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Salinity drives the distribution of a top-order predator, the tiger shark (*Galeocerdo cuvier*), in an inverse estuary

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Understanding how dynamic environmental processes influence the distributions of top-order predators is fundamental to assess top-down effects on ecosystems. Tiger sharks (*Galeocerdo cuvier*) are a large top-predator that can trigger trophic cascades and structure communities. However, the dynamic physical processes that influence the distributions of these animals in coastal systems are largely unknown. Here, we assess the environmental processes influencing tiger shark movements in the inverse estuary of Shark Bay, Western Australia, a shallow coastal embayment with salinities consistently above that of the adjacent ocean. We applied Bayesian generalized linear mixed-effects models to generate dynamic predictions of suitable habitat for tiger sharks in this region. These habitats were associated with dense and shallow seagrass beds and largely reflected the spatial variability of hypersaline water (<40). Under future climate scenarios, coastal areas worldwide are predicted to experience inverse estuarine conditions. We anticipate that the physical processes that influence tiger shark distributions in this study will become applicable to numerous other species of gill-breathing fauna in coastal ecosystems across the globe.

Keywords Habitat suitability model, Marine megafauna, Regional Ocean Modelling System, Satellite telemetry, Sharks, Species distribution model

Top-order predators can have a profound impact on the energy flow and trophic structure of ecosystems[1–3]. These predators are affected by several physical (e.g., rainfall, temperature, topography[4,5]) and biological factors (e.g., prey distribution, vegetation coverage[6]) that can alter their behaviour and redistribute entire populations[7,8]. This is particularly true in pelagic systems, where dynamic oceanographic processes can govern access to resources[9,10] and limit use of habitats[11], which in turn may determine when and where top-predators can exert their influence on prey communities.

Tiger sharks (*Galeocerdo cuvier*) are a large, top-order predator[12] that occurs in tropical and warm-temperate marine environments. The movements of these sharks can influence the distribution and behaviour of prey through consumption and by inducing threat-response behaviours[13,14]. Where tiger sharks are more common, prey species may forgo foraging and avoid habitats (e.g., shallow seagrass banks) that increase the risk of their predation[15–17]. More broadly, the response of prey to the presence of tiger sharks can trigger trophic cascades across communities, which can reduce grazing pressure on vegetated coastal habitats (e.g., seagrass meadows, macroalgae etc.) that maintains the productivity of these systems[14,18]. Such trophic effects can occur at large spatial (100–1000's km) and temporal (weeks–months) scales[19] because tiger sharks are migratory, routinely moving between coastal and oceanic habitats[20–22].

The oceanic movements of tiger sharks are often associated with seasonal shifts in water temperature and meso-to large-scale (10–1000's km) oceanographic features (e.g., shelf break, slope, frontal systems etc.) that amass prey[23–26]. However, tiger sharks also occupy habitats on coastal shelves for prolonged periods spanning

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many months[20,27]. In these systems, currents interact with inputs from estuaries, wind patterns and obstructions in the form of reefs, islands and banks to generate a very complex oceanographic environment[28]. At present, it is unclear how dynamic physical processes in coastal systems drive habitat selection and distribution of tiger sharks. This information is important to predict how these animals will respond to the high levels of anthropogenic modification now occurring within coastal habitats (e.g., climate change and habitat loss[29]).

A key challenge associated with assessing the environmental preferences of highly mobile marine fauna such as tiger sharks is the measurement of in-situ data at the spatio-temporal scales relevant to their movements[30,31]. Ocean circulation models, such as the Regional Ocean Modelling System (ROMS; obtained from coastaloceanography.org[32]), can assist with overcoming this issue because they can be used to generate oceanographic data at sub-mesoscales (1–10 km) and at temporal intervals of hours to days[33]. Incorporating these data when analysing the movements of animals using habitat suitability models (HSMs) provides a powerful method to evaluate the physical processes that determine the distributions of individuals, and can also be used to predict their responses to dynamic environmental conditions[34]. Here, we combine data obtained from ROMS and satellite telemetry to develop HSMs that reveal the physical processes influencing the distribution patterns of tiger sharks within Shark Bay World Heritage Area in Western Australia. We assess how the habitat suitability of tiger sharks is affected by the key physical processes of this shallow ecosystem, which features extensive seagrass meadows and inverse estuarine conditions[35]—defined as a body of water where salinities consistently exceed that of the adjacent ocean[36]. We used a suite of dynamic (e.g., salinity, sea surface temperature, frontal zones etc.) and static (e.g., bathymetry, seagrass density maps and other habitat types) environmental variables that are thought to influence the movement patterns of this species throughout the region. We generated dynamic habitat suitability maps on a monthly and seasonal basis to examine the underlying environmental processes that might determine the distribution of tiger sharks in Shark Bay.

Results

Tiger shark satellite tracks

A total of 10 tiger sharks were captured and tagged using baited drumlines in the eastern and western gulfs of Shark Bay during the summer (October–March; n = 5) and winter (April–September; n = 5) of 2022 (Fig. 1). Tag deployment durations ranged from 29 to 301 days (mean = 180, Standard deviation 96 days; hereafter ± SD; Table 1). Location estimates obtained per deployment ranged from 2 to 255 (mean = 86 ± 89 locations; Table 1). Two sharks were removed from HSM analyses because the tags reported fewer than 10 location estimates (Shark 226172 and 238332; Table 1). Tiger sharks travelled distances ranging from ~ 20 to over 2600 km (mean = 1238 ± 1006 km). The four largest individuals (3.17 to 4.06 m TL) in the dataset displayed large-scale (100’s km) migratory movements away from Shark Bay during the winter months before returning during summer (Figure S1). Two females (4.06 and 3.17 m TL) migrated 435 and 446 km north to Coral Bay and Exmouth Gulf respectively, and one female (3.17 m) and one male (3.51 m) migrated 369 km south to the Abrolhos Islands (Fig. 2A; Figure S1). The other six individuals remained in the general vicinity of Shark Bay throughout the duration of tracking (Fig. 2B; Figure S1).

Local oceanography and tiger sharks

Average sea surface temperatures (SST) across Shark Bay derived from ROMS models were warmer in the summer (range 17.47–30.72 °C, mean = 24.64 ± 1.01 °C) than winter (range 10.68–27.48 °C, mean = 20.81 °C ± 1.7 °C; Figure S2). There was no seasonal fluctuation in mean sea surface salinity (herein a dimensionless unit, see methods; Figure S3). However, during the summer, hypersaline water was largely restricted to the southern regions in both the eastern and western gulfs (Figure S3), compared to the winter, when plumes of hypersaline water flowed north towards oceanic waters (Figure S3). Two persistent thermal frontal systems spanned between the Naturaliste and Geographe channels (Figure S4). The magnitude strengths of these were weaker in the summer (2.11 ± 0.53) and intensified during the winter (2.82 ± 0.77) when the waters within Shark Bay become cooler than the adjacent ocean (Figure S2 and 4).

Tiger sharks were typically found within a narrow range of SSTs and salinities (Table 1; Figure S5 and 6). The SST each shark experienced in Shark Bay ranged from 21.25 to 22.58 °C (mean = 21.8 ± 0.26; Table 1). Tiger sharks stayed within the general vicinity of Shark Bay even as SST began to cool and remained within or near water masses with temperatures above 21 °C (Figure S5). Tiger sharks also occupied a narrow range of salinities, from 35.29 to 39.77 (mean = 36.6 ± 0.90; Table 1) and avoided areas with hypersaline waters (salinities > 40, Supplementary Video 1). The movements of tiger sharks did not seem to be associated with thermal frontal systems (Figure S7). Tiger sharks with larger body sizes (> 3.10 m) occupied significantly higher salinities (Wilcoxon rank sum test: W = 33,180, p-value < 0.01) and SSTs (Wilcoxon rank sum test: W = 28,211, p-value < 0.01), than sharks with smaller body sizes (< 3.10 m; Figure S8). There was no significant difference between the magnitude strength of thermal frontal systems experienced by smaller (> 3.10 m) and larger (< 3.10 m; Wilcoxon rank sum test: W = 13,800, p-value = 0.22) sharks.

Habitat suitability model

A suite of Bayesian GLMMs were built with combinations of environmental variables using a filtered tracking data that contained position errors of less than 1.5 km to match the resolution of the oceanographic data (see “Methods” section below). The model with the highest statistical support (wAICc ~ 1) included the variable salinity with the interaction terms of percentage of grid area covered by dense seagrass and bathymetry (Table S1). Our choice of pseudo-absences had no effect on model selection (Table S2). The top-ranked model explained 26% of deviance with a mean area under the curve (AUC) score of 0.75 (tenfold cross validation range of 0.71–0.79), Kappa (*k*) of 0.42 (tenfold cross validation range of 0.36–0.49) and true skill statistic (TSS) of 0.43 (tenfold cross validation range of 0.36–0.49). The grouping variable of shark ID explained ~ 1% of total model deviance.

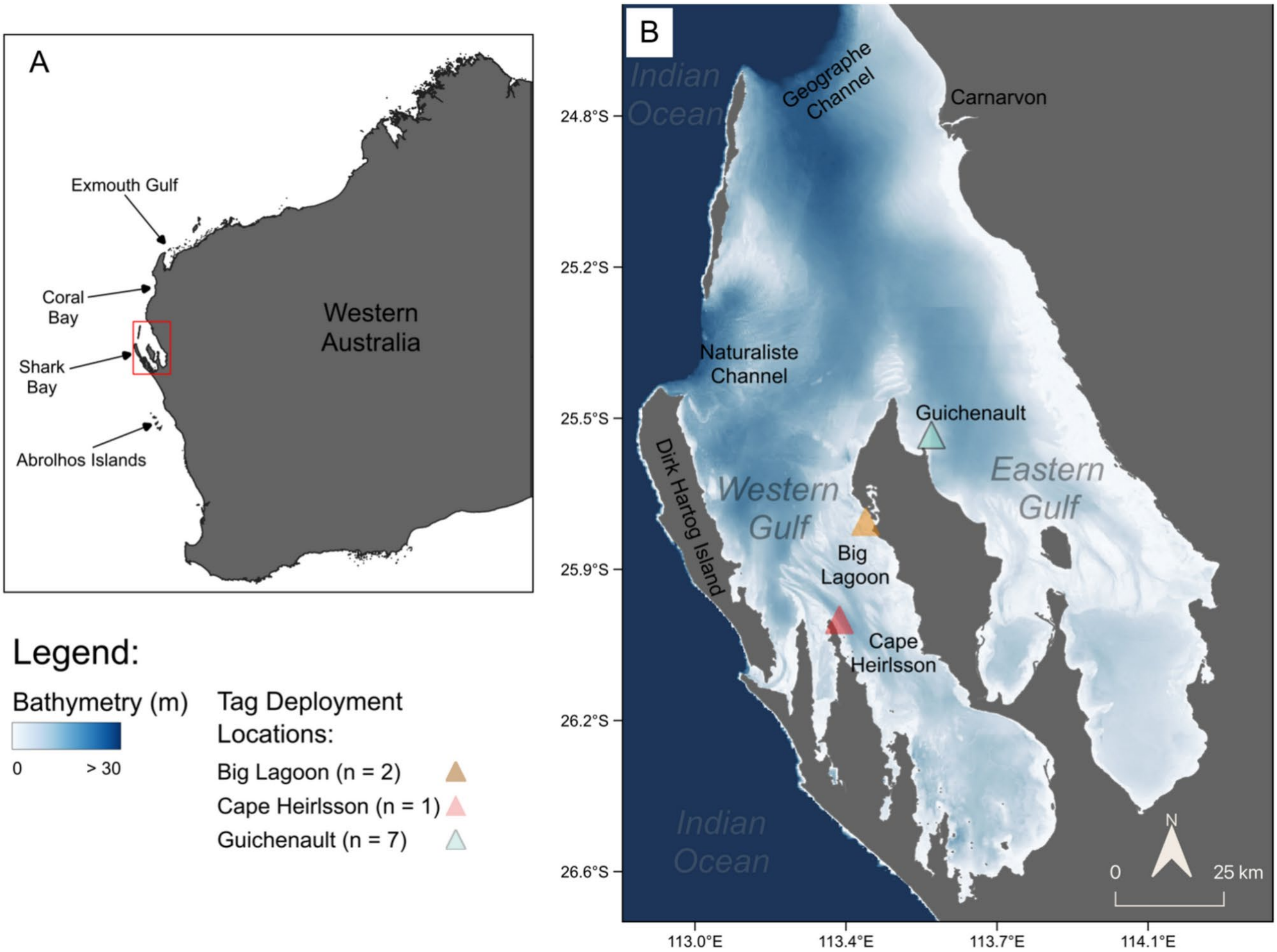

Fig. 1. (**A**) An overview map showing the position of study area of Shark Bay (red square) in relation to other areas of interest and to Western Australia. (**B**) A map showing the bathymetry of Shark Bay and the tag deployment locations in the eastern and western gulfs (Big Lagoon, Cape Heirlsson and Guichenault). The legend shows the number of individuals tagged in each location.

TS ID	Sex	Size (m)	No. of raw locations	No. of filtered locations	Tracking duration (days)	SST °C (mean ± SD)	Salinity (mean ± SD)	Front magnitude (mean ± SD)	Tagging location
112952	Female	3.17	14	2	120	21.8 ± 1.75	36.1 ± 1.08	0.5 ± 0.36	Eastern Gulf
226167	Female	2.77	96	51	140	21.7 ± 0.28	35.6 ± 0.37	0.5 ± 0.35	Western Gulf
226168	Female	2.44	22	14	114	21.5 ± 0.03	35.3 ± 0.01	0.1 ± .15	Western Gulf
226169	Male	3.13	159	52	301	21.8 ± 0.17	36.6 ± 0.49	0.4 ± 0.37	Eastern Gulf
226170	Male	3.51	78	16	298	21.7 ± 0.15	36.0 ± 0.73	0.4 ± 0.29	Eastern Gulf
226171	Female	4.06	34	18	203	22.0 ± 0.24	37.0 ± 0.54	0.4 ± 0.24	Eastern Gulf
226172	Female	3.00	7	6	85	21.9 ± 0.09	35.4 ± 0.37	0.5 ± 0.17	Eastern Gulf
238332	Female	2.47	2	1	29	21.5 ± 0.01	37.3 ± 0.01	0.5 ± 0.01	Western Gulf
238333	Female	3.17	187	94	232	21.8 ± 0.20	36.5 ± 0.69	0.5 ± 0.38	Eastern Gulf
238336	Female	3.12	255	151	283	22.0 ± 0.26	37.2 ± 0.91	0.5 ± 0.31	Eastern Gulf
Mean ± SD		3.08 ± 0.47	86 ± 89	40 ± 48	180 ± 96	21.8 ± 0.26	36.6 ± 0.90	0.5 ± 0.34	

Table 1. Summary statistics for each tiger shark in the tracking data set. *TS* tiger shark, *SST* sea surface temperature.

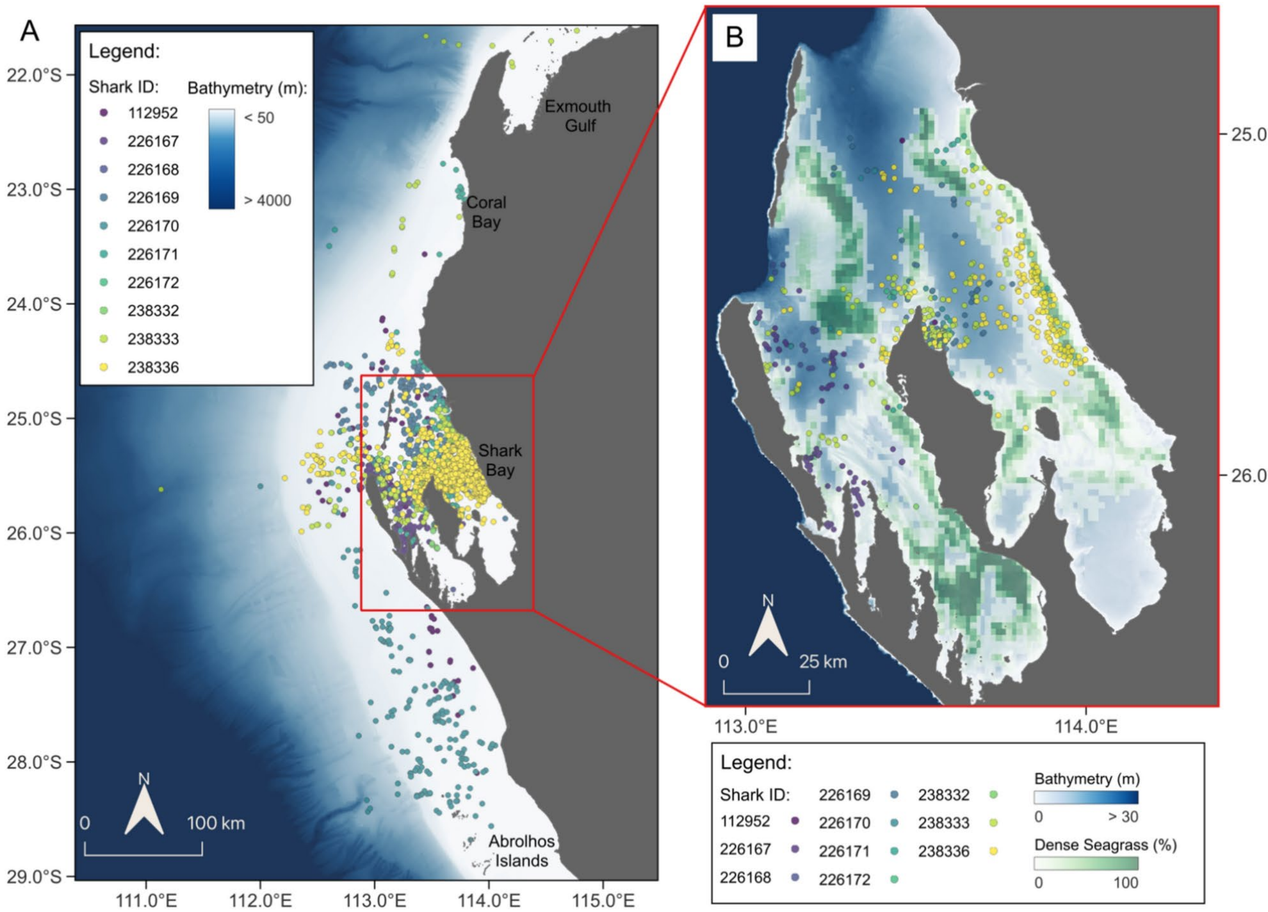

Fig. 2. (**A**) Raw location estimates for all tracked sharks. (**B**) The location estimates for the filtered tracking dataset (location error < 1.5 km) within Shark Bay for all sharks combined, overlayed on the habitat variables of dense seagrass (% coverage) and bathymetry (m).

The response curve of salinity showed that the probability of occurrence of tiger sharks peaked at salinity values ~ 37, with a significant non-linear effect (95% CI 0.45–0.53, $p < 0.01$), followed by a steep decline in the probability of occurrence at salinity levels exceeding > 37 (Fig. 3A). The conditional effect term of bathymetry, which was held at a mean value, had a positive and significant effect (95% CI: 1.19–1.92, $p = 0.01$) indicating that shallower areas were associated with higher habitat suitability (Fig. 3B). The conditional effect term of dense seagrass had a weak and non-significant effect (95% CI: 0.73–1.11, $p = 0.30$) at its mean value, suggesting little influence on habitat suitability (Fig. 3C). The interaction between dense seagrass and bathymetry was significant and positive (95% CI: 1.25–1.89, $p < 0.01$), indicating that the influence of dense seagrass on habitat suitability increased with shallower depths (Fig. 3D).

Monthly maps of predicted habitat suitability showed seasonal trends between summer (October–March) and winter (April–September) with suitable habitat restricted to areas of the Bay with salinities < 40 (Fig. 4, Figure S9 and Supplementary video 2). During the summer months (October–March), suitable habitat (> 0.6) was identified far south into both the western and eastern gulfs of the bay with areas of higher suitability (> 0.80) identified where there was shallow bathymetry and higher coverage of dense seagrass (Fig. 4, Figure S9 and Supplementary Video 2). The model also predicted that in the cooler months (April-September), suitable habitat for tiger sharks was largely restricted to the northern regions of Shark Bay and within more oceanic waters (Fig. 4, Figure S9 and Supplementary Video 2).

Discussion

We found strong evidence that outflowing plumes of hypersaline water originating in the southern portions of Shark Bay strongly influenced the available habitat for tiger sharks in this region, which were associated with shallow depths and dense seagrass beds. The seasonal advance and retreat of hypersaline water determined use of these habitats by tiger sharks, which were highly suitable in the summer, but unsuitable in winter when waters with salinity > 40 inundated the seagrass banks. Despite tracking a limited number of sharks, our results could explain the outcomes of earlier studies that showed that similar seasonal patterns in the abundance of tiger sharks in Shark Bay that could not be explained by shifts in prey distribution or changes in SST[37,38].

Although it is possible that we had more location estimates from tags when sharks were in shallow depth, and thus more likely to have the antenna out of the water to allow transmission, the preference by sharks for

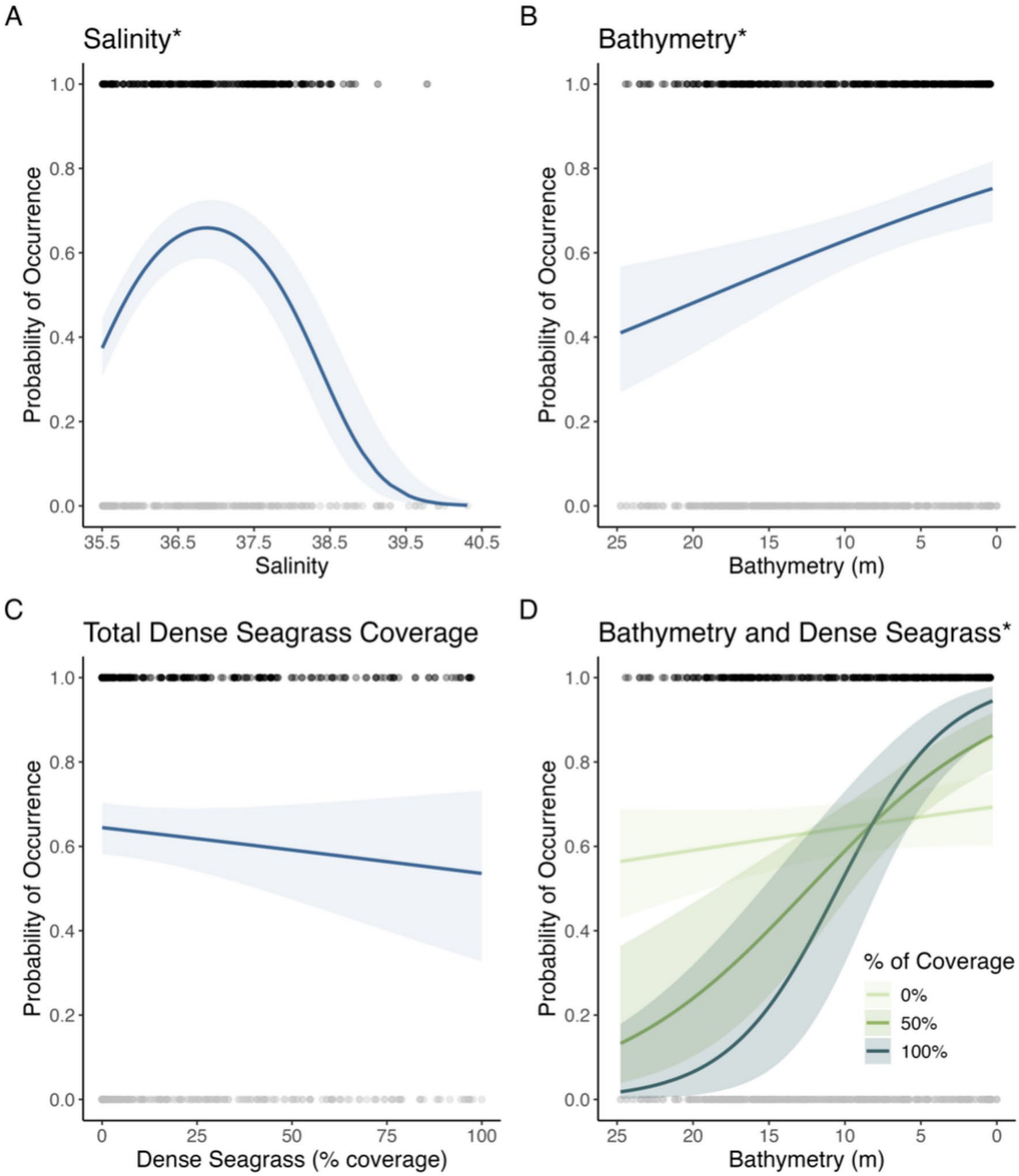

Fig. 3. Conditional effects of the fixed effects of the top Bayesian generalized linear mixed-effects model. The 95% credible interval is represented as the shading around the fitted line.Points along the x-axis indicate the distribution of all presence (black) and pseudo-absence (grey) data for the predictor variable. Note that in plot D, the effect of the interaction between dense seagrass and bathymetry is shown at specified intervals of the percent of dense coverage. Significance of predictor variables indicated with an asterisk.

shallow seagrass habitats is known to be associated with foraging, given this is where their preferred prey (e.g., sea turtle, dugong and sea snakes) are most abundant in Shark Bay[15,17,39]. Tiger sharks are visual predators and foraging in shallow environments could allow individuals to better identify the motion cues of potential prey[40]. There is also evidence that foraging in these habitats may be more efficient, as search patterns can easily include both the seabed and surface habitats[41,42]. Capture of large-bodied prey by tiger sharks is thought to improve in shallow environments and at the air–water boundary when prey are potentially less vigilant, and can be trapped at the surface[41,42].

Our models suggest that suitable habitat available for tiger sharks decreases as salinities exceed ~ 37 and revealed that these animals refrain from utilising areas inundated with hypersaline water (salinity above 40). This likely reflects some physiological limit for tiger sharks, given they are stenohaline gill-breathers and lack the physiological adaptations to osmoregulate in hypersaline conditions[43]. Exposure to hypersaline conditions

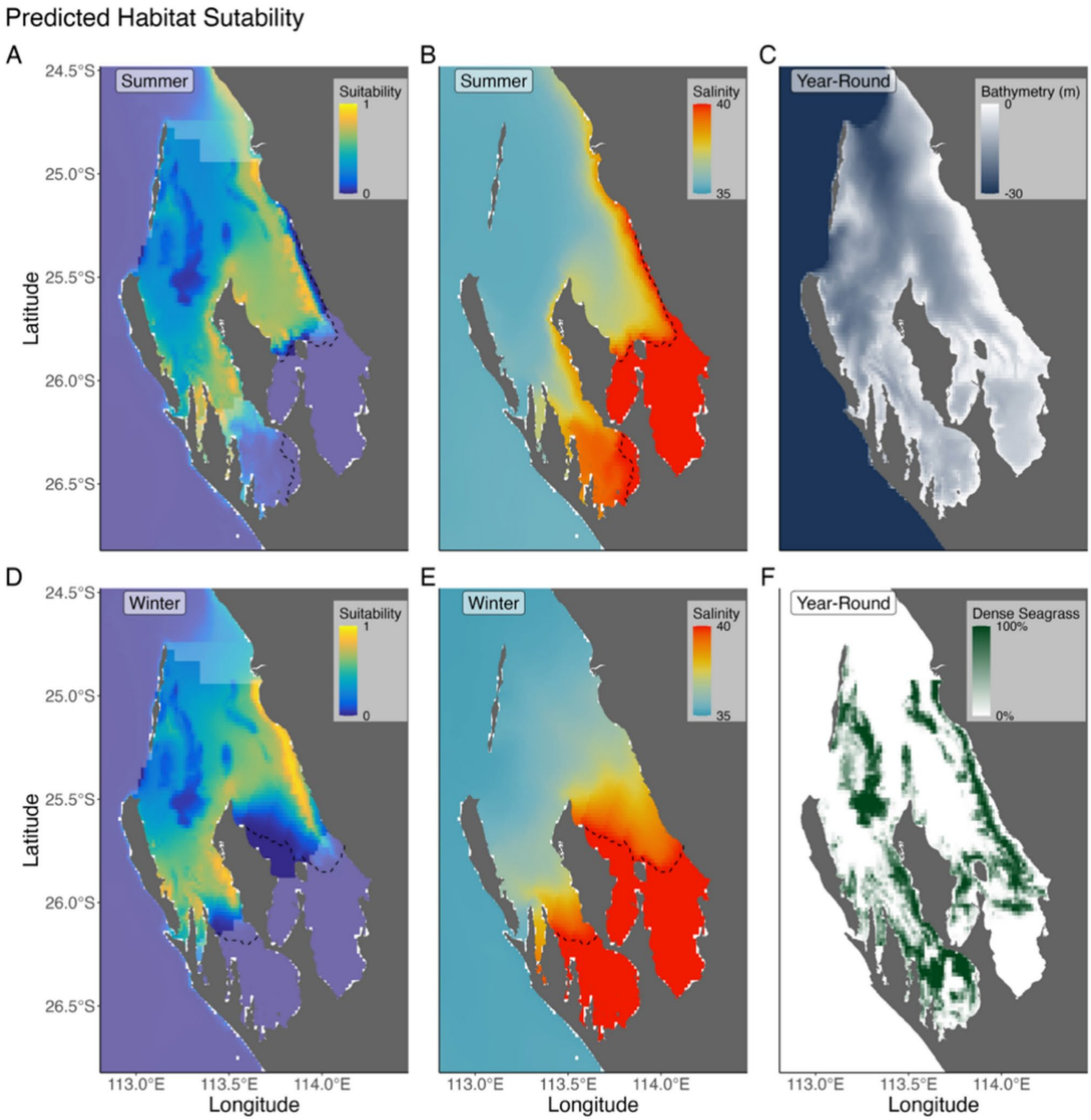

Fig. 4. Spatial predictions of habitat suitability for tiger sharks in Shark Bay and corresponding monthly mean salinity for January (**A** and **B**), the middle month of summer, and June (**D** and **E**), the middle month of winter. The darker colours represent the spatial predictions made within the grid extent and the lighter colours represent extrapolated predictions to the entire of the study area. The dashed black line (**A**, **B**, **D** and **E**) represent the contour line of water with salinity above 40. Static environmental predictor variables of bathymetry (m) and % of dense seagrass cover shown as (**C**) and (**F**) respectably.

can reduce the efficiency of oxygen consumption rates for teleost fishes[44] and gradients of salinity are known to influence the distributions of other large sharks in similar coastal environments[45]. Differences in residency related to size provide further evidence of a physiological basis for habitat suitability[46], with larger individuals (>3.10 m TL) occupying waters of higher salinity (up to 40) than smaller (<3.10 m TL) sharks, which never ventured into waters of salinities >37.3. Smaller sharks are known to be less tolerant to changes in salinity[47] due to higher ratios of gill surface area to body volume than larger sharks, which increases the relative cost of osmoregulation[43].

Size segregation is common among numerous species of sharks in costal systems. Typically, smaller individuals avoid certain habitats to reduce competition with larger individuals that might provide a potentially lethal threat[48]. We found some evidence of this in Shark Bay, with the four largest tiger sharks (all > 3.10 m TL) conducting broad scale (100–1000's km) migrations away from the region during winter, whereas the six smaller individuals (< 3.10 m TL) moved into less saline water but remained within the Bay throughout the duration of the study. If hypersaline water does restrict access to shallow foraging areas for tiger sharks in Shark Bay, perhaps larger individuals migrate elsewhere to access habitats where they can more efficiently capture highly profitable prey items (e.g., turtles and marine mammals) or fulfill other important life history requirements. Prey remain in the Bay year-round[39,49–52], so this migration of larger sharks is likely not a response to a redistribution of these species. For smaller individuals, remaining in the general area could reduce competition for resources despite being less than optimum for their physiology. Shifts in the salinocline may also increase the availability of prey that are sensitive to changes in salinity, such as teleosts and sea snakes[53,54], by aggregating them against salinity boundaries[55–57]. Additionally, hypersaline water exits Shark Bay along the seabed[58] and could improve the foraging efficiency for tiger sharks by compressing the distributions of prey sensitive to high salinity to the upper layers of water column or near the surface[41]. Although salinities are uniform across depths in shallow (less than 10 m) portions of Shark Bay[36], future studies could explore this relationship further by linking the 3-dimensional movements of sharks to data on the vertical structure of the water column in deeper areas of the Bay that is provided by ROMS[32,59].

Despite the fact that tiger sharks are ectotherms and temperature is known to influence their distributions at other locations[24,25,60], SST did not seem to be an important predictor of habitat suitability for the species in Shark Bay. This lack of any relationship could occur because the range of temperatures the tagged sharks experienced while in this environment (10–28 °C) did not exceed the broad thermal niche for the species[61]. Indeed, tiger sharks are capable of occupying water temperatures ranging from 4 to 33 °C[25,62], and have been caught by fisheries in the sub-Arctic waters off the coast of Iceland[63]. The movements of many other species of sharks, particularly in open ocean ecosystems are frequently linked with temperature fronts and thermoclines[64]. Typically, this association between marine predators and temperature fronts is due to foraging as these oceanographic features can accumulate high densities of prey that markedly increase food availability[65,66]. However, it seems unlikely that these phenomena entrain prey for tiger sharks in Shark Bay, given the water temperatures here are within the physiological range of prey species such as marine mammals[67,68], which are endothermic, and marine reptiles, which have large temperature tolerances[69,70].

For tracking data, sample sizes of up to 10 individuals are useful for identifying responses to environmental processes and their influence on the movement of mobile marine megafauna[71]. However, we acknowledge that our findings are based on a limited number of tagged sharks and that more data is required to examine population-level patterns of space use. Despite this, it is very likely that the trends identified in this work will reflect species-wide preferences within Shark Bay because our results were comparable to the outcomes of earlier studies that evaluated seasonal catch rates based on sample sizes of more than 900 individuals[14,37,38]. Unlike hyposaline conditions, few fishes can occupy hypersaline water for protracted periods because such conditions require physiological adaptations that reduce the osmotic permeability of gill membranes[43]. There is no evidence for these mechanisms in tiger sharks and examining how salinity affects the physiology of these animals could be an avenue for future research.

In the past, studies that have attempted to identify the drivers of movement patterns of tiger sharks found a high degree of variability both within and among populations, with some emergent seasonal trends[20,25,26,72,73]. Despite the complexity of our study system, clear patterns emerged in the environmental factors that influenced habitat suitability in Shark Bay. In other estuarine systems, salinity is also a key driver of distributions of elasmobranchs, although in such cases most species avoid areas of hyposaline waters, typical of freshwater inflows into classical estuarine systems[47,74,75]. Under future climate scenarios, inverse estuarine ecosystems will likely become more saline[76], and plumes of hypersaline water will persist through a greater portion of Shark Bay[77]. Based on our model predictions, the persistence of hypersaline flows further into the western gulf will probably shift a large area of highly suitable habitat for tiger sharks into the northern portion of the bay. This might have implications for the management for the species, as commercial trawl fisheries operate in this area year-round[78]. Likewise, extended exposure to hypersaline water would also impact seagrass communities through physiological stress that could reduce coverage in some areas of Shark Bay[79]. The loss of seagrass would further restrict available habitat for tiger sharks, likely due to shifts in the distribution of prey species and may obstruct their role as a top-order predators in Shark Bay. This has broad implications that would reduce the overall productivity of the ecosystem[18,80,81].

Our study advances the understanding of the distribution patterns of tiger sharks in coastal systems by revealing the important environmental processes influencing the movement patterns of tiger sharks within the complex inverse estuary of Shark Bay, Western Australia. We show that hypersaline conditions and the availability of shallow and dense seagrass beds govern the habitat suitability for this species in the Bay. Under future climate scenarios, an increasing number of coastal embayments are predicted to evolve into inverse estuarine systems[82–84], and it is likely that the physical processes influencing the distributions of tiger sharks within Shark Bay could become applicable to a wider range of large gill-breathing predators. If this occurs, hypersaline conditions in coastal environments could release prey communities from the top-down pressures imposed by sharks potentially altering the structure of coastal ecosystems.

Methods

Study area and local oceanography

Shark Bay is a large, semi-enclosed coastal embayment, covering approximately 14,000 km^2 (Fig. 1). It has a semi-arid climate that experiences two main seasons: warm/hot summers (October–March) and mild winters (April–September). Due to evaporation exceeding the input of fresh water, Shark Bay functions as an inverse estuary so that nearshore waters are consistently more saline than the surrounding ocean[35,85]. Salinity increases substantially (up to ~ 65 in the innermost reaches of the Bay) during the summer and pulses of hypersaline water, defined here as salinity levels exceeding 40, are released from the southernmost portions of both the eastern and western gulfs into the rest of Shark Bay when wind-driven vertical mixing and tidal forcing is reduced in winter[36]. These plumes of hypersaline water flow along the seabed and generate strong longitudinal gradients of salinity that fluctuate between seasons (summer and winter) and extend from the oceanic waters towards the innermost reaches of the Bay[35]. Temperature gradients in Shark Bay are also seasonal, becoming warmer than adjacent oceanic water in summer and cooler in winter[86]. Seagrass is the most dominant habitat in Shark Bay and supports globally significant populations of sea turtles (*Chelonia mydas*, *Caretta caretta*[15]) and dugong (*Dugong dugon*[51]), which are key prey items for tiger sharks in this region[12,37,87].

Oceanographic model predictors

Oceanographic and habitat variables were selected based on the ecology of tiger sharks in Western Australia[20,37,42]. Daily oceanographic data was sourced from a ROMS model implemented for the extent of the Shark Bay study region[88,89]. The model output included 24-h gridded (1.5 × 2.5 km) sea-surface temperature (°C; SST) and values of sea-surface salinity (a dimensionless variable) for the duration of the tracking data set (11th of March 2022 to 7th of September 2023). Salinity is defined as the total amount of dissolved salts in seawater), when all carbonates are turned into oxides, bromides and iodides into chlorides and all organic matter completely oxidised. A gradient-based and edge detection algorithm following Belkin et al.[90] was then applied to SST data using the R package "grec" in the statistical software R[91] to generate daily maps of frontal systems and calculate the front magnitude (Fmag). We then used the "sp" package to measure the distance (meters) to the nearest frontal system for each tracked shark location. Static habitat maps at 10 m resolution were derived from Strydom et al.[92] and consisted of two habitat categories: dense seagrass cover (seagrass coverage per grid cell > 40%) and other (sand, colonizing seagrass, coral, macroalgal, pavement and microbial mat) classified from 2016 imagery. A 1.5 × 2.5 km grid was then overlayed onto the habitat map and the percentage of each grid cell area occupied by each habitat category was calculated using the R package "landscapemetrics"[93]. Bathymetry data were obtained from Geoscience Australia, at a resolution of 30 arc-second interval grids (~ 250 × 250 m grid). The spatial resolution for each environmental variable was resampled to a 1.5 × 2.5 km grid by averaging values of smaller grid cell resolutions.

Satellite tracking data

Tiger sharks were caught using drumlines that were equipped with a single 18/0 circle hook baited with fish frames acquired from local commercial fisheries. Three drumlines were deployed ~200 m apart between 07:45 and 16:00 local time, with lines checked every 30 min. Once a shark was caught, it was secured alongside the research vessel using the leader line and a tail rope to keep the shark close to the boat. We measured pre-caudal, fork and total length of each shark, and identified the sex based on the presence or absence of claspers. We used SPOT-258 satellite tags measuring 110 mm × 45 mm × 20 mm L × W × H (from Wildlife Computers, Seattle, Washington) mounted on the dorsal fin of the tiger sharks. All tags relayed satellite positions via the ARGOS satellite network and were assigned a location class (LC) based on the error associated with the location estimate (ranges from 0.50 km to 10.28 km[94]). The total length of tagged individuals ranged from 2.47 to 4.06 m (3.08 ± 0.47 m; Table 1). Of these individuals, 8 were female and 2 were male (Table 1). The distance travelled by each shark was calculated using the cumulative straight-line distance (km) between successive position estimates. To assess whether body size influenced the habitat preferences of tiger sharks, we classified individuals as large (n = 6) or small (n = 4) based on a total length of > 3.10 m, as this size when larger prey items (e.g., turtles and dugongs) are more prevalent in their diet for this region[37,87].

Satellite tracks were initially processed by removing duplicated timestamps and location estimates that contained errors larger than 1.5 km to match the resolution of the oceanographic data (see section "Oceanographic model predictors" above). Using the R package "aniMotum"[95], we also fitted a Bayesian switching state-space model (SSM[96,97]) to compare the model performance and predictive power (see section "Habitat suitability modelling" below) of SSM data with the filtered raw tracking dataset[98]. The SSMs were fitted for each individual independently using a correlated random walk model (CRW) to account for location errors and regularise location estimates at equal time intervals[95]. A temporal resolution of 24 h was used to generate SSM tracks with one location per day. This time interval was selected by considering the mean timestep between location estimates (19 h) for all shark tracks combined. Model convergence was checked following standard procedures outlined by Jonsen et al.[99].

Presence and pseudo-absence generation

We gridded the tracking dataset using a 1.5 × 2.5 km grid-cell resolution (Figure S10) to generate the presence/pseudo-absence dataset to be used in the habitat suitability models. The gridded area included the extent of all shark tracks combined, spanning from latitude 24.7° S to 26.2° S and longitude 112.9° E to 114.0° E. The grid resolution was chosen to match the grid size of the Regional Ocean Modelling System (ROMS; obtained from coastaloceanography.org[32]), the source of the oceanographic predictor variables for subsequent modelling (see "Oceanographic model predictors" section above). Grid-cells were then classified as a presence if they included a location estimate from the tracking dataset on a specific day for each unique shark ID and timestamp throughout the dataset (Figure S10). This allowed grid cells classified as presences to vary among individuals and through time (~ 24 h).

Given the inherent biases of tracking data[98], presence and pseudo-absences were generated and assessed independently for both filtered and SSM tracking datasets (Table S2). There are many techniques used to generate pseudo-absences that range from background sampling to simulations of animal movement trajectories (e.g., movement persistant models[100]). However, for satellite tag data, background sampling performs best across all model evaluation metrics and provides the most ecologically realistic predictions of species distributions[98,100,101]. Therefore, we randomly generated pseudo-absences at a ratio of 1:1 to presences using background sampling techniques. We did this by drawing (without replacement) locations among non-presence grid cells (following recommendations from O'Toole et al.[98]) within the extent of area where presence data from all tracks had been obtained (Figure S10). The selection of pseudo-absences was based on location and time, so that grid-cells were considered as presence when a location was obtained within that grid-cell at a particular time (~ 24 h) and could be selected as pseudo-absence on a different date (Figure S10). Together, this provided daily presence/pseudo-absence dataset spanning 19 months, from March 2022 to September 2023. The pseudo-absence sampling procedure was repeated 10 times to test if pseudo-absence selection had any effect on our modelling results and performance metrics (Table S2). The results from both the raw and SSM datasets were assessed and compared. The raw tracking dataset outperformed the SSM data and was thus used for subsequent analysis (see Table S2 and S3).

Habitat suitability modelling

We developed a binominal Bayesian Generalized Linear Mixed-Effects Model (GLMMs) with a logit link function using the 'bglmer' function in the 'blme' R package[102]. Unlike other Bayesian approaches (e.g., rstanarm or brms), models fit with 'blme' are implemented as an extension of more traditional frameworks (e.g., 'lme4'[103]) using maximum posteriori estimation and Bayesian regularisation[104]. The models were fit with the default number of iterations, and priors. Convergence were checked using the R package 'Performance'[105] and diagnostics were assessed using the R package 'DHARMa'[106]. We selected GLMMs over alternative modelling frameworks (e.g., additive mixed models, regression trees etc.) because we wanted to focus on the general trends of tiger shark presence/pseudo-absence in relation to environmental processes[107]. Due to the large range of values across predictor variables, we scaled all predictor variables using Z-scores (e.g., mean = 0, SD = 1) prior to model fitting. Our model set consisted of a null model plus various combinations of oceanographic and habitat variables (Table S1). We assessed the correlation between predictor variables using the R package "corrplot"[108], and following Queiroz et al.[109], did not include variables that were highly correlated (> 0.75) in the same model (Figure S11). All models included shark ID as a grouping variable. Quadratic terms were included for SST and salinity using the poly function in the "stats" R package to account for non-linear dependencies of tiger shark occurrences with these predictors. Models fit with quadratic terms were compared with linear terms of SST and salinity to ensure non-linear dependencies performed better. Models in our model set were ranked using Akaike's information criterion corrected for small sample sizes (AICc[110]) and corresponding model weights (wAICc; Table S1). Due to the importance of using multiple metrics for HSM evaluation[111], we assessed the predictive skill and power of the top ranked models using three common evaluation metrics: Area Under the Curve (AUC), True Skill Statistic (TSS) and Cohen's Kappa statistic (k). Model performance was considered good when values of AUC were > 0.7, and values of TSS and $k > 0.4$. A tenfold cross validation was used to calculate all evaluation metrics using 75–25% split into training and testing data, respectively. The ability of the model to explain variability within the dataset was assessed using the percentage of deviance explained. We then used the top ranked model to create spatial predictions of habitat suitability for tiger sharks using the "terra" r package[112] for each month in our presence pseudo-absence dataset (March 2022–September 2023). Model predictions were only made within the spatial extent of Shark Bay because of our aim was to assess the relationships between tiger sharks and the complex oceanographic processes of inverse estuarine systems.

Data availability

Gridded data and code used to develop the models for analysis is deposited in Dryad (https://datadryad.org/stash/share/qsJuN7csmjj6ETonAnNzZenORXeHvJFGOguvjghsYts).

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Author contributions

B.D. and A.M.M.S. conceptualised the study. B.D., A.M.M.S., M.D.T, C.B.P collected the data with help from acknowledged field assistants. B.D., A.M.M.S. developed the predictive models, interpreted and analysed the data. C.B.P developed the oceanographic models. B.D., A.M.M.S., M.M., L.C.F, C.B.P and M.D.T, wrote the manuscript with input from all authors.

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Competing interests

The authors declare no competing interests.

Ethics approvals

Field work was conducted under the University of Western Australia ethics permit 2020/ET000026. Permits for wild-caught tiger shark operations are licenced under DPIRD Exemption 250964122 and DBCA licence FO25000390.

Additional information

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