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Spatially explicit risk assessment of marine megafauna vulnerability to Indian Ocean tuna fisheries

Leslie Roberson[1,2] | Chris Wilcox[3] | Germain Boussarie[4] | Emma Dugan[5] | Cristina Garilao[6] | Kristofer Gonzalez[5] | Madeline Green[3,7,8] | Salit Kark[5] | Kristin Kaschner[9] | Carissa J. Klein[1,2] | Yannick Rousseau[7,10] | Dan Vallentyne[11] | James E. M. Watson[1] | Jeremy J. Kiszka[4]

[1]School of Earth and Environmental Sciences, University of Queensland, St Lucia, Queensland, Australia

[2]Centre for Conservation and Biodiversity Science, The University of Queensland, St Lucia, Queensland, Australia

[3]CSIRO Oceans & Atmosphere, Castray Esplanade, Battery Point, Hobart, TAS, Australia

[4]Institute of Environment, Department of Biological Sciences, Florida International University, North Miami, Florida, USA

[5]School of Biological Sciences, The University of Queensland, St Lucia, Australia

[6]GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany

[7]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Australia

[8]Centre for Marine Socioecology, University of Tasmania, Hobart, TAS, Australia

[9]Department of Biometry and Environmental System Analysis, University of Freiburg, Freiburg, Germany

[10]Future of Marine Ecosystems Lab, Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada

[11]Shark Stewards, Berkeley, California, USA

Correspondence
Leslie Roberson, School of Earth and Environmental Sciences, University of Queensland, St Lucia, 4072, Australia, Email: l.roberson@uq.edu.au

Abstract

By-catch is the most significant direct threat marine megafauna face at the global scale. However, the magnitude and spatial patterns of megafauna by-catch are still poorly understood, especially in regions with very limited monitoring and expanding fisheries. The Indian Ocean is a globally important region for megafauna biodiversity and for tuna fisheries, but has limited by-catch data. Anecdotal and scattered information indicates high by-catch could be a major threat. Here, we adapt a Productivity Susceptibility Analysis tool designed for data-poor contexts to present the first spatially explicit estimates of by-catch risk of sea turtles, elasmobranchs, and cetaceans in the three major tuna fishing gears (purse seines, longlines, and drift gill nets). Our assessment highlights a potential opportunity for multi-taxa conservation benefits by concentrating management efforts in particular coastal regions. Most coastal waters in the northern Indian Ocean, including countries that have had a minimal engagement with regional management bodies, stand out as high risk for fisheries interactions. In addition to species known to occur in tuna gears, we find high vulnerability to multiple gear types for many poorly known elasmobranchs that do not fall under any existing conservation and management measures. Our results indicate that current by-catch mitigation measures, which focus on safe-release practices, are unlikely to adequately reduce the substantial cumulative fishing impacts on vulnerable species. Preventative solutions that reduce interactions with non-target species (such as closed areas or seasons, or modifications to gear and fishing tactics) are crucial for alleviating risks to megafauna from fisheries.

KEYWORDS

by-catch, Indian Ocean, marine megafauna, Productivity Susceptibility Analysis, risk assessment, tuna fisheries

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Fishing, either targeted or incidental, is the primary threat directly driving population declines and extinction risk for many species of cetaceans, sea turtles, seabirds and elasmobranchs (Brownell et al., 2019; Costello et al., 2010; Lewison, Crowder, Read, & Freeman, 2004; Ripple et al., 2019). Tuna fisheries are some of the world's largest and most valuable fisheries, with an annual landed value of US$12.2 billion generated mostly by industrial purse seine and longline sectors (Rogers et al., 2016). By-catch—which in this context includes unmanaged by-product or non-target species, such as many elasmobranchs—remains one of the major management problems for tuna fisheries globally (Juan-Jordá, Murua, Arrizabalaga, Dulvy, & Restrepo, 2018). Given the magnitude, value and vast geographic footprint of tuna fisheries, addressing the substantial by-catch issue in these fleets is essential for their future viability.

Indian Ocean fisheries contribute 20% of the global commercial tuna catch (WWF, 2020). The region is unique among the world's tuna fisheries because of the large gill net sectors, especially the expansion of large pelagic gill nets ('drift nets') in addition to more traditional inshore nets (Temple et al., 2018). Gill nets are a broad category of relatively cheap and simple-to-operate gear that can be anchored or drifting and are increasingly common in the coastal and continental shelf waters in developing countries (Northridge, Coram, Kingston, & Crawford, 2017). Gill nets catch at least as much volume as the industrial purse seine and longline sectors in the Indian Ocean, which is atypical compared with the rest of the world (Aranda, 2017). Gill net vessels target a wide range of species in addition to the 16 tuna and tuna-like species that fall under the mandate of the Indian Ocean Tuna Commission (IOTC), including many elasmobranchs (Jabado et al., 2018). Countries are required to report information about some fishing gears to the IOTC but not about where gill net fisheries operate or how many vessels are involved (Roberson, Kiszka, & Watson, 2019).

Gill nets (and drift nets in particular) have emerged as a primary concern for marine biodiversity because they are associated with high mortality per unit of fishing effort for megafauna globally (Lewison et al., 2004; Read, Drinker, & Northridge, 2006; Reeves, McClellan, & Werner, 2013). For the Indian Ocean, estimates of annual catch in tuna gill net fisheries include 100,000 cetaceans (Anderson et al., 2020), 97,000 tonnes of elasmobranchs (Murua et al., 2013) and 29,500 sea turtles (Nel, Wanless, Angel, Mellet, & Harris, 2013). However, there are limited empirical data about gill net impacts on large marine vertebrates from this region (Anderson et al., 2020; Clarke et al., 2014; Garcia & Herrera, 2018; Lewison et al., 2014), and the many loopholes in the existing regulatory framework result in severely incomplete catch monitoring of these species (WWF, 2020).

Previous research shows that fishing—both incidental and targeted—is a primary direct threat to marine megafauna in the Indian Ocean, including sea turtles (Bourjea, Nel, Jiddawi, Koonjul, & Bianchi, 2008; Wallace et al., 2013; Williams et al., 2018), cetaceans (Böhm et al., 2013; Elwen, Findlay, Kiszka, & Weir, 2011; Kiszka et al., 2021) and elasmobranchs (Davidson & Dulvy, 2017; Dulvy et al., 2014; Jabado et al., 2018). Available data suggest that sea turtles are vulnerable to capture in all three tuna gears but have lower mortality in purse seines than in longlines and gill nets (Williams et al., 2018). Cetaceans are considered to be at the greatest risk from drift gill nets; particularly, small- and medium-sized Delphinidae such as spinner dolphins (*Stenella longirostris*), bottlenose dolphins (*Tursiops truncatus*) and common dolphins (*Delphinus delphis*), and a few larger delphinids—particularly Risso's dolphin (*Grampus griseus*), false killer whales (*Pseudorca crassidens*) and short-finned pilot whales (*Globicephala macrorhynchus*)—depredate longlines, but the interactions are less lethal than entanglement in other gears (Clarke et al., 2014; Garcia & Herrera, 2018; Huang & Liu, 2010; Kiszka et al., 2021; Murua et al., 2018; Wallace et al., 2010). Oceanic and pelagic elasmobranchs are the most frequently reported by-catch in all three tuna gears (by numbers of individuals). The most commonly reported species are silky sharks (*Carcharhinus falciformis*, Carcharhinidae) in all three gears; blue sharks (*Prionace glauca*, Carcharhinidae) and oceanic whitetip sharks (*Carcharhinus longimanus*, Carcharhinidae) in longlines and purse seines; shortfin makos (*Isurus oxyrinchus*, Lamnidae) and pelagic batoids (e.g. Myliobatidae, Mobulidae) in purse seines and drift nets; pelagic stingrays (*Pteroplatytrygon violacea*, Dasyatidae) in drift nets and longlines; hammerheads (*Sphyrna* spp, Sphyrnidae) and crocodile sharks (*Pseudocarcharias kamoharai*, Pseudocarchariidae) in longlines; and whale sharks (*Rhincodon typus*, Rhincodontidae) in drift nets (Briscoe, Maxwell, Kudela, Crowder, & Croll, 2016; Clavareau et al., 2020; Escalle et al., 2015; Fernando & Stewart, 2021; Garcia & Herrera, 2018; Moazzam, 2012; Murua et al., 2018).

Overall, purse seine fleets reportedly have the lowest by-catch rates per unit of fishing effort (especially for cetaceans), lower mortality for sea turtles and cetaceans, and fewer species that are caught in large numbers compared with drift nets and longlines (Clavareau et al., 2020). However, the magnitude of purse seine effort can still result in large volumes of by-catch (Forget et al., 2021). Furthermore, the available literature for the Indian Ocean notes the lack of quality data for megafauna by-catch relative to other regions (for all gear types), and there are many contradictory reports. For example, no shortfin makos were reported by purse seines fleets in the IOTC data (Garcia & Herrera, 2018), compared with substantial shortfin mako catch reported in a study of the Spanish purse seine fleet operating in the IOTC Area (Clavareau et al., 2020).

Limited by-catch data are an issue across all ocean regions, including in many wealthy countries, especially for unselective fishing gears that catch many species (e.g. small- or medium-mesh gill nets) and for species that are rarely encountered or difficult to identify (Clarke et al., 2014; Lewison et al., 2014). This problem is amplified in the Indian Ocean, where a comparative study of ecosystem-based management approaches—including by-catch management—rated the IOTC as the worst-performing Regional Fisheries Management Organization (RFMO) for tropical tuna (Juan-Jordá et al., 2018). The IOTC faces considerable challenges in managing 31 contracting Parties in addition to massive distant water fleets from Europe and Asia, and compared with the other four tuna RFMOs, it has the most recently developed fisheries, countries with the lowest average per capita GDP, high economic dependency on tuna fisheries, the smallest vessels and the most vessels (Pons, Melnychuk, & Hilborn, 2018; Sinan & Bailey, 2020). Of the many species reportedly caught in tuna fisheries and in large-scale fisheries more broadly, relatively few are actively monitored and managed by fisheries agencies (Costello et al., 2012; Ricard, Minto, Jensen, & Baum, 2012). Species often interact with multiple gears in one area or across their range, and these cumulative impacts are difficult to detect and monitor (Riskas, Fuentes, & Hamann, 2016). By-catch rates vary across regions due to different environmental conditions, species abundances and fishing effort dynamics, even for the same species and fishing gear, which means trends from one ocean or region may not be representative of another area (Clarke et al., 2014; Lewison et al., 2014). In general, multi-taxa or multi-gear studies of by-catch species are rare or lack a spatial component, and this gap is particularly glaring for the Indian Ocean (Lewison et al., 2014).

Evaluating the risk that fishing poses to marine biodiversity requires accurate information about both the threat and the impacted species. Data-limited approaches—such as Ecological Risk Assessment methods—have been used extensively to estimate risk in these data-poor contexts, often by incorporating expert knowledge with available quantitative or empirical data (Georgeson et al., 2020; Hobday et al., 2007; Zhou et al., 2013; Zhou, Hobday, Dichmont, & Smith, 2016). The Productivity Susceptibility Analysis (PSA) is a semi-quantitative risk assessment tool that compares life history characteristics and susceptibility to fisheries catch, and identifies potentially high-risk species that merit additional assessment (Hobday et al., 2011). It has been widely used to estimate potential impact from fisheries for data-poor species (Arrizabalaga et al., 2011; Moore et al., 2013; Murua et al., 2018). The PSA incorporates categorical scores (e.g. low, medium or high overlap with fishing), where information is missing or highly uncertain. However, there are two main drawbacks of this method relevant to the context of by-catch in Indian Ocean tuna fisheries. First, some resolution of the relative risk estimates is lost in the repeated binning and averaging, which makes it difficult to compare risk and prioritize species when considering multiple fishing sectors and many potentially impacted species. Second, the PSA is not spatially explicit—although it includes a parameter for geographic overlap—which limits the utility of the results in a case like the Indian Ocean, where risk is not evenly distributed over the large management area.

The primary objectives of this study were to estimate the magnitude and location of tuna fishing effort in the Indian Ocean, including drift gill nets, and to quantify the risk to megafauna species from the three major tuna fishing gears. We adapt a semi-quantitative Ecological Risk Assessment method (described in Hobday et al., 2007; Hobday et al., 2011) to present the first spatially explicit estimated risk to species across multiple gears and taxa in the Indian Ocean. These results can serve as a baseline to guide regional management organizations such as the IOTC, national governing bodies and conservation organizations to better prioritize how and where to invest limited resources in reducing fishing impacts on threatened species.

2 | MATERIALS AND METHODS

2.1 | Species distributions

We used species distribution maps from AquaMaps (Kaschner et al., 2016), which models species-specific envelopes of environmental preference based on occurrence records from published databases and includes variables such as temperature, depth and salinity (Ready et al., 2010). The model estimates a probability of occurrence for each species in each 0.5° grid cell. Although species distribution models can generate inaccurate predictions, we opted to use model-derived maps from AquaMaps instead of expert-drawn range maps from the IUCN because the probability of occurrence can be used as a rough proxy for species' density, whereas the IUCN maps are presence–absence maps (Selig et al., 2014; Weber, Stevens, Diniz-Filho, & Grelle, 2017). In general, there is a good alignment between AquaMaps and IUCN maps, although the AquaMaps model sometimes produces discontinuities at the edges of species' predicted ranges (O'Hara, Afflerbach, Scarborough, Kaschner, & Halpern, 2017).

We first selected all probabilities of occurrence for 405 species (348 elasmobranchs, 51 cetaceans and six sea turtle species) that the AquaMaps models predict to occur in the upper 400-m depth column within IOTC Area of Competence (hereafter 'IOTC Area'), which covers the Indian Ocean (including the Persian Gulf and the Red Sea) to 45° and 55° South in the western and eastern Indian

Ocean, respectively. There have been many recent changes in taxonomic classifications of elasmobranchs—and cetaceans to a lesser extent—meaning some names have changed or species have been redefined (IUCN, 2021). We maintained the species names and classifications used in the AquaMaps database. Experts have reviewed 168 of the 405 (41%) maps used in our analysis.

2.2 | Fishing effort

Reporting of catch and effort is not consistent across the tuna sectors in the Indian Ocean. Countries with fleets targeting tuna are required to report their catch to the IOTC at a maximum spatial aggregation of 1°×1° grid cells for purse seines and 5°×5° cells for longlines (IOTC, 2020). There are fewer requirements for gill nets because they are classified as artisanal gears; where gill net catch or effort is reported, the data may refer to irregular areas (e.g. per port of unloading) (IOTC, 2020). For a standard index of fishing effort across the three gear types, we used a global and spatially explicit model of fishing effort that reports effort in terms of engine power and fishing days (kW days per year) (Rousseau, 2020; Rousseau, Watson, Blanchard, & Fulton, 2019). The standardized unit of fishing effort incorporates the size, length overall, engine power and fishing days of the vessels, but not the amount of gear in the water. From a by-catch per unit effort perspective, a 3-km longline with 3000 baited hooks might represent different fishing intensity than a 3-km gill net, even if they are deployed for the same number of hours. However, there is very little information available on gear dynamics or catch rates in the Indian Ocean, so we use this standardized unit of fishing effort as the best available proxy for fishing intensity, allowing comparison of the three main tuna gears across the management area.

The model uses data from FAO and country-specific reports to divide each country's vessels into classes and associate effort with a corresponding catch (Rousseau, 2020; Rousseau et al., 2019). The effort was mapped in 0.5-degree cells using a ratio to the total catch and including assumptions about major ports and the distance that different types of vessels can travel from the coast. Incompatibilities between effort and catch were resolved by comparing broader families of gears (e.g. lines instead of longlines, bottom nets instead of bottom trawls). For countries where there was no information on the link between tonnage, length and engine power, missing data were filled with information from neighbouring countries, which improves upon earlier approaches where missing data were replaced with global averages derived from the larger industrial fleets (Rousseau et al., 2019).

In the Indian Ocean, there is considerable variability in the characteristics and configuration of gill nets and what species are targeted, compared with longline and purse seine sectors. Country reports rarely include specific information about their gill net fleets, such as the number of vessels that use gill nets, mesh sizes, and whether they are bottom-set or drifting. Most of the fleets using drift nets to target tuna and tuna-like species have a stretched mesh size of 13–17 cm (Kiszka et al., 2021). However, these nets can be used to target a variety of other species in addition to tunas, including demersal sharks and rays, Spanish mackerels (Scombridae), catfish (*Arius* spp., Ariidae) and seabreams (Sparidae), and can be used interchangeably as a bottom-set gill nets and drift nets depending on the season and target species (Khan, 2017; Shahid, Khan, Nawaz, Abdul Razzaq, & Ayub, 2016). Vessels also frequently use multiple gears in combination, such as drift gill nets with snoods attached along the lead line or nets hung between pelagic longlines, which further complicates estimates of fishing effort (Henderson, McIlwain, Al-Oufi, & Al-Sheili, 2007; Jabado & Spaet, 2017; Winter, Rudianto, Laglbauer, Ender, & Simpfendorfer, 2020; Yulianto et al., 2018). We attempted to capture the boats more likely using drift gill nets by selecting only powered vessels for the gear types longlines, purse seines and gill nets, and two target catch categories (pelagics 30–90 cm length and pelagics larger than 90 cm).

We corrected for extreme spatial skewness by adjusting outlier cells to the 95th percentile value for the respective gear. We then scaled the fishing effort 0–1 across all gears. The resulting value represents a relative likelihood or intensity of fishing effort, measured on the same scale for all three gears, in each grid cell. The resulting effort remains heavily skewed, but we assume the skewness derives from real patterns in fishing effort. For example, smaller gill net vessels are clustered near certain ports and population centres, and in some areas are known to concentrate near fish aggregating devices.

2.3 | Productivity susceptibility analysis

We adapted a PSA to compare risks to species across the three tuna fishing gears (Figure 1). This tool estimates a threat's potential impact on a species or population, incorporating expert judgement where empirical data are not available (Hobday et al., 2011). The PSA quantifies a species' relative vulnerability to a fishing threat by incorporating information about the species' productivity (factors that influence the intrinsic rate of increase, such as reproductive rate and longevity), as well as its susceptibility to fisheries mortality (factors influencing in the intensity of damage from fishing gear) (Hobday et al., 2007).

We selected five life history traits to estimate each species' productivity: number of offspring per year, lifespan, age at sexual maturity, reproductive strategy, and maximum size, based on recommendations from Hobday et al., 2011 and other PSAs of elasmobranchs, cetaceans, or sea turtles (Breen, Brown, Reid, & Rogan, 2017; Clarke, Espinoza, Romero-Chavez, & Wehrtmann, 2017; Georgeson et al., 2020; Williams et al., 2018). There are three categories for each trait, corresponding to scores of 1, 2 or 3 for high, medium and productivity (Table 1). We used the same trait categories for all taxa, except for maximum size, which was scaled differently for cetaceans, elasmobranchs and sea turtles. Following the precautionary principle, we assigned the more conservative category where there was uncertainty between categories. For instance, life history traits of many species vary

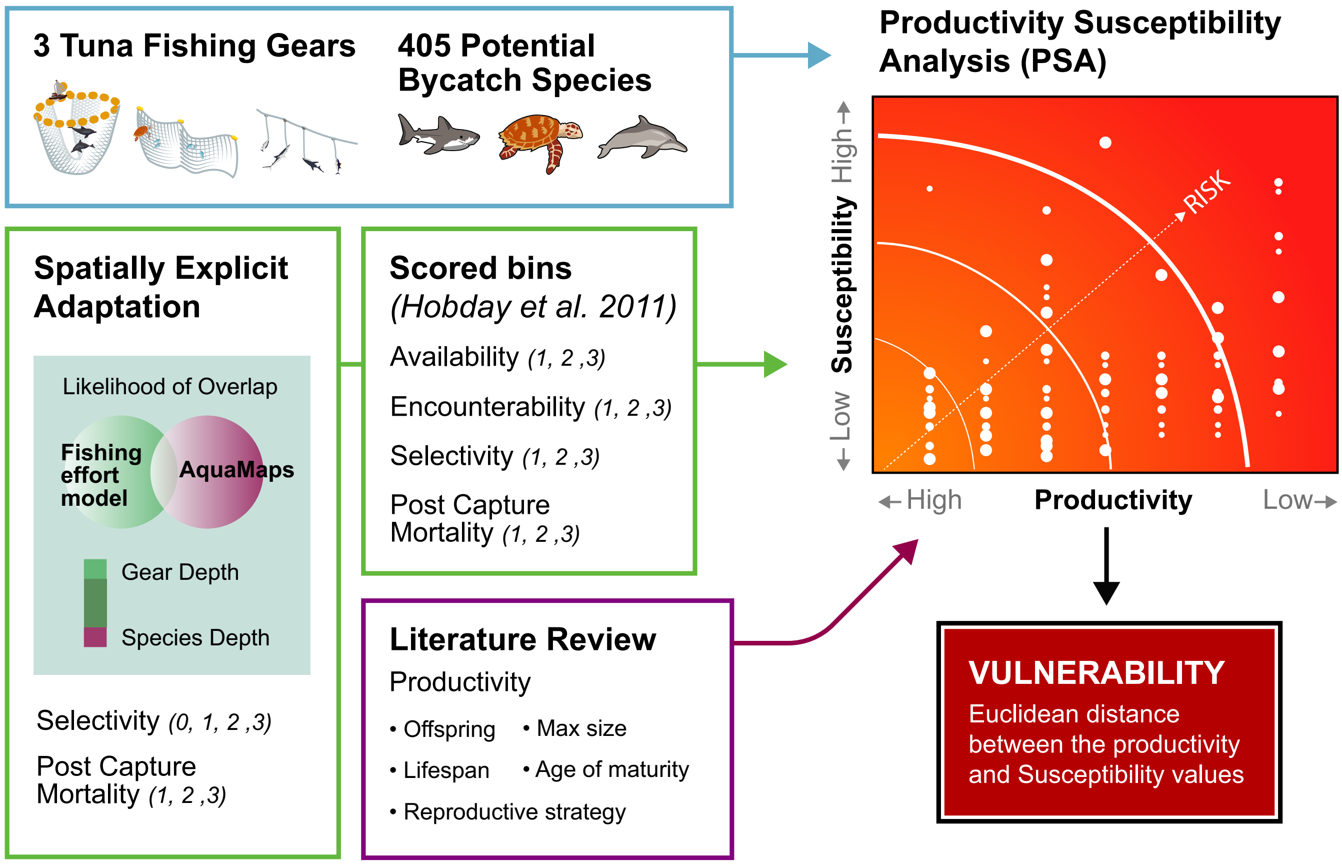

FIGURE 1 Schematic diagram of the methods used in this analysis, with the PSA approach outlined in Hobday et al. (2011) and the spatial adaptation where the availability and encounterability parameters are expressed as a likelihood of horizontal and vertical overlap

TABLE 1 Cut-off scores for species attributes related to its productivity and growth rate, adapted from Hobday et al. (2011) and other PSAs of cetaceans, elasmobranchs or sea turtles

Attribute	High productivity (low risk, score = 1)	Medium productivity (medium risk, score = 2)	Low productivity (high risk, score = 3)
Average offspring per year	More than 5	1 to 5	Less than 1
Average age at maturity	Less than 5	5 to 10	More than 10
Average maximum age	Less than 10	10 to 25	More than 25
Reproductive strategy	Egg layer	Live birth unattended	Live birth and care
Average max. size (cetaceans)	Up to 300	300 to 900	More than 900
Average max. size (elasmobranchs)	Up to 100	100 to 200	More than 200
Average max. size (sea turtles)	Up to 50	50 to 100	More than 100
Data quality score	**Good**	**Decent**	**Poor**
	Empirical data available for most life history traits	Some empirical data available; other traits assumed from closely related species (e.g. genus)	No empirical data available for the species or any closely related species (e.g. genus)

considerably between sexes, often with females maturing more slowly than males; in this case, we used the females' attributes. Basic biological information is missing entirely for many species, particularly benthic and deep-sea elasmobranchs. We filled missing information with data from related species and scored the quality of each species' life history data as 'poor', 'decent' or 'good' as a rough indicator of the uncertainty in the estimate of the productivity parameter (Tables 1, S1).

The productivity score is the mean of the five parameters:

$$\text{Productivity} = \sqrt[5]{\text{Offspring} \times \text{Lifespan} \times \text{Age mature} \times \text{Reproductive strategy} \times \text{Max size}}$$

Most PSAs use different calculations for the productivity and susceptibility attributes, with the arithmetic mean for productivity and the geometric mean for susceptibility (Cotter & Lart, 2011). Since the geometric mean is always smaller than the arithmetic mean, susceptibility is down-weighted compared with productivity. The inherent assumption is that life history traits are more important to a species' vulnerability to fishing than its susceptibility to capture, which has no basis in empirical data. Here, we use the geometric mean for both attributes.

Next, we used four parameters to quantify a species' susceptibility to fishing gear, where its susceptibility is a combination of the likelihood of capture and the potential lethality of the incident—or, 'how bad is it?' (Hobday et al., 2011). *Availability* is the horizontal overlap of the species and the fishing gear, *encounterability* is the vertical overlap of the animal and the gear in the water column, *selectivity* is the specificity of the gear to entangle that animal, and *post-capture mortality* represents the severity of the outcome if the animal is entangled (Tables 2, S2).

To calculate availability, we converted the fishing effort and species' distribution maps to raster files, then multiplied the probability of occurrence for each species and the scaled fishing effort value in each grid cell. The resulting values are proxies for density of animals and fishing gear (assuming more fishing gear in high effort cells and more animals present in a cell with a high probability of occurrence). In this per capita framing of risk, the availability represents the likelihood that an individual animal and fishing gear are both present in that cell.

$$\text{Availability}_{\text{cell}} = \text{Probabaility of occurrence} \times \text{Fishing intensity}$$

We calculated the availability of each species in each grid cell and then summed those values across all cells in the IOTC Area, for a relative measure of horizontal overlap with fishing.

$$\text{Availability}_{\text{cumulative}} = \sum_{i}^{n} A$$

This calculation of availability does not account for temporal variability (e.g. diurnal vertical migrations, time of day of fishing operations), seasonal variability (e.g. annual migrations, shifting fishing effort around the monsoon season), or ontogenetic shifts of species (e.g. sea turtles and many elasmobranchs have juvenile phases with distinct life histories). These assumptions lead to overestimations of risk where the actual overlap between fishing and animals is lower than predicted, and underestimations of risk where the overlap is greater than predicted because seasonal or diurnal densities coincide.

To estimate encounterability (vertical overlap), we conservatively assumed all gears are deployed from the surface to 20 m for drift gill nets (Aranda, 2017), 280 m for purse seines (Romanov, 2002) and 400 m for longlines (Song et al., 2009). For species' depth ranges, we used depth ranges from the AquaMaps model but adjusted

TABLE 2 Cut-off scores for species attributes related to its susceptibility to fishing, adapted from Hobday et al., 2011 and other PSAs of cetaceans, elasmobranchs or sea turtles

Attribute	Low susceptibility (Low risk, score = 1)	High susceptibility (Medium risk, score = 2)	High susceptibility (High risk, score = 3)
Availability: horizontal overlap of species and fishery (scored bins)	Low horizontal overlap with fishing effort (<33% of species' range in the IOTC Area)	Moderate horizontal overlap with fishing effort (34–66% of species' range in the IOTC Area)	High horizontal overlap with fishing effort (>66% of species' range in the IOTC Area)
[a]Availability: likelihood of horizontal overlap with gear (continuous)	Probability that species occurs in grid cell (proxy for density of species) x Fishing effort in grid cell (kW/fishing days per year), summed over all overlapping cells		
Encounterability: vertical overlap of species and fishing gear	Low vertical overlap with fishing gear (<25% of species depth range)	Moderate vertical overlap with fishing gear (25–50% of species depth range)	High vertical overlap with fishing gear (>50% of species depth range)
[a]Encounterability: likelihood of vertical overlap with gear	Proportion of species' depth range that overlaps with a depth range of fishing gear (continuous value, not location-specific)		
Gear selectivity	Species is not physically similar to targeted species (e.g. much larger or much smaller, different foraging ecology, habitat use or attraction to bait), or there is evidence species can escape the gear	Species has some similarities to targeted species, but there is evidence that it sometimes escapes	Species is a by-product, has similar physical and life history traits to targeted species, or has traits that attract it to the fishing gear
Post-capture mortality	Evidence of post-capture release and survival	Likely to be released alive	Often retained or has value as a by-product species, or majority dead when released

[a]For the spatial adaptation, the continuous values were scaled 1-3 to calculate an overall vulnerability score for each species.

depths for most species based on available empirical information (Supplementary Info S1). We then calculated the proportion of each species' depth range that overlaps with each gear type, assuming that both species and fishing gears are evenly distributed throughout the overlapping range and that the overlap is uniform across all cells. This assumption leads to underestimates of encounterability for species and gears that more often concentrate in the same shallow portion of their depth ranges, and overestimates for species that spend more time at depths beyond the range where most of the fishing effort is concentrated (e.g. many demersal-associated elasmobranchs are less likely to encounter tuna gears than the depth overlaps suggest).

$$\text{Encounterability}_{(\text{species,gear})} = \frac{\text{Overlapping depth range}}{\text{Species depth range}}$$

Less empirical information is available for the third parameter (gear selectivity) because relatively few studies have quantified the likelihood of entanglement in fishing gears independent of species abundance and fishing effort. We compiled a database of the 405 species and used information from the peer-reviewed and grey literature to group species according to life history traits that lead to a similar propensity for entanglement in fishing gear. We considered a variety of factors including body size and shape, swimming style, adult habitat use and occupancy in the water column, foraging ecology, and attraction to bait or fish aggregating devices (FADs) (Table 3). We conservatively assumed that all purse seines are fishing around FADs, which has become the dominant (although not universal) practice in Indian Ocean tuna fisheries (Davies, Mees, & Milner-Gulland, 2014). Purse seine sets on FADs have by-catch levels approximately three times those on free-swimming sets, in addition to capturing more species (Davies et al., 2014; Lezama-Ochoa et al., 2015).

Once entangled, the severity of the outcome (post-capture mortality) depends on the animal's ability to escape the gear, or to survive if released by the crew. There is very little information available about post-release survival in general, or about compliance with safe-release practices in the Indian Ocean (Zollett & Swimmer, 2019). We adapted the categories in Hobday et al., 2011 (Table 2) and made several assumptions about fishing practices in the region. We assumed that all longline fleets use monofilament leaders, which are easier for larger species to break compared with wire leaders (Gilman, 2011). However, vessels that are targeting (or subtargeting) sharks will likely use wire leaders and there is no comprehensive information about targeting dynamics across the wide variety of longline fleets operating in the region (Ardill, Itano, & Gillett, 2013). Pelagic longlines allow hooked animals to move but are usually set at depth and can also have long set times (usually more than 12 h and sometimes more than 24 h) (Chen, Song, Li, Xu, & Li, 2012; Clarke et al., 2014), and survival rates are highly variable for individuals that are successfully released (Carruthers, Schneider, & Neilson, 2009). Releasing entangled animals entangled in gill nets is usually ineffective because they are static and typically deployed overnight, so air-breathing species or elasmobranchs that need to swim to breathe are likely to die (Zollett & Swimmer, 2019). Compared with longlines and gill nets, survival rates of species released from tuna purse seines are expected to be higher for sea turtles and cetaceans, although post-capture mortality is difficult to study (Escalle et al., 2015; Hamilton & Baker, 2019; Zollett & Swimmer, 2019). Available data suggest much lower post-release survival rates for pelagic elasmobranchs caught in purse seines (Eddy, Brill, & Bernal, 2016).

The overall susceptibility score is the geometric mean of the attributes:

$$\text{Susceptibility} = \sqrt[4]{\text{Availability} \times \text{Encounterability} \times \text{Selectivity} \times \text{Post Capture Mortality}}$$

Many studies have adjusted this formula to suit different contexts, such as incorporating additional attributes, weighting attributes deemed to be more important, or using an additive (arithmetic) mean instead of a geometric mean (Brown, Reid, & Rogan, 2015; Grewelle, Mansfield, Micheli, & De Leo, 2021; Micheli et al., 2014). We made two key adjustments to the calculation of susceptibility outlined in Hobday et al., 2011. First, we allowed attributes to score zero, for instance, if a species' depth range does not overlap with fishing gear or the gear does not select for that species because of its habitat or how it uses the water column (e.g. deep-sea benthic skates in drift gill nets). Second, we added a cell-specific susceptibility score to make a spatially explicit estimate of species' susceptibility to capture in fishing gear. We first expressed availability and encounterability as probabilities of encountering gear (values between zero and one) in each grid cell. We weighted this probability by the severity of the outcome (the mean of selectivity and post-capture mortality scores), resulting in a relative susceptibility score for each species in each grid cell. We summed these scores across all species for each gear to create a map of relative susceptibility across the IOTC Area. Then, to calculate an overall vulnerability score for each species and gear type, we scaled the species' cumulative availability (sum of availability in each grid cell) and its encounterability score from 1 to 3. This gives all four attributes equal weight in the calculation of susceptibility.

The overall vulnerability score for each species is the Euclidean distance between the productivity and susceptibility axes:

$$\sqrt{\text{Productivity}^2 + \text{Susceptibility}^2}$$

We used these scores to assess the relative vulnerability of each species and gear type. We then compared the vulnerability scores with the approach described in Hobday et al., 2011, where all attributes are scored 1–3 and there are fixed-width bins for availability and encounterability. We used conservation assessments from version 2021–3 of the Red List as an additional indicator of potential priority species for management (IUCN, 2021; Pacoureau et al., 2021). We also searched published and unpublished literature to see which species appear in available by-catch reports, recognizing that information on non-target catch in the Indian Ocean is scarce and reporting is not standardized, so frequency of by-catch records does not necessarily correlate with frequency of catch. For instance, easily

TABLE 3 Fifteen species groups for ranking gear selectivity and post-capture mortality, based off habitat use, physical characteristics and known interactions with fisheries

Taxonomic group	Subgroup name	Description
Cetaceans	Baleen whales	Coastal and oceanic baleen whales
Cetaceans	Inshore dolphins and porpoises	Nearshore species primarily in shallow (<50 m) depths
Cetaceans	Large oceanic dolphins	Large oceanic dolphins (beyond continental shelf)
Cetaceans	Oceanic toothed whales	Beaked and toothed deep-diving whales (including all sperm whales) with oceanic distribution
Cetaceans	Small oceanic and coastal dolphins	Small- or medium-sized dolphins found in oceanic or coastal areas primarily >50-m depth
Elasmobranchs	Benthic elasmobranchs	Primarily feeds on benthic species and remains near the seafloor (at any depth), usually sedentary lifestyles and ambush hunting strategies
Elasmobranchs	Deep-sea elasmobranchs	Benthic or demersal species anywhere along the continental shelf and upper slope > 200 m depth, or deep-sea pelagic species >400-m depth (species primarily outside the depth range of tuna gears)
Elasmobranchs	Deep-shelf pelagic elasmobranchs	Pelagic species anywhere along the continental shelf and upper slope > 200-m depth
Elasmobranchs	Demersal generalist elasmobranchs	Primarily feeds or lives near the bottom, occupies range of depths and range of habitats
Elasmobranchs	Filter feeder elasmobranchs	Filter feeders that primarily feed or live in the pelagic zone, occupy a range of depths and range of habitats
Elasmobranchs	Inshore elasmobranchs	Shallow (<100 m depth), common in coastal and estuarine areas (continent & island) including shallow reefs and muddy or sandy bottoms
Elasmobranchs	Oceanic elasmobranchs	Pelagic species found in open ocean (beyond continental shelf)

identifiable by-catch such as whale sharks could be rare occurrences but are possibly more likely to be recorded than less impressionable animals.

3 | RESULTS

3.1 | Tuna fishing effort

We selected motorized fishing effort associated with catch of large pelagic fishes from 2015 to 2017 in the IOTC Area and found vessels flagged to 77, 74 and 79 countries for gill nets, purse seines and longlines, respectively. Pakistan and India had by far the greatest average gill net effort, whereas differences in effort among the top countries for the other two gears were less dramatic, with India and Tanzania ranked highest for purse seines and Taiwan and Sri Lanka ranked highest for longlines (Table 4). Tuna fishing effort is highest in coastal areas of the Indian Ocean, particularly for drift gill nets (Figure 2). Drift gill net effort is extremely high along almost the entire northern Indian Ocean coastline, including the Red Sea, Persian Gulf and Gulf of Oman, around Sri Lanka, and the Bay of Bengal, along the western coast of Indonesia, and in the Seychelles. Most of these regions also have high purse seine and longline effort.

Although the fishing effort model incorporates multiple data sources, including AIS and other vessel tracking information, it is a global model and some discontinuities arrive at finer geographic scales (Rousseau, 2020). For example, drift gill nets are deployed predominantly within countries' EEZs; the appearance of low gill net effort across the entire IOTC region in Figure 2 is due to the assumptions used in the model of fishing effort to connect landed catch with a gear type (Rousseau, 2020). This is particularly complicated in the Indian Ocean because vessels often deploy multiple gear types, and there are hot spots of transhipment activity that involve a wide range of poorly monitored vessels (Miller, Roan, Hochberg, Amos, & Kroodsma, 2018; WWF, 2020). Additionally, catch data from the Indian Ocean indicate there are substantial purse seine and longline efforts off the coast of Somalia, with drift gillnetters also operating in this area although the artisanal effort is unreported and essentially unregulated (Heile, 2017; Kaplan et al., 2014). The standardized units of effort used in this analysis are not directly comparable to available purse seine and longline catch data, but in general, these data indicate that there is more longline effort spread across most of the IOTC Area and more purse seine effort spread across the Western Indian Ocean than the model of fishing effort used here suggests (Kaplan et al., 2014). Certain areas that appear devoid of tuna fishing are due to errors in the model caused by disparities between the location of fishing and the port where catch was landed. There is a large tuna fishery operating in the Maldivian EEZ, but it is almost exclusively pole and line and was therefore not included in this analysis (Ardill et al., 2013).

TABLE 4 Top 20 Flag States for fishing effort in the Indian Ocean Tuna Commission Area of Competence for the three main tuna fishing gears

	All gears		Drift gill nets		Purse seines		Longlines	
Rank	Flag state	Effort	Flag state	Effort	Flag state	Effort	Flag state	Effort
1	Pakistan	96,179	Pakistan	94,794	India	8249	Taiwan	17,388
2	India	91,315	India	83,067	Tanzania	8152	Sri Lanka	11,656
3	Sri Lanka	32,797	Thailand	28,580	Sri Lanka	5104	Madagascar	6758
4	Thailand	30,771	Sri Lanka	16,038	Malaysia	4354	Seychelles	5056
5	Indonesia	17,606	Bangladesh	13,511	Japan	4291	South Korea	5010
6	Taiwan	17,388	Indonesia	8652	Seychelles	4069	Indonesia	4927
7	Bangladesh	15,036	Malaysia	8495	Indonesia	4027	Oman	4731
8	South Korea	13,685	South Korea	7922	Thailand	2160	Tanzania	3572
9	Malaysia	12,849	Yemen	5184	Spain	1235	Australia	2500
10	Tanzania	11,733	Iran	3218	South Korea	753	Yemen	2171
11	Seychelles	9142	UAE	1710	Australia	548	Bangladesh	1525
12	Yemen	7509	Saudi Arabia	1643	France	307	Pakistan	1384
13	Madagascar	6758	Australia	744	Italy	227	Spain	531
14	Oman	4731	France	564	South Africa	214	Egypt	436
15	Japan	4354	Spain	516	China	195	Saudi Arabia	366
16	Australia	3792	Kuwait	513	Egypt	167	France	208
17	Iran	3256	Qatar	317	Mozambique	157	South Africa	205
18	Spain	2282	China	308	Yemen	154	Italy	169
19	Saudi Arabia	2130	South Africa	303	Saudi Arabia	120	Grenada	163
20	UAE	1795	Reunion	211	UAE	86	Angola	120

Only effort associated with catch of large pelagics (tuna and tuna-like species >30 cm) by powered vessels is included, and is shown in thousands of kW/fishing days per year (averaged over 2015–2017).
UAE, United Arab Emirates.

3.2 | Species vulnerability

We analysed 405 species distribution maps from the AquaMaps database and found 319 cetaceans, elasmobranchs or sea turtles that potentially interact with tuna fisheries in the Indian Ocean. There are 208 species susceptible to catch in gill nets, 240 in purse seines and 282 in longlines. We adapted a PSA method to incorporate spatial information on species ranges and fishing effort in each grid cell in the IOTC management area and found that cumulative susceptibility overlaps closely with predicted fishing effort and is concentrated in coastal regions, particularly in the northern Indian Ocean and around certain island territories (Figure 2). Most species with high susceptibility scores also ranked high for their overall vulnerability (Figure 3). The species with the highest vulnerability scores were great white sharks (*Carcharodon carcharias*, Carcharhinidae) in all three gears, oceanic manta rays (*Mobula birostris*, Mobulidae) in gill nets, great hammerheads (*Sphyrna mokarran*, Sphyrnidae) in longlines, and sei whales (*Balaenoptera borealis*, Balaenopteridae) in purse seines (Table 5). Most of the highest vulnerability scores for longlines and purse seines are elasmobranchs, whereas for gill nets, more cetaceans (primarily inshore dolphins and porpoises) have a relatively higher risk. In general, high vulnerability scores were driven more by high susceptibility to fishing for elasmobranchs and by low productivity scores for cetaceans, especially for longlines and purse seines (Figure 3). The high vulnerability species either had large ranges with consistent overlap with fishing gear, or small ranges with high susceptibility values in each cell.

Many species groups have high vulnerability to all three gears, such as sea turtles and filter feeder, oceanic, pelagic generalist, and shallow shelf elasmobranchs (Figure 4, Table S3). Not surprisingly, there was a wider range of vulnerability scores for the more taxonomically diverse elasmobranch groups compared with sea turtles or cetaceans. Several species groups were scored zero for selectivity in certain gears, meaning they are considered not at risk from that fishery even if they overlap.

The PSA approach is designed to be conservative and tends to overestimate risk in many cases. For example, most cetaceans (especially baleen whales) have high scores because they have low productivity and their horizontal and vertical ranges overlap closely with fishing gear, although available data indicate entanglements are rare (Escalle et al., 2019). Benthic and inshore elasmobranchs (e.g. guitarfish, Rhinobatidae; angelsharks, Squatinidae; and *Urolophus* spp., Urolophidae) are probably less susceptible to catch than estimated by the PSA because they are unlikely to interact with surface

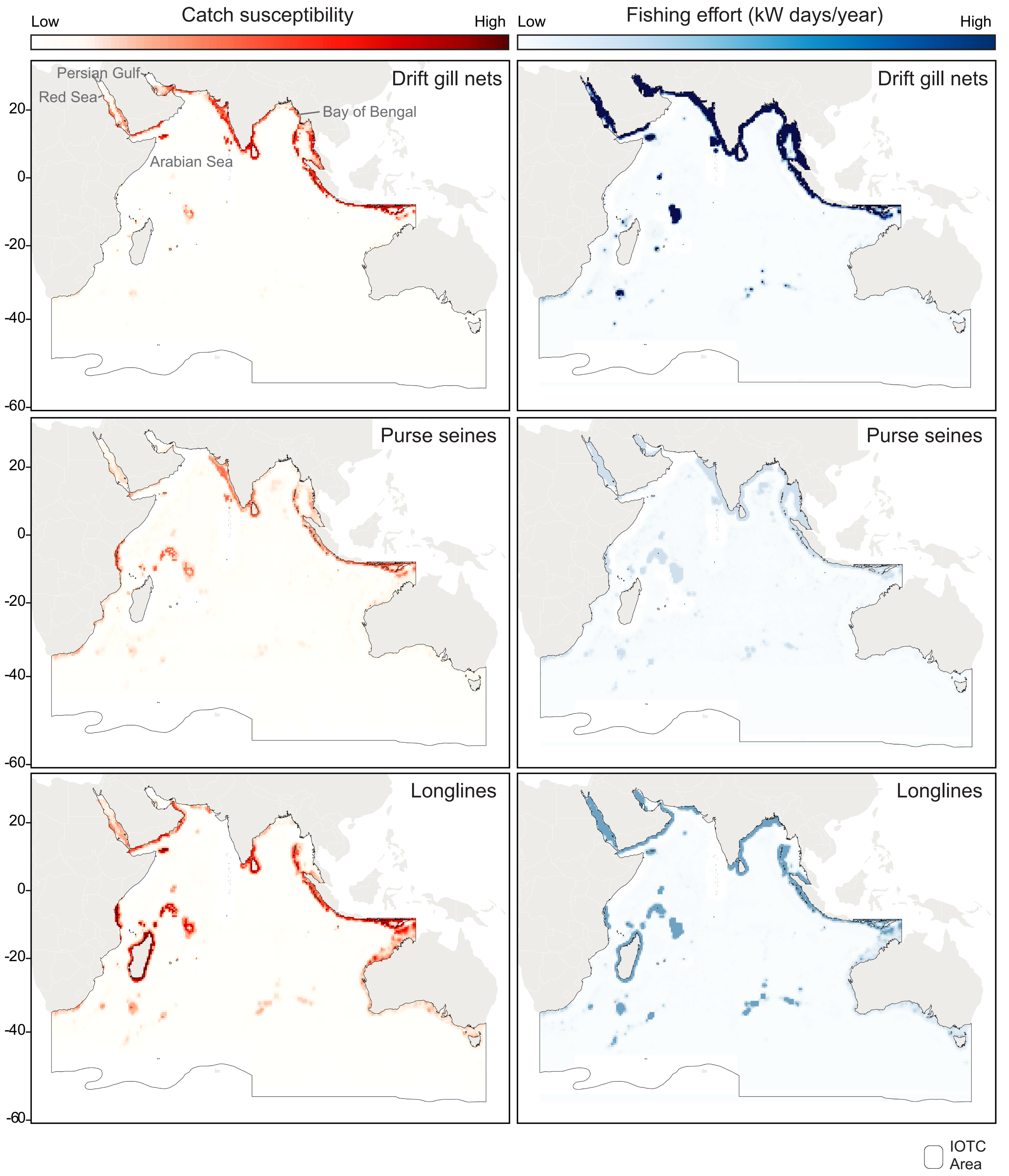

FIGURE 2 Maps of susceptibility (left) and fishing effort (right) for drift gill nets, purse seines and longlines in the IOTC Area of Competence. Susceptibility values are summed across all species in each grid cell. Fishing effort is for all powered vessels associated with catch of two pelagic size classes (30–90 cm and >90 cm). Effort is standardized to the same 0–1 scale across all three gear types

or pelagic gears, although their depth ranges and horizontal distributions result in a high calculated overlap. For example, the long-tailed butterfly ray (*Gymnura poecilura*, Gymnuridae) has high catch susceptibility in gill nets, even though it is a benthic species that feeds mainly on crustaceans and clams and is unlikely to be captured in a surface-set net (IUCN, 2021).

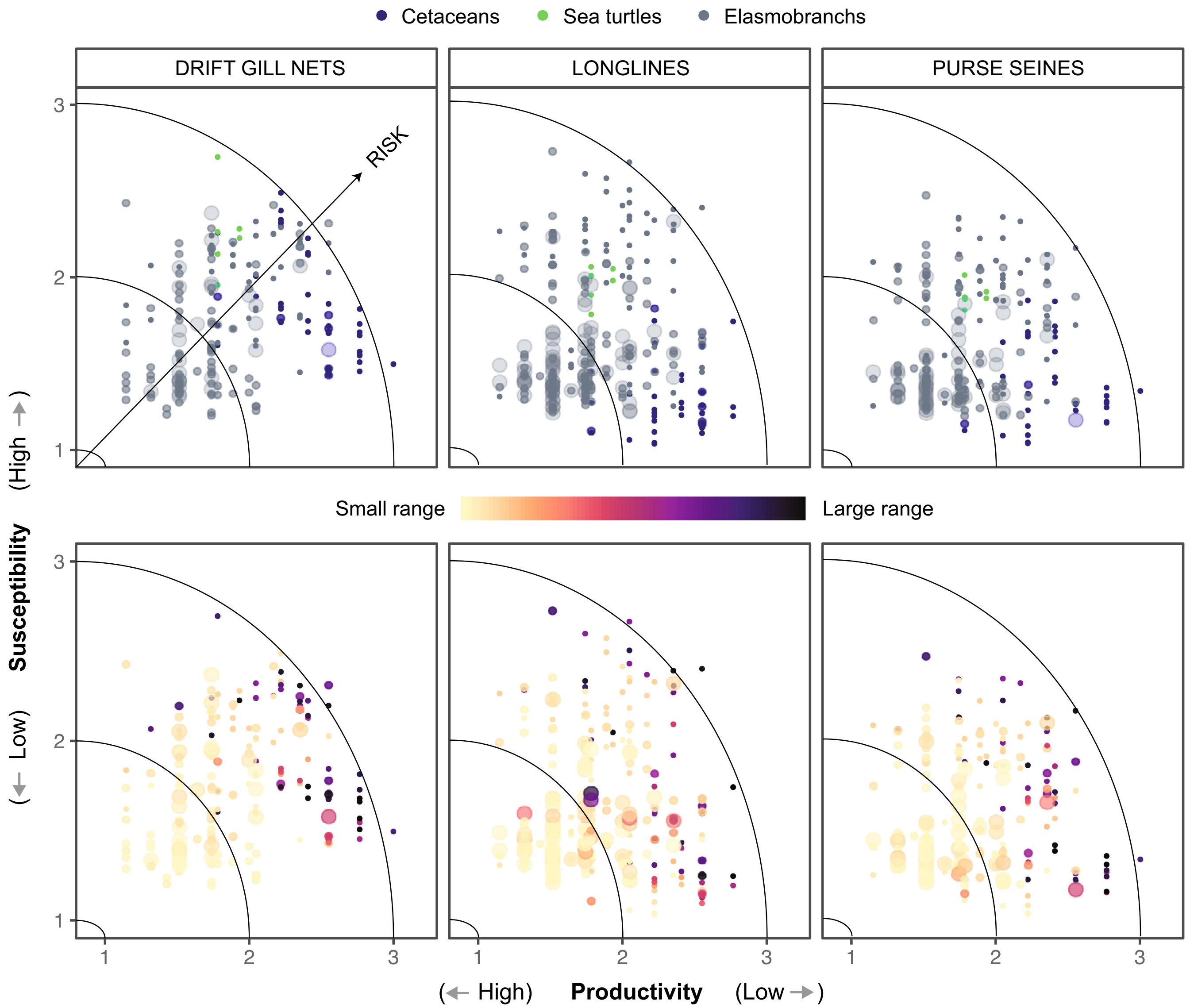

FIGURE 3 PSA results from the spatial adaptation method for the 319 species with the potential to interact with tuna gill nets, purse seines or longlines in the Indian Ocean. Top panel shows taxonomic group; bottom panel shows species' range size (number of cells with probability of occurrence >0.1). Transparency and size of dot correspond to data quality score for the productivity traits (scores of 1, 2 or 3; larger and more transparent dots are lower quality data)

Although conservative, this cross-taxa PSA approach could also underestimate the relative vulnerability of some species or groups. For example, sea turtles produce many eggs and thus score higher for productivity compared with cetaceans, but egg survival rates can be very low. The vulnerability could also be underestimated for data-poor species. Nineteen per cent of the species in our analysis were given a 'poor' data quality score; all were elasmobranchs except for two beaked whales (Figure 3, Table S1). Information on reproductive traits was especially scarce for small sharks (e.g. catsharks, Scyliorhinidae) and many groups of stingrays and skates (e.g. torpedo rays, Torpedinidae; softnose skates, Arhynchobatidae), even for some shallow and inshore species such as the porcupine ray (*Urogymnus asperrimus*, Dasyatidae) or sharpnose stingray (*Maculabatis gerrardi*, Dasyatidae). Most of these poor data quality species scored low for vulnerability to tuna fishing gears. However, many benthic or demersal elasmobranchs are endemic to national waters or have small ranges (Figure 3) and may be a conservation concern due to cumulative and local threats.

Compared with our adjusted PSA, the binned score approach described in Hobday et al., 2011, resulted in higher vulnerability scores for most species, particularly for longlines and purse seines (Figures 5, S1). The difference is more pronounced for certain groups of species and gears, in particular, shallow shelf elasmobranchs, pelagic generalist elasmobranchs, and sea turtles in both longlines and purse seines. We found that the spatial adaptation allows mapping of risk across grid cells and better resolves relative differences in susceptibility among species. However, many low productivity species end up with high vulnerability scores even though they are

TABLE 5 Attribute scores for the top ten highest risk species for each gear (ranked by vulnerability score, *V*). V_{123} = vulnerability score using the approach from Hobday et al. (2011), *S* = susceptibility, *P* = productivity. Red List categories are as follows: CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; and DD = Data Deficient. No. gears = number of tuna fishing gears species is susceptible to

Name	Group	V	V123	S	P	Red List	Num. Gear
Drift gill nets							
Mobula birostris	Filter feeder elasmobranchs	3.44	3.42	2.28	2.55	EN	3
Carcharodon carcharias	Pelagic generalist elasmobranchs	3.37	3.42	2.28	2.55	VU	3
Balaenoptera borealis	Baleen whales	3.35	3.53	1.86	3	EN	2
Sousa chinensis	Inshore dolphins and porpoises	3.33	3.73	3	2.22	VU	3
Balaenoptera brydei	Baleen whales	3.31	3.33	1.86	2.77	DD	2
Alopias vulpinus	Oceanic elasmobranchs	3.3	3.28	2.28	2.35	VU	3
Stenella attenuata	Small oceanic and coastal dolphins	3.28	3.32	2.28	2.41	LC	3
Balaenoptera edeni	Baleen whales	3.26	3.33	1.86	2.77	LC	2
Tursiops truncatus	Small oceanic and coastal dolphins	3.26	3.18	2.28	2.22	LC	3
Mobula alfredi	Filter feeder elasmobranchs	3.26	3.42	2.28	2.55	VU	3
Longlines							
Carcharodon carcharias	Pelagic generalist elasmobranchs	3.5	3.72	2.71	2.55	VU	3
Sphyrna mokarran	Shallow shelf elasmobranchs	3.36	3.63	3	2.05	CR	3
Alopias vulpinus	Oceanic elasmobranchs	3.35	3.59	2.71	2.35	VU	3
Carcharhinus albimarginatus	Pelagic generalist elasmobranchs	3.31	3.59	2.71	2.35	VU	3
Isurus oxyrinchus	Oceanic elasmobranchs	3.29	3.59	2.71	2.35	EN	3
Orcinus orca	Large oceanic dolphins	3.27	3.45	2.06	2.77	DD	3
Alopias superciliosus	Oceanic elasmobranchs	3.27	3.59	2.71	2.35	VU	3
Sphyrna zygaena	Shallow shelf elasmobranchs	3.24	3.63	3	2.05	VU	3
Galeocerdo cuvier	Pelagic generalist elasmobranchs	3.22	3.5	2.71	2.22	NT	3
Alopias pelagicus	Oceanic elasmobranchs	3.21	3.47	2.71	2.17	EN	3
Purse seines							
Carcharodon carcharias	Pelagic generalist elasmobranchs	3.35	3.42	2.28	2.55	VU	3
Balaenoptera borealis	Baleen whales	3.29	3.46	1.73	3	EN	2
Alopias pelagicus	Oceanic elasmobranchs	3.18	3.47	2.71	2.17	EN	3
Alopias vulpinus	Oceanic elasmobranchs	3.17	3.4	2.45	2.35	VU	3
Mobula birostris	Filter feeder elasmobranchs	3.17	3.54	2.45	2.55	EN	3
Carcharhinus albimarginatus	Pelagic generalist elasmobranchs	3.16	3.59	2.71	2.35	VU	3
Isurus oxyrinchus	Oceanic elasmobranchs	3.13	3.4	2.45	2.35	EN	3
Alopias superciliosus	Oceanic elasmobranchs	3.12	3.4	2.45	2.35	VU	3
Sphyrna mokarran	Shallow shelf elasmobranchs	3.12	3.4	2.71	2.05	CR	3
Balaenoptera physalus	Baleen whales	3.08	3.26	1.73	2.77	VU	2

relatively unsusceptible, and where empirical data are lacking, it is difficult to validate these results.

Although both methods likely overestimate vulnerability for some species and groups, we identified many potentially high-risk species that are not listed in available catch reports (Figures S2–S4). As an additional indicator of which species might be conservation priorities, we assessed species' IUCN statuses and found that 42% are listed as Threatened (Critically Endangered, Endangered or Vulnerable). Apart from hawksbill turtles (*Eretmochelys imbricata*, Cheloniidae), the Critically Endangered species are all elasmobranchs, including common eagle rays (*Myliobatis Aquila*, Myliobatidae), scalloped and great hammerhead sharks (*Sphyrna lewini* and *S. mokarran*), sand tiger sharks (*Carcharhinus taurus*, Carcharhinidae), oceanic whitetip sharks (*Carcharhinus longimanus*) and Pondicherry sharks (*C. hemiodon*, Carcharhinidae); the latter might be extinct (Dulvy et al., 2021). These species are susceptible to all three tuna gears

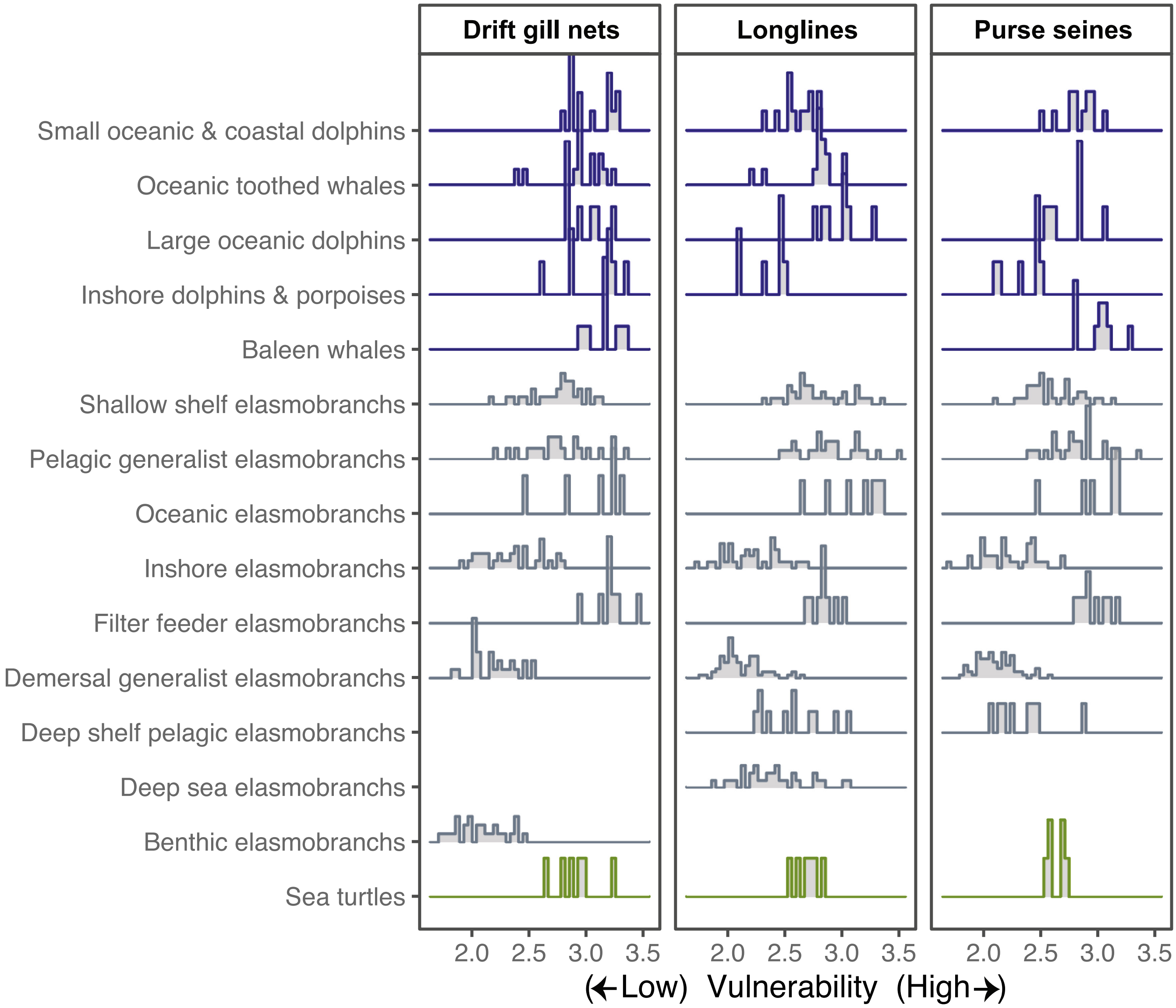

FIGURE 4 Distributions of vulnerability scores in drift gill nets, longlines and purse seines for species in the 15 species groups. Purple groups = cetaceans; grey = elasmobranchs; and green = sea turtles

and several rank relatively high for vulnerability to multiple gears (Figures S2–S4). Twenty-six of the 30 highest vulnerability species are Threatened (Table 5), and proportionally more of the Threatened species are susceptible to all three tuna gears (Figure 6). In total, almost half (49%) of the 319 species are susceptible to all three gears, and these species tend to have higher average vulnerability scores (Figure 6).

4 | DISCUSSION

4.1 | Species vulnerability

We adapted a common PSA method to provide the first spatially explicit risk assessment of over 300 megafauna species in Indian Ocean tuna fisheries. Our results indicate that sea turtle, cetacean and elasmobranch species face substantial cumulative risks from the tuna gill net, purse seine and longline fisheries. Many high-risk species are listed as Threatened (Critically Endangered, Endangered or Vulnerable) on the IUCN Red List and have few protections (Jabado et al., 2018; Pacoureau et al., 2021). We found high vulnerability for known risk groups such as small cetaceans in drift nets (Anderson et al., 2020; Brownell et al., 2019; Kiszka et al., 2021; Reeves et al., 2013; Temple, Westmerland, & Berggren, 2021), mesopelagic sharks and rays in longlines and purse seines (Amande et al., 2012; Garcia & Herrera, 2018; Murua et al., 2018), and sea turtles in all three gears (Ardill et al., 2013; Lewison et al., 2014; Ortiz et al., 2016; Varghese & Somvanshi, 2010; Wallace et al., 2013).

Additionally, we found that many poorly known or monitored elasmobranchs have high vulnerability scores for one or more gears (e.g. smalleye stingray, *Megatrygon microps*; Dasyatidae, sicklefin weasel shark; *Hemigaleus microstoma*, Hemigaleidae; and many

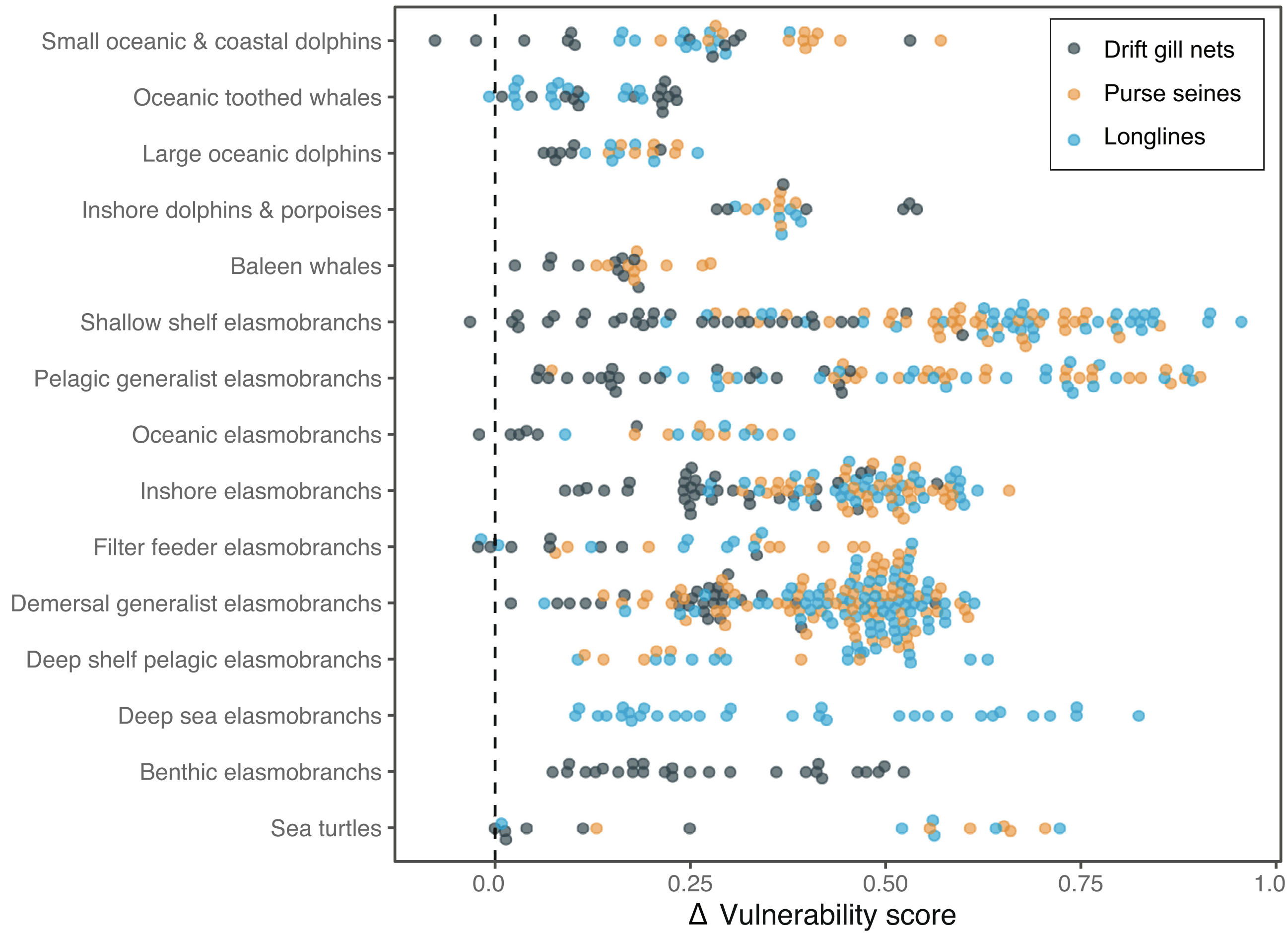

FIGURE 5 Differences in the vulnerability scores for 319 species in the three tuna gears using two different PSA methods. Most vulnerability scores were higher using the score-based PSA (delta vulnerability is positive)

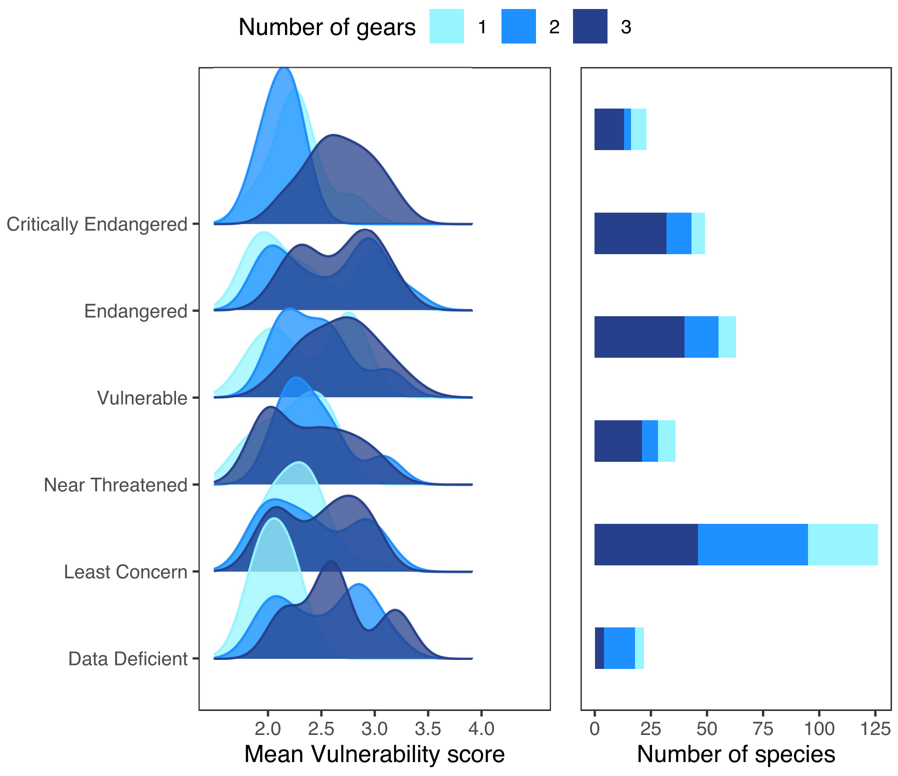

FIGURE 6 Vulnerability scores (left), number of species (right) and the number of gears (colours) that the species in each Red List category is susceptible to. Vulnerability score is the average across the gears each species interacts with

Carcharhinus spp., Carcharhinidae). Most of these species are rarely (if ever) specifically listed in available catch reports from the Indian Ocean, either because they are rarely caught (perhaps because they are not abundant), the catch is not being recorded, or it is only recorded in aggregated groups (e.g. 'pelagic sharks'). The latter is likely the case for many of the high-risk pelagic and semi-pelagic elasmobranchs, which can be difficult to identify even for trained observers (Roman-Verdesoto & Orozco-Zoller, 2005; Smart et al., 2016).

Basic biological information is also lacking for many potentially high-risk species. While not surprising for deep-sea species, many relatively visible and accessible species (e.g. eagle rays, Myliobatidae; or inshore whiprays, Dasyatidae) are also poorly studied. There has been a consorted effort to address these knowledge gaps, and we relied heavily on the recently updated IUCN assessment material for life history traits of elasmobranchs (Dulvy et al., 2021; IUCN, 2021). Some productivity traits are quite difficult to study, for instance, interbirth intervals, age of maturity or maximum age. If these elasmobranchs are slower growing and less fecund than we assume, they would be categorized as much higher risk.

The PSA is designed to be conservative, and we may overestimate risk from tuna gears for some species and groups (e.g. benthic and demersal elasmobranchs). We assume uniform vertical distribution of species and fishing gear throughout their depth ranges, which results in unrealistically high susceptibility scores for species that spend most of their time near the seafloor and are unlikely to encounter pelagic fishing gears. Although probably not high conservation priorities for the IOTC, it is possible that some of these species are caught in tuna gears. The Indian Ocean contains numerous seamounts that are relatively shallow, and where many elasmobranchs make diurnal migrations through wide ranges of the water column, making them simultaneously epipelagic, mesopelagic and bathypelagic (Heard, Rogers, Bruce, Humphries, & Huveneers, 2018; Sims et al., 2006; Speed, Field, Meekan, & Bradshaw, 2010; WWF, 2020). The encounterability attribute could be improved by estimating the distribution of species and fishing effort throughout the depth range, at least by the susceptibility group (e.g. sea turtles, benthic elasmobranchs), or incorporating habitat-specific depth ranges (Temple et al., 2021).

Another likely overestimation is vulnerability to purse seines, especially for cetaceans. We assume that no by-catch mitigation tactics are in place for any gears, even for species with little market value (such as small deep-sea skates and rays). Since some Indian Ocean purse seiners do use safe-release practices, which are reasonably effective for cetaceans, turtles and some elasmobranchs, we likely overestimate risk to these taxa from this gear type (Amande et al., 2012; Bourjea et al., 2008; Clavareau et al., 2020; Escalle et al., 2015). We also assume that all purse seiners set on fish aggregating devices (FADs), which increases selectivity for species attracted to floating objects. However, known by-catch rates in purse seine sets on FADs do not account for the additional mortality from ghost fishing, where pelagic sharks and sea turtles in particular can get entangled in the net hanging below the raft (Davies et al., 2014).

There remains some subjectivity in the interpretation of the PSA results. For instance, we may overestimate risk to species with high vulnerability scores but low susceptibility to catch—such as baleen whales. Alternatively, their very low productivity could mean populations truly are at high risk from rare catch events (Thomas, Reeves, & Brownell, 2016). The method implies that the susceptibility and productivity components are equally important drivers of vulnerability, where a unit of susceptibility is equivalent to a unit of productivity (Hordyk & Carruthers, 2018). There is no biological or empirical evidence for this assumption, but this framing provides a reasonable way to incorporate both elements into the calculation of risk and interpret the results (Grewelle et al., 2021). Depending on the context, practitioners may be more concerned about the vulnerable species with higher susceptibility scores (e.g. many oceanic elasmobranchs), or about low susceptibility, low productivity species such as large cetaceans.

4.2 | Summarizing risk across space

We adjusted the score-based PSA outlined in Hobday et al., 2011, by framing the catch susceptibility component as a likelihood of an animal encountering fishing gear in horizontal and vertical space, weighted by the severity of that event (selectivity of gear for that species and lethality of the gear if entanglement occurs). This allowed us to achieve two goals, which would not have been possible with the purely score-based approach. First, we could calculate a susceptibility value for each species in each grid cell, and therefore map susceptibility across the IOTC Area. We found that susceptibility to tuna fisheries is concentrated in a relatively small proportion of the IOTC Area along certain coastlines, which suggests that targeted interventions in specific geographic areas could have important benefits for a range of species. Second, basing the availability score on a per-cell calculation of risk allowed us to compare relative susceptibility across hundreds of species, whereas the score-based approach results in highly aggregated risk groups.

There are important limitations to this approach to calculating risk across space. We used models of species occurrence and fishing effort as proxies for the density of animals and fishing gear. Both models are static and fail to capture the strong seasonal and temporal patterns of where species and fishing occur. Where better information is available, data sources such as satellite transponder or vessel tracking systems could certainly improve estimates of where species and fishing gear will overlap. This information may not exist in the data-poor contexts the PSA is designed for. It would be worthwhile to explore different ways to use available spatial information such as AquaMaps range maps in PSAs to better quantify the likelihood of species encountering gear. However, it becomes complicated to summarize and interpret risk across space and time for many species, so additional nuance comes at increased computational expense.

Ultimately, the PSA is not a replacement for stock assessments or other quantitative tools because it does not assess the true impact (e.g. biomass removal) of the fishery (Hobday et al., 2011). The absence of quantitative data limits what can be estimated by the PSA; for instance, it is not intended to estimate a total number or volume of animals caught in fishing gear. Instead, the value of the PSA is that it can provide a baseline comparison of relative risk across species and threats in data-poor contexts and help identify priorities for additional monitoring or more robust assessment tools (Gallagher, Kyne, & Hammerschlag, 2012; Hobday et al., 2011; Lucena-Frédou et al., 2017). Recently, there have been several proposed improvements to the PSA that could better resolve risk estimates, focusing primarily on how attributes are selected and scored and how the overall vulnerability score is derived (Grewelle et al., 2021; Hordyk & Carruthers, 2018).

4.3 | Reducing by-catch mortality in tuna gears

Improving our understanding of the dynamics of the diverse fishing sectors in the Indian Ocean is a crucial first step in directing conservation resources and designing interventions to mitigate by-catch and protect threatened species (Teh, Teh, Hines, Junchompoo, & Lewison, 2015). The gill net sector is of particular concern because it is extremely diverse and essentially unmonitored. Although we attempt to focus on drift gill nets by only including fishing effort associated with catch of large pelagic fishes, gill net fleet dynamics are poorly known in the majority of high-risk coastal areas (Davies et al., 2014). Some of this effort may be aimed at species outside of the IOTC mandate, including small pelagic fish in estuarine habitats (FAO, 2014; Sekadende et al., 2020). There is also a sizeable bottom-set gill net sector that uses slightly larger mesh nets to target sharks and rays, particularly in the northern Indian Ocean (the Arabian Sea, Bay of Bengal, and western coast of Indonesia), in eastern Africa and in Western Australia (Henderson et al., 2007; Jabado, Al Ghais, Hamza, & Henderson, 2015; Temple et al., 2018). Standardized gill net subcategories—even if they were broad—would greatly improve our knowledge and understanding of this important sector. The IOTC is working to improve reporting, but this will require substantial investment in helping member countries to inventory their fleets and monitor catch, especially for countries with very limited management capacity such as Somalia or Yemen (Sinan & Bailey, 2020).

A major concern for many species in our analysis (including demersal elasmobranchs) is additional impacts from other fishing sectors not managed by the IOTC, such as the set gill net, demersal longline and bottom trawl fisheries (Georgeson et al., 2020; Jabado et al., 2018). The limited conservation and management measures under the IOTC mandate only cover incidental catches of a relatively short list of non-target species, which is especially concerning for elasmobranchs as fishing patterns shift and demand from Asian markets grows (Jabado & Spaet, 2017; WWF, 2020). Sea turtles and cetaceans are usually less marketable than elasmobranchs, but in some contexts, they have value for subsistence, bait or other traditional purposes, particularly in many coastal gill net fisheries (Temple et al., 2021). Better catch monitoring—especially in the essentially unmonitored gill net sectors—will be critical for the management of fishing pressure on all by-catch species, particularly for the most vulnerable species for which populations are naturally small (e.g. small cetaceans), or severely depleted by high by-catch levels.

In general, there are two main strategies for reducing mortality in fishing gears: reducing entanglement and reducing post-release mortality (Carruthers et al., 2009; Senko, White, Heppell, & Gerber, 2014). Techniques that reduce encounters and entanglement include time-area closures (e.g. marine protected areas or closed areas for certain seasons or gears), modifications to the gear itself (e.g. hooks, leaders, or mesh size and materials), the use of acoustic deterrents or other alerting devices (e.g. LED lights, pingers), or changing how the gear is deployed (e.g. setting gill nets lower in the water column, prohibiting purse seine sets on cetaceans or restricting the use of FADs) (Gilman, 2011; Kiszka et al., 2021; Northridge et al., 2017; Senko et al., 2014). The second broad strategy is to improve survival after entanglement—usually by implementing safe-release practices—although tactical measures such as shortening the time the gear is deployed can also reduce mortality (Carruthers et al., 2009; Zollett & Swimmer, 2019). Some strategies are widely effective in mitigating by-catch of a variety of species—such as restricting FADs or switching from wire to mono leaders—although target catch rates may be affected (Gilman, 2011). Other strategies are more variable depending on the context and species, and in some cases may reduce one type of by-catch but increase catch rates of another species (Gilman, Chaloupka, Swimmer, & Piovano, 2016).

Very few by-catch regulations are in place in the Indian Ocean. The region has a relatively small number of MPAs, and none in international waters. The period of increased piracy around Somalia in the early 2000s initially functioned as a de facto MPA, but evidence suggests that over time the governance void has resulted in increased illegal fishing in that area (Glaser, Roberts, & Hurlburt, 2019). The IOTC has fewer by-catch monitoring and mitigation requirements compared with the other tuna RFMOs, and it is the only organization that does not implement spatial closures or gear restrictions (Boerder, Schiller, & Worm, 2019). There is a global ban on setting drift nets longer than 2.5 km in the high seas, and some scattered management measures within the IOTC Area, such as prohibiting purse seines from intentionally encircling whale sharks or marine mammals, some regulation of FADs, and some requirements for safe-release practices (Garcia & Herrera, 2018). However, the lack of a common definition for FADs limits their effective management and reports indicate high rates of non-compliance across all types of fishing regulations (e.g. gear and area restrictions) within most EEZs and on the high seas (Jabado & Spaet, 2017; Kaplan et al., 2014; Swimmer, Zollett, & Gutierrez, 2020; WWF, 2020).

While safe-release practices can reduce species' mortality and therefore are an important component of the by-catch mitigation portfolio, they can still have significant effects on the animal's fitness (Adams, Fetterplace, Davis, Taylor, & Knott, 2018; Wilson, Raby, Burnett, Hinch, & Cooke, 2014). Furthermore, the safe release is only relevant to certain species and gears. Our results corroborate the growing evidence that sea turtles and many small- and medium-sized cetaceans are highly vulnerable to gill nets, and these nets pose an additional threat to many elasmobranch species that are already heavily impacted by other fisheries in the region (Dulvy et al., 2021; Kiszka et al., 2021; Temple et al., 2021; Williams et al., 2018). Many vulnerable species that entangle in gill nets die before the net is hauled, so devoting limited resources to safe-release practices is not an effective strategy to reduce this threat. Studies show that gill nets are also difficult to effectively modify (Brownell et al., 2019; Senko et al., 2014), although there are potential modifications that have not been rigorously tested across different areas and megafauna species (e.g. type and colour of net filament, type of float-line, weight of lead line, net hanging ratio) (Northridge et al., 2017). There has been some success using acoustic pingers to reduce gill net by-catch of beaked whales and some small cetaceans (e.g. harbour porpoise *Phocoena phocoena*, Phocoenidae), although they are relatively expensive to purchase and maintain (Carretta, Barlow, & Enriquez, 2008; Hamilton & Baker, 2019). Thus, the most promising solutions to reducing by-catch impacts from gill nets are likely to be low-cost tactical changes in how the gear is deployed (e.g. setting slightly below the surface) and restricting their use at certain high-risk times or areas (Hamilton & Baker, 2019; Kiszka et al., 2021).

Although the magnitude of drift gill net fishing presents a unique challenge for the Indian Ocean, it is only one component of the problem. Our results corroborate the increasingly urgent calls for controls on fishing effort in the Indian Ocean, across all the major gear types, national or non-industrial sectors, distant water fleets. Currently, tuna fishing is essentially unlimited, posing a serious threat to both target and non-target species (Juan-Jordá et al., 2018; Kaplan et al., 2014). The importance of fish for protein provision and food security to millions of people in the region makes overfishing a particularly tricky problem to combat (Sinan & Bailey, 2020). Any market-based solutions to controlling fishing effort will have to account for the wide variety of supply chains in the region, some oriented towards low-value regional subsistence and others aimed at high-value international markets (Lecomte, Rochette, Laurans, & Lapeyre, 2017).

The current regulatory framework in the Indian Ocean—which includes the IOTC mandate—has substantial limitations and loopholes that allow fishing impacts on marine megafauna to continue at unsustainable levels (WWF, 2020). The IOTC alone does not have the capacity to close these loopholes; effective by-catch management in the Indian Ocean will require coordinated efforts from all the RFMOs in the region, as well as Regional Fisheries Bodies, national governments and agencies (e.g. US Marine Mammal Commission), non-governmental organizations, other international agencies (e.g. International Whaling Commission) and the seafood industry itself. We find that risk to megafauna is concentrated in coastal areas within Exclusive Economic Zones, which highlights the importance of the coastal States in managing fishing in their waters. Given the limited governance capacity of many Indian Ocean countries, improving national fisheries management institutions will require substantial assistance from regional organizations and better-resourced governments (Sinan & Bailey, 2020). Although voluntary, international commitments such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the Convention on Migratory Species (CMS) also provide opportunities to strengthen regulations around data collection and management measures for sea turtles, cetaceans and elasmobranchs. Currently, the CMS and CITES provide some protections to sea turtles and cetaceans but few high-risk elasmobranchs are protected by these agreements. Better catch documentation would help identify species that merit consideration of CITES or CMS listings, including the many IUCN-listed Threatened elasmobranchs that our results suggest are potentially caught in tuna fisheries.

Despite the challenges of improving by-catch monitoring and mitigation, there are promising solutions emerging that are advancing beyond gear modifications, for example integrating satellite and other data sources to build dynamic management tools and by-catch warning systems, or working directly with fisher organizations to develop context-specific tactics to avoid catching protected species (Hall et al., 2007; Hazen et al., 2018; Howell et al., 2015). Electronic monitoring systems—which contribute to basic catch documentation and enforcement of regulations—are becoming increasingly feasible (Suuronen & Gilman, 2020). Given the challenging management context in the Indian Ocean and the diversity of fishers, fishing fleets and seafood supply chains, by-catch mitigation tactics will likely be intractable without early and consistent engagement with fishers and local management bodies (Gladics et al., 2017; McCluney, Anderson, & Anderson, 2019; Sinan & Bailey, 2020). While baseline information on species biology and catch should remain a priority for management agencies in the Indian Ocean, there is an urgent need to implement by-catch reduction strategies, as threatened species could be declining too rapidly to wait for complete documentation of the problem before taking actions.

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DATA AVAILABILITY STATEMENT

Two primary databases were used in this study: a publicly available database of marine species distributions (AquaMaps) and a database of global non-industrial fishing effort, which is available upon request from the authors. We used version 2021.3 of the IUCN Redlist, which is freely available at https://www.iucnredlist.org/.

The code and data required to reproduce the figures and results in this paper will be made freely available as RMarkdown and csv files on a publicly accessible GitHub repository (https://github.com/lroberson/indianocean_bycatchPSA_ms).

ORCID

Leslie Roberson https://orcid.org/0000-0002-7490-0795
Yannick Rousseau https://orcid.org/0000-0003-0765-7518

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