

# Seasonal distribution patterns and conservation gaps of blue sharks in the Indo-Western Pacific Ocean

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## Abstract

**Aim:** Oceanic sharks play an important role in maintaining the stability and biodiversity of marine ecosystems, and yet they are among the most threatened taxa worldwide. Currently, large spatial-scale distribution patterns and conservation gaps are poorly known for most species since they are challenging to study. To address the problem, we here use an integrated approach with an illustration with the blue shark (*Prionace glauca*), a common bycatch oceanic species.

**Location:** Indo-Western Pacific Ocean (IWPO).

**Methods:** We first collated decades of species occurrences and marine environmental datasets from open-access sources. We then applied ensembled species distribution models (SDMs) to predict its seasonal distributions and evaluated the model performance using true skill statistic (TSS) and area under the receiver-operating characteristic curve (AUC). We finally conducted spatial analyses (e.g. bivariate hotspot analyses) to identify conservation gaps/opportunities based on the predicted distribution maps and two additional datasets, namely, marine protected areas (MPAs) and fishing effort.

**Results:** (1) Both seasonal SDMs performed well (mean TSS > 0.8, AUC > 0.95), and the results suggested that blue sharks were widely distributed in the IWPO with some seasonal differences in ecological niches and distributions (mainly in the West Indian Ocean and the Northwest Pacific Ocean); (2) large MPAs and shark sanctuaries covered comparable, small portions (4%–9%) of blue shark habitats, but these locations (in MPAs and sanctuaries) varied between seasons; (3) fishery-shark conflict hotspots also varied between seasons with some located in or close to large MPAs and sanctuaries.

**Main conclusions:** We provide seasonal (cold vs. warm) distribution maps of blue sharks across the IWPO to advance their conservation and management. We highlight the importance of strengthening management both in and near large MPAs and shark sanctuaries. Our study contributes a feasible integrated approach to reveal seasonal distribution patterns and conservation opportunities for oceanic sharks.

## KEYWORDS

conservation planning, marine protected areas, overfishing, pelagic shark, seasonal habitat uses, species distribution model

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## 1 | INTRODUCTION

Given the significance and threatened status of oceanic sharks, conservation efforts pertaining to these apex predators have become a focal point in the field of marine biodiversity conservation (Sherman et al., 2023). Oceanic sharks play an extremely important role in maintaining marine biodiversity and ecosystem stability (Ferretti et al., 2010). These sharks are large, pelagic, widespread, and may undertake long-distance migrations. Most of them are top predators in various marine ecosystems around the world. The decline of oceanic sharks could have serious ecological consequence, such as triggering a trophic cascade effect and leading to fishery collapses (Ferretti et al., 2010; Myers et al., 2007). Unfortunately, our human activities (especially overfishing) have driven oceanic sharks to be one of the most threatened fauna worldwide (Myers et al., 2007; Pacoureaux et al., 2021). The abundance of 18 well-studied populations of oceanic sharks and rays have declined by approximately 71% over the past half century, with three-quarters of these populations classed as threatened with extinction (Pacoureaux et al., 2021).

Oceanic sharks are difficult to study, given they have dynamic distribution patterns (Sequeira et al., 2012). To address this challenge, scientists have applied fishery-dependent surveys and satellite-tag tracking projects, which have significantly advanced our understanding of the distributions and movement patterns of some oceanic sharks (Queiroz et al., 2016; Zhu et al., 2023). We now know that the distribution of oceanic sharks is often correlated with environmental factors such as temperature, salinity, and currents, which exhibit seasonal variations. Such seasonality may drive oceanic sharks to migrate to suitable habitats over different seasons (Queiroz et al., 2016; Schlaff et al., 2014). Furthermore, oceanic sharks use different habitats for seasonal mating and reproduction (Coelho et al., 2018). However, we still know little about seasonal distributions of most oceanic sharks at broad spatial scales due to the expensive cost in observing and tracking their movements (Zhang, 2022). In the recent decade, species distribution models (SDMs) have been applied to predict suitable habitats for some oceanic sharks (Báez et al., 2020; Druon et al., 2022). SDMs are powerful as they can utilise limited species occurrences and relevant environmental data to predict the distributions of target species across the vast oceans (Elith & Leathwick, 2009). The accuracy of SDMs in predictions can be evaluated with multiple statistical metrics (Naimi & Araújo, 2016). However, most previous SDMs studies on oceanic sharks used annual data rather than seasonal ones to construct SDMs, which can mask the potential seasonal variations in species distributions.

Understanding the seasonal distributions of oceanic sharks is essential for a more comprehensive evaluation of the effectiveness of marine protected areas (MPAs) and fisheries management (Graham et al., 2016; Queiroz et al., 2016). MPAs are important tools in conserving marine biodiversity mainly through prohibiting or constraining fishing activities by setting up no-take zones or restrictions on allowable fishing gears. For highly migratory species like oceanic sharks, establishing large MPAs is crucial since these MPAs may provide more safe and suitable habitats for sharks by

reducing the likelihood of these species encountering fishing gears (Bonnin et al., 2021). In addition, shark sanctuaries (a large area protected specifically for sharks through a series of measures such as prohibiting commercial shark fishing) are also recommended and it is generally acknowledged that they will have a stronger protection for sharks (largely coastal sharks) than regular MPAs (MacKeracher et al., 2019). However, currently we know little about the contribution of large MPAs and shark sanctuaries in protecting many oceanic sharks, in particular whether they have covered a considerable amount of suitable habitats of the oceanic sharks, and whether fishing activities (with high catch/bycatch rates of oceanic sharks) are greatly reduced in and near these protected areas. The exposure risk of oceanic sharks to fishing activities (e.g. pelagic longline) has been a great concern, given many pelagic fishing gears targeting other fishes (e.g. tuna) can catch large numbers of bycatches of oceanic sharks, leading to a considerable level of fishing mortality (Campana et al., 2009; Queiroz et al., 2016). Such a risk is often mapped with an 'exposure risk index' (mainly based on the product of species presence probability and fishing intensity in each grid) to identify conflict hotspots (Queiroz et al., 2019; White et al., 2019), which sometimes can be misleading. For instance, this index could not discriminate an area frequently used by sharks but not heavily fished from another area rarely used by sharks but heavily fished. For decision makers, these two areas may require very different countermeasures. To address this drawback, the bivariate hotspot mapping may be a valuable alternative but has been rarely used in fishery-shark conflict studies (Maure et al., 2023).

The blue shark (*P. glauca*) is one of the most widespread oceanic sharks and common bycatch species, deserving great concerns in fisheries management (Druon et al., 2022; Simpfendorfer & Dulvy, 2017). Blue sharks have been found in both tropical and temperate waters from 62°N to 54°S (Coelho et al., 2018; Last & Stevens, 2009). They are an important bycatch species in pelagic longline and gillnet fisheries, accounting for over 50% of the total catch in some Atlantic longline fisheries (Coelho et al., 2012). The blue shark is now classified as near threatened (NT) on the IUCN Red List with decreasing population trends (IUCN, 2018), but it has not received significant attention from fisheries management organisations and few fishing restrictions are in place for it (Simpfendorfer & Dulvy, 2017). Currently, studies on the distribution of blue sharks have primarily focused on the Atlantic and Eastern Pacific Oceans, while populations in the Indo-Western Pacific Ocean (IWPO) are poorly studied (Coelho et al., 2018; Druon et al., 2022). The IWPO is of particular interest given (1) the high fishing pressures on oceanic sharks (Pacoureaux et al., 2021) and (2) the recent increase in large MPAs (Davidson & Dulvy, 2017).

Our study integrates multiple approaches to reveal the seasonal distribution patterns and conservation opportunities for blue sharks in the IWPO. We first collated species occurrences and environmental datasets from open-access sources. We then applied SDMs to predict the seasonal distributions of blue sharks in the cold and warm seasons. Finally, we analysed the spatial overlaps and mismatches

among the seasonal distribution of blue sharks and two additional datasets, namely, large MPAs & shark sanctuaries, and fishing effort. This study enhances our understanding concerning the spatial ecology and conservation status of blue sharks in the IWPO, and our approaches can be applied to reveal distribution patterns and conservation opportunities for many other oceanic sharks.

## 2 | MATERIALS AND METHODS

### 2.1 | Data collection and treatment

#### 2.1.1 | Species occurrence data

We collected blue shark occurrences in the IWPO (52°N–66.5°S, 30°E–180°E) from the Global Biodiversity Information Facility (GBIF, 2023) and the Ocean Biodiversity Information System (OBIS, 2023). As a manner of data quality control, we only used the occurrences from 1960 to 2022 since we considered the coordinates prior to 1960 (~<1% of all available occurrences) were likely less reliable in terms of spatial resolutions. We also removed those unreliable occurrences with recorded coordinates that were located on land. Finally, we collated a total of 3940 independent occurrences for blue sharks with an average spatial precision of  $33.6 \pm 23.2$  km (mean  $\pm$  SD; Figure S1a). Majority of them (~67%) were recorded between 1990 and 2022, generally matching the temporal range of our predictor data (Table 1).

#### 2.1.2 | Predictors data

We gathered data for model predictors, which were categorised into three groups: (1) original environmental variables, (2) oceanic fronts derived from environmental data and (3) fishing effort (Table 1). The original environmental data include monthly spatial datasets of six variables derived from the Copernicus Marine Service (CMEMS, 2023; Table S1 for details) and bathymetry data from the General Bathymetric Chart of the Oceans (GEBCO, 2023): sea surface temperature (SST), sea surface salinity (SSS), current velocity (CV), net primary production (NPP), diffuse attenuation coefficient at 490 nm ( $K_d(490)$ , a proxy of water turbidity), sea level anomaly (SLA) and bathymetry (depth). Additionally, we derived monthly oceanic front intensity based on SST ( $OF_t$ ) and SSS ( $OF_s$ ), respectively, using a moving window approach in ArcGIS (version 10.3, See Supplementary Information). As a top predator, the blue shark often searches for areas with higher abundance of preys where fishing efforts may also tend to be higher. Considering blue sharks are mainly caught by longlines, gillnets and purse seines (Queiroz et al., 2019; Vögler et al., 2011), we calculated the annual average cumulative fishing effort (FE, 2016–2020) of these fishing gears based on data from the Global Fishing Watch. Subsequently, the data from different sources were resampled in ArcGIS to a resolution of  $0.25 \times 0.25$  arc-degree (approximately 28 km at the equator).

#### 2.1.3 | Splitting data to cold versus warm seasons

Given the seasonal asynchrony between the northern and southern hemisphere, we split our species and predictors data based on the actual seasons in both hemispheres. We defined the warm season as March–August of the northern hemisphere combined with January–February and September–December of the southern hemisphere, and the cold season as January–February and September–December of the northern hemisphere combined with March–August of the southern hemisphere. All species occurrences and predictors data were then split to these two seasons. Seasonal statistics (mean and SD) of the predictors were calculated for further analyses.

#### 2.1.4 | Regular large MPAs and shark sanctuaries

We obtained geographic maps of MPAs and shark sanctuaries within the IWPO from the World Database on Protected Areas and Pew Charitable Trusts. Given the vast home range of blue sharks (approximately 3,000,000 km<sup>2</sup>; Conners et al., 2022), large MPAs are more meaningful than small ones in protecting this species. We therefore adopted the IUCN's definition to screen out large MPAs with an area greater than 150,000 km<sup>2</sup> for subsequent analyses (Lewis et al., 2017). A total of seven regular large MPAs and six shark sanctuaries were selected (Table S2 and Figure S2).

### 2.2 | Seasonal SDMs construction and prediction

Based on seasonal occurrences and predictors data, we constructed SDMs for warm and cold seasons using the ENMTEML function in R (Andrade et al., 2020). Three algorithms, they are boosted regression tree (BRT), random forest (RDF) and maximum entropy (MaxEnt, with default settings), were employed to build ensemble models. The modelling process was narrated as follows.

#### 2.2.1 | Model settings

To reduce correlation and collinearity of predictors, we excluded redundant variables with Pearson correlation  $|r| > .7$  or variance inflation factor (VIF)  $> 10$  (Figure S3). To reduce sampling biases of occurrences, we filtered occurrences by a 'double cellsize' method (a parameter in ENMTEML function) to ensure that the minimum spacing between each occurrence (c. 56 km) was approximately twice the resolution of the environmental data (Zhang, 2022). Given the filtering process can generate a slightly different dataset in each run, we performed 30 runs. After spatial filtering, the final number of occurrences used in each the model was 771–775 for the warm season and 466–467 for the cold season. For each seasonal SDM, we ran our models 30 times correspondingly with each time using one of the 30 different datasets of filtered species occurrences. We chose an environmental constrain method to generate pseudo-absences

**TABLE 1** Summary of all potentially significant predictors used for modelling, including their temporal range, units, sources and resolutions. These predictors can be categorised into three groups: marine environmental observation, oceanic front and fishing effort data.

Data category	Covariate	Temporal range	Unit	Source of original data	Original resolution (°)
Marine environmental observation data	Mean sea surface temperature	1993–2020	°C	Copernicus Marine Service	0.25
	Standard deviation of sea surface temperature	1993–2020	°C	Copernicus Marine Service	0.25
	Mean sea surface salinity	1993–2020	‰	Copernicus Marine Service	0.25
	Standard deviation of salinity	1993–2020	‰	Copernicus Marine Service	0.25
	Mean velocity	1993–2020	ms <sup>-1</sup>	Copernicus Marine Service	0.25
	Standard deviation of velocity	1993–2020	ms <sup>-1</sup>	Copernicus Marine Service	0.25
	Mean net primary production	1993–2020	mg m <sup>-3</sup> day <sup>-1</sup>	Copernicus Marine Service	0.25
	Standard deviation of net primary production	1993–2020	mg m <sup>-3</sup> day <sup>-1</sup>	Copernicus Marine Service	0.25
	Diffuse attenuation coefficient at 490 nm	1997–2021	m <sup>-1</sup>	Copernicus Marine Service	0.04
	Standard deviation of diffuse attenuation coefficient at 490 nm	1997–2021	m <sup>-1</sup>	Copernicus Marine Service	0.04
	Mean sea level anomaly	1993–2020	m	Copernicus Marine Service	0.25
	Standard deviation of sea level anomaly	1993–2020	m	Copernicus Marine Service	0.25
	Bathymetry	NA-2023	m	GEBCO (GEBCO_2023)	0.0083
Oceanic front	Oceanic front based on sea surface temperature	1993–2020	—	Copernicus Marine Service	0.25
	Oceanic front based on sea surface salinity	1993–2020	—	Copernicus Marine Service	0.25
Fishing effort	Annual average cumulative fishing effort of longline, gillnet and purse seine	2016–2020	h/km <sup>2</sup>	Global Fishing Watch	0.01

Abbreviation: GEBCO, general bathymetry chart of the oceans.

within predicted low suitability areas at presences-absences ratio of 0.5 (Zhang, 2022). Based on the above process, we constructed two scenarios of SDMs (cold vs. warm) with all selected predictors (hereafter, full models).

## 2.2.2 | Model evaluation

Following a previous SDM study (Zhang, 2022), we evaluated the importance of each variable in predicting distributions of blue sharks. We selected the top six variables of relatively higher importance in each seasonal full model to construct their simplified models (30 runs with the same model settings as the full model except for predictors). We used these simplified models to derive response curves for these important variables to demonstrate species-environment relationships. This process was done with the *sdm* package in R (Naimi & Araújo, 2016).

To evaluate the model performance (for both the full models and simplified models), we calculated two metrics: true skill statistic (TSS) and area under the receiver-operating characteristic curve (AUC). The TSS considers both presence and absence prediction accuracy. It is independent of presence rate (a.k.a., prevalence) and spatial extent,

but dependent on the probability threshold used to discriminate presences from absences (Allouche et al., 2006). Here, we adopted the commonly used threshold that maximised TSS. In contrast, the AUC measures the overall model capacity in discriminating presences from absences, independent of the threshold, but this metric is sensitive to prevalence and spatial extent (Allouche et al., 2006; Lobo et al., 2008). A higher value of the metric indicates a more accurate model. We used block-cross validation to divide the occurrences into training data and test data, effectively reducing the impact of spatial autocorrelation on the evaluation of model performance (Valavi et al., 2019).

## 2.2.3 | Model prediction

For each modelling scenario, we selected algorithms with TSS higher than the average level to construct an ensemble model (weighted by TSS; Andrade et al., 2020). We then compared the TSS values between the ensembled full models and the ensembled simplified models in each season, and used the ensembled models that have higher TSS values to predict species distributions (presence probability and presences/absences). The final presence probability was determined by calculating the mean probability across the 30 runs

(see Section 2.2.1). We converted each probability map ( $n=30$ ) into a presence/absence map using a threshold that maximised TSS in each run. If more than half of the 30 runs predicted the species occurred in the same grid, we determined that blue shark was present in this grid. To facilitate the comparison between our predicted maps with previous studies that narrated blue shark distributions based on quarters of the year (rather than seasons), we also exchanged the northern (or southern) predicted distributions between the two seasons to map the predicted distributions into two durations: March–August versus September–February (next year).

## 2.3 | Spatial analyses

To initially verify the reliability of the model predictions, we overlapped the predicted presence map of blue sharks with the species range map delineated by the IUCN. We calculated the proportion of the predicted presences that was not covered by the IUCN range area (hereafter, mismatched area). A low value of such a proportion implies our predictions are generally reliable.

We examined the spatial relationships between the predicted seasonal maps of blue sharks (probability or presence/absence) and each of the following datasets in the IWPO: (1) MPAs (mainly large MPAs & shark sanctuaries) and (2) seasonal fishing intensity. First, based on the predicted seasonal presence/absence maps, we calculated the coverage of each MPA/sanctuary on the seasonal distributions of the species, and examined whether the coverage varied significantly between seasons (cold vs. warm) or MPA categories (large MPAs vs. shark sanctuaries) using Mann–Whitney  $U$ -tests. We also treated all large MPAs as a whole (so as to all shark sanctuaries, respectively), and calculated an overlap ratio (i.e. intersection area divided by the union) of the protected habitats (i.e. the predicted presences) between the two seasons. A lower overlap ratio indicates a higher divergence between seasons. Second, we used bivariate maps to illustrate the relationship between species presence probability and fishing intensity in each season. We defined hotspot locations as those grids for which values of seasonal presence probability and fishing intensity lay in the highest 20% of respective values (nulls were removed) across the IWPO. We calculated the proportions of (1) the predicted seasonal distributions covered by these hotspots and (2) the hotspots covered by MPAs.

## 3 | RESULTS

### 3.1 | Seasonal SDMs

#### 3.1.1 | Model performance and predictions

In general, both seasonal SDMs (the full and the simplified) performed well (mean TSS  $>0.8$  and AUC  $>0.95$ ), with the cold season performing slightly better than the warm season and the simplified performing slightly better than the full models (Table S3). The

predicted seasonal distributions of blue sharks are highly consistent with the occurrence points and broadly spread in the IWPO (Figure 1). Although the distributions of predicted presence probability of the two seasons were largely similar (Schoener's  $D=0.728$ ), we found areas with prominent divergences, in distribution patterns between two seasons (or month groups), and there were also some differences between the two hemispheres and the two oceans (Figure 1a,b). In the Indian Ocean, the predicted distributions of both the north and the south hemispheres were more contracted towards the equator from September to February (next year, see boxes I and II in Figure 1c,d). In the West Pacific Ocean, the predicted distributions in the northwest were more contracted towards the subtropical and tropical patches from September to February (next year, see box II in Figure 1c,d), while the distributions in the southwest Pacific Ocean exhibited little variation.

#### 3.1.2 | Important predictors and response curves

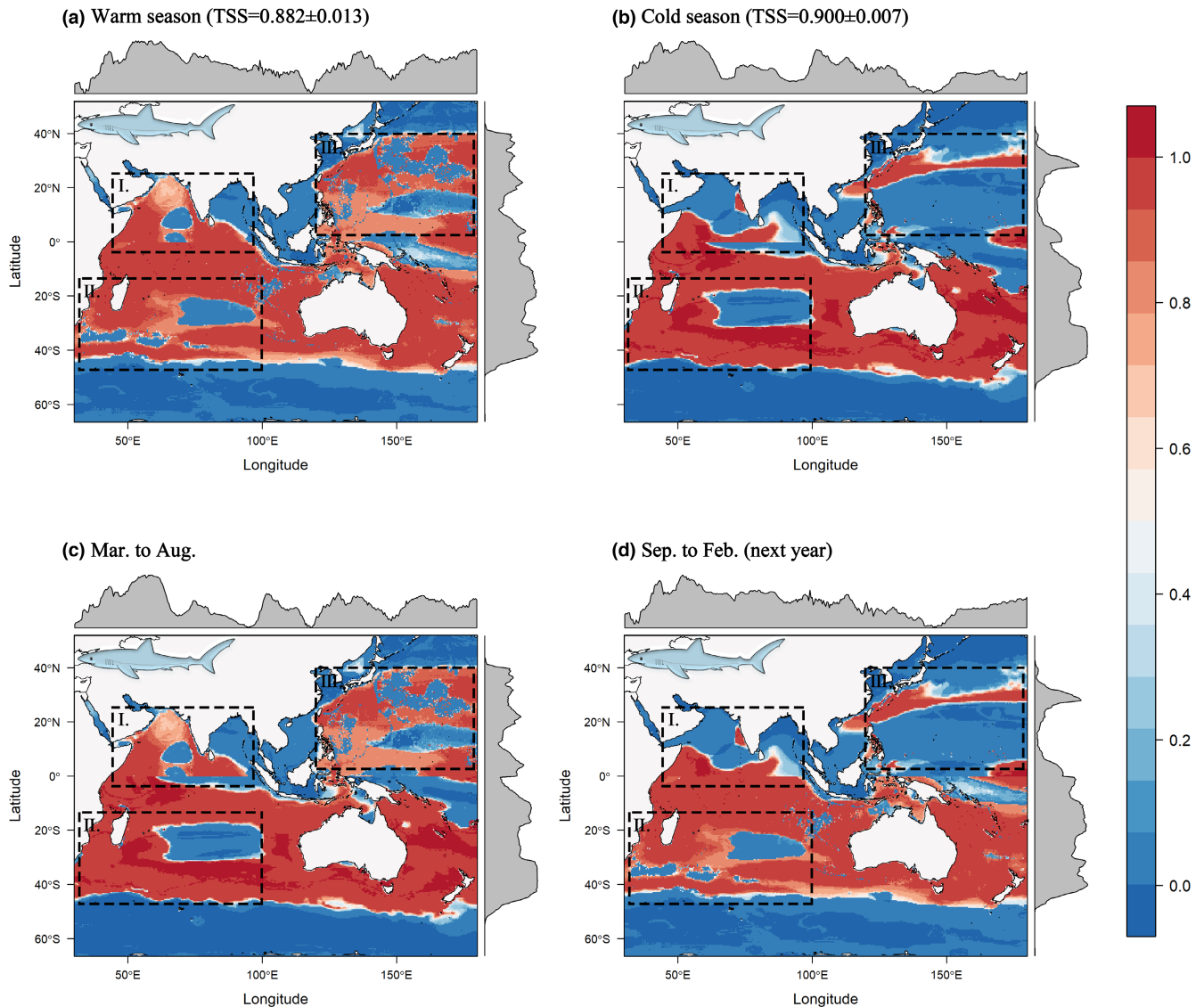
We found that the top four important predictors in predicting the distributions of blue sharks in both seasons were SSS,  $K_d(490)$ , SST, and SSS sd (Figure S4). The fifth and sixth important predictors were depth and  $OF_s$  for the warm season and SST sd and CV for the cold.

The response of blue sharks to SSS followed a narrow bell-shaped curve. The optimal SSS range for the species was approximately 34.7–35.8‰, with a slightly broader niche towards high salinities in the warm season (Figure 2a). The response of blue sharks to SST exhibited a trapezoid curve, with preferred SST about 13–29°C in the warm season and 8–29°C in the cold (Figure 2b). Additionally, the responses to  $K_d(490)$  and SSS sd were similar and right skewed (Figure 2c,d), showing peaks at lower values. This indicates a preference for habitats with lower water turbidity and more stable SSS over years. Less important variables were different across seasons and cannot be compared to analyse seasonal response relationships (Figure S5).

### 3.2 | Conservation and management gaps/opportunities

The predicted suitable distribution areas for blue sharks were generally confined within the range defined by the IUCN, except for some mismatched areas at fringes in the southern Indian Ocean in both seasons and in the Sea of Japan in the warm season (Figure S6). The percentages of these mismatched areas were very minimal (2.16% and 3.53% in warm and cold seasons respectively), and we retained them in the following analysis.

When individual MPAs were treated as independent samples, we did not find significant difference in MPA coverage between pairwise seasons or MPA categories (Mann–Whitney tests, both  $p > .05$ ). When the MPAs of each category were treated as a whole, although the seasonal divergence (warm vs. cold) in MPA coverage measured by all regular large MPAs was relatively minor (3.70% vs. 4.53%),



**FIGURE 1** Predicted presence probability of blue sharks (*Prionace glauca*) in (a) the warm season, (b) the cold season, (c) March–August and (d) September–February (next year) with prominent seasonal divergence highlighted by dashed boxes (I–III) and the latitudinal/longitudinal stacked probability plotted in grey areas. TSS: True skill statistic (model performance).

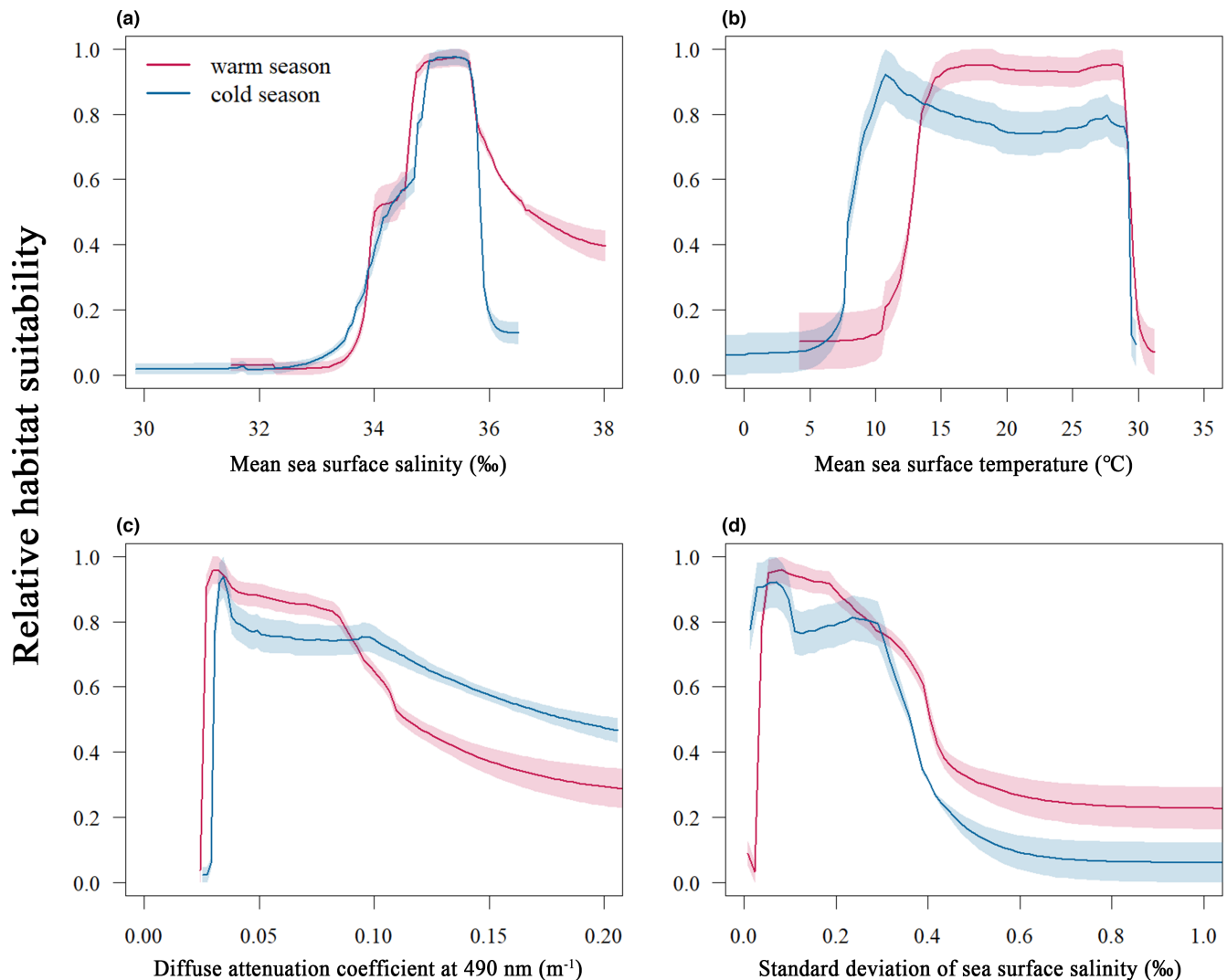
such divergence was more prominent in terms of all shark sanctuaries (9.09% vs. 4.62%; Figure 3). The predicted habitats of blue sharks covered by all considered MPAs (as a whole) in the warm season amounted to 76.34 million km<sup>2</sup> (Figure 3a), while in the cold season, the area declined to 57.77 million km<sup>2</sup> (Figure 3b). The overlap ratio of the whole protected habitats between the two seasons was high (86.08%) in terms of large MPAs, but the ratio in terms of shark sanctuaries was much lower (37.32%).

Our bivariate maps revealed a high spatial heterogeneity in the spatial relationship between the presence probability of blue sharks and fishing intensity in each season (Figure 4a,b). In the warm season, the fishery–shark conflict hotspots were largely located on the high seas in the northwestern Indian Ocean (50–60°E, 0–10°N) and in the subtropical band (20–30°N) in the northwestern Pacific Ocean (Figure 4c). While in the cold season, the hotspots moved further east–west and south (40–80°E, 15°S–10°N), with major hotspots in

Somalian waters, surrounding the British Indian Ocean Territory, and additional dispersive hotspots in the southwest Indian Ocean and the southwest Pacific Ocean (Figure 4c). Generally, hotspots were absent from MPAs, with 2.77%–2.82% and 0.65%–0.79% of the hotspots located within large MPAs and shark sanctuaries respectively. However, some large MPAs (e.g. British Indian Ocean Territory MPA) and shark sanctuaries (e.g. Maldives EEZ) are surrounded by hotspots (Figure 4c). Additionally, some proposed large MPAs that have not yet been implemented (e.g. Amirantes to Fortune Bank Area of Outstanding Natural Beauty) are also located near hotspots (Figure 4c).

## 4 | DISCUSSION

The present study is among the first to reveal seasonal distribution patterns and conservation gaps/opportunities for blue sharks, which

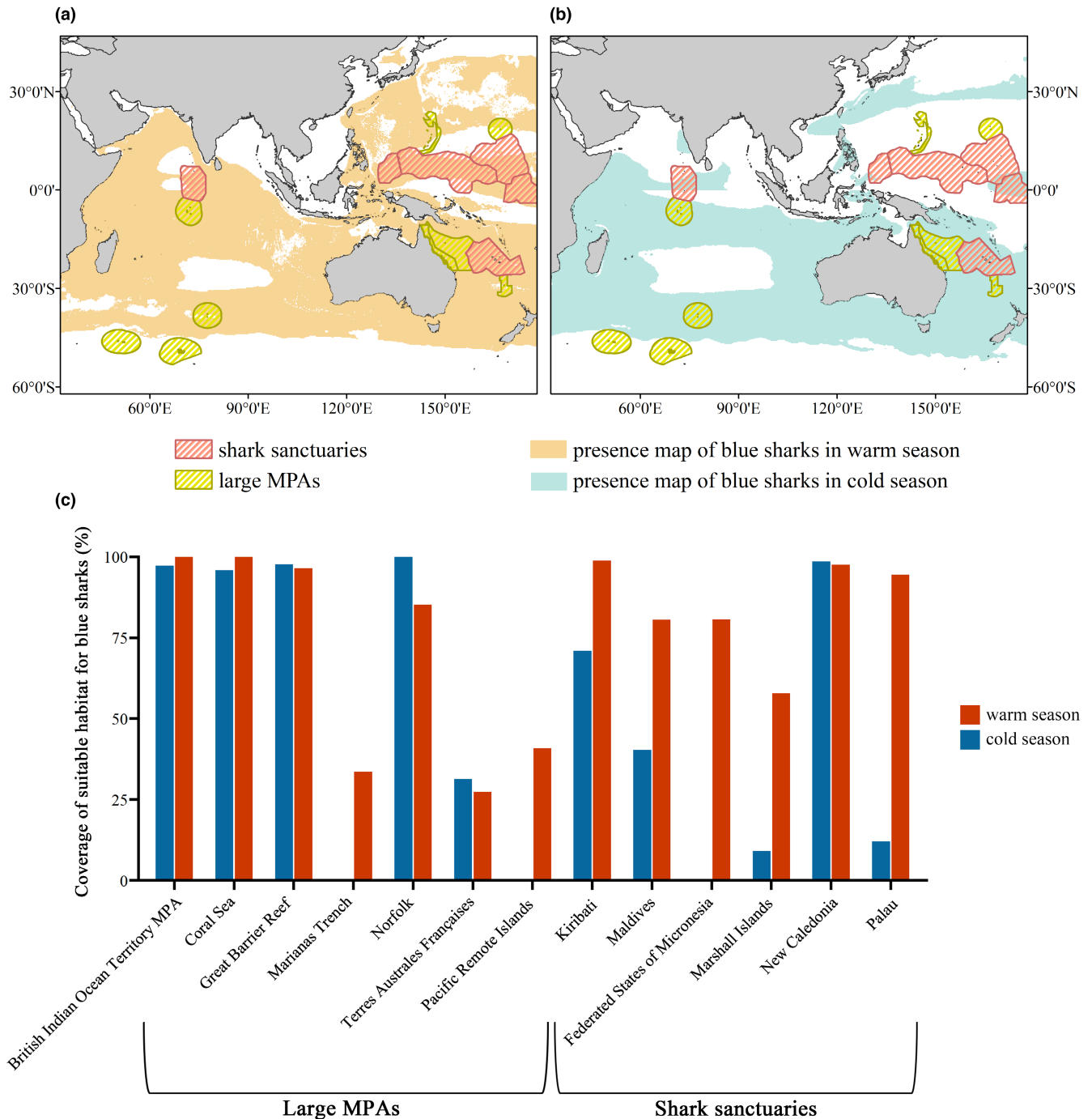


**FIGURE 2** Plots of species response curves of blue sharks in different seasons to (a) mean sea surface salinity (SSS), (b) mean sea surface temperature (SST), (c) diffuse attenuation coefficient at 490 nm, i.e.  $K_d(490)$  and (d) standard deviation of SSS in warm (red dots) and cold (blue dots) seasons.

urgently required to inform their conservation and management in the IWPO given their threatened status (Coelho et al., 2018). Our predicted seasonal distribution maps are generally consistent with the IUCN range map and previous findings based on fishery-dependent surveys and satellite-tag tracking studies, encouraging the use of ensemble SDMs in predicting seasonal habitat uses for oceanic sharks (Zhang, 2022). We show a significant gap in the MPA coverage of the habitats of blue sharks in the IWPO, and given a similar coverage was found in the Atlantic and Eastern Pacific (Conners et al., 2022), future conservation efforts are required to protect this species at the global scale. Furthermore, we reveal that some existing MPAs (especially shark sanctuaries) in the IWPO are still impacted or surrounded by intense fishing efforts, as in the North Atlantic (Graham et al., 2016). This highlights the urgent need to strengthen spatial optimisation and network construction of MPAs and to reduce fishing pressure within and around these areas. Our approaches can be helpful to reveal seasonal distribution patterns and conservation opportunities of other oceanic sharks.

#### 4.1 | Seasonal differences in the distribution and ecological niche of blue sharks

Our predictions on the large-scale seasonal distributions of blue sharks in the IWPO are generally consistent with previous findings (Coelho et al., 2018; Fujinami et al., 2021; Kai et al., 2017; Zhu et al., 2023), and the seasonal divergences may be caused by the migration of blue sharks. The predicted distribution contraction of both the northern and southern populations towards the equator during the September to February (next year) in the Indian Ocean is likely due to the synchronous migration of adult blue sharks from both hemispheres for mating as shown by fishery-based studies (Coelho et al., 2018; Zhu et al., 2023). The unchanged distributions in the temperate waters in the southwest Indian Ocean and southwest Australia are likely driven by the juvenile sharks given they mainly concentrate in these high-latitude zones and do not change habitats over the year (Coelho et al., 2018). Predicted seasonal distributions in the northwest Pacific Ocean are likely driven by the

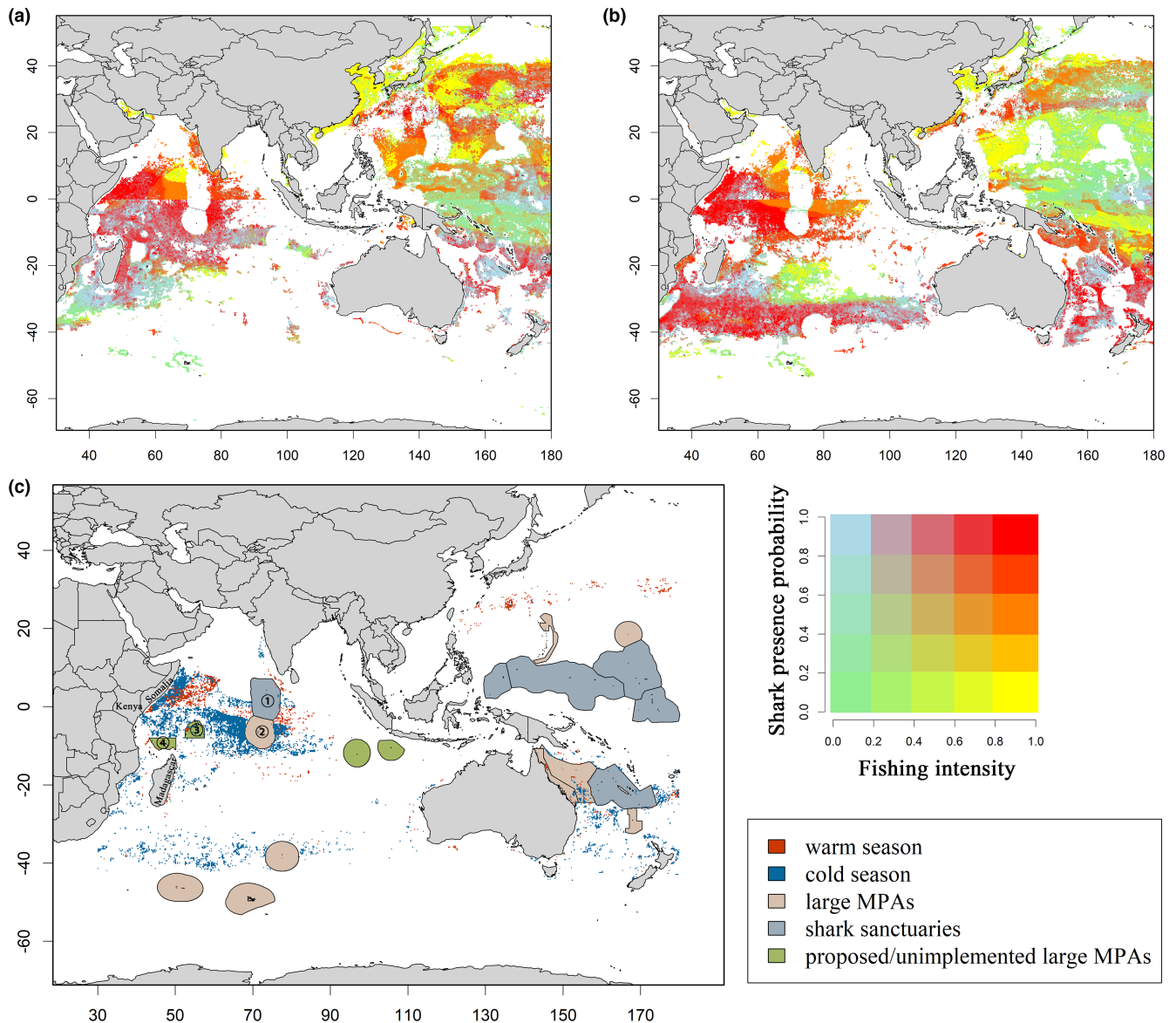


**FIGURE 3** Maps of protected habitats for blue sharks in (a) the warm season and (b) the cold season and (c) coverage of habitats for blue sharks in large MPAs (area > 150,000 km<sup>2</sup>) and shark sanctuaries in each season.

seasonal migrations of adult males and females as shown by a recent tagging study (Fujinami et al., 2021). This tagging study reveals that adult males follow the North Pacific Gyre (a clockwise large-scale current), leaving the equatorial region in spring and mating with females in summer in subtropical waters (around 30°N) where females usually reside. Pregnant females then migrate northeasterly and give birth in temperate waters mainly in autumn, while the adult males continue clockwise movement, returning to the equator through the eastern Pacific coast (which was beyond our focal range) during autumn and winter. In the southwestern Pacific Ocean, the predicted

wide-spread distributions (similar between cold and warm seasons) might be largely driven by the wide-range movements (across the subtropical and temperate waters) of adult males in each season as found by a recent tagging study (Elliott et al., 2022).

The seasonal distribution divergences due to migration at different life-history stages might be essentially driven by environmental factors, such as changes in salinity and temperature which showed seasonal differences in some areas (Figure S7). Salinity has an important effect on the distribution of blue sharks in the IWPO, which is consistent with previous studies in the Northeast Pacific



**FIGURE 4** Bivariate maps of fishing intensity and blue shark presence probability in (a) the warm season and (b) the cold season. Colour scales are based on quantile intervals (in 20% increments) with each class containing an equal number of values. (c) Twenty per cent hotspots for shark presence probability and fishing intensity in each season, overlaid with protected areas. Annotated protected areas: 1, Maldives Shark Sanctuary; 2, British Indian Ocean Territory MPA; 3, Amiranthes to Fortune Bank Area of Outstanding Natural Beauty; 4, Aldabra Group Marine National Park.

(Vögler et al., 2011). Most sharks are stenohaline, and movement within suitable salinity ranges can reduce energetic costs involved in osmoregulation (Froeschke et al., 2010). Blue sharks in our study have a slightly wider tolerance in salinity during the warm season, presumably because they can allocate more energy to regulate osmotic pressure balance in warm season and thus become less sensitive to salinity. Ocean temperature plays an important role in crucial metabolic physiological processes (e.g. digestion and reproduction) of ectotherms (Bernal et al., 2012). Our model results also indicate that the blue sharks in the IWPO exhibit a wide temperature tolerance, with a higher tolerance during the cold season compared to the warm season (8–29°C vs. 13–29°C). When the external environment changes, sharks need to weigh the risks of moving to suitable

habitats (e.g. increased chance of predation) against the energetic costs of staying in adverse conditions (Schlaff et al., 2014). Therefore, blue sharks in the temperate cold waters, which are largely juveniles (Coelho et al., 2018), may stay in lower water temperatures during the cold season to avoid the risks associated with migration.

## 4.2 | Conservation opportunities for blue sharks

Large MPAs and shark sanctuaries are crucial for the conservation of oceanic sharks with long-distance migratory abilities (Graham et al., 2016). However, our study reveals that the current proportion of suitable habitat for blue sharks in the IWPO covered by MPAs

(including large MPAs and sanctuaries) is relatively low (about 9% and 13% in cold and warm seasons respectively), so as to the populations in the Atlantic and Eastern Pacific (Conners et al., 2022). These findings together suggest that more MPAs or shark sanctuaries might be required to protect this NT species in the future. The waters surrounding Australia have many MPAs, and a significant amount of blue shark occurrences were located in this region. This suggests if these MPAs and sanctuaries were managed effectively in terms of excluding high bycatch fishing activities (currently not; Devillers et al., 2020), they might serve as important refuges for blue sharks, as for some reef sharks (Simpfendorfer et al., 2023). In contrast, we identified shark-fishery hotspots in the warm season in the subtropic northwest Pacific, where there is a lack of large MPAs or sanctuaries. To the best of our knowledge, very few studies have focused on blue-shark conservation planning in this region, which should be a priority area for new MPAs.

Our study reveals potential shortfalls and management gaps/opportunities in current shark sanctuaries, which are rarely addressed in literature (MacKeracher et al., 2019). Previous studies suggest shark sanctuaries can provide better refuges to sharks than normal MPAs (Ward-Paige, 2017). We imply that this may not be true for blue sharks given statistically the coverage of blue shark's habitats by a shark sanctuary was not significantly different from that by a large MPA. Interestingly, we showed that fishing efforts within and around shark sanctuaries were significantly higher than those of large MPAs. This may be partly because there are no regulations specifically prohibiting the exploitation of other fisheries resources in shark sanctuaries. As a result, blue sharks are still likely to be caught as bycatch even within areas where shark fishing is prohibited (Hyde et al., 2022). A recent study has indicated that mortality rates of blue sharks are very high in shark sanctuaries near the equator (i.e. Federated States of Micronesia, Palau and Marshall Islands; Shea et al., 2023). Therefore, it is necessary to modify or prohibit fishing gears (e.g. longlines and purse seines) and issue retention bans in (and around) shark sanctuaries to mitigate shark bycatches.

### 4.3 | The contributions and caveats of our study

Our study encourages the use of open-access data and SDMs to predict seasonal distribution patterns for the highly-mobile blue shark, which is otherwise normally examined through expensive fishery-dependent surveys or satellite tags (Maxwell et al., 2019; Zhu et al., 2023). However, due to data limitations, we are unable to predict distribution patterns for different sexes and life history stages. This drawback is mainly due to the potential poor logging of captured sharks in field, and it is recommended that fisheries management improve species occurrence records to provide more detailed data for crowd-sourced data collection initiatives such as GBIF and OBIS. Nonetheless, our study highlights that building seasonal SDMs is valuable for oceanic sharks that are highly mobile and migrate seasonally (Gibson et al., 2021; Mannocci et al., 2017; Sequeira et al., 2014). Notably, we find some prominent seasonal variations in the distribution maps, suggesting that previous non-seasonal SDM studies might

have masked important habitat-use dynamics over the year (Báez et al., 2020; Braun et al., 2023). The statistical test results for comparing MPA coverage between seasons should be taken with cautions given the small sample sizes of MPAs available in our study area. That is why we also calculated the seasonal differences in MPA coverage in terms of all MPAs as a whole and that of each category (regular large MPA vs. shark sanctuary). The results of these additional analyses revealed a prominent seasonal divergence in MPA coverage particularly in terms of shark sanctuaries. Therefore, a dynamic approach to MPA networks (at least for shark sanctuaries) might be helpful for protecting oceanic sharks with seasonal habitats (Zhang, 2022), and our study provides maps to do so. Additionally, we are among the first to apply bivariate hotspot analyses to identify shark-fishery conflict hotspots and conservation opportunities, in contrast to previous studies that rely on an exposure risk index (White et al., 2019), which could mask the different values between shark frequency and fishing intensity. In summary, we provide a feasible integrated approach to inform large-scale conservation planning and fishery management for blue sharks and many other sharks alike.

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### CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13828>.

### DATA AVAILABILITY STATEMENT

All data and R code used in our analyses are available from Figshare (doi: [10.6084/m9.figshare.23815971](https://doi.org/10.6084/m9.figshare.23815971)).

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#### BIOSKETCH

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Author contributions: XZ contributed to the research idea and methodology. YZ conducted the data collection and analyses, and wrote the manuscript under the supervision of XZ. PL provided help with data analyses and comments to improve the manuscript.

#### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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