malan et al. 2020). Further downstream of Stockton, chl *a* is driven by a strong seasonal cycle, with 152% increases in phytoplankton biomass each spring (Everett et al. 2014). The high productivity of the Stockton region, as well as upwellings occurring twice as often upstream of the EAC separation as downstream (Rossi et al. 2014), could explain the high occurrence of sharks in the Stockton to Port Macquarie region and off the northern NSW coast, while to the converse, low-productivity waters further south may explain the reduction in the area-restricted movement of sharks along the central and southern NSW coast (Fig. 5).

Occurrence and habitat selection increased as the chl *a* gradient increased (Figs. 3d & 4f), with the latter also increasing with SST gradients of ~1 and greater than 4°C (Fig. 4d) despite low concurvity between chl *a* and SST gradient in the models. As well as increasing chl *a* concentrations, upwellings produce chl *a* (Everett et al. 2014) and temperature (Schaeffer et al. 2013, Armbrecht et al. 2015, Schaeffer & Roughan 2015) gradients in surface waters and at depth. Therefore, the relationships observed in this study could be in response to such oceanographic events. However, upwelling intensity, which is measured by the depth of the 14°C isotherm in this region, or sub-surface properties were not included in this study. Further research could explore how white shark spatio-temporal distributions change with sub-surface conditions. Alternatively, the relationship with chl *a* and chl *a* gradient observed in this study could have been influenced by the size of the grid cells over the continental shelf and slope. Surface chl *a* concentrations are higher on the continental shelf (closer to the coast) and decrease offshore (Everett et al. 2014). If the sharks were in mid- to offshelf regions, the surface chlorophyll may be lower here than by the coast and result in chl *a* and chl *a* gradient being included in the models.

In addition to other possible oceanographic conditions, this region is known to be eddy rich (Suthers et al. 2011, Everett et al. 2012). Anticyclonic eddies off south-eastern Australia have similar hydrodynamic properties to the EAC proper (i.e. no eddies; Baird et al. 2011), given that they are shed from the jet itself. So it makes sense that no eddy is similar to anticyclonic eddy, as observed in each of the models. Eddies are more prevalent in waters south of the EAC separation point (32° S) to east of Bass Strait (39° S), with cyclonic eddies having higher chl *a* concentrations and lower SST than surrounding waters and anticyclonic eddies having lower chl *a* concentrations (Everett et al. 2012) and higher SST. Therefore, the relationships observed between habitat selection and chl *a* and SST gradient could also be influenced by their preference for cyclonic eddies. This preference for the more productive cold-core eddies is in contrast to that observed by adult white sharks in the North Atlantic, which apparently prefer warm-core, anticyclonic eddies (Gaube et al. 2018). This may highlight the relative difference in absolute temperature within eddies between the 2 locations or may highlight differing habitat selection by white sharks during different life stages.

4.2. Implications for mitigation of human–shark interactions

Although white sharks were less likely to occur in shallow nearshore waters (Fig. 3a), when they were present, they were more likely to exhibit short-term area-restricted movement (Fig. 6a). This, coupled with a higher probability of them displaying area-restricted movement in shallow waters (<60 m depth) with an SST of ~19 to 23°C and high chl *a* concentrations, has implications for informing measures used for shark surveillance and to minimize shark–human interactions and by-catch of white sharks in nearshore fisheries. Nearshore temperatures along the northern and central NSW coast reach 19 to 23°C during the late austral winter and early spring (Lee et al. 2018b), which coincides with detections from acoustically tracked sharks (Bruce et al. 2019) and higher white shark catches in the NSW Shark Meshing Program (Reid et al. 2011, Lee et al. 2018a). Smaller sharks (<200 cm TL) had the highest probability of movements being area restricted, which has implications for managers of shark mitigation programs trying to reduce anthropogenic threats to this vulnerable age class in the nearshore regions and the likelihood of interaction with beach users (especially board riders). More than 85% of the Australian population lives within 50 km of the eastern seaboard of Australia (Clark & Johnston 2017), with 45% of people along the stretch of coastline between Brisbane, Queensland, and Sydney, NSW (calculated from Australian Bureau of Statistics 2019). This stretch of coastline is the centre of the eastern Australian white shark's distribution.

The results from this study highlight the broad-scale oceanographic conditions associated with juvenile white shark occurrence and habitat use. The results of this study provide previously lacking insight into the distribution of juvenile white sharks in relation to key oceanographic and bathymetric features of the region. This is important contextual information which could be used as an input into decisions on the spatial and temporal allocation of shark bite mitigation measures (e.g. drones, SMART drumlines, shark spotters, aerial surveillance) by enabling authorities to implement or enhance these measures during times when oceanographic conditions increase the potential for high nearshore densities of juvenile and sub-adult white sharks. These data will now be used to inform predictive models of shark distribution.

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