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Original Research Article

Shark conservation hindered by lack of habitat protection

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ABSTRACT

Many of the world's shark populations are in decline, indicating the need for improved conservation and management. Well managed and appropriately located marine parks and marine protected areas (MPAs) have potential to enhance shark conservation by restricting fisheries and protecting suitable habitat for threatened shark populations. Here, we used shark occurrence records collected by commercial fisheries to determine suitable habitat for pelagic sharks within the Australian continental Exclusive Economic Zone (EEZ), and to quantify the amount of suitable habitat contained within existing MPAs. We developed generalised linear models using proportional occurrences of pelagic sharks for three families: Alopiidae (thresher), Carcharhinidae (requiem), and Lamnidae (mackerel) sharks. We also considered aggregated species from the Lamnidae and Carcharhinidae families ('*combined* sharks' in the models). Using a set of environmental predictors known to affect shark occurrence, including chlorophyll-*a* concentration, salinity, sea surface temperature, and turbidity, as well as geomorphological, geophysical, and sedimentary parameters, we found that models including sea surface temperature and turbidity were ranked highest in their ability to predict shark distributions. We used these results to predict geographic regions where habitat was most suitable for pelagic sharks within the Australian EEZ, and our results revealed that suitable habitat was limited in no-take zones within MPAs. For all shark groupings, suitable habitats were found mostly at locations exposed to fishing pressure, potentially increasing the vulnerability of the pelagic shark species considered. Our predictive models provide a foundation for future spatial planning and shark management, suggesting that strong fisheries management in addition to MPAs is necessary for pelagic shark conservation.

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1. Major inferences

Suitable pelagic shark habitat within the Australian continental EEZ occurs predominantly outside marine protected areas (MPAs), or within MPAs in areas where fishing is allowed, highlighting a lack of protection of suitable habitats and potentially hindering shark conservation efforts.

2. Introduction

Sharks are globally threatened due to overexploitation, and efficient management is now critical to their conservation (Davidson and Dulvy, 2017). Many shark species have direct high economic value, with global revenues estimated at over US $ 800 million for fisheries (Dulvy et al., 2017) and US $ 314 million for ecotourism (Cisneros-Montemayor et al., 2013). In addition, as top predators, sharks have a profound impact on ecosystem functioning and stability (Ferretti et al., 2010; Hammerschlag et al., 2019). Nevertheless, 17.4% of chondrichthyan (sharks, rays and chimaeras) species are estimated to be threatened with extinction, with 15.9% of shark species categorised as 'Threatened' and another 20.1% of shark species categorised as 'Data Deficient' by the International Union for Conservation of Nature (IUCN; Dulvy et al., 2014). Many shark species are particularly vulnerable to overexploitation because of their slow growth, late age at maturity, and low fecundity (Cortés, 2000; Garcia et al., 2008), suggesting that effective fisheries management is likely to be essential if viable populations are to be maintained. Because sharks connect habitats and ecosystems by transferring energy through food webs, potentially shaping marine communities over large spatial scales (Ferretti et al., 2010; Heupel et al., 2015), and affect fundamental aspects of ecosystem function (Heupel et al., 2014; Roff et al., 2016; Dulvy et al., 2017), a better understanding of their habitat requirements, population status and distribution is critical for their protection and management.

Although the primary purpose of marine protected areas (MPAs) is the protection of biodiversity and the marine environment (Barr and Possingham, 2013) to meet the needs of a wide range of stakeholders, well-managed MPAs can assist in protecting shark populations (Edgar et al., 2014). Depending on multiple-use management arrangements, a variety of activities are often permitted in MPAs, and can include tourism, fishing, mining and scientific research (Day, 2002; Barr and Possingham, 2013). MPAs may also include no-take areas. Such areas, being free from all extractive activities, including fishing (Roberts et al., 2018), offer the highest level of protection for fish species including sharks (Zupan et al., 2018). As the foremost threat to shark populations is fishing (Dulvy et al., 2014), well enforced and large no-take MPAs that include suitable shark habitat could provide important protection for shark populations, including those with broad geographic ranges (Edgar et al., 2014; Davidson and Dulvy, 2017).

Pelagic sharks can range over large geographic areas (Rogers et al., 2015) and information exists on their distribution patterns and habitat use over large spatial scales in the Pacific (e.g., Block et al., 2011; Musyl et al., 2011; Carreon-Zapiain et al., 2018), Atlantic (e.g., Casey and Kohler, 1992; Queiroz et al., 2016; Coelho et al., 2017) and Indian Oceans (e.g., Rogers et al., 2015; Coelho et al., 2017), as well as globally (Queiroz, 2019). In Australia, most studies of shark distributions have been conducted in nearshore waters, with the majority of research on pelagic species focussed on tagged shark movements or fisheries catch data in localised areas (e.g., Pepperell, 1992; Pillans et al., 2010; Heard et al., 2017). However, sharks comprise approximately 27% of the total catch by number in Australian pelagic longline fisheries (Gilman et al., 2008). To understand and effectively manage pelagic shark populations it is important to investigate their habitat use and distribution on a continental scale.

In Australia, MPAs were first established over 80 years ago (Barr and Possingham, 2013) and have expanded since then to become one of the largest MPA networks in the world (Devillers et al., 2015). However, a recent revision of zoning in Australia has led to a 54% decrease in the total no-take area within redefined MPAs (Buxton and Cochrane, 2016). Here, we use existing fisheries data to assess habitat suitability for a suite of pelagic sharks across the entire Australian continental Exclusive Economic Zone (EEZ), which extends up to 200 nautical miles offshore and covers an area of approximately 7,000,000 km^2 including coastal waters and the inshore Territorial Sea (Huang et al., 2014). This study area spans a latitudinal range of 5000 km from tropical (9°S) to temperate (47°S) latitudes (Butler et al., 2010) with marked differences in temperature, and a longitudinal range of 109°E to 163°E comprising a variety of geomorphologic features and habitats, with unique biodiversity in ecosystems ranging from coastal areas to abyssal zones (Huang et al., 2011). Our analyses examine the extent of Australia's continental MPAs protecting suitable pelagic shark habitat within the EEZ, and provide insights into the overlap of current MPAs, including no-take zones, with respect to predicted suitable habitat for pelagic sharks.

3. Methods

3.1. Shark occurrence data and environmental predictors

We analysed occurrence records of 4339 sharks from 8 species of 3 families (Table S1) available through the online database Global Biodiversity Information Facility (Larcombe, 2017) from the Bureau of Rural Sciences National Commercial Fisheries dataset. These data were compiled from logbooks and commercial fisher returns for the years 2000, 2001 and 2002, and included catch location (latitude and longitude) and species composition (Larcombe et al., 2006). Catch records primarily represented offshore fishing effort in Commonwealth managed fisheries and sharks were primarily caught using commercial longlines (Gilman et al., 2008). Pelagic sharks comprised 43% of the total shark catch, dominated by requiem sharks

(Carcharhinidae, 56% of pelagic catch) with blue (*Prionace glauca*, 33% of pelagic catch) and oceanic whitetip sharks (*Carcharhinus longimanus,* 19% of pelagic catch) being the most commonly caught species in this group. Mackerel sharks (Lamnidae), predominantly IUCN classified 'Endangered' shortfin mako sharks (*Isurus oxyrinchus*), made up 31% of the pelagic catch, with the remainder comprising thresher sharks (Alopiidae, 8%). We focused our analysis on the 3 pelagic shark families that had sufficient occurrence data for statistical analysis (Table S1) and an additional grouping ('*combined* sharks') including all species from the mackerel and requiem families (Table S1). As a response variable, we used the probability of success in catching a shark, i.e. the number of sharks encountered in each grid-cell divided by the number of boats occurring in the same grid-cell (hereafter referred to as the probability of occurrence; Benejam et al., 2010). Fishing effort, measured as the number of commercial fishing boats using gear that could catch pelagic sharks within each 9 km × 9 km grid cell (the highest resolution currently available for all predictors), was made available by the Australian Bureau of Agricultural and Resource Economics and Sciences (ABARES; Fig. 1). To account for the bias in fishing effort across the entire EEZ, we randomly generated 1000 sets of pseudo-absences within the grid-cells where no fishing effort was recorded, with the number of pseudo-absences in each set equal to the number of presences of each shark family group (following Barbet-Massin et al., 2012). We did this by using the simple random sampling without replacement function srswor () from the *sampling* package (Tillé and Matei, 2016Tillé and Matei, 2016) in R statistical software (R Core Team, 2017). We then used these sets iteratively to ensure the modelling results were not biased by our pseudo-absence selection.

We collated environmental and spatial predictors (Table S2) known to affect shark occurrence (Schlaff et al., 2014). These included satellite-derived chlorophyll-*a* concentration (chl-*a*), shown to be an important predictor for pelagic shark occurrence in previous studies (Block et al., 2011; Carvalho et al., 2011) (but see Hutchinson et al., 2019); sea surface temperature (SST) known to influence the occurrence of requiem (Tolotti et al., 2015; Hueter et al., 2018) (but see Stevens et al., 2010), and mackerel sharks (Rogers et al., 2015); and turbidity, caused by physical processes causing suspended sediments (e.g. sand and sediment runoff) inshore (Moore, 1977; Jennings and Kaiser, 1998), and patchily distributed plankton (included in our models using the proxy chl-*a*) in offshore waters (Martin, 2003), shown to affect mackerel and requiem shark catches in South Africa (Wintner and Kerwath, 2018). All environmental variables were available via the Marine Geospatial Ecology Tool (Roberts et al., 2010). We included salinity (downloaded from National Oceanic and Atmospheric Administration, 2016) in our models because most shark species have a narrow tolerance range (Carrier et al., 2004). We also included geophysical (depth, distance to shore and bathymetric slope; downloaded from MARSPEC; Sbrocco, 2013) and geomorphological parameters (reef, seamount, and canyon; available from Australian Government, 2017) which represent ecologically important habitats for mackerel sharks in Australian waters (Rogers et al., 2015), and sediment characteristics (i.e., percentage of carbonate, sand

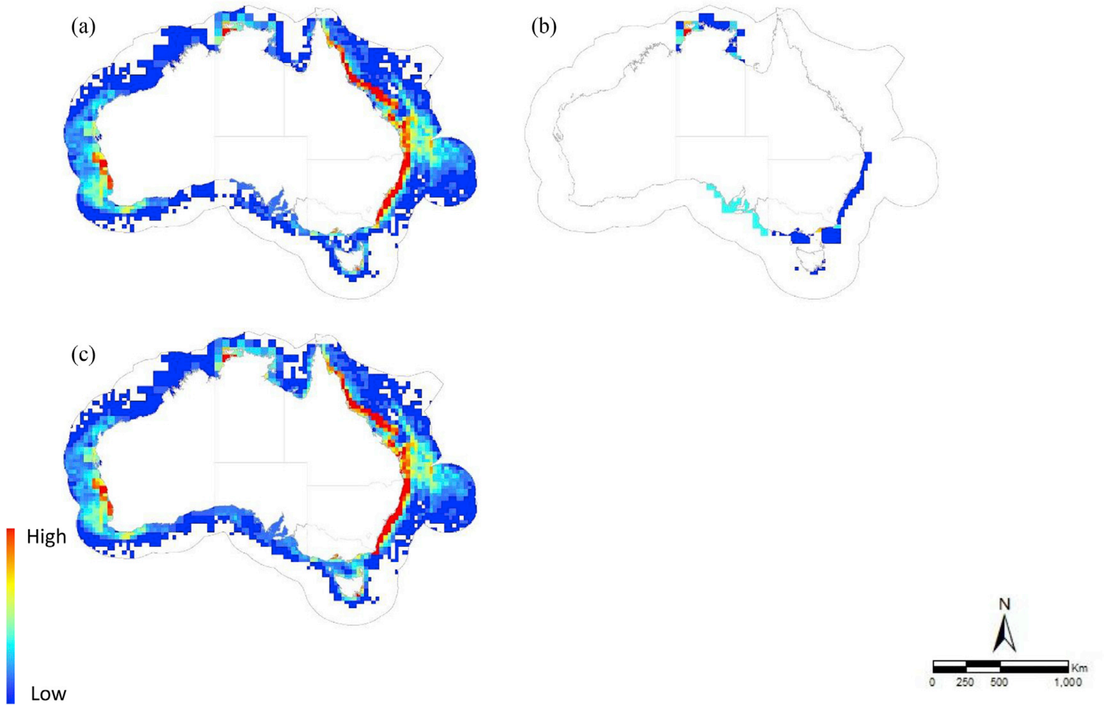

Fig. 1. Spatial representation of fishing effort in the Australian EEZ including location and number of commercial fishing boats per year from 2000 to 2002 and by fisheries method: (a) line fishery boats (min: 2.5, max: 157), (b) other fishery boats (min: 2.5, max: 43), and (c) both methods combined (min: 2.5, max: 160.5). Sharks were caught using mainly bottom-set and pelagic longlines (more detailed data unavailable). Hooks and lines were used, including hand operated and mechanised handlines and pole-lines, set and drifting longlines, trolling and vertical drop lines.

and gravel; available through Australian Government, 2006). We calculated monthly means for satellite data and salinity within the study period and at the extent at which the predictors were available using ArcGIS 10.3 (ESRI, 2014). We assessed collinearity between predictors using variance inflation factors through the VIF function from the package *car* in R statistical software (Fox and Weisberg, 2011). We assessed spatial autocorrelation in occurrences as a function of distance between grid cells based on Moran's I (Diggle and Ribeiro, 2007). To stabilise parameter estimation we standardised all predictors to z-scores (Zuur et al., 2007) using the scale function in R (R Core Team, 2017) before inclusion in the models (James et al., 2015).

3.2. Modelling of habitat suitability

We developed generalised linear models with binomial distributed response for the *i*th grid-cell within the region considered (O_i; based on the probability of success in finding a shark according to fishing effort, i.e. number of $Boats_i$ trials) with a logit link function for each of the three pelagic shark families and for the group of *combined* sharks (Table S1). To account for differing amounts of effort in datasets due to unbalanced fishing effort within the entire EEZ, we included effort (i.e. number of Boats; Fig. 1) as a model weight. Our model structure can be represented as shown below, where α is the model intercept, and β_j represents the coefficients for each predictor X_j, and n is the maximum number of predictors per model:

$$O_i \sim \text{Binomial}\ (p_i,\ Boats_i)$$

$$\text{logit}(p_i) = log\left(\frac{p_i}{1 - p_i}\right) = \alpha + \sum_{j=1}^{n} \beta_j X_{ji}$$

Our model set included several combinations of the environmental and spatial predictors in line with our hypotheses (Table 1). We hypothesised that chl-*a* and SST would influence shark occurrence and expected to find pelagic sharks offshore in less turbid waters. We also hypothesised salinity would limit these species to higher and more stable salinities offshore (Hammerschlag, 2006; Bernal et al., 2012) due to the high cost of osmoregulation (Pang et al., 1977), and that geophysical and geomorphological parameters would influence shark occurrence in different locations rather than sediment characteristics.

To account for potential preferential ranges for depth and SST, we included quadratic terms for these predictors using the poly () function from the *stats* package in R statistical software (R Core Team, 2017). We used the Akaike's information criteria corrected for small sample size (*AICc*) to assign relative strengths to candidate models (Burnham et al., 2011) and its weight (*wAICc*) to compare each model's performance. We used the percentage of deviance explained (% DE) to quantify goodness-of-fit for each model, and then predicted shark habitat suitability using the predict () function from the *stats* package in R

Table 1
Summary of generalised linear models relating the probability of shark occurrence to ecological predictors, *Chl-a*: concentration of chlorophyll-*a*, *Depth*: depth of the seafloor, *Distance*: distance from the center of grid cell to shore, *Geo*: geomorphology including canyon, reef and seamount, *Null*: intercept-only model, *Sal*: salinity, *Sed*: sediment variables including percent carbonate, gravel and sand, *Slope*: bathymetric slope, *SST*: sea surface temperature, *Turb*: the coefficient of light attenuation at 490 nm; shown for each model are the mean weight of the Akaike's information criterion corrected for small sample sizes (wAICc; SD lower than 0.01 for all model iterations) and mean percentage of deviance explained (% DE, SD lower than 0.16% for all model iterations).

Model	Thresher		Requiem		Mackerel		Requiem and mackerel families *Combined*	
	wAIC$_C$	% DE	wAIC$_C$	% DE	wAIC$_C$	% DE	wAIC$_C$	% DE
Evaluation								
1. Sed	–	10.08	–	24.52	–	27.08	–	28.82
2. SST^2 *+ chl-a*	–	13.13	0.003	28.54	–	32.54	0.001	34.73
3. Factor(Geo)	–	0.93	–	0.29	–	0.75	–	0.49
4. Sal + Turb	–	8.98	–	30.65	–	34.39	0.013	37.82
5. SST^2 *+ Turb*	1	17.14	0.996	31.64	1	36.13	0.986	38.49
6. $SST^2 + Depth^2$	–	11.57	–	22.77	–	28.99	–	28.31
7. Slope + Distance	–	10.10	–	20.05	–	27.32	–	26.93
8. Null	–	–	–	0	–	–	–	0

Table 2
Results of the 10-fold cross-validation of binomial generalised linear models for all shark groupings, we iterated the cross-validation 1000 times and compared the predicted and observed values based on the Pearson's R for each iteration of the cross-validation procedure, after removal of outliers more than 3 SD from the mean (SD shown in parentheses).

	Thresher	Requiem	Mackerel	Requiem and mackerel families *Combined*
Mean	0.14 (0.12)	0.4 (0.07)	0.49 (0.1)	0.43 (0.12)
Minimum	0	0.2	0.19	0.2
Maximum	0.34	0.62	0.81	0.79

statistical software. To predict shark occurrence relative to our response variables, we averaged the contribution of each model based on the wAICc results (Araújo and New, 2006). We used a 10-fold cross-validation (Mosteller and Tukey, 1968), iterated 1000 times to validate the predictions, and then compared the predicted and observed values based on the Pearson's R for each iteration cross-validation procedure (Table 2). The resulting predicted values for shark habitat suitability (ranging between 0 and 1) were grouped into the following 3 categories: low suitability < 0.3, $0.3 \leq$ suitable < 0.6, and high suitability ≥ 0.6.

3.3. Level of protection within MPAs

Internationally, MPAs may be entirely or partly assigned to any of the 6 IUCN zoning categories (Fig. 3, Table S3). These IUCN zones range in levels of protection, with zones I and II prohibiting extractive activities (e.g., fishing), zone III protecting natural features (e.g., seamounts), zone IV allowing extraction (including fishing) but with restrictions on some activities such as dredging (Dudley, 2008), and zones V and VI allowing sustainable harvesting of fish, corals and mineral resources. In Australia, zones I and II are matched with no-take areas where fishing (both commercial and recreational) is not permitted, but some fishing is allowed in zones III through to VI (Barr and Possingham, 2013). We obtained MPA boundaries and zonings for the Australian EEZ from the Australian Government (2015) and then used ArcGIS 10.3 to overlay the zones on our predictions of habitat suitability for the species of sharks included in our study. We then calculated the number of grid cells within each IUCN zone for each habitat category (i.e. low suitability, suitable, high suitability).

4. Results

Our results showed highest support (wAICc ≥ 0.89) for the model including SST and turbidity (model 5) as predictors of shark occurrence for all shark groupings (Table 1). The percentage of deviance explained by this model was highest for our *combined* group of species (38.49%), followed by mackerel (36.13%), requiem (31.64%), and lowest for thresher (17.14%) sharks. The models with salinity and turbidity (model 4), and SST and chlorophyll-*a* (model 2) also explained a large percentage of deviance for *combined* (37.82% and 34.73%, respectively), mackerel (34.39% and 32.54%) and requiem (30.65% and 28.54%) sharks, with a negative correlation found between chlorophyll-*a* and shark occurrence across all shark groupings in our study. Values of variance inflation factors were below the *a priori* cut-off of 3 (Zuur et al., 2010) for all models and only minor spatial structuring (Moran's $I < 0.3$) was found in the models' residuals. Our cross-validation results were highest for mackerel sharks with a Pearson's R [SD] value of 0.49 [0.1], followed by *combined* (0.43 [0.12]), and requiem (0.40 [0.07]), and were lowest for thresher sharks (0.14 [0.12]) (Table 2). We therefore, did not consider the thresher shark dataset in any further analysis.

We found only a small percentage of the Australian EEZ contained habitat in the highest suitability class (0.6–1) for requiem and mackerel (only 3% for both groups, corresponding to *ca.* 210,000 km^2), and *combined* sharks (4%, i.e. *ca.* 280,000 km^2), even though the amount of habitat protected in Australian waters increased between the time of collection of the shark catch data (2000–2002) and the marine park rezoning (2016; Roberts et al., 2018). Regions where habitat was predicted in this highest suitability class varied by family, with southern Australia being highly suitable for mackerel and *combined* sharks, and north-eastern Australia for requiem sharks (Fig. 2). Overlaying MPA zoning on our habitat predictions, we found that only 1% (i.e. *ca.* 70,000 km^2) of highly suitable habitat for each of mackerel, requiem and *combined* sharks within MPA zones. This high suitability area was mostly in unprotected areas and that occurring inside MPA was always in areas open to fishing (i.e. IUCN zone IV).

Within the Australian EEZ, habitat classed as suitable (i.e. predicted habitat suitability 0.3–0.59) encompassed the largest area for the *combined* grouping of sharks (19% of the entire continental EEZ; i.e. *ca.* 1,330,000 km^2), followed by requiem (17%; i.e. *ca.* 1,190,000 km^2), and mackerel sharks (16%; i.e. *ca.* 1,120,000 km^2). Southern and south-western Australia included suitable habitat for mackerel and *combined* sharks, with north-eastern Australia also providing suitable habitat for *combined* and requiem sharks (Fig. 2). The area of suitable habitat within the EEZ that included protection from fishing (IUCN zone II) equated to 0.2% of the total EEZ for *combined* and requiem sharks (i.e. *ca.* 2637 km^2) and 0.1% (i.e. *ca.* 1164 km^2) for mackerel sharks. The remainder of the region (77% for *combined*, 80% for requiem, and 81% for mackerel sharks) therefore included low suitability habitat (≤ 0.29) for all shark groupings.

5. Discussion

Fisheries management is required for the effective conservation of shark populations and MPAs can be of assistance, especially for threatened species such as the oceanic whitetip (requiem family) and mako sharks (mackerel family) (Dulvy et al., 2008). Using Australia as a case study, we found that most Australian continental MPAs primarily include habitat of low suitability for these pelagic sharks, and that available highly suitable habitat is relatively unprotected, being located in areas where fishing is allowed. Our results highlight that Australian MPAs are unlikely to contribute significantly to pelagic shark conservation and, importantly, that species globally classified as 'Endangered' or 'Vulnerable to extinction' by the IUCN (see Table S1) are exposed to commercial and recreational fishing, both within and outside Australian MPAs. Weakly regulated MPAs have been shown to be ecologically similar to unprotected areas (Zupan et al., 2018), and therefore, protection of highly suitable habitat in no-take MPAs is needed to promote shark conservation, as well as to support sustainable fisheries (Kerwath et al., 2013).

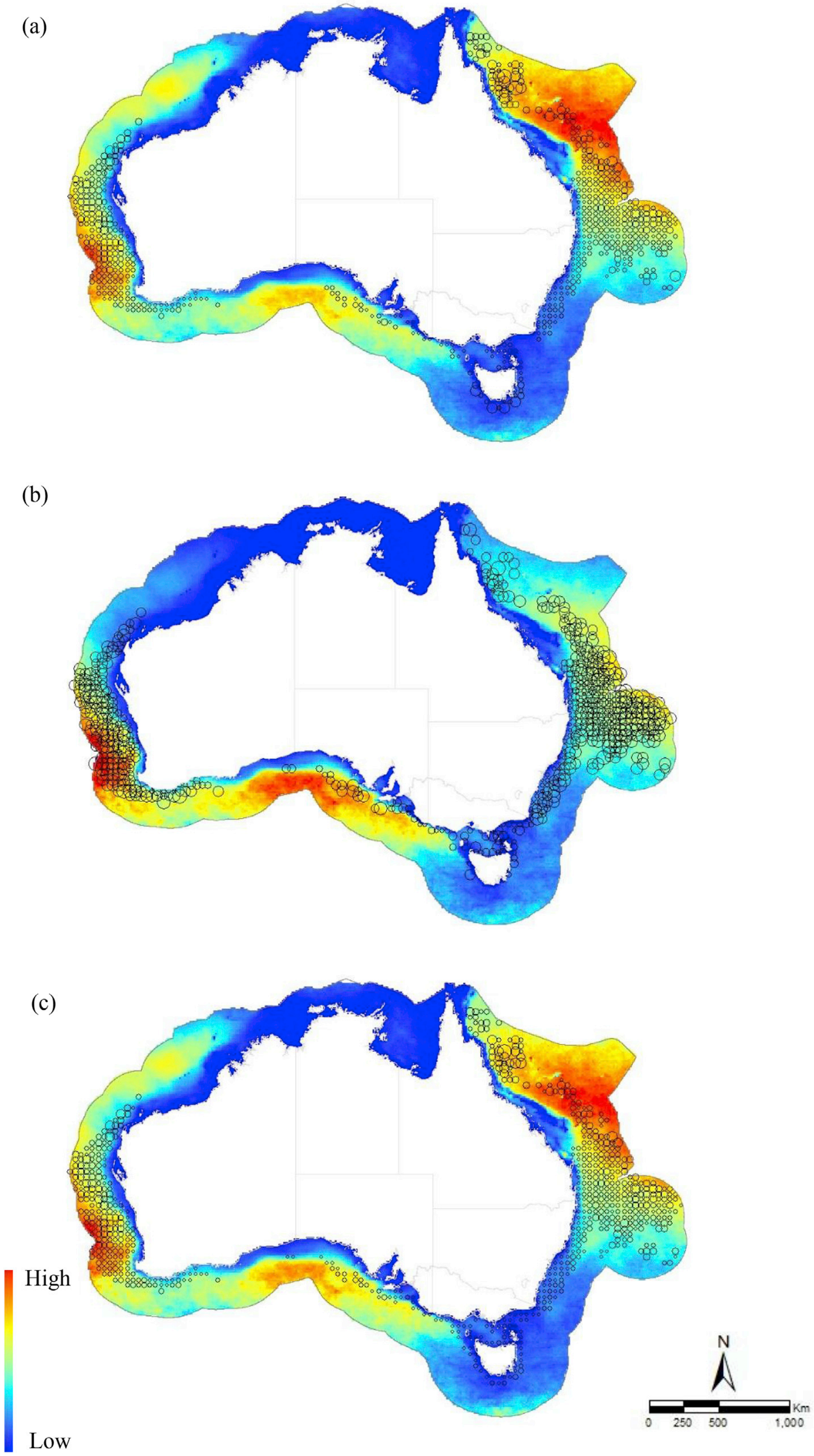

Fig. 2. Predicted habitat suitability within the Australian EEZ for 9 × 9 km grid cells for: (a) requiem (Mean: 0–0.77, SE: 0–0.04), (b) mackerel (Mean: 0–0.87, SE: 0–0.04) and (c) *combined* (Mean: 0–0.8; SE: 0–0.03) sharks, with probability of occurrence (open circles) of sharks used as inputs in generalised linear models.

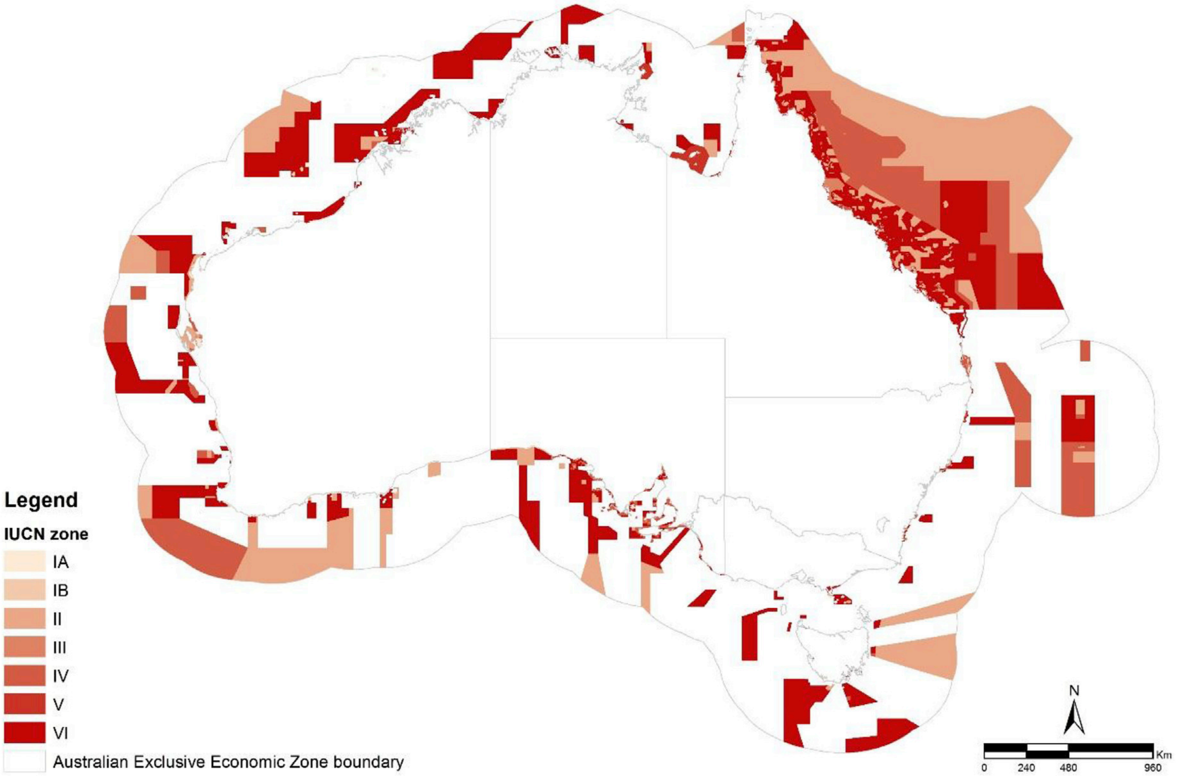

Fig. 3. International Union for Conservation of Nature (IUCN) protected area management categories and locations of marine protected areas within the Australian Exclusive Economic Zone.

In our study, regions with suitable habitat for pelagic sharks varied by family and generally included offshore areas in the southern, north-eastern and, to a lesser extent, the south-western coast of Australia, which is in agreement with existing knowledge on the distribution and occurrence of these species (e.g. Simpfendorfer et al., 2002; Last and Stevens, 2009; Rogers et al., 2015; Coelho et al., 2017; Corrigan et al., 2018). The model based on sea surface temperature and turbidity was ranked highest for all the shark groups we considered. Temperature may be an important determinant of habitat suitability because sharks, with the exception of mackerel sharks, are ectotherms (Bernal et al., 2012). In Australian waters, pelagic sharks have been recorded regulating their depth in ways that suggest they occupy regions of favourable temperatures, although this behaviour could also be related to prey movements (Rogers et al., 2009; Stevens et al., 2010; Heard et al., 2017). It is not possible to measure the temperature of the sea below the surface from satellites, but the effect of sea surface temperature was nevertheless an important variable determining the distribution of our *combined* sharks category, which included many wide-ranging pelagic species known to aggregate along particular temperature gradients (e.g. blue sharks and oceanic whitetip sharks, both species from the requiem family; Queiroz et al., 2016). Turbidity was also in the highest ranked model alongside temperature. As expected, we found a negative correlation between the probability of occurrence of pelagic sharks and turbidity highlighting their absence in more turbid nearshore areas, and affinity for offshore areas with low turbidity. This affinity of pelagic sharks for clear-water may be due to a relatively high reliance on vision for hunting active, fast-moving prey species (Lisney and Collin, 2007) when compared to coastal shark species (Lisney et al., 2012). Interestingly, the model including SST and chlorophyll-*a* concentration (which was highly correlated with turbidity) also explained a large amount of deviance for some shark families additionally indicating a negative correlation between shark occurrence and chlorophyll-*a*. This negative correlation aligns with previous studies in Australian waters where blue (requiem family) sharks ranged across areas of both high and low chlorophyll-*a* concentrations (Stevens et al., 2010), and shortfin mako (mackerel family) sharks utilised areas with low chlorophyll-*a* concentrations (Rogers et al., 2015). These findings may be partly explained by a deep chlorophyll maximum layer forming in oligotrophic oceanic waters (Cullen, 1992) at depths between 60 m and 100 m off Australia (Gibbs, 2000; Parslow et al., 2001; Moore et al., 2007). This layer provides foraging areas for pelagic fishes (Childers et al., 2011) and may be present even when chlorophyll and other nutrients appear to be depleted near the surface and not observed in satellite-based imagery (Hutchinson et al., 2019).

Our findings suggest strong fisheries management is needed to supplement MPAs for the protection of pelagic shark species. Although Australian MPAs were established to conserve biodiversity based on habitat designation, and deep pelagic waters are generally not biodiversity hotspots, extension of MPAs to include adjacent pelagic areas can be crucial to protect migratory species, such pelagic sharks with concerning IUCN conservation status. Although pelagic sharks inhabit very large geographic areas with complex movement and spatial distribution patterns (Carvalho et al., 2018), individuals may have some degree of residence in comparatively small geographic areas for extended periods of time (Rogers et al., 2015; Corrigan et al., 2018; Nasby-Lucas et al., 2019). This can be the case, for example, while foraging in core areas within national EEZs (Bird et al., 2018; Francis et al., 2019). As such, MPAs located in these ecologically relevant provisioning areas (Bird et al., 2018), as well as at aggregation sites and along migration corridors (Boerder et al., 2019), would be beneficial to the conservation of these sharks. However, as MPAs serve a variety of different objectives, not all biological (Giakoumi et al., 2018), they are often established in areas residual to extractive activities (Devillers et al., 2015).

While MPAs in Australian waters are not contributing significantly to shark conservation, Australia has strict fisheries legislation protecting pelagic sharks, including listing some species as no-take (Woodhams and Harte, 2018; Commonwealth of Australia, 2019). However, as pelagic sharks range over large geographic areas and are capable of crossing international boundaries, these migratory species may be vulnerable in other waters due to a lack of management throughout their ranges. As such, in countries where shark quotas are unregulated and shark fisheries not well managed, MPAs could be critical for pelagic shark conservation, especially if such refugia can be shown to have significant protective effects on these species. This study provides a foundation for future research by providing a basis for spatial planning and conservation management to predict habitat of high conservation value for pelagic sharks. Studies such as this, using remotely-sensed environmental information and occurrence data from fisheries over a large spatial scale, are important for effective spatial management planning, especially for pelagic species with broad geographic ranges. With sea surface temperature a strong driver of shark distribution across all families analysed, future changes in sea temperature will likely shift distribution and locations of suitable habitat (Chin et al., 2010; Lezama-Ochoa et al., 2016). These changes need to be explored, not least because climate change may alter the way in which MPAs need to be managed if they are to meet the needs of all stakeholders. However, analyses such as the one we present here need to be used with caution when using smaller datasets over large areas. For instance, our model validation was weak for thresher sharks, possibly due to a lack of data over such a large spatial scale. Broad-scale studies are required for pelagic species and effective management is urgently needed for the globally threatened shark species in our study, such as oceanic whitetip, porbeagle and ‘Endangered’ mako sharks, as well as heavily fished species such as blue sharks (Gilman et al., 2008; Sims et al., 2018; Queiroz, 2019). In conclusion, a multi-pronged management approach combining MPAs with fishery-based catch and effort restrictions may provide the most comprehensive conservation approach (Boerder et al., 2019).

Article impact statement

Suitable pelagic shark habitat within the Australian EEZ is mostly unprotected and improved marine protected areas should be supplemented with robust fisheries management of pelagic shark species.

Declaration of competing interest

We have no conflicts of interest to disclose.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00862.

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