



Environmental controls of billfish species in the Indian Ocean and implications for their management and conservation

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Abstract

Background and aim: Billfish are epipelagic marine predators facing increasing pressures such as overfishing and rising global temperatures. Overfishing is a major concern, as they are caught by industrial longline fishers targeting tuna. Billfish are targeted by multiple fishing sectors, which provides food, socio-economic and cultural benefits. To support effective billfish management and conservation, it is essential to understand their spatial distribution and the environmental factors that may influence it.

Location: The focus of this study is the Indian Ocean (IO), where there are gaps in understanding the interactions between fisheries and billfish distribution. Three of six billfish species are at risk from overfishing. Therefore, determining their distribution is crucial to their management and conservation.

Methods: Using Ocean Biogeographic Information System (OBIS) occurrence data, Indian Ocean Tuna Commission (IOTC) catch data, and environmental covariates, we applied species distribution models to investigate the spatial extent of the realized niches of six billfish species in the IO. We also determined the role and relative importance of environmental drivers. Moreover, we evaluated the association between species' spatial distribution and the fishing effort distribution.

Results: We found niche partitioning and overlap among the six species identified spatial distribution, with higher species richness in the northern region of the IO and off the East coast of Africa. Temperature, mixed layer depth and salinity were identified as the most important predictors of species distribution, with moderately warm and stable environments preferred by most billfish species. Areas with high species richness and high fishing effort overlap were primarily found in the Areas Beyond National Jurisdiction (ABNJ). In contrast, areas with high species diversity richness and low fishing effort were found mainly in the Exclusive Economic Zone (EEZ).

Main conclusion: Spatial overlap between fishing effort and billfish projected distribution suggests inadvertent fishing pressure on billfish populations as they are caught together with targeted tuna. Spatial distribution transcends maritime zones,

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reinforcing a need to formulate effective management policies for marine areas beyond national jurisdictions.

KEYWORDS

bycatch, ensemble modelling, fishing pressure, niche overlaps, spatial ecology, species distribution modelling

1 | INTRODUCTION

Billfish are epipelagic predators distributed widely throughout the tropical, subtropical and temperate waters of the world's oceans (Nakamura, 1985; Restrepo et al., 2016; Reygondeau et al., 2012). The Indian Ocean (IO) is home to six species of billfish, including the black marlin (*Istiompax indica*), sailfish (*Istiophorus platypterus*), striped marlin (*Kajikia audax*), blue marlin (*Makaira nigricans*), shortbill spearfish (*Tetrapturus angustirostris*) and swordfish (*Xiphias gladius*). These species are targeted by multiple fishing sectors, including small-scale, commercial and recreational fishers for food, socio-economic and cultural benefits (Doyle, 2018; Kadagi et al., 2021; Techera, 2020). Despite their significance, billfish are currently facing environmental pressures and overexploitation, threatening their sustainability of fisheries (Dell'Apa et al., 2018; Juan-Jordá et al., 2011; McIlgorm, 2010).

Historical trends suggest that global billfish catches increased steadily from 1950 to 2000 but have declined recently in other oceans except for the IO, where reported catch has been rising (Pons et al., 2017; Sharma et al., 2018). The exploitation status of billfish species differs among the three major oceans. For instance, in the Atlantic Ocean, approximately over 70% of the billfish populations are considered overfished or undergoing overfishing, compared to the Pacific and IO, where 62% and 50% of the populations are overfished or undergoing overfishing respectively (IOTC, 2020a; Restrepo et al., 2016). However, a disproportionate effort is expended towards billfish studies among ocean basins. In the IO, gaps still exist in understanding the interactions between fisheries and billfish distribution in space and time, which is necessary for informing their conservation measures.

Recent stock assessments of IO billfish species reported that the black marlin, blue marlin and striped marlin are overfished, while sailfish are undergoing overfishing (Andrade, 2016; IOTC, 2020a; Yokoi & Nishida, 2016). The stock status of the shortbill spearfish remains unknown due to limited data, while the swordfish stocks are not subject to overfishing (IOTC, 2020a). Here, management recommendations are often entirely dependent on aggregated catch and effort trends, with less consideration of the spatial distribution of billfish and associated factors. This may be particularly problematic as climate-driven pressures influence environmental conditions that determine habitat use of billfish species, with implications for their exploitation and conservation (Dell'Apa et al., 2018). Therefore, besides monitoring fish stocks and fishing efforts, there is a need to understand the relative role and potential impacts of environmental pressures such as increased water temperature on billfish distribution to inform conservation and management decisions at national and oceanic scales.

Environmental factors are known to influence billfish movements and foraging habits, and several studies globally have described the strong relationships between their distribution and environmental covariates such as temperature, oxygen, and salinity (Block et al., 1992; Block et al., 1992; Boyce, 2004; Carlisle et al., 2017). Studies on billfish distribution indicate spatially distinct niche preferences based on physiological requirements (Lam et al., 2015; Ricklefs et al., 2014; Shimose et al., 2010). Understanding correlations between billfish distributions and environmental variables may help determine their niche preferences, including potential niche overlaps (Boyce, 2004; Boyce et al., 2008; Reygondeau et al., 2012). When coupled with stock assessments, such information is critical in developing spatio-temporal management and conservation measures (Boerder et al., 2019; Carlisle et al., 2017; Hazin & Erzini, 2008; Sedberry & Loefer, 2001). However, a lack of information on environmental controls, niche distribution, and overlaps of billfish species in the IO hinders the ability to advance their spatio-temporal management.

Common approaches to delineating the distribution of species involve using species distribution models (SDMs) that require presence and absence data and environmental covariates to predict habitat use of species. SDMs have been used widely to characterize the niches of highly migratory species such as birds and seals (Elith & Leathwick, 2009; Raymond et al., 2015; Scales et al., 2016). SDMs can address challenges related to data deficiency for species requiring management intervention by modelling distributions and identifying potential interactions with threats such as fishing activities (Escalante et al., 2013; Queiroz et al., 2016).

Here, we addressed critical knowledge gaps on the effects of environmental controls on billfish in the IO. First, we used SDMs to investigate the spatial distribution and niche partitioning of each of the six billfish species. Second, we evaluated environmental covariates' role and relative importance in predicting the identified Spatial distribution. Finally, we examined the potential risk of commercial fishing to billfish stocks by estimating the overlap between the projected billfish distributions and fishing activity. The results of our study will enhance the understanding of critical environmental controls their influence on the distribution of billfish species and contribute to sustainable management efforts.

2 | DATA AND METHODS

2.1 | Data

From the Ocean Biodiversity Information System (OBIS) database (www.obis.org), we collected 2314 occurrence records for black marlin, sailfish, striped marlin, blue marlin, shortbill spearfish and

swordfish across the IO (Table S1). The OBIS database contains species occurrence data harmonized from multiple sources and quality checked (Costello et al., 2007; Klein et al., 2019). The occurrence records in the OBIS database for billfishes in the IO primarily comprises data from commercial fishery logbooks and/or observer programmes. Occurrence records from the OBIS database have previously been utilized to estimate species distributions in other regions (Coro et al., 2016; Jensen et al., 2017). On closer examination of OBIS records within our region of interest, we found data gaps and geographical bias in the occurrences due to underreporting of billfish data and little fishing effort in some areas. Consequently, we processed and used fisheries catch data from IOTC to fill the data gaps.

Fisheries data containing nominal effort (number of hooks) and catches (number of fish) were obtained from the IOTC database (<https://iotc.org/data/datasets>). These data are reported to IOTC in a gridded format at $1^{\circ} \times 1^{\circ}$ and $5^{\circ} \times 5^{\circ}$ by day, month, year and grid, based on countries' reports for their vessels operating in the region. We extracted longline catch data from 2008 to 2018 for the IO region and re-gridded it onto a $1^{\circ} \times 1^{\circ}$ grid for consistency. We used longline catch data because longline vessels accounted for approximately 70% of historical total billfish catches reported to IOTC from the 1990s up to the early 2000s (IOTC, 2020b). Over the past few years, longline vessels have caught a smaller share of total billfish, up to 30% in 2018, with offshore gillnet fleets playing an increasingly important role. However, longline data are more readily accessible, as many countries operating in the IOTC region do not report most of their billfish catches from gillnets.

For a merged IOTC and OBIS occurrence dataset, we first created IOTC occurrence points in all 10×10 grid areas where IOTC catches were reported. Using the OBIS occurrence points, we removed all IOTC points that occurred over a known OBIS point. The IOTC spatial data does not undergo the same quality checks as the OBIS database. Therefore, to increase the certainty of the occurrence, we only considered IOTC grids with the highest catch ($\geq 50\%$ quantile) as occurrence points.

2.2 | Environmental data and physiological mechanisms

The distribution and abundance of marine fishes are highly dependent on physiological mechanisms (Jørgensen et al., 2012). Using existing hypotheses of environmental influence on billfish physiology, we identified covariates that best represent the environmental cause of physiological significance. Several environmental variables have been found to influence billfish habitat preference and distribution (Carlisle et al., 2017; Lam et al., 2015; Sedberry & Loefer, 2001). These include seawater temperature, mixed layer depth (MLD), productivity, sea surface height (SSH), depth and salinity.

Temperature and salinity affect billfish physiological processes such as metabolic rate (Carlisle et al., 2017; Neilson et al., 2009; Reygondeau et al., 2012; Rooker et al., 2012). Ocean productivity indicates the availability of food for small fish preyed upon by billfish.

The Chl-a level offers information on an area's primary production (Sedberry & Loefer, 2001; Seki et al., 2002). The billfish's vertical movements, food availability and oxygen levels are influenced by depth. The amount of light required for primary production is lower in deeper areas, and thermoclines may impede oxygen circulation (Block et al., 1992; Carlisle et al., 2017). MLD is a measure of how well surface waters mix with deeper water due to temperature differences, and it can influence billfish vertical movement (Lam et al., 2015; Williams et al., 2017). SSH denotes oceanic features such as gyres, eddies and upwelling areas that influence MLD and primary productivity.

The appropriate covariates for use in the SDMs were derived from the above hypothesis (Table S2). We obtained the covariates' respective time series (2010–2020) data from the Global Ocean Physical Reanalysis and Global Ocean Biogeochemistry hindcast on the Copernicus website (<http://marine.copernicus.eu/services-portfolio/access-to-products/>). Monthly time series data were aggregated into long-term averages and coefficients of variation (CV).

2.3 | Data analysis

2.3.1 | Billfish niche partitioning

We investigated billfish niche partitioning, and the mechanisms influencing their niche using SDMs implemented using R $\times 64$, 4.1.0 (R Core Team, 2021) package *sdm* (Naimi & Araujo, 2016). Before fitting SDMs, we tested the occurrence data for geographical and sampling biases using the R package *Sampbias* (Zizka et al., 2020). We also tested for multicollinearity among the environmental covariates by applying variance inflation factor (VIF) tests using the *usdm* R package (Babak Naimi, 2015). VIF values of < 3 indicate that multicollinearity is not a serious concern. However, because our objective was to compare relative importance among the covariates, we applied a more conservative VIF threshold of 1.5.

To fit SDMs, we used presence-only records as the response variable against six environmental covariates. Most SDMs require both presence and true absence datasets. Because our occurrence data lacked true absence records, we used the method 'gRandom' in the *sdm* package to generate a set of pseudo-absence records for each species that matched the number of the presence points (Naimi & Araujo, 2016). The algorithm uses environmental spatial data layers and the presence points to model suitable areas for the species. It randomly selects locations least ideal for the species as pseudo-absence points. Matching points are then removed to verify that no pseudo-absence is placed over a known presence point (Barbet-Massin et al., 2012; Senay et al., 2013).

We accounted for the strengths and weaknesses of different SDM approaches, including regression-based models and tree-based machine learning approaches. Four algorithms were run by applying ensemble modelling: Generalized Linear Models (GLMs), Generalized Additive modelling (GAMs), Gradient Boosting Machines (GBMs) and Random Forests (RFs). All models were run using the following settings,

replicatin = 'sub', test.percent = 30, n = 10 (evaluates using 10 runs of subsampling replications taking 30 per cent as a test) (Naimi & Araujo, 2016). The RF algorithm has 'hyper-parameters', which are not estimated from the data (unlike parameters of a statistical model) and are set by the user to influence model performance. The number of trees (ntree) and the number of random samplings from the set of predictors (mtry) are the most influential for the RF models (Probst et al., 2019). To determine a combination of mtry (1–10) and ntree (1–500) that produced the best performance for each of the alternative models, we used the *caret* package in R (Kuhn et al., 2020). We then ran the models using the identified parameters. GAMs and GLMs were fitted using binomial error distributions with logit link function, while GBMs were fitted using Bernoulli distributions and default hyperparameters values in *sdm*.

We evaluated model performance using the 'true skill statistic' (TSS) that measures the model performance based on sensitivity and specificity (Allouche et al., 2006). Before predicting each of the four models spatially over the IO, we confirmed that ranges of predictor variables in the sampled area were comparable to that of the study area's background data to avoid model extrapolation. To obtain a harmonized prediction for each of the six species, we generated model ensembles based on the weighted mean by the model performance of the four models (R. A. Garcia et al., 2012; Grenouillet et al., 2011; Jensen et al., 2017; Scales et al., 2016; Zanardo et al., 2017).

Temperatures and MLD experience seasonal variations in the IO (Keerthi et al., 2016). Testing for seasonality in SDMs is complicated by a lack of data on seasonal observations. Environmental variability metrics are often used as proxies for seasonality in SDMs. For example, standard deviation (Bazzato et al., 2021), the difference between the temperature of the warmest and coldest month as a proxy for seasonality (Jarvie & Svenning, 2018; Tyberghein et al., 2012), and coefficient of variation (Porfirio et al., 2014) can be used as proxies for seasonality in SDMs. Here we used the CV to infer seasonality. To evaluate the potential influence of seasonality on the species' spatial distributions, we plotted the probabilities of occurrence against CVs for temperature and MLD. This essentially created a bivariate occurrence space illustrating the association (or lack of) between seasonality and distribution. Finally, the predicted habitat suitability was converted to presence-absence using the highest kappa threshold (Liu et al., 2016).

2.3.2 | Niche overlap

To evaluate overlap in the billfish niches, we applied the 'niche overlap' function in the *r* package DISMO (Hijmans et al., 2017; Warren, Glor, & Turelli, 2008). The niches rasters were stacked to create a billfish species richness map.

2.3.3 | Spatial congruence between billfish distribution and longline fishing

We evaluated the spatial congruence between species richness and the Global Fishing Watch data (GFW) derived effort distribution.

GFW computes the global distribution of fishing effort using the location data of fishing vessels obtained from the Automatic Identification System (AIS). GFW retrieves the location data of the fishing vessels and maps the fishing effort (hours) distribution at a resolution of a 10 km grid (Guiet et al., 2019). We retrieved daily global data in spreadsheets to obtain annual GFW effort estimates for the IO. This was done by first obtaining the total fishing effort for 1°×1° grid for each year. The average for all the years was obtained by summing the annual total fishing effort, divided by years. These were subsequently mapped into 1°×1° grid and clipped to the IO extent.

The spatial interaction between billfish species and fishing effort was calculated by first dividing the fishing effort and species layers into two categories: low (less than 50 percent quantile) and high (greater than 50 percent quantile). The two layers were then intersected to provide four interaction categories: low species-low fishing, low species-high fishing, high species-low fishing and high species-high fishing.

2.3.4 | Data and methodological approach sensitivity test

The outcome of SDMs is as good as the data and the algorithms used. We opportunistically used a different dataset version and alternate algorithm to function as a sensitivity test to our methodological approach. In this second approach, we create a dataset with absence points instead of the pseudo-absence points method used in the first approach. Since the presence data used is primarily from longline vessels that target swordfish, we generate the absence data of all the other species by comparing them with the swordfish presence data. Each species' presence data was matched with the swordfish presence points. In cases where there was no overlap between the species' presence and swordfish presence, the swordfish presence point was considered absent points for the species. This was similar to the approach used by Torreblanca et al. (2019). We then compared the projected realized niches for each species using the 'niche overlap' function in the *r* package DISMO to dictate possible differences between the two approaches.

3 | RESULTS

3.1 | Billfish niche partitioning

There was clear niche partitioning among the six billfish species. For most species, the projected spatial distributions are centred in Western IO, Northern IO, and western Australia (Figure 1a-f). There were differences and similarities in the individual species' niches. Black marlin and striped marlin had the highest niche overlap index (0.85). In contrast, the species with the least potential for niche overlap were the blue marlin and shortbill spearfish, with a niche overlap index of 0.25. (Figure 2).

Striped marlin had the largest projected distribution, with the projected realized niche occurring in the Western IO, Northern IO, and western Australia (Figure 1a). The least distributed species is the shortbill spearfish, with a projected niche occurring mainly in the south-western IO and western Australia (Figure 1f). Our findings also show that marlins had similar projected niches compared to the other species, which corresponds to the IOTC stock status, as all three marlin species are overfished in the region, while species that had contrasting projected niches, such as the swordfish, having better stock status (Figure 2).

3.2 | Role and relative importance of environmental covariates

There were agreements among model types on variable importance for most species, except for salinity, which was indicated as important in GLM models and not in the other three (GAM, GBM and RF) (Table S6). Temperature, MLD and salinity were the most important variables in predicting distribution in all species across all the model types but with a species-specific difference in relative importance. For example, temperature and salinity were the most important predictors for black marlin, blue marlin and sailfish. Similarly, MLD and

salinity were the most important predictors of striped marlin and swordfish occurrences (Figure 3).

The average temperature was positively associated with the occurrence of all species, with an optimal mean range between 22 and 30°C (Figure 4a). Our results show that swordfish has the largest temperature tolerance ranging between 18 and 30°C, while sailfish was predicted to occur within a narrow mean temperature range of 23 and 29°C (Figure 4a, Figure S4). A high probability of occurrence was associated with low MLD and optimal MLD values of 20 and 40 m (4d). For salinity, GLM, GBM and RF models revealed a similar trend of increasing probabilities between the range of 32 and 36psu (4b). Although depth was less important in influencing the distributions of some species, swordfish and shortbill spearfish showed a stronger positive association with depth with decreasing probabilities of occurrence in shallower depth (Figure 4c).

The distribution ranges for temperature, MLD, salinity and depth varied among the species (Figure 4). The species with the highest depth ranges were shortbill spearfish (−1542 to −4756), while the striped marlin showed the narrowest depth range (−2773 to −5081) (Figure 4c). Areas with the highest suitability of finding swordfish also had the greatest MLD range (19 and 33 m). In contrast, sailfish displayed the smallest MLD ranges with the highest probability between mean MLD values of 7 and 32 m (Figure 4d).

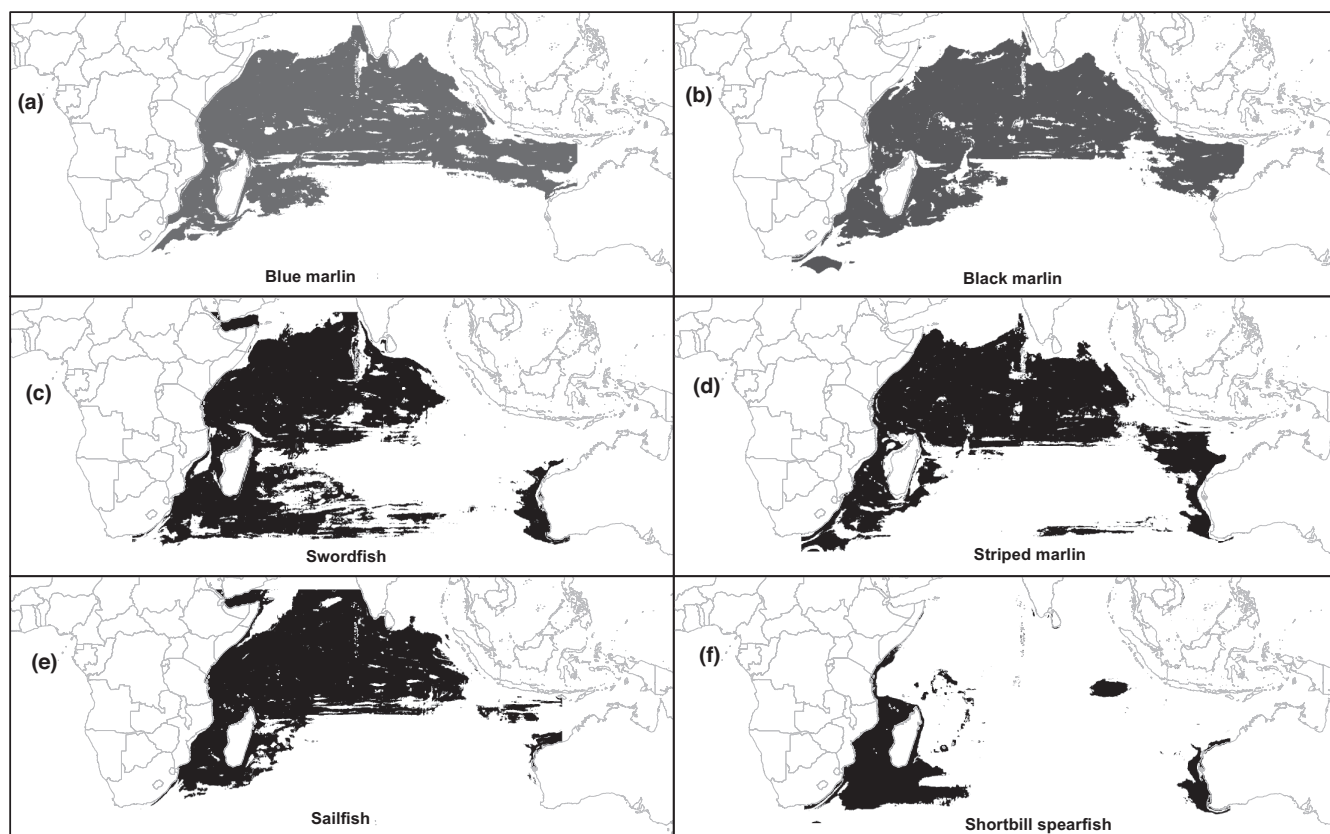
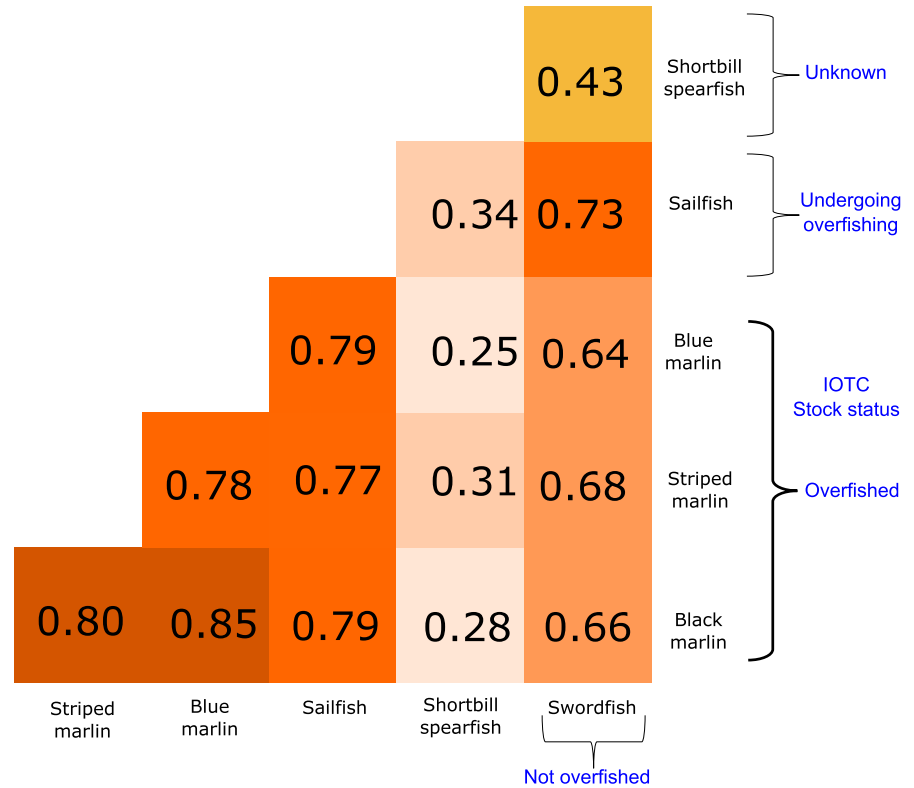


FIGURE 1 Projected current distributions for billfish species in the Indian Ocean. The maps show the areas that are more suitable for each species. Projected distributions result from converting the habitat suitability to 0 and 1 (black) by applying a threshold where kappa is maximised. The initial suitability maps are shown in the Supporting Information. Projected distributions are ordered from the largest to the smallest

FIGURE 2 Tests of niche overlap among the six billfish taxa, with 0 and 1 representing no overlap and perfect overlap, respectively. Taxa stock assessments are also illustrated based on the recent IOTC report (IOTC, 2019; Yokoi & Nishida, 2016; Andrade, 2016)



Our results show relationships between the spatial distribution of the species and seasonal changes in temperature and MLD. The species distribution fall in regions with a low CV in mean temperature and a higher MLD CV, especially for the marlins and sailfish (Figure 5). Swordfish and shortbill spearfish did not exhibit clear seasonality effect on their niche distributions.

3.3 | Fishing effort interaction within billfish spatial distributions

We found species richness hotspots (high niche overlap) for the six billfish species off the eastern coast of Africa, the northern region of the IO and Australia's western coast. In contrast, the southern IO is characterized by fewer billfish species (Figure 6a). Areas with many billfish species present were also found to experience high fishing pressure.

The EEZ and the high seas are essential areas for billfish, with 55% of the billfish spatial distributions found in the EEZ of the IO nations, while 45% were found in the high seas. Areas with a high probability of occurrence for most species and high fishing effort overlap were primarily found in the Areas Beyond National Jurisdiction (ABNJ). In contrast, areas with high species diversity and low fishing effort were found mainly in EEZ (Figures 6b,7a). The areas with the highest predicted occurrences of billfish also varied among countries, with some countries in the Western Indian Ocean (WIO) such as Mozambique, Seychelles, Madagascar and Mauritius being 'hot spots' for species occurrence (Figures 6a,7b).

3.4 | Sensitivity test

Using two approaches to modelling: pseudo-absences and an alternate method that considers swordfish presence as believable absences, our sensitivity test reveals a minor difference in billfish distribution projections. The overall spatial pattern of projected distribution along the IO is quite similar; however, the exhibited similarity was >than 78% for all species, except for the shortbill spearfish, where the similarity between the two projected distributions was 60%. The pseudo-absence method was more conservative and projected a relatively smaller distribution than the swordfish presence - pseudo-absence method (Figure S5).

4 | DISCUSSION

We investigated the spatial distribution of six billfish species in the IO and their dependence on the prevailing environmental conditions. To evaluate the likely effects of fishing pressure on billfish species, we tested whether observed fishing effort overlapped with inferred spatial distributions. Overall, our findings show that billfish species in the IO exhibit distinct spatial distributions. Niche partitioning existed among the six species based on physiological tolerances for temperature, MLD and salinity. Furthermore, our study revealed regions where billfish species were strongly associated with the longline fishing effort distribution, suggesting that there may be a need to accelerate measures for billfish management in the EEZs and ABNJs.

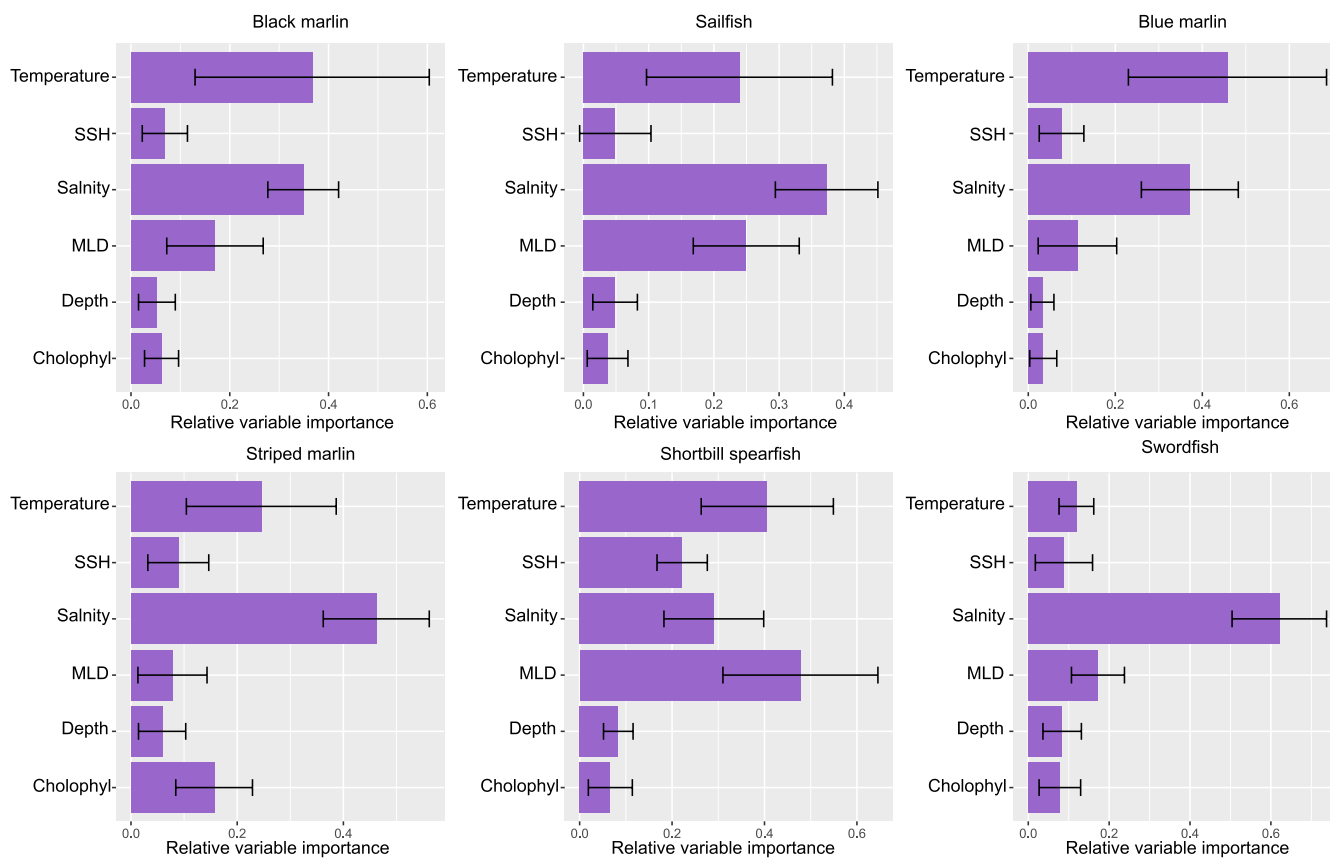


FIGURE 3 Relative importance of predictor variables used for predicting billfish species in the Indian Ocean. The relative importance compares the importance of a variable in a model with the other variables in the same model and ranges from 1 to 0). Relative variable importance is based on Pearson correlation coefficients weighted by AUC values of contributing models

4.1 | Spatial distribution of billfish

The results of our study demonstrate that billfish species in the IO exhibit both niche partitioning and co-occurrence. Based on billfish species' occurrence records in public databases, we identified potential species distributions and associated environmental limits. The northern, western and eastern IO are vital distribution regions for billfishes. High niche distribution of all species for specific areas, particularly in the northern and western IO areas, may be influenced by high productivity (Prasanna Kumar et al., 2009; Wiggert et al., 2005). Our findings are consistent with reports of shifts in black marlin distribution primarily driven by high nutrients and warm SST from coastal upwelling in the Pacific Ocean (Farchadi et al., 2018). High billfish diversity in Africa's northern and east coast suggests that these areas are conducive environments for billfishes. However, this finding should be subjected to further investigation given fewer occurrence records for this area in the database (Lévy et al., 2007; McCreary et al., 2009).

4.2 | Relative importance of environmental covariates

The most important variables in billfish habitat suitability were temperature, MLD and salinity. The IO exhibits a wide range of

environmental factors (Figure 4). For example, the northern IO, off the eastern coast of Africa, and Western Australia experiences high temperatures with minimal seasonal variation because of little exchange with external water masses (Wafar et al., 2011). In contrast, the southern IO region experiences lower temperatures with strong seasonal variability due to the water exchange between the IO and the Atlantic Ocean at high latitudes and between the IO and the Pacific Ocean at low latitudes (Longhurst, 2010; Reygondeau et al., 2012; Wafar et al., 2011). Ocean conditions in northern IO are also influenced to a large extent by the monsoon cycle. The interchange between the northeast and southwest monsoon creates a distinct zone with a subtropical gyre that leads to upwelling and higher productivity and subsequently wider distribution of the billfish species in this region (Schott and McCreary, 2001; Shankar et al., 2002).

The extent of the predicted spatial distributions varied among the six billfish species. These variations may be mainly due to differences in environmental ranges in the predicted distribution. For example, the swordfish had a broader geographical range, while the marlins had a much narrower geographical range. Our results reinforce previous findings that swordfish have wider temperature ranges than the other billfish species (Boyce, 2004; Boyce et al., 2008). Wider geographical ranges confer species' resilience to climate change, while species with narrow ranges are more exposed to climate impacts (Ofori et al., 2017).

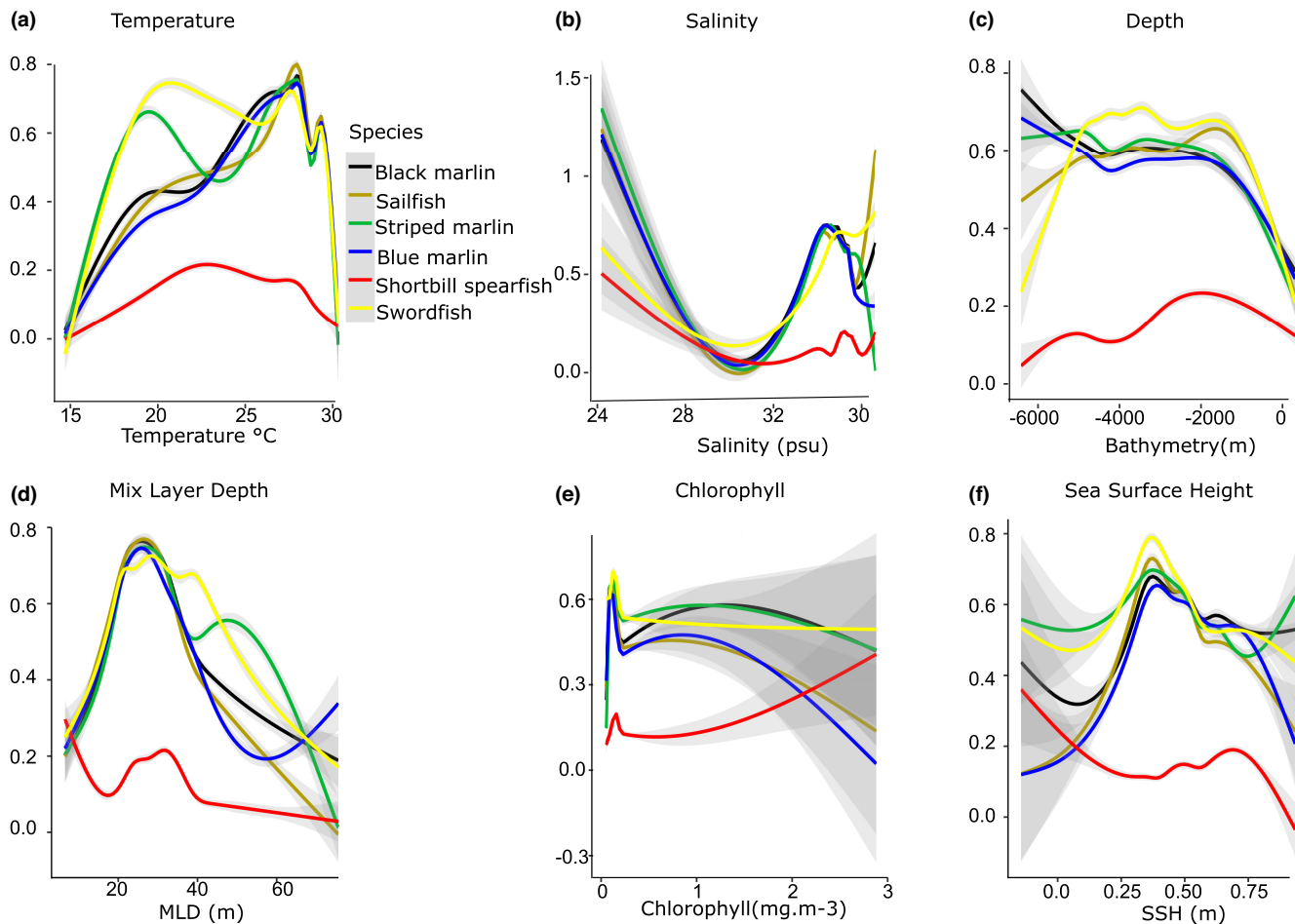


FIGURE 4 Response curves showing the effects of the predictor variables on billfish species' probability of occurrence. Environmental variables are plotted on the X-axis, and the Y-axis represent habitat suitability

4.3 | Potential unintended effects on billfish from the longline fishing effort

The high niche overlap of the six billfish species in the northern IO is also consistent with the catch and effort distribution of other pelagic species such as tuna, which are commonly caught together with billfish in various industrial fishing gears, especially longline and offshore gillnet fisheries (IOTC, 2020a; Lee et al., 2005; Mohri & Nishida, 1999). Longline fishing in the IO mainly targets high-value tunas and swordfish (IOTC, 2020b). Since billfish are highly susceptible to becoming bycatch in tuna and other fisheries, an increased effort targeting tuna can significantly impact billfish populations. Our findings demonstrate that overfished species (black marlin, blue marlin and striped marlins) highly overlap with zones of high fishing effort. The high overlap between the species' spatial distributions and fishing effort corresponds to recent stock assessments (Andrade, 2016; IOTC, 2020a; Yokoi & Nishida, 2016). The high spatial overlap between longline fishing effort and spatial distribution of black marlin, blue marlin and striped marlin might explain the overfished status of the three species.

4.4 | Management implications

Our research has key implications for the conservation and management of billfish species in the IO. First, identifying the billfish spatial distributions and niche overlap can inform billfish management as single species, multispecies or an ecosystem-based approach to management (Möllmann et al., 2014; Vinther et al., 2004). Currently, billfish in the IOTC's area of competence are managed chiefly as single stocks. Our findings on species' distinct niche preferences and niche overlap demonstrate that the IO provides important habitats for these species, underscoring the need for ecosystem-based management both within EEZs and high seas. Second, identifying heavily fished areas relative to the billfish spatial distribution highlights the necessity to identify important marine areas where area-based management approaches could be applied. Third, understanding the critical environmental variables which correlate with billfish distribution may be important in determining how climate change may impact species occurrence in the future.

In a multispecies fishery, it is important to understand the level of species interaction to determine the levels of control to put in place, such as total allowable catch (TAC), especially when vulnerable and threatened species exist together with key targeted species (Pascoe,

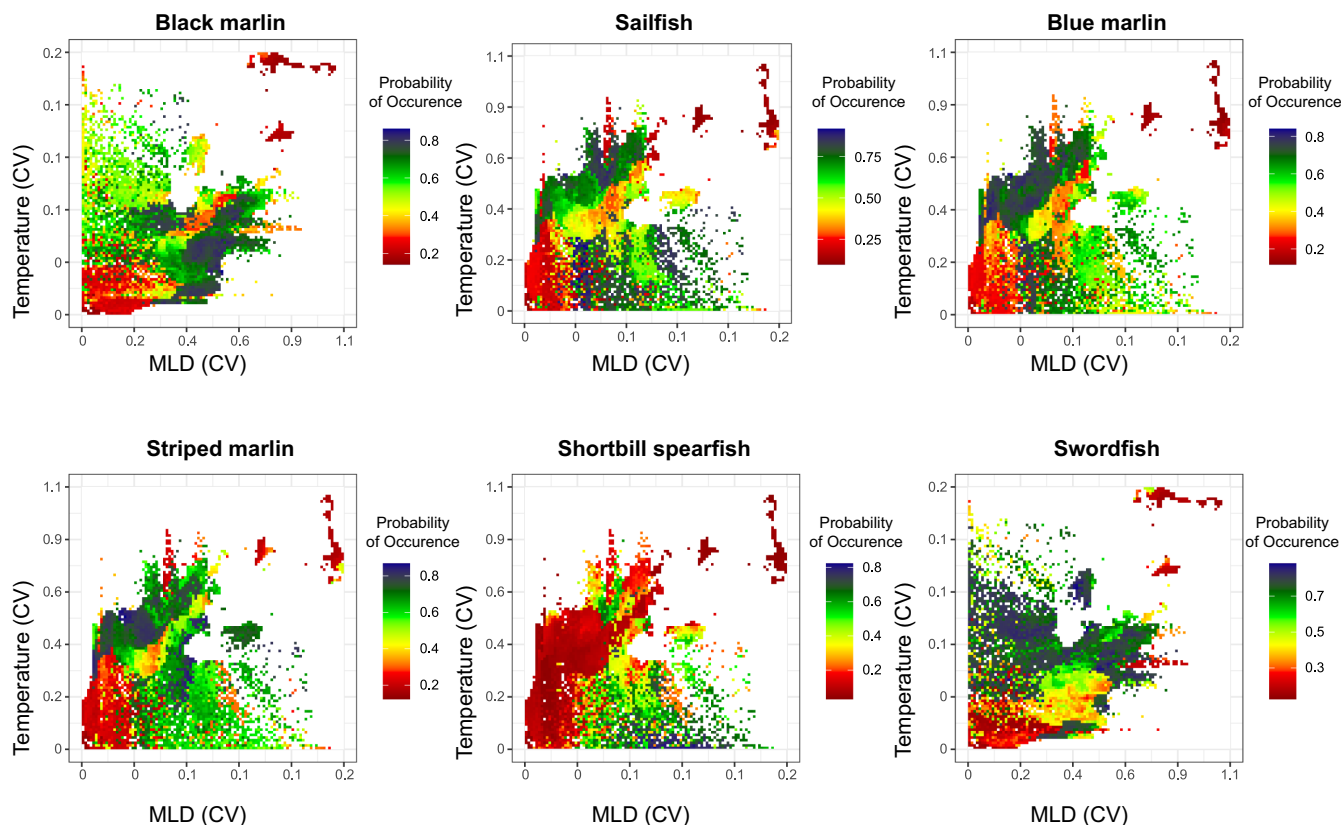


FIGURE 5 Habitat suitability for six billfish species visualised against axes of MLD and temperature coefficients of variation, used as measures of seasonality across the IO

2000). Given that three of the billfish species are considered overfished, specific strategies can be formulated accordingly to reduce the detrimental impact of fisheries. Our study demonstrates a significant niche overlap between the overfished species (black marlin, blue marlin and striped marlin) and those not classified as overfished species. Therefore, unregulated exploitation in these areas of overlap may further increase species' susceptibility to overexploitation, especially for co-caught species such as blue marlin and striped marlin. The interaction between billfish species and other commonly targeted fish species such as tuna and swordfish represents both a risk and reward for implementing management measures (Crespo et al., 2018; Fonteneau & Richard, 2003). The co-exploitation of these species raises management concerns and indicates that the protection of depleted stocks can only be achieved by reducing the overall catches of billfish and related target species in the IO. However, such an approach would be challenging due to the opportunity cost of other commercially viable species, such as swordfish and some tuna species, which are still being exploited at sustainable rates in the region (IOTC, 2020a; Pascoe, 2000; Pascoe et al., 2015). Even though this choke species scenario does not represent optimal management, the requirement for fisheries to be managed according to the principles of ecologically sustainable development and the precautionary principle should prevent the continual overexploitation of depleted stocks over the short-term economic gains (Baudron & Fernandes, 2015).

Currently, the stock status of shortbill spearfish in the IO is unknown. Our results indicate that the shortbill spearfish has the smallest

spatial distribution, which overlaps strongly with areas of high fishing effort, especially in the south-western IO. For the first time, we show that the predicted distribution of shortbill spearfish overlaps highly with fisheries and may require a targeted management response, including intensified data collection to address the substantial data gaps. Precautionary fisheries management approaches could be applied mainly in the EEZs of the Western IO, where its niche is centred (S. M. Garcia, 1994; González-Laxe, 2005; Karim et al., 2020). The high seas occupy approximately half of the study area and comprise the spatial distributions of most of the billfish species. Yet fishing effort has increased tremendously in the high seas (Swartz et al., 2010). The limitations associated with monitoring, control and surveillance of the EEZs and high seas in the IO predisposes the billfish species to overfishing (Agnew et al., 2009; Riskas et al., 2018). The need to provide additional management measures to safeguard species caught within the high seas has been of interest to the international community (Crespo et al., 2019; Marsac et al., 2020). Our paper further emphasizes this need by identifying that high billfish species richness overlaps with fishing pressure. These areas may provide focal points for fisheries management approaches within the high seas. Also identified are areas with high species diversity and low fishing effort, which could be a priority for establishing spatial conservation measures. Additionally, we point out specific nations that may be more significant for billfish management.

Climate-driven changes, such as changes in water temperatures, have been shown to have likely impacts on billfish species (Dell'Apa

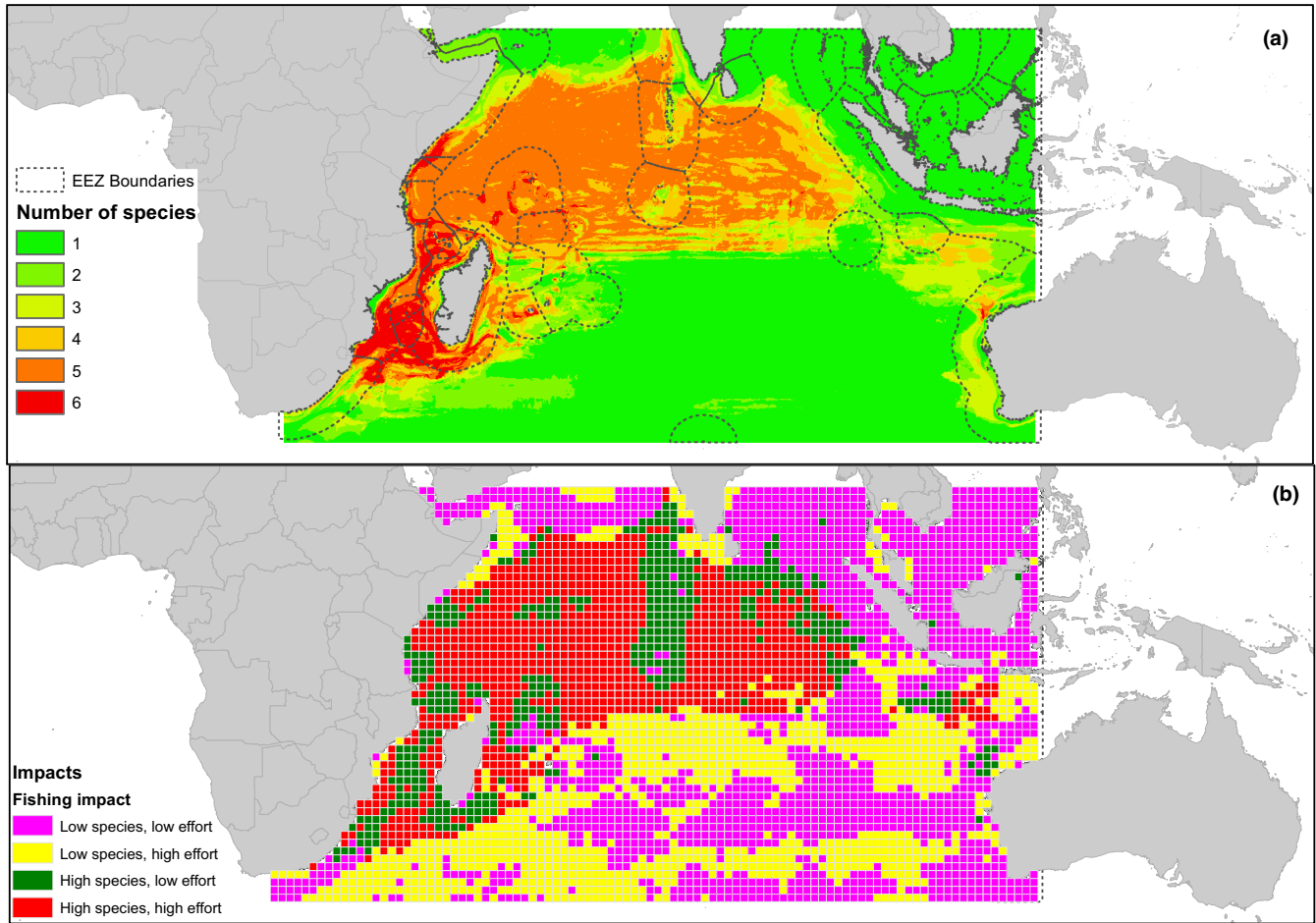


FIGURE 6 (a) Distribution map of the six billfish species showing the extent of overlapping distributions and the EEZ boundaries (b). Species richness across a gradient of fishing effort, Areas with a high (>50% quantile) number of species had a higher (>50% quantile) mean monthly fishing effort

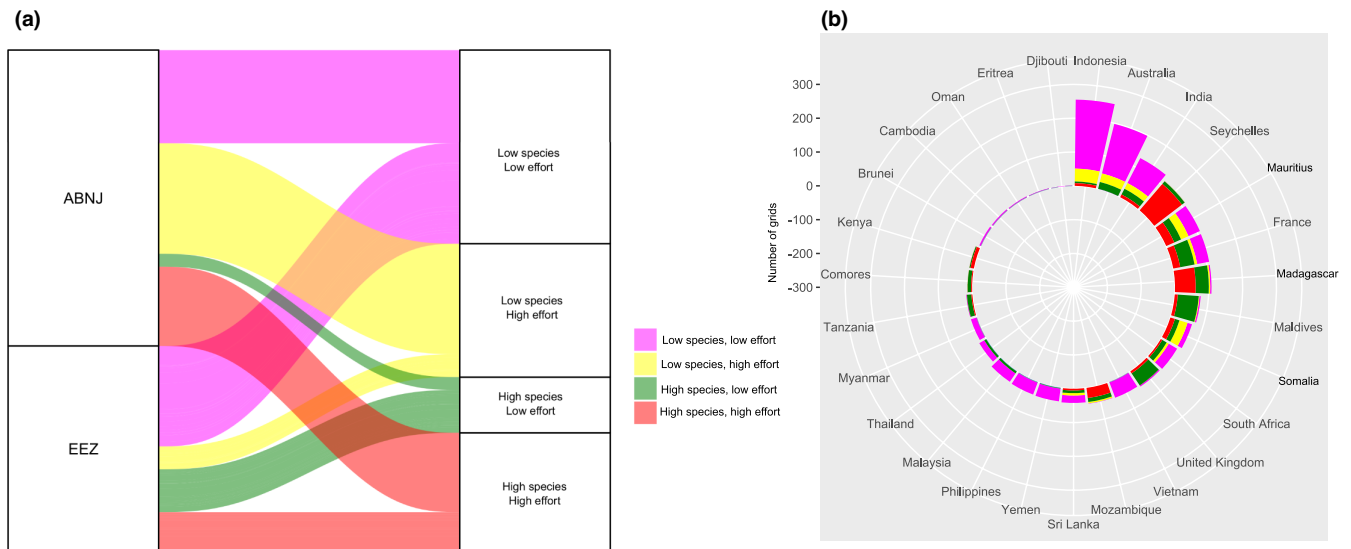


FIGURE 7 (a) Impacts of fishing effort on the Distribution of billfish species, areas are categorised according to the level of fishing effort (Low, high) and the number of species (Low, High) in the EEZ ABNJ. (b) Alluvial plot showing the proportion of EEZ and ABNJ occupied by the different billfish species classes and fishing effort interaction. The species and fishing effort interaction classes are similar to those presented in Figure 6b

et al., 2018). Our study indicates that temperature and MLD significantly influence the occurrence of billfish species in the IO. This shows that future climate change uncertainties continue to pose a threat to billfish fisheries and the coastal populations that rely on them for survival (Dell'Apa et al., 2018; Grose et al., 2020). Hence an adaptive management framework should be considered when developing billfish management actions in the region (Chang et al., 2019; Walters, 1986). Adaptive management considers uncertainties, such as potential changes in water temperature and capacities of species to adapt to these changes, which is a more practical approach to addressing climate-driven changes in fisheries (Daw et al., 2009; Ogier et al., 2016).

4.5 | Limitations

Models may be limited by the data used to generate them. This study was carried out in a data scarcity context and within the data availability limitations, particularly in areas where billfish data and longline fishing effort are under-reported or/and lacking. Our findings are based primarily on longline fishing effort, given the data scarcity. In particular, the determination of the spatial congruence between the identified spatial distributions and fishing effort should be interpreted with caution, given that catch data (albeit from other sources) were used in generating the spatial distribution maps. Moreover, data from offshore gillnet fisheries, conventional and satellite tagging from recreational fishers and artisanal landings in future studies may provide improved predictions of billfish partitioning in the other areas within the IO. Nevertheless, our findings provide a starting point to understanding the influence of various fisheries sectors and environmental factors on billfish distribution, emphasizing the urgent need for comprehensive data.

5 | CONCLUSION

Our findings depict niche partitioning and overlap of the six billfish species in the IO, greatly influenced by temperatures, MLD and salinity. Our analysis suggests that more effort is required to record billfish occurrences and fishing effort adequately. Our results highlight species' hotspots' that could provide a focus for billfish management, including ecosystem-based, adaptive, and precautionary approaches to managing these threatened species across maritime zones. These findings can inform countries' actions in the IO towards sustainable exploitation and management of billfish, which is necessary for securing socio-economic and cultural security for local communities dependent on fisheries (Kadagi et al., 2021; Okafor-Yarwood et al., 2020).

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CONFLICT OF INTEREST

We wish to confirm that there are no known conflicts of interest associated with this publication. In addition, all funding and support for the research detailed in this publication has been acknowledged.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the following repositories, www.obis.org, <https://iotc.org/data/datasets> and <http://marine.copernicus.eu/services-portfolio/access-to-products>

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BIOSKETCH

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