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A systematic conservation plan identifying critical areas for improved chondrichthyan protection in South Africa

Nina Faure-Beaulieu [a,b,*], Amanda T. Lombard [c], Jennifer Olbers [a], Victoria Goodall [c], Charlene da Silva [d], Ryan Daly [e,f], Gareth Jordaan [e], Sven E. Kerwath [d], Alison Kock [f,g], Bruce Q. Mann [e], Taryn S. Murray [f], Patricia Albano [h], Geremy Cliff [i], Natalie A. dos Santos [j], Enrico Gennari [k,l], Neil Hammerschlag [h], Aletta E. Bester-van der Merwe [j], Ralph Watson [m], Sara Andreotti [n], Anthony T.F. Bernard [f,o], Paul D. Cowley [f], Lauren De Vos [p], Natalia Drobniewska [q], Chantel Elston [f], Chris Fallows [r], Toby D. Rogers [s,t], Grant Smith [u], Michaela van Staden [j], Pierre de Villiers [v], Timothy Guy Paulet [q], Jean Harris [a]

[a] Wildlands Conservation Trust, PO Box 21450, Mayors Walk, Pietermaritzburg 3208, South Africa
[b] Department of Zoology, Nelson Mandela University, South Africa
[c] Institute for Coastal and Marine Research, PO Box 77000, Nelson Mandela University, Gqeberha, Port Elizabeth 6031, South Africa
[d] Department of Forestry, Fisheries and the Environment, Cape Town 7700, South Africa
[e] Oceanographic Research Institute, PO Box 10712, Marine Parade, 4056 Durban, South Africa
[f] South African Institute for Aquatic Biodiversity (SAIAB), Private Bag 1015, Makhanda 6140, South Africa
[g] Cape Research Centre, South African National Parks, Cape Town, South Africa
[h] Rosenstiel School of Marine & Atmospheric Science, University of Miami, 1320 S Dixie Hwy, Coral Gables, FL 33146, United States
[i] School of Life Sciences, University of KwaZulu-Natal, Durban, South Africa
[j] Department of Genetics, Stellenbosch University, Private Bag XI, Stellenbosch, South Africa
[k] Oceans Research, Mossel Bay, South Africa
[l] Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown, South Africa
[m] Dyer Island Conservation Trust, 5 Geelbek Street, Kleinbaai, Western Cape 7220, South Africa
[n] Evolutionary Genomics Group, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Stellenbosch 7600, South Africa
[o] Department of Zoology and Entomology, Rhodes University, Makhanda 6140, South Africa
[p] Save our Seas Foundation, Rue Philippe Plantamour 20, Geneva 1201, Switzerland
[q] South African Shark Conservancy, Hermanus, South Africa
[r] Apex Shark Expeditions, Quayside Building Simonstown, Cape Town, South Africa
[s] Institute for Communities and Wildlife in Africa (iCWild), University of Cape Town, Cape Town 7701, South Africa
[t] Shark Spotters, Cape Town 7945, South Africa
[u] Sharklife Conservation Group, Sodwana Bay, Kwa-Zulu Natal 3974, South Africa
[v] Marine and Coasts Operations, Conservation Operations, Cape Nature, South Africa

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ABSTRACT

The International Union for Conservation of Nature (IUCN) estimates that over a third of all chondrichthyan species (sharks, rays and chimaeras) are threatened with extinction, primarily by overfishing (as target or bycatch species). Owing to the wide-ranging distributions of many chondrichthyans, they are often overlooked in marine protected area (MPA) design. South Africa is a biodiversity hotspot for chondrichthyan species diversity, and to improve the conservation status of these species in the country's continental exclusive economic zone (EEZ), we collaborated widely to collate existing occurrence data. Ensemble models were developed for 87 species' distributions, which informed a systematic conservation planning analysis for 64 threatened and endemic species. We assessed the current representation of these species in South Africa's MPA network and identified priority areas for protection, avoiding fishing pressure where possible. Results show that many MPAs are well placed to protect chondrichthyans, especially along the east coast (KwaZulu-Natal province). Unfortunately, permissive fishing regulations within many MPA zones reduces their effectiveness at protecting

* Corresponding author at: Wildlands Conservation Trust, PO Box 21450, Mayors Walk, Pietermaritzburg 3208, South Africa.
E-mail address: nina-fb@outlook.com (N. Faure-Beaulieu).

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chondrichthyans. Improved regulations designed to protect chondrichthyans within all MPAs should be considered a high priority. Priority areas for increased spatial protection were identified along the west coast continental shelf, the Agulhas Bank off the south coast, and south coast embayments. We found that supplementing the current MPA network by an additional 5 % of the EEZ would be sufficient to protect >30 % of the range of all 64 species, provided there is adequate enforcement. As South Africa prepares to expand its MPA estate to meet international targets, these findings can ensure that chondrichthyans are well represented.

1. Introduction

Overfishing has been identified as the primary threat to chondrichthyans (Dulvy et al., 2021) and approximately 100 chondrichthyan species are impacted by fisheries in South Africa's continental Exclusive Economic Zone (EEZ). These fisheries include the demersal shark longline, inshore and offshore demersal trawl, midwater pelagic trawl, large pelagic longline, demersal hake longline, commercial line-fishing, recreational line-fishing, emerging small-scale fisheries, and the bather protection programme in KwaZulu-Natal (KZN) (da Silva et al., 2015; DFFE, 2022a). Many threatened pelagic species have distributions that also extend to the high seas, beyond South Africa's EEZ, where they have limited refuge from commercial fishing pressure (Queiroz et al., 2019). Chondrichthyans are highly vulnerable to overexploitation, largely due to their life-history characteristics such as long gestation periods, late maturity, slow growth, high longevity and low fecundity (Cortés, 2000).

South Africa's drive to "unlock an ocean economy", focusing on oil and gas exploration, sea-bed mining, marine infrastructure development, aquaculture, and tourism, brings additional stressors to vulnerable species (Findlay, 2018). The scale of these activities is of concern for a coastline with many threatened endemics. Furthermore, the location and timing of many nursery and breeding areas are still unknown for most species. There is also concern that climate change may shift or limit species to narrower distribution ranges, decreasing carrying capacity and increasing vulnerability (Currie et al., 2019; O'Brien et al., 2013).

Fisheries management, and spatial management measures, must be applied to mitigate against chondrichthyan population declines. Marine Protected Areas (MPAs) are one of many conservation management tools to protect species and habitats from anthropogenic threats (Agardy, 1997). The benefits of MPAs for biodiversity have led to several international goals for increased spatial area protection coverage, the most recent being target three of the Kunming-Montreal Global Biodiversity Framework (GBF). Target three calls for conservation of at least 30 % of terrestrial, inland water and coastal marine areas by 2030 (CBD/COP/15/L25).

South Africa has already designated 5 % of its continental EEZ (which excludes the Prince Edward Islands in the Southern Ocean) as 41

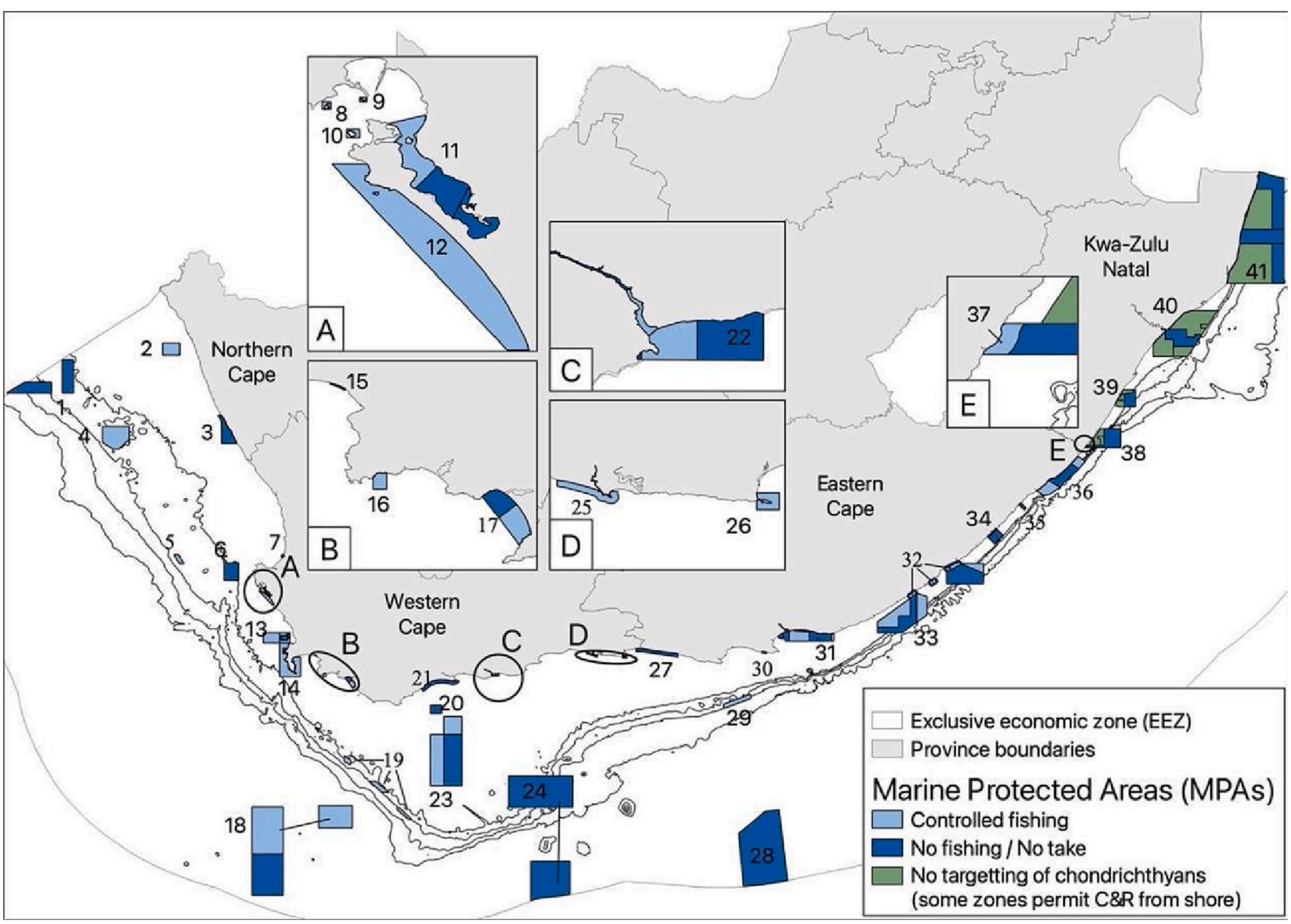

Fig. 1. South Africa's 41 continental Marine Protected Areas (MPAs)24. These cover 5 % of the continental exclusive economic zone (EEZ), no-take zones cover 3 %. The inshore zonation (200 m out to sea) is not captured here and differs from the offshore zonation for some MPAs. The 250 m, 500 m, 1000 m and 2000 m isobaths are shown.

MPAs (Fig. 1) (RSA, 2019), with 20 of these having been recently proclaimed as a result of systematic conservation planning (SCP) and a lengthy stakeholder engagement process over several years (Operation Phakisa, 2014; Sink et al., 2019). Most of South Africa's MPAs are subdivided into zones, which dictate permitted activities within them. No-take zones prohibit harvesting of any kind, including catch-and-release angling, and cover 3 % of the continental EEZ. Various fisheries are permitted in the remaining mixed-use zones, and these permitted fisheries vary by MPA and may affect chondrichthyans directly, or indirectly as by-catch. For example, chondrichthyan by-catch occurs within offshore MPAs that allow for pelagic longlining. Whilst direct catches are permitted in some MPA zones by commercial and recreational line-fishing. Only the MPAs in KZN explicitly prohibit targeting chondrichthyans in these mixed-use zones, but still permit the catch and release of chondrichthyans caught from the shore. In addition, several species are also caught in the bather protection nets and drumlines found within three of the five MPAs in KZN (Cliff and Dudley, 2011).

Owing to the generally wide-ranging spatial distributions and movement characteristics of chondrichthyans, they have largely been overlooked as focal species in the designation of MPAs globally (Giménez et al., 2020), including in South Africa. Of South Africa's 41 MPAs, chondrichthyans are mentioned in the published gazettes as conservation objectives in only five of them. Some fisheries data on sharks and rays were used for the spatial planning of the new offshore MPAs (DFFE, 2022a) but these were never explicitly taken into account.

However, MPAs alone are not sufficient to protect some of the more transient and pelagic species (Shiffman and Hammerschlag, 2016; Simpendorfer and Cook, 2019). Therefore, fisheries management is also necessary in the form of gear restrictions, size and catch limits, and spatial or temporal closures. Many of these measures have shown success worldwide in reducing chondrichthyan mortality (Simpendorfer and Cook, 2019). Spatial or temporal fisheries closures are a variant of MPAs, and have been described as "other effective area-based conservation measures" (OECMs). However, some studies on migratory fishes suggest that MPAs, if properly placed, can have disproportionately positive benefits (Bond et al., 2017; Daley et al., 2015; Kerwath et al., 2009), and some locally exploited species can benefit from protection within MPAs (Albano et al., 2021; da Silva et al., 2013, 2021). A network of well-placed MPAs has been shown to be one of the most effective measures to protect certain species of sharks and rays as this enables habitat connectivity and reduces exposure to fisheries across several areas (Simpendorfer and Cook, 2019). This is especially relevant in South Africa, home to a network of 41 MPAs.

Spatial protection for chondrichthyans in the form of MPAs, also referred to as "shark sanctuaries" cover just over 3 % of the world's oceans (Ward-Paige and Worm, 2017). The lack of these sanctuaries can often be attributed to a paucity of data to help direct where these sanctuaries would be best placed. There is a growing international support and need for shark and ray directed protection (Davidson and Dulvy, 2017), and this is evident through the recent emergence of a global strategy led by the IUCN to identify important shark and ray areas (ISRAs) (Hyde et al., 2022). ISRAs have not yet been identified in South Africa but they will make a strong contribution to this work when they are identified.

This study aimed to build up-to-date Species Distribution Models (SDMs) for threatened and endemic chondrichthyan species. The SDMs were used to conduct a gap analysis on the existing representation of chondrichthyans across South Africa's MPA network. A gap analysis was also conducted using available IUCN ranges since these are a widely used resource in global spatial analyses of sharks and rays (Derrick et al., 2020; Finucci et al., 2021; Sherman et al., 2023) and were therefore considered as useful comparisons with the SDMs produced in this study. The SDMs were then used as input into a Systematic Conservation Plan (SCP). SCP methods use spatial prioritisation algorithms to identify areas for protection based on explicit quantitative targets or goals (Margules and Pressey, 2000). Known (or modelled) distributions of species and habitats, as well as the spatial distribution, intensity and impacts of threats typically form the base data. The SDMs and SCP developed in this study aimed to assess the representation of chondrichthyan species in South Africa's current MPA network. This study supports one of the priorities outlined in South Africa's National Plan of Action for Sharks II (NPOA-II), which acknowledges the need for increased spatial management of chondrichthyans (DFFE, 2022a).

This study is a preliminary step in developing methods towards systematic conservation planning for chondrichthyans. Further studies should encompass additional socio-economic variables, incorporate aggregation spot information and ISRAs when available, and conduct stakeholder engagement before any areas are implemented. This study can serve as a blueprint methodology to be built upon for other countries and regions on how priority areas can be identified for expanded spatial protection targeted at these species.

2. Material and methods

2.1. Species occurrence data

During a collaborative exercise spanning approximately seven months, chondrichthyan occurrence data were collated from research institutions, individual researchers, the scientific literature, and online repositories. Data collation was focused on endangered and endemic species. Given that many of the datasets contained a mixture of different species, we initially accepted data from non-endemic and non-threatened species. Data sharing agreements were established, and it was agreed that the raw data would not be made publicly available. Each data record needed to include the following information: genus and species name, date, and, either a GPS coordinate or location description with a minimum resolution of 10 × 10 km. A resolution of 10 × 10 km was chosen as this is the highest resolution achieved for the majority of the environmental variables used for modelling (Tyberghein et al., 2012) (Appendix 1). The temporal scale of the data collated ranged from 1950 to 2021 to represent current and historical distribution ranges. Data collected originated from various sampling methods including, but not limited to, baited remote underwater video (BRUV) surveys, fisheries catch records, mark-recapture data, acoustic telemetry data, citizen science projects and underwater visual census (UVC) surveys. We created a separate data sheet per species with the GPS coordinates of the occurrence data, as well as information on date, dataset and sampling method. Due to data sharing agreements however these raw data sheets will not be made available. A description of datasets and dataset-specific cleaning steps (when applicable) are available in Appendix 1.

2.2. Expert consultations

In addition to data collation, ongoing discussions with experts as well as expert mapping workshops were conducted to discuss the species data collated, existing distribution ranges as well as distribution maps produced through this study for several species. The experts highlighted potential issues with transient species, geographic ranges, or species identification. Since some data points were sourced from online repositories, it can be challenging to assess the accuracy of the information collated. It was thus critical to evaluate this taxonomic information against the expert knowledge of workshop participants. Some of the issues identified at workshops were: (1) Taxonomic revisions and species misidentifications, (2) data scarcity, (3) data resolution and location accuracy, and (4) transient and oceanic species. See Appendix 1 for more information on how these issues were addressed. Several transient and oceanic species were omitted (n = 18) as the spatial coverage of the data collated was not sufficient to model their movement across the whole planning area. When dealing with wide-ranging species, MPAs will only be of benefit if these species predictably use the same areas (Simpendorfer and Cook, 2019). Due to current gaps in this information, we found it more appropriate to remove these species from the analyses and avoid biases in our spatial prioritisations.

2.3. Species distribution models (SDMs)

All analyses were conducted using R version 4.2.1 (R Core Team, 2022), RStudio (RStudio Team, 2022), and the tidyverse package (Wickham et al., 2019), and all codes are available on GitHub (https://github.com/ninzyfb/wildoceans-scripts). An example dataset is available within the repository to run the code. All individual and ensemble models were built using the biomod2 package (Thuiller et al., 2021). We describe our species distribution models (SDMs) following the ODMAP (Overview, Data, Model, Assessment, Prediction) protocol for SDMs (Fitzpatrick et al., 2021; Zurell et al., 2020), which facilitates standardised reporting of SDMs. Here, the overview section is provided, whilst the remaining ODMAP sections (containing the technical details) are in Table B.1 of Appendix 2.

The statistical techniques used here assume that the response data are random samples. However, as with most large and collated datasets, this is not the case. Spatial autocorrelation, temporal autocorrelation and nesting are three issues that can affect the non-independence of data. To deal with these issues we started by 'thinning' each dataset (Steen et al., 2021). This involves reducing the number of data points per species to keep one data point per 10 × 10 km grid cell, therefore assigning each grid cell to a binary presence or absence value for each species.

This reduced the effect of sampling bias and spatial autocorrelation. Background or pseudo-absence data were also generated for each model to account for sampling bias across the various datasets. Spatial bias of presences will result in environmental bias (Phillips et al., 2009) so it is important to account for this when running SDMs. We randomly generated 5000 pseudo-absence points per species per model algorithm as recommended by (Barbet-Massin et al., 2012). The model objective for the SDMs was to predict single species occurrence in space as continuous occurrence probabilities. Each model was restricted to the boundaries of South Africa's continental EEZ.

Predictor variables included remotely sensed environmental data (e.g., sea surface temperature (SST), chlorophyll-a) as well as physical data (bathymetry, slope, habitat). A set of 27 predictor variables was selected based on their known influence on chondrichthyans (Schlaff et al., 2014) (Appendix 1). Prior to model building, predictor variables were checked for collinearity (Dormann et al., 2013). We used the correlation_groups function from the sdmpredictors package (Dormann et al., 2013). This function calculates the pairwise correlation among variables and flags highly correlated variables (Pearson's r correlation coefficient of $>|0.7|$). Variables were removed from the highly correlated pairs after assessing for biological importance and 18 variables remained.

Three different modelling algorithms were fitted independently per species using the BIOMOD_Modeling function of the biomod2 package (Thuiller et al., 2021): generalised linear models (GLM) with a binomial error distribution (logit link), general additive models (GAMs) with a binomial error distribution (logit link), and maximum entropy models (MaxEnt). All three model outputs were then averaged using the BIOMOD_EnsembleModeling function. The final ensemble model accounts for algorithmic uncertainty. Each ensemble model per species combined and averaged the model outputs from our three chosen models (GLM, GAM, Maxent); this method has been shown to have better predictive performance than individual models (Araújo and New, 2007). Ensemble predictions from SDMs were derived using un-weighted ensemble means. Predictive model performance was assessed using a commonly used assessment score known as the True Statistics Skill (TSS) score. The TSS balances sensitivity and specificity and is independent of the prevalence of observations. TSS values range from −1 to 1, with negative values indicating that models are no better than chance and values of 1 indicating a perfect agreement. TSS values >0.6 are considered good. Only models with a TSS >0.7 were incorporated into the final ensemble model. The TSS values of all individual models run are available for download.

Each SDM produced was verified against current knowledge of the distribution of the species using (Ebert et al., 2021) and expert consultations. This is because a high TSS score does not necessarily equate to an accurate SDM. The TSS score is calculated based on the model's performance in predicting the presence and absence of the species. If the model makes correct predictions for the available data points, it can yield a high TSS score. However, this does not guarantee that the model's predictions accurately reflect the actual distribution of the species in areas where data is limited or unavailable. SDMs for 17 species were flagged as inaccurate (detailed in Appendix 1) due to the resulting distribution being considerably different to the actual distribution of those species. This was based on visual inspection of these models and discussions with experts. This resulted in a final set of 87 SDMs.

2.4. Binarizing the SDMs (core range)

The final ensemble model for each species was a map depicting the continuous probability of occurrence values for each 10 × 10 km grid cell. Moving forward with the prioritisation algorithm, we wanted to include areas only with high probability of occurrence values (i.e., each species' core range). We binarized each continuous probability map using a threshold value above and below which cells would be given a value of 1 or 0, respectively. When dealing with presence and pseudo-absence (background) data such as was done in this study, one of the suggested threshold techniques to use is that of the maximisation of the TSS (max-TSS) (Liu et al., 2013). This was done using the Find.Optim.Stat function within the Biomod2 package, which iterates through 1000 fitted values to determine the optimal TSS score and the associated threshold cut-off for converting the continuous values to binary.

2.5. Gap analysis on representation of chondrichthyans across MPA network

The overlap between each SDM (n = 87) and the MPA network was assessed by using the st_intersection function from the sf package (Pebesma, 2018). The same was carried out for all equivalent and available IUCN ranges (n = 81). IUCN ranges were unavailable for the following six modelled species: *Himantura leoparda*, *Neotrygon caeruleopunctata*, *Pateobatis fai*, *Rhinoptera jayakari*, *Carcharhinus amblyrhynchos*, *Etmopterus granulosus*. The gap analysis was conducted on three groupings of MPA zones: all MPAs, zones which prohibit the catching of sharks and rays, and no-take zones.

2.6. Spatial planning

2.6.1. Overview of spatial prioritisation process

Spatial prioritisation was performed using the Prioritizr package (Hanson et al., 2021), which allows users to build and solve conservation planning problems in R using mathematical optimization. This package can find cheaper solutions and in a shorter time period than the commonly used Marxan software. We used GurobiTM as our optimization algorithm. Each conservation scenario built using Prioritizr requires a conservation objective, which in our case was to maximise the protection of chondrichthyan species within South Africa's EEZ. The solver will then identify which planning units (PUs) are required to meet the conservation objective whilst also minimising the total cost of the solution. Two broad categories of conservation scenarios were developed: Biodiversity scenarios (n = 24) and Management scenarios (n = 6). Biodiversity scenarios were built to understand which key areas within South Africa's EEZ are identified for sharks and rays, regardless of existing constraints such as MPAs or fishing pressure. Whilst these are interesting from an ecological perspective, they might fail to capture realistic options for increased spatial protection and are likely to be deemed impractical from a management perspective. Management scenarios on the other hand incorporated existing constraints such as MPAs, fishing pressure, a maximum area budget for expansion, and known critical biodiversity areas (CBAs). The combination of parameters for each scenario is outlined in Fig. 2. Regardless of which category a conservation scenario fell in, 100 solutions were generated and summed per scenario, resulting in an irreplaceability map highlighting key areas identified across all 100 solutions.

2.6.2. Planning units

The planning region was the South African continental EEZ, divided into 10 × 10 km planning units (PUs) (10,426 in total).

2.6.3. Conservation features

Conservation features included the core range of 87 shark and ray species produced through species distribution modelling. In some scenarios only the subset of endangered and South African endemic species was used (n = 64). A layer representing critical biodiversity areas (CBAs) natural and restore was also used as a conservation feature in some scenarios. See Appendix 2 for full details on how the CBA layer was coded to the PUs.

2.6.4. Costs

Two different cost layers were developed for the conservation scenarios: area-based and scaled by fishing pressure. In the area-based cost layer, each PU was assigned a value of 1. This ensures that the total cost of the solution is a surrogate for the total area required to meet the targets. In the cost layer that was scaled by fishing pressure, all pressure layers were scaled between 0 and 1, summed together, and then the summed values were scaled between 0 and 1.

2.6.5. Targets

Targets specify the minimum area of the biodiversity feature that is required in the solution to the conservation scenario. For example, a 10 % protection target indicates that a minimum of 10 % of the PUs that make up the total area of a biodiversity feature need to be selected in the final solution. We developed species-specific targets based on their endemic or threatened status. Therefore, we chose a baseline target of 30 % protection based on targets set in other conservation planning projects on chondrichthyan species. This is also in line with the baseline target used to develop South Africa's CBA maps (Harris et al., 2022). Targets were increased for species of higher concern (endemic and threatened (Critically Endangered, CR; Endangered, EN; Vulnerable, VU)) (Table 1). The two species with the highest target of 60 % were the puffadder shyshark *Haploblepharus edwardsii* and the twineye skate Raja ocellifera because they are endemic to South Africa and categorised as EN. We also ran scenarios with a uniform target of 30 % across all species to compare the solution outputs.

2.6.6. Other design considerations

2.6.6.1. Boundary penalties. Boundary penalties define how clumped or

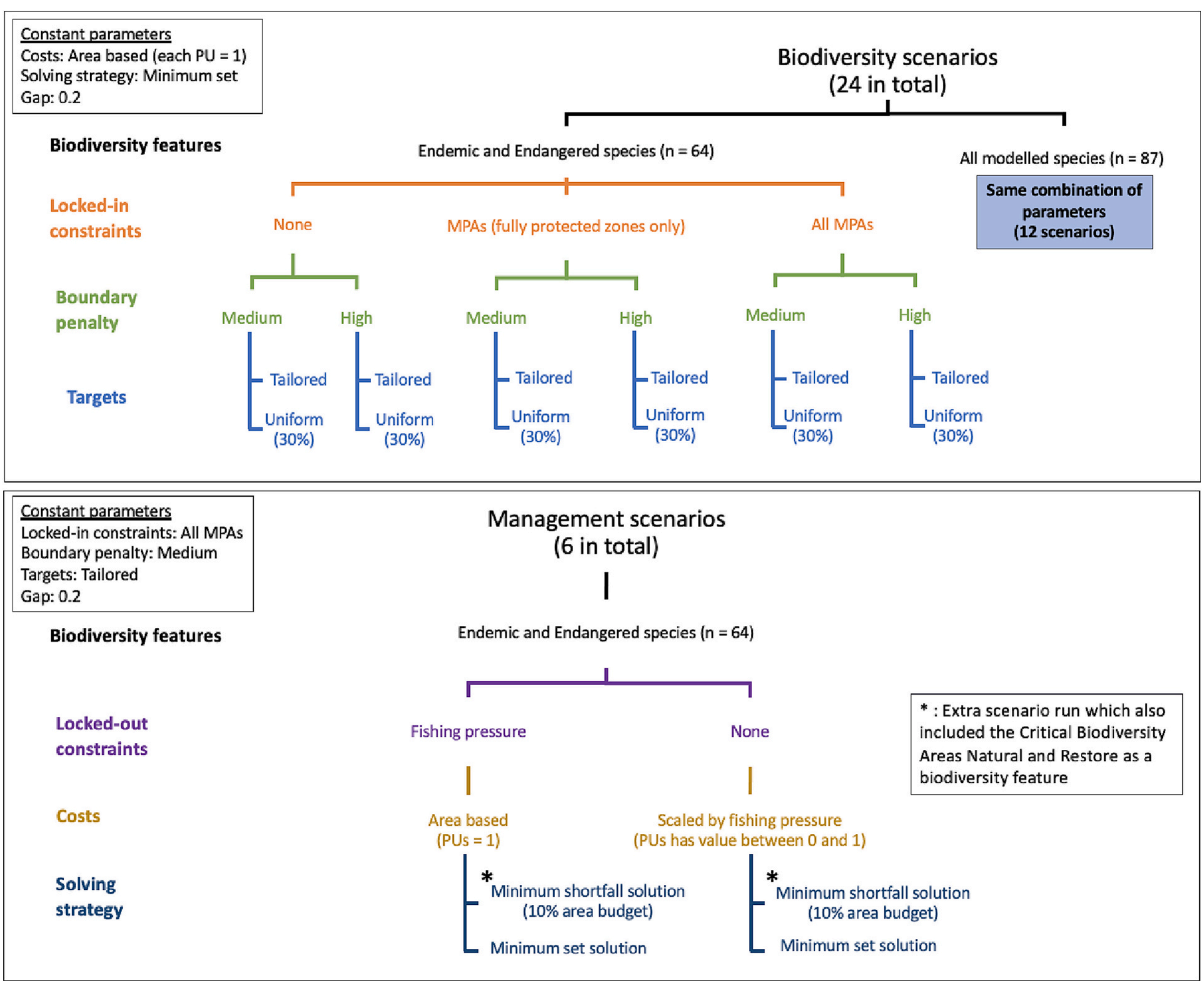

Fig. 2. Overview of parameters set across all planning scenarios run in this study using prioritizr. A total of 30 scenarios were run, 24 biodiversity scenarios and 6 management scenarios.

Table 1
Species-specific protection targets assigned to species based on endemism and IUCN Red List status.

	Not endemic to Southern or South Africa	Southern Africa endemic	South Africa endemic
Data deficient	30 %	30 %	40 %
Critically endangered	50 %	50 %	60 %
Endangered	50 %	50 %	60 %
Vulnerable	30 %	40 %	50 %
Near threatened	30 %	30 %	40 %
Least concern	30 %	30 %	30 %

fragmented the final solution should be. This is equivalent to the boundary length modifier in Marxan. Each scenario was run with a low (0), medium (0.0001) or high (0.00001) boundary penalty to limit the fragmentation of each final solution. These values were obtained through visual inspection of their impact on the scenario outputs.

2.6.6.2. Locked-in planning units. South Africa's existing network of 41 Marine Protected Areas (MPAs) was overlaid over the PUs and these PUs were locked-in for certain scenarios. In some instances, only the fully no-take zones across all MPAs were locked in. This means they are forced into the solution. See Appendix 2 for full details on how the MPAs were coded to the PUs.

2.6.6.3. Locked-out planning units. In some of the planning scenarios, PUs with high fishing pressure values were locked-out. This was done by excluding any PUs across all fisheries with pressure values above 0.8.

2.6.6.4. Solving strategy. One of two solving strategies was used across all scenarios: minimum set solution or minimum shortfall solution. If a minimum set solution was applied, this meant that all targets must be met irrespective of how many PUs this required. If a minimum shortfall solution was applied, this meant that a maximum budget could be set (maximum number of PUs available for selection), and as a result the algorithm minimised the overall shortfall of as many targets as possible, whilst ensuring that the total cost of the solution did not exceed the given budget. This is a useful solving strategy for the management scenarios as it allowed us to set a total budget of 10 % of the EEZ, which represents realistic expansion strategies.

2.6.6.5. Optimality gap. Each scenario was run using an optimality gap of 0.2 which indicates that the solution must be at a maximum 20 % from optimality. This allowed for reduced processing times, an optimality gap of 0 means the software can run for several days until the most optimal solution is found.

3. Results

3.1. Data collation and species distribution models

At least one occurrence was collated for 164 out of the 194 chondrichthyan South African species. The number of data points collated per species is summarised in Appendix 1. Species distribution models (SDMs) were produced for 87 species (Fig. 3) and are available upon request. Differences in the predicted range between the IUCN range and the core range extracted from the SDMs averaged at 594 grid cells. They ranged from a difference of 0 for whitetip reef shark *Triaenodon obesus* to a difference of 2429 grid cells for leafscale gulper shark *Centrophorus squamosus* (Fig. 5). See Appendix 3 for differences across all species for which an IUCN range was available (n = 81).

3.2. Gap analysis: representation within the current marine protected area (MPA) network

On average, 26.2 % (±23.9 % SD) of the core range area across all 87 species overlapped with MPAs. The value dropped to 22.2 % (±23.4 % SD) when using equivalent IUCN ranges (n = 81). However, when considering only the no-take zones, area overlap decreased to 9.8 % (±7.9 % SD). When considering no-take zones as well as MPA zones where the targeting of chondrichthyans is prohibited, area overlap is 22.2 % (±24.2 % SD). How these values varied by threatened status is shown in Fig. 4. Fig. 5 shows the difference in range protection across different MPA zones as well as by endemic and threatened status. The percentage of each species' range found within MPAs varied greatly per species (Fig. 5). Only two species had >30 % of their range overlapping with no- take zones (grey reef shark *Carcharhinus amblyrhynchos*, silvertip shark *C. albimarginatus*). All estimates are available in Appendix 3.

Overall, species of Least Concern (LC) showed the least overlap between their range and MPAs, with most of their ranges overlapping <20 % with MPAs (Appendix 3). Of the threatened (CR, EN, VU) species, the ones with <20 % of their range overlapping with MPAs were also the ones with little to none of their range overlapping with either no-take zones or no chondrichthyan targeting zones (Fig. 6). The ten species with the smallest proportion of their range within MPAs were all deep-water demersal species found on the west coast: black dogfish *Centroscyllium fabricii* (LC), Portuguese shark *Centroscymnus coelolepis* (NT), Long-snouted african dogfish Squalus bassi (LC), Sculpted lanternshark Etmopterus sculptus (LC), Southern lanternshark *E. granulosus* (LC), African softnose skate *Bathyraja smithii* (LC), Smoothback skate *Rajella ravidula* (LC), Munchkin skate *R. caudaspinosa* (LC), Leopard skate R. leoparda (LC), Roughskin skate *Malacoraja spinacidermis* (LC). All had <5 % of their range overlapping with MPAs.

The ten species with the largest proportion of their range within MPAs, all have relatively small ranges within South Africa and are restricted to the northern KZN coast (Fig. 6, Table C.1 in Appendix 3). Seven of these 10 species are rays (Blue-spotted fantail ray *Taeniura lymma* (LC), Reef manta ray Mobula alfredi (VU), Shortfin devil ray *M. kuhlii* (EN), Giant manta ray *M. birostris* (EN),Pink whipray Pateobatis fai (VU), Reticulate stingray *Himantura uarnak* (EN), Leopard whipray H. leoparda (VU)) and the remaining three are sharks (Grey reef shark *Carcharhinus amblyrhynchos* (EN), Silvertip shark *C. albimarginatus* (VU), and Whitetip reef shark *Triaenodon obesus* (VU)). All these more tropical species are threatened except for *T. lymma*, and they all have at least 60 % of their range overlapping with MPAs, given that their ranges in South Africa are restricted to within the iSimangaliso MPA on the north-eastern border of the country with Mozambique.

3.3. Irreplaceable areas resulting from spatial prioritisation

Irreplaceable PUs are defined here as any PUs systematically chosen across all 100 output solutions to a conservation problem. A PU chosen across all 100 solutions means that this PU is essential to achieving the targets of the conservation problem and therefore can be deemed irreplaceable. A total of 30 different conservation scenarios was run, with 100 solutions produced for each one of these 30 scenarios. Only a select few are discussed here but all outputs are available upon request. An important consideration when describing these scenario outputs is the variability in which planning units (PUs) are chosen owing to differences in scenario parameters. For example, the boundary penalty can have an important effect on how the PUs are chosen, with high boundary penalties favouring more clumped solutions. This needs to be kept in mind when interpreting any of the outputs and is why several scenarios were run so that the effect of different parameters could be understood.

Scenarios were run using different approaches to target setting. Species-specific targets indicate that the target for each species was set based on their IUCN and endemic status. Uniform targets indicate that the target for each species was set at 30 % range protection. For

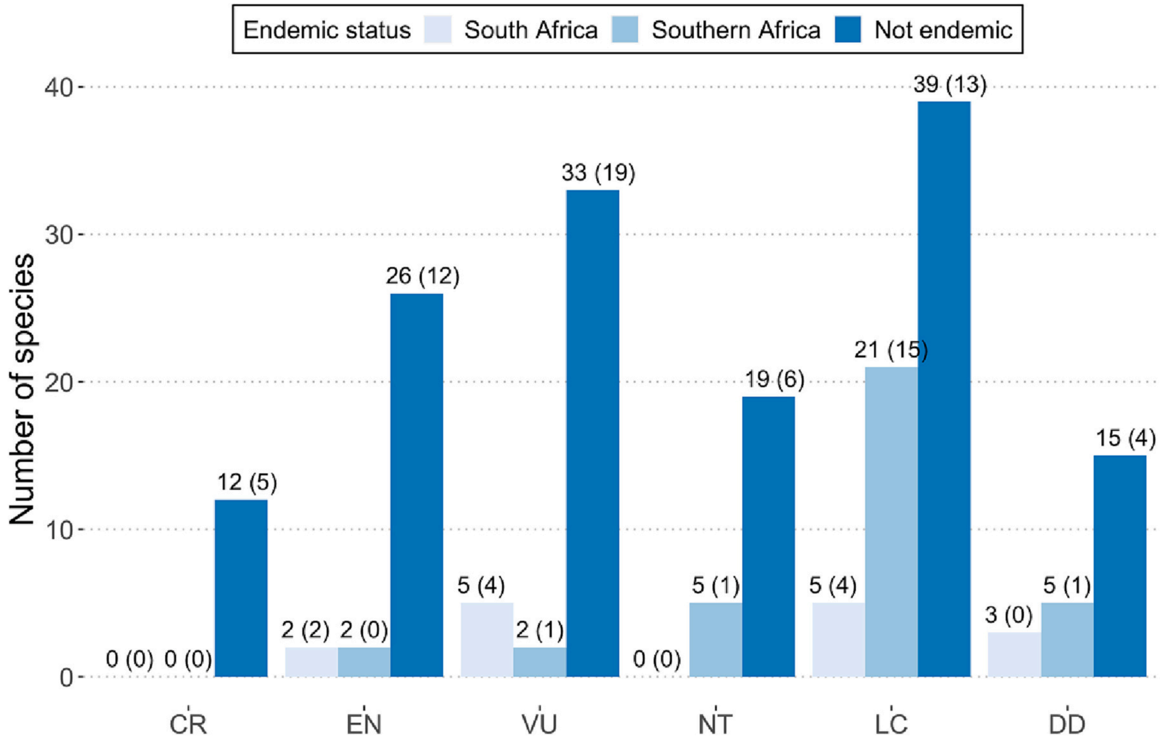

Fig. 3. Endemic and Red List status for 194 chondrichthyan species recorded in South African waters. Numbers in parentheses are species for which a species distribution model (SDM) was produced. CR – Critically Endangered, EN – Endangered, VU – Vulnerable, NT – Near Threatened, LC – Least Concern, DD – Data Deficient.

biodiversity scenarios with no locked-in constraints, the percentage of EEZ required to meet species-specific or uniform targets was 12 % and 8 % respectively (Fig. 7, A1 & B1). These scenarios provide insight into how representative of chondrichthyans the MPA network is by looking at the overlap with irreplaceable PUs. With uniform targets, the irreplaceable PUs did not overlap as much with existing MPAs as when species-specific targets were used, especially with regards to the coastal MPAs. This is likely a result of species-specific targets requiring more area to meet the targets, which provides more opportunity for overlap. There were some major differences in important areas chosen between these two biodiversity scenarios. When using species-specific targets (Fig. 7, B1), a large portion of the Agulhas shelf is irreplaceable, as well as many of the coastal embayments across the Western Cape. The Benguela shelf off the west coast is highlighted regardless of the target type, but with more irreplaceable PUs chosen when species-specific targets were used. The PUs chosen along the KZN coast were similar across both scenarios.

When the MPA network was locked in, the average area required to meet species-specific and uniform targets increased to 15 % and 12 % respectively, likely due to the offshore MPAs not overlapping with any biodiversity features. Neither scenario using either uniform (Fig. 7, A2) or species-specific (Fig. 7, B2) targets required additional PUs to the existing MPAs along the KZN coast. The MPAs on the Agulhas shelf did reduce the number of additional PUs required, especially on the southern region of the shelf (Fig. 7, B2). The lack of MPAs on the Benguela shelf resulted in little differences in the number of PUs chosen, even with the MPA network locked in.

When considering the management scenarios incorporating additional constraints such as fishing pressure, there was less flexibility in where the necessary PUs could be chosen, resulting in more irreplaceable PUs. Management scenarios also resulted in reduced differences between scenarios using uniform (Fig. 7, A3) or species-specific (Fig. 7, B3) targets, especially along the western Benguela shelf. However, on the Agulhas shelf, there were far more irreplaceable PUs when using species-specific compared to uniform targets (Fig. 7, B3). High fishing pressure along the Western Cape coast resulted in fewer PUs available to be chosen in this region. This region of the coast is now more "expensive" owing to the demersal inshore trawl fishery and the small pelagic fishery.

Often however, a total EEZ area budget rather than species protection target will dictate the location of new conservation areas (i.e., 10 % by 2020 or 30 % by 2030). Therefore, a management scenario was run to understand what targets could be achieved within a 10 % EEZ area budget. This scenario locked-in the existing MPAs, incorporated fishing pressure, and included a 30 % target for CBAs (Fig. 8). The areas that were identified as most irreplaceable included regions along the 100 m isobath on the Agulhas shelf, and regions between 500 m and 1000 m along the Benguela shelf. The eastern coast of False Bay and the areas directly surrounding de Hoop, Tsitsikamma and Addo Elephant National Park MPAs were also prioritised. Not all species-specific targets could be met; however, a minimum of 30 % range protection was achieved across all species within this 10 % area budget. Fig. 9 shows the difference in protection achieved when comparing the current MPA network with the 10 % area budget scenario. Within the current MPA network (5 % of the EEZ), the species-specific targets and a 30 % range protection target was achieved for 23 out of 64 threatened and/or endemic species. When increasing the spatial protection to 10 % of the EEZ, 30 % protection was achieved across all 64 species and the species-specific targets were met for an additional 26 species, 10 of which are threatened (Fig. 9). Species not meeting the species-specific targets even with an additional 5 % EEZ protection included yellowspot skate *Leucoraja wallacei* (VU), lesser guitarfish Acroteriobatus annulatus (VU), smoothhound *Mustelus mustelus* (EN), leafscale gulper shark *Centrophorus squamosus* (EN), spearnose skate *Rostroraja alba* (EN), and soupfin shark Galerohinus galeus (CR). These species have a combination of relatively large distributions and high targets due to their threatened status, which explains why their targets were not met when constrained by a limited area budget.

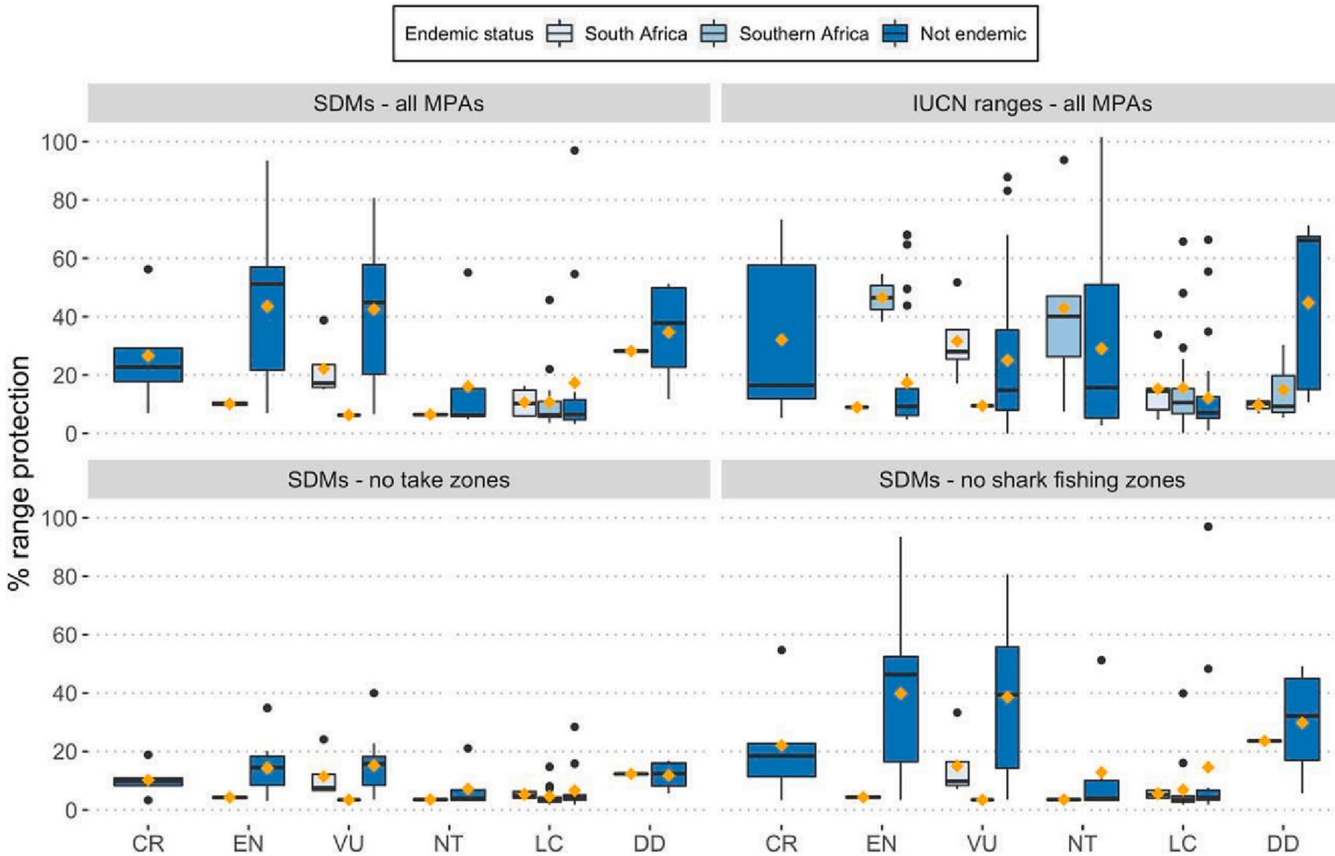

Fig. 4. Boxplots depicting the percentage of range protected within South Africa's MPA network for chondrichthyan species using the Species Distribution Models produced in this study and available IUCN ranges. Blue triangles represent the mean in each group. CR – Critically Endangered, EN – Endangered, VU – Vulnerable, NT – Near Threatened, LC – Least Concern, DD – Data Deficient. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

This study presents a systematic conservation plan (SCP) for chondrichthyans in South Africa. Only a few studies have used a SCP to identify important areas for chondrichthyans (Giménez et al., 2020; Haupt et al., 2017), most likely due to a paucity of data. This study represents an attempt at a wide-reaching collaboration to collate all available data on chondrichthyan occurrences within South Africa. This exercise highlighted the abundance of data in South Africa and the benefits of broad-scale data collaborations. SDMs were generated for 87 species, several of which, until now, lacked an up-to-date distribution map. For six of these species, no IUCN distribution map had previously been available (Leopard whipray H. leoparda (VU), Bluespotted maskray Neotrygon caeruleopunctata (LC), Pink whipray Pateobatis fai (VU), Oman cownose ray Rhinoptera jayakari (EN), Grey reef shark *C. amblyrhynchos* (EN), and Southern lanternshark *Etmopterus granulosus* (LC)). Some modelled ranges closely matched IUCN ranges, this was most often the case for species with restricted ranges in South Africa (i.e., Whitetip reef shark *Triaenodon obesus* (VU)). Contrastingly, for species with larger ranges, there were larger variations in predictions, such as for the Leafscale gulper shark *Centrophorus squamosus* (EN), a demersal species found along the Benguela shelf slope on the west coast.

4.1. Spatial protection within the current MPA network

Spatial protection for chondrichthyans in South Africa exists mainly within proclaimed MPAs. In 2019, South Africa expanded its MPA estate within continental EEZ waters from 0.4 % to 5.4 % (Kirkman et al., 2021). However, only 3 % of the continental waters are designated as no-take zones. Current levels of range protection across no-take zones averaged 10 % across all 87 modelled species. Protection was much lower for several CR and EN species, including both Endangered South African endemics (*H. edwardsii* and R. ocellifera), at 5 % and 4 % respectively. When considering additional protection conferred by zones prohibiting targeting of chondrichthyans in KZN, average range protection across species more than doubled to 22 %. However, these additional zones cannot be considered to offer the same level of protection as no-take zones since they allow for line-fisheries to operate and catch-and-release of chondrichthyans from the shore; therefore chondrichthyans are caught unintentionally wherever fishing is permitted (Smith et al., 2021). Finally, shark nets are installed in several KZN MPAs, which results in high levels of chondrichthyan catches (Cliff and Dudley, 2011). A case study using research shore fishing in iSimangaliso MPA concluded that allowing for catch-and-release was incompatible with no-take zones owing to sensitive species, mostly teleosts, suffering high levels of post-release mortality (PRM) (Mann et al., 2018). Unfortunately, there is limited information on PRM for chondrichthyans (Ellis et al., 2017). For the VU Thresher shark *Alopias vulpinus* and CR Raggedtooth shark *Carcharias taurus*, PRM varied across studies and seemed to be highly dependent on fight times, hook placement and handling. In addition to the issue of PRM, *C. taurus* has shown evidence of post-release jaw injuries (Bansemer and Bennett, 2010) as well as other species showing premature birth or abortion following release (Adams et al., 2018). In the absence of more information, concerted efforts must be made to educate both commercial and recreational fishers on how to effectively release hooked chondrichthyans to minimise mortality.

When considering all MPA zones, average range protection across species rose to 26 %, and was far greater for some species. These results

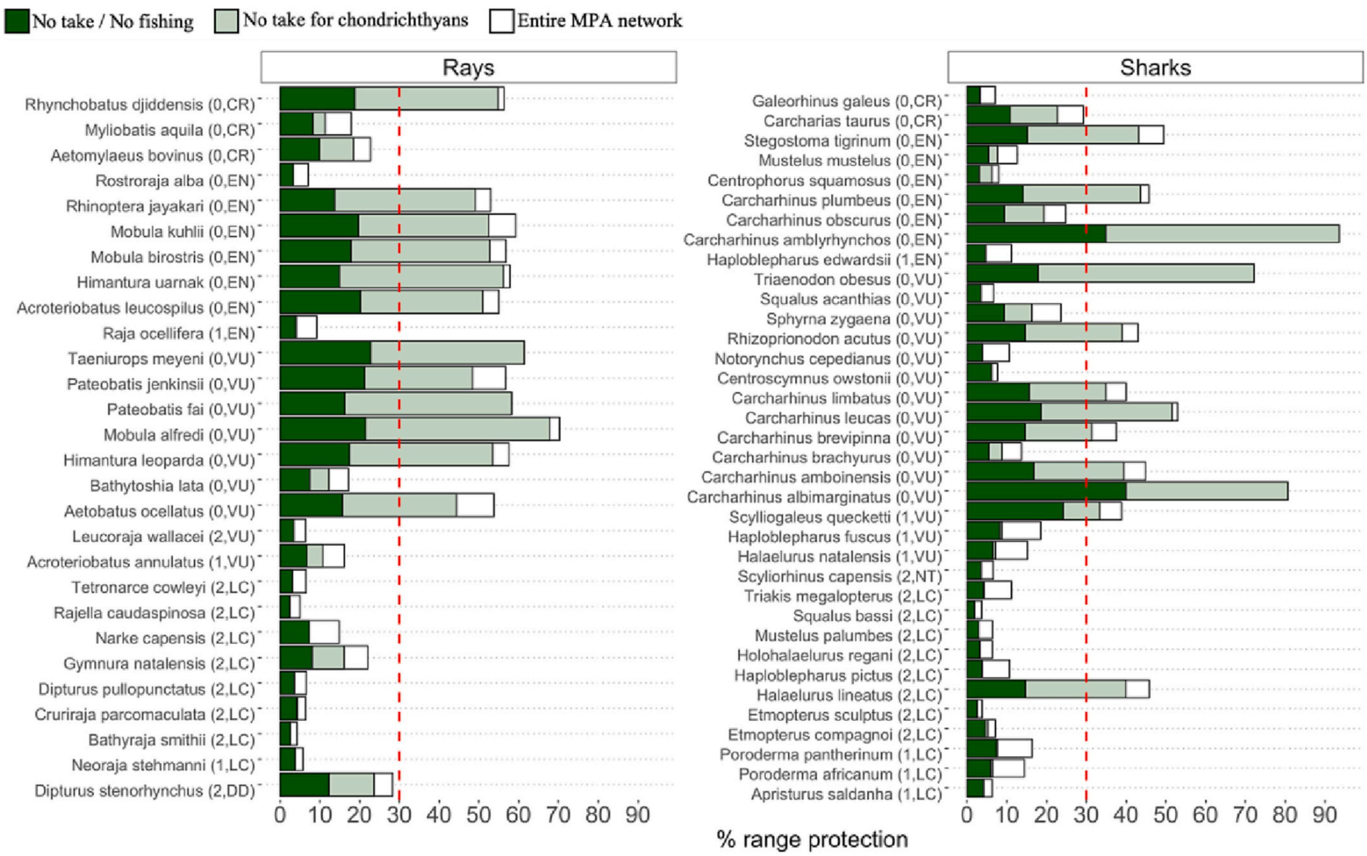

Fig. 5. Percentage range protection across South Africa's MPA network categorised by MPA zonation for threatened and/or endemic chondrichthyan species (n = 64). Species are ordered first by threatened status, then by endemic status. The red dashed line represents the 30 % target for spatial protection. 0 - not endemic, 1 - South African endemic, 2 - southern African endemic. CR – Critically Endangered, EN – Endangered, VU – Vulnerable, LC – Least Concern. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

are promising, as there is a potential to increase the protection of South Africa's chondrichthyan populations considerably if better management and stricter rules were applied to their extraction across all MPA zones. The National Environmental Management: Protected Areas Act allows management authorities of MPAs to apply such internal rules, which can form part of management plans, without having to change the legislation as it appears in the Government Gazette (RSA, 2004), but stakeholder engagement is essential.

4.2. Spatial protection beyond the current MPA network

For some species, expanding protection within the current MPA network will be insufficient to protect them adequately. For example, only 7 % of the range of the CR *G. galeus* is protected across all MPAs. In addition, this species is caught in high numbers across the line and trawl fisheries and is an official target in the demersal shark longline fishery (DFFE, 2022a). Using this SCP, we identified important areas beyond existing MPAs where increased protection should be focussed, whilst also considering fishing pressure and CBAs. These included offshore off the west coast on the southern Benguela continental shelf, the Agulhas shelf, and the southern coast and its embayments. The west coast offshore areas are very important for several demersal and deep-water species such as *G. galeus*. This is also a heavily fished area for the offshore demersal trawl and demersal hake longline, both of which have high levels of chondrichthyan by-catch. The southern coast embayments are a target area of the demersal inshore trawl, the small pelagic fishery and the commercial and recreational line-fishery. Interestingly, the areas offshore of the Addo Elephant National Park, Tsitsikamma and De Hoop MPAs were all prioritised (Fig. 9). Extending the boundaries of these MPAs further offshore into deeper water or where there is more unconsolidated sandy habitat could greatly increase their effectiveness. Generally, such MPA extensions are easier to achieve and obtain the necessary stakeholder buy-in than establishing new MPAs (BQM, pers. obs.). Our results found that the MPAs on the KZN coastline are sufficient and large enough that this region would likely rather benefit from improved management of existing MPAs. An issue of importance on the KZN coast is the presence of bather protection gear (large mesh gillnets and baited drum lines) designed to target large species such as white shark *Carcharodon carcharias*, tiger shark *G. cuvier*, and bull shark *Carcharhinus leucas*, but which have a high associated bycatch (Cliff and Dudley, 2011). In addition, the commercial and recreational line-fishery and, to a lesser extent due to the recent closure of the inshore component as a result of the declaration of the uThukela Banks MPA in 2019, the crustacean trawl fishery all place considerable pressure on chondrichthyans occurring in, and passing through, this stretch of coastline. Improved implementation and awareness of regulations designed to protect chondrichthyans within KZN's MPAs should therefore be considered as a high priority. A promising finding from the various conservation scenarios was that a 10 % area target of the South African continental EEZ is sufficient to meet a 30 % target across all modelled species and targets up to 60 % for other species. This is also provided that these 10 % have adequate fisheries regulations to protect chondrichthyans. Additional MPAs will require thorough stakeholder engagement processes, which can sometimes result in different areas being set aside for protection because of compromise. Therefore, range protection provided by a 10 % area target, will vary by species depending on how these additional areas are finally delineated.

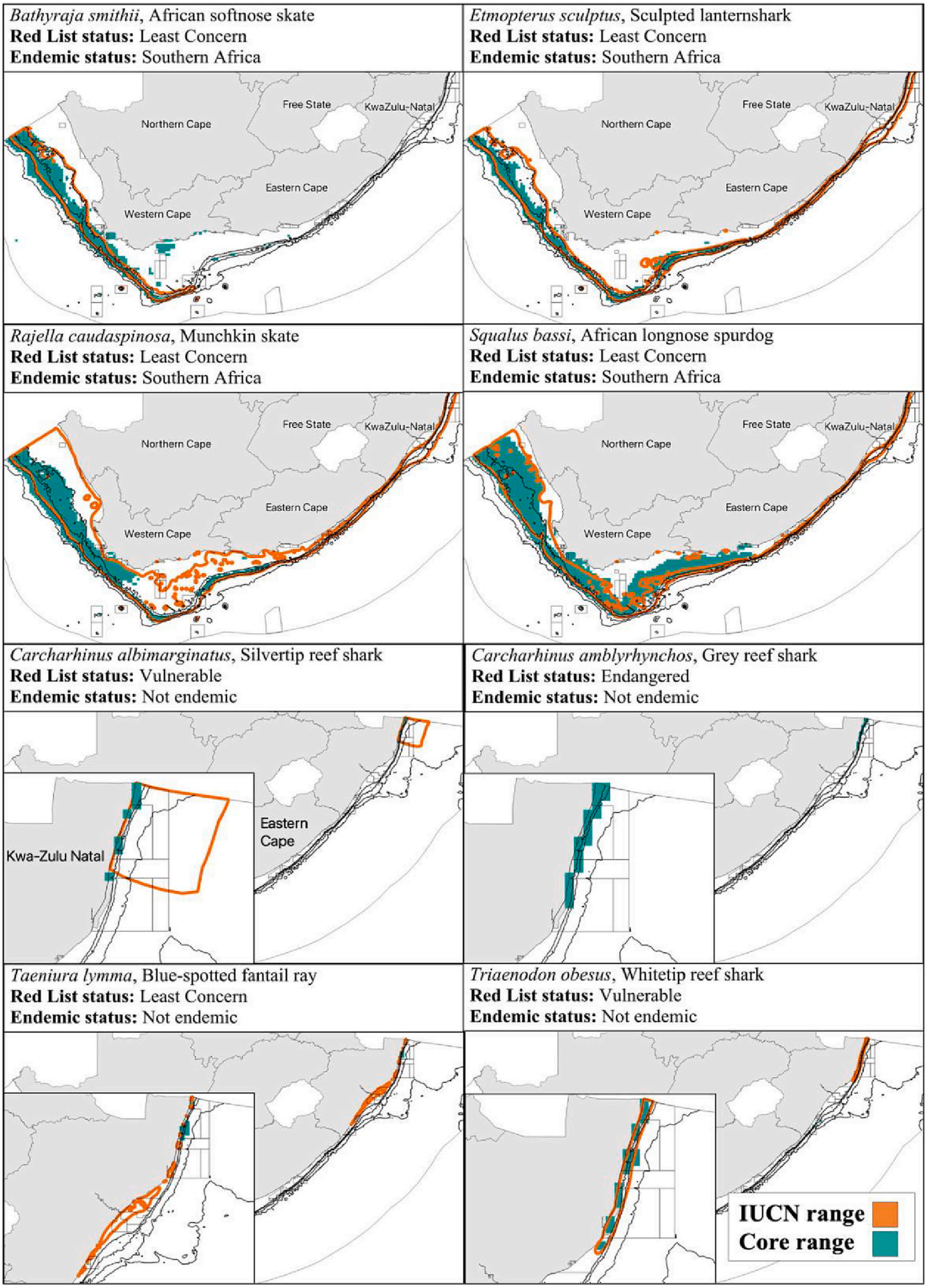

Fig. 6. Core ranges for the chondrichthyan species with the smallest overlap (top 4 panes) and largest overlap (bottom 4 panes) between their range and the South African MPA network. No IUCN range was available for *Carcharhinus amblyrhinchos*. Blue: core range, Orange: IUCN range. The 250 m, 500 m, 1000 m and 2000 m isobaths are shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

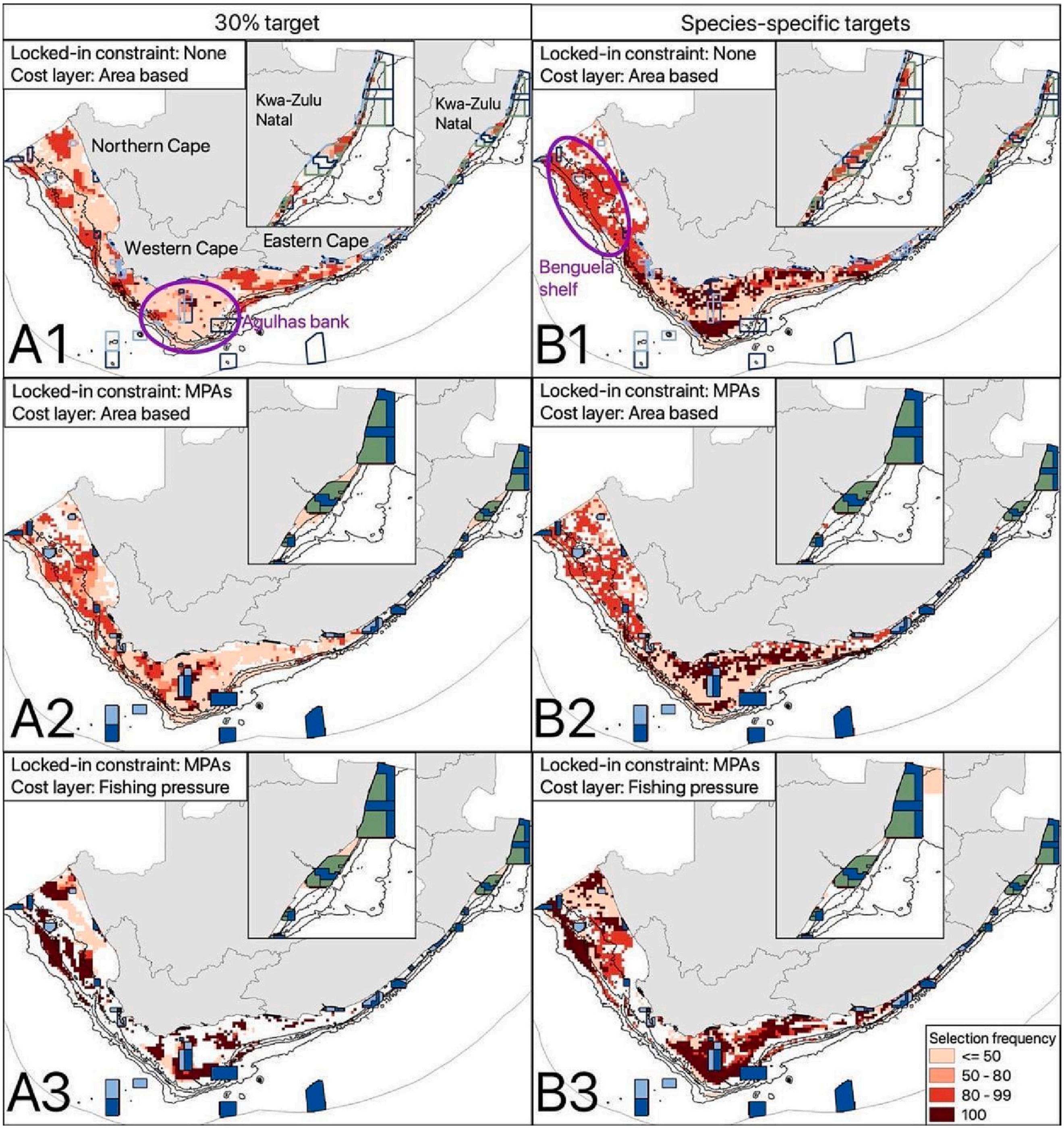

Fig. 7. Frequency selection from different conservation scenarios all run on 64 threatened or southern African endemic chondrichthyan species. Left panel (A1,2,3): 30 % protection target across all species. Right panel (B1,2,3): species-specific protection targets. The KwaZulu-Natal coast is shown as an inset. The 250 m, 500 m, 1000 m and 2000 m isobaths are shown. MPAs are shaded according to zonation: dark blue (no-take), light blue (controlled fishing), green (controlled fishing but not for chondrichthyans). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.3. General effectiveness of MPAs for chondrichthyans

Whilst MPAs are an effective management tool, the scientific consensus is that they are most effective when complemented with other conservation or fisheries management tools (MacNeil et al., 2020). MPAs for chondrichthyans must be informed by region-specific space-use information (van Zinnicq Bergmann et al., 2022) and must be carefully designed to succeed. Some chondrichthyan species may not benefit from spatial protection during their life-history stages when they undergo large-scale pelagic migrations (Simpendorfer and Cook, 2019). However, MPAs can still protect these species when they aggregate for feeding, mating, or pupping. For example, South Africa's population of white shark *C. carcharias* includes transient and resident individuals, with the latter spending more time in coastal MPAs than outside, likely due to increased food availability inside MPAs (Kock et al., 2022). Another study showed that the tiger shark *G. cuvier* also aggregates along the KZN coast, showing a 24 % overlap with existing MPAs (Daly et al., 2018). This evidence strengthens the argument for increased restrictions on chondrichthyan fishing within MPAs.The NEOLI principles (i.e., no-take, well enforced, old [>10 years], large [>100 km2] and

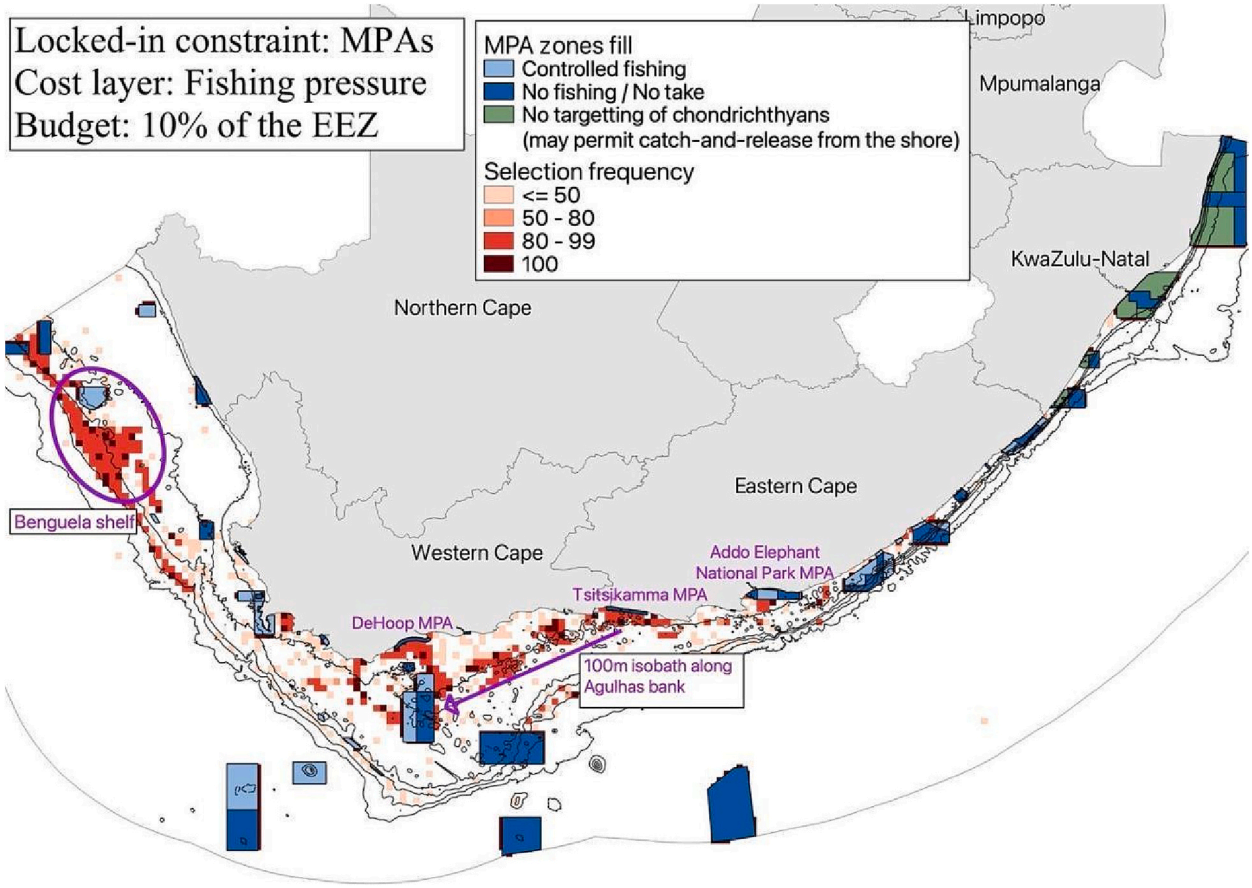

Fig. 8. Frequency selection from a conservation scenario run on 64 threatened and/or southern African endemic chondrichthyan species. This scenario included Critical Biodiversity Areas as a layer. MPAs were locked-in and a maximum area budget of 10 % of the EEZ was set. Species-specific targets were used. The 100 m, 250 m, 500 m, 1000 m and 2000 m isobaths are shown.

isolated) detail the characteristics of successful MPAs (Edgar et al., 2014). In addition, a 2019 guide to MPAs for chondrichthyans outlined key behavioural characteristics that would determine the success of an MPA: residency and site fidelity, philopatry and seasonal aggregations (Simpendorfer and Cook, 2019). MPAs have been shown to help conserve and facilitate recovery of shark and ray species when adequately designed (Bond et al., 2017; Henderson et al., 2016; MacNeil et al., 2020). In South Africa, a study demonstrated the benefit of the no-take zones of the Langebaan Lagoon MPA for soupfin shark *M. mustelus* (da Silva et al., 2013). Specifically, this MPA was identified as a nursery ground due to the large concentrations of neonate and juvenile individuals found in higher abundances over several years within the no-take area (da Silva et al., 2021). Another study within the De Hoop MPA demonstrated that medium to small endemic shark species have greatly benefited from the establishment of a no-take zone and have shown higher relative abundance within the MPA compared with areas outside the MPA (Albano et al., 2021). Whilst this study did not take into account aggregation areas, areas of highest chondrichthyan diversity were modelled and this can be seen as a start to assess the representation of sharks and rays in our MPA network.

Without adequate enforcement even a perfectly designed MPA will not be successful. Cocos Island National Park is a large isolated MPA in Costa Rica, and one of the world's oldest MPAs. Nevertheless, research has shown decreases in the abundance of eight out of 12 chondrichthyan populations in this MPA over the past 20 years (White et al., 2015), driven by illegal fishing pressure within and surrounding the park, resulting from a lack of effective enforcement. Thus, enforcement of MPA regulations is key to their success, which is currently lacking across many South African MPAs (RJ. Adams and Kowalski, 2021; Brill and Raemaekers, 2013; Chadwick et al., 2014). A recent study assessing the NEOLI principles across South Africa's MPAs found that enforcement (E) was the single criterion that consistently scored the poorest (Kirkman et al., 2021).

It is important to note that the IUCN shark specialist group has developed a global strategy to identify important shark and ray areas (ISRAs) (Hyde et al., 2022) in a similar manner that these areas have been identified for important bird (IBAs) and marine mammal (IMMAs) areas in the past. There are four main criteria for an area to be designated as an ISRA, which are: vulnerability, range restriction, life-history and special attributes (distinctiveness and diversity). We have outlined below how this conservation plan aligns with some of these criteria. The vulnerability criterion is accounted for in our protection targets, which were set higher for threatened and endemic species. This ensures that a larger proportion of their range is protected, which contributes to the persistence and recovery of threatened sharks as detailed in the ISRA criteria. The range restricted criteria was accounted for during our species selection process in which we omitted transient and oceanic species and ensured all endemic species were included. We acknowledge that these species may be better protected by other tools such as fisheries management measures and that spatial-based management measures such as MPAs are better suited to habitat- associated species that occupy the same areas year-round or seasonally as detailed in the ISRA criteria. Our consideration of the life-history criteria was greatly hampered by a paucity of life-history data for most of South Africa's chondrichthyan species (Cliff and Olbers, 2022). Trying to incorporate aggregation areas was an ongoing discussion since quantitative data on their location and timing is currently not available. We opted to omit any data that was driven purely by an expert- driven process in this conservation plan.

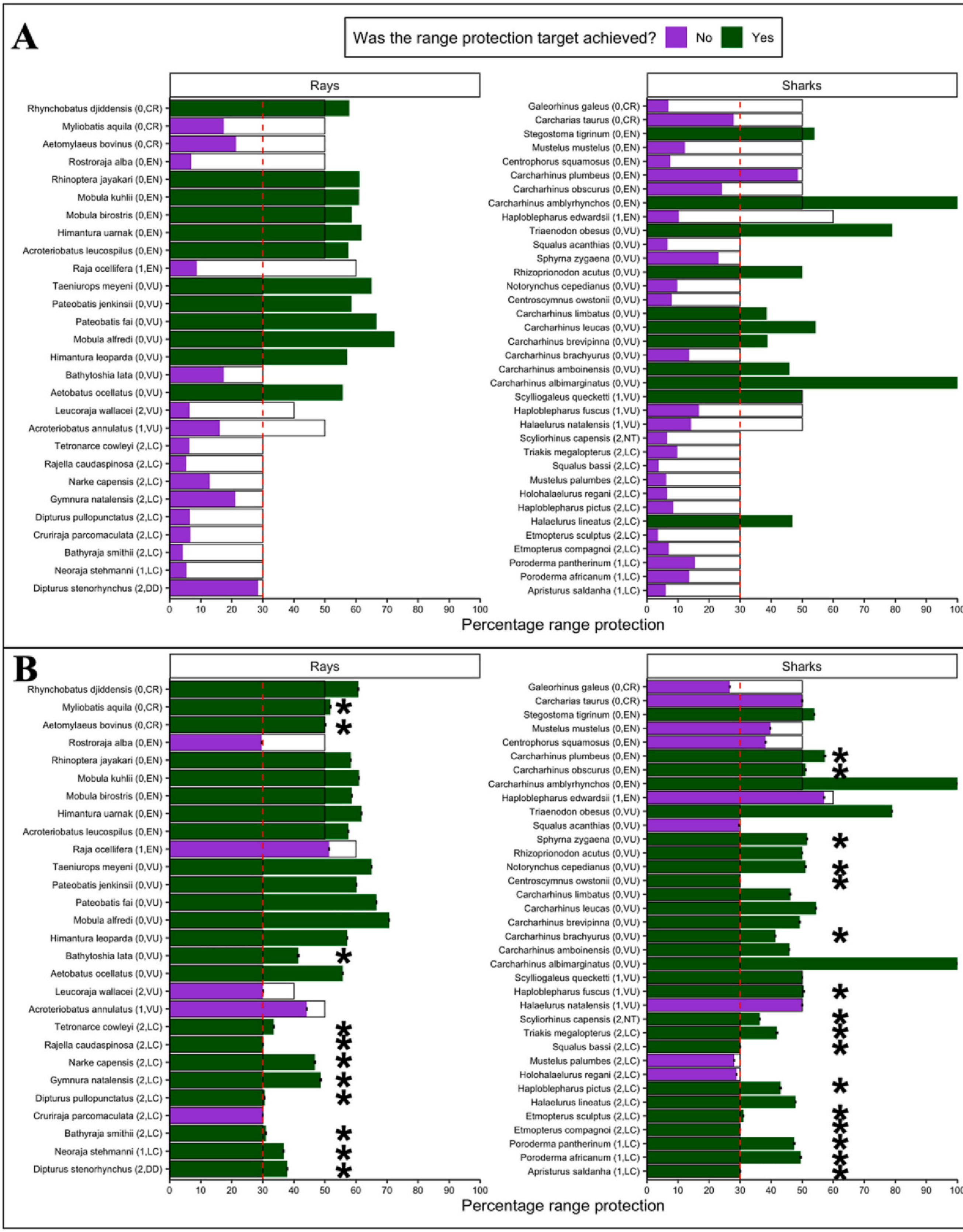

Fig. 9. Percentage range protection achieved across 64 threatened or endemic species. The outline represents the species-specific target set for each species. A: protection conferred solely by South Africa's MPAs, B: protection conferred by South Africa's MPAs and an additional 5 % of the EEZ. An asterisk (*) shows species where the additional 5 % was sufficient to meet the species-specific targets. The red dashed line shows a 30 % range protection threshold. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Finally, the special attributes criteria (distinctiveness and diversity) is the most appropriate for our SCP process since the prioritisation algorithm aims to fulfil as many targets as possible across all species. The areas identified, especially in the conservation scenarios, answer well to this criterion, specifically to sub criterion D2 "Areas that sustain an important diversity of sharks". In conclusion, we believe that there is some alignment between the SCP process and the ISRA process, the main difference being that the SCP process is data-driven and not purely ecological since it also considers existing MPAs as well as socio-economic pressure layers.

4.4. Conclusion and future directions

The outputs from this SCP provide important mechanisms and guidance on how to improve chondrichthyan protection in South African waters. The study provides an assessment of the current protection of threatened sharks and rays in existing MPAs, identifies which MPAs need to strengthen their management objectives and zonation to be effective in protecting these species, and identifies the focal areas of the EEZ where these threatened chondrichthyans would benefit most from increased spatial protection. Establishment of sanctuaries in new or expanded MPAs and OECMs in the priority areas identified through this study would contribute to achieving target three of the Kunming-Montreal GBF, and South Africa's current commitment to achieving 28 % marine protection by 2036 (DFFE, 2022b).

This study provides an opportunity to ensure that chondrichthyans are well represented in the expanded MPA network. Furthermore, this work will support goals identified in South Africa's NPOA II (which recognises increased spatial protection as a need), and it provides guidance to the National Biodiversity Management Plan recently developed for public comment and adoption.

Currently, the protection of threatened chondrichthyans is considered inadequate in some MPAs due to the lack of restrictions with regards to chondrichthyan extraction through commercial and recreational fishing rules within certain zones. These regulations could be adjusted to restrict the extraction of chondrichthyan species or to improve awareness about how to handle and release them with reduced PRM. Increasing spatial protection for sharks and rays within the current MPA network would be less costly and potentially more acceptable for stakeholders than creating new MPAs. Whether the patently needed protection for these highly threatened species is achieved through MPA zonation or expansion, or through OECMs, it will be important to ensure inclusive stakeholder consultations to minimise socio-economic impacts whilst maximising conservation benefits, and to reduce the conflict between different user groups. Support from local communities that live on, near the MPA, or rely upon the area for resources, including extractive, cultural, spiritual and recreational is crucial for any spatial-based protection to be successful. The social and economic impact of South Africa's MPAs on local communities and small-scale fishers has not been extensively studied (Mann-Lang et al., 2021). Information is generally lacking on the interaction between local communities and chondrichthyans, and how increased restrictions regarding the extraction of these species would be received and this would be a fruitful area for future research.

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CRediT authorship contribution statement

Nina Faure-Beaulieu: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Amanda T. Lombard:** Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition. **Jennifer Olbers:** Writing – review & editing, Project administration, Supervision. **Victoria Goodall:** Conceptualization, Methodology, Software, Validation, Formal analysis, Resources, Writing – review & editing, Supervision. **Charlene da Silva:** Investigation, Writing – review & editing. **Ryan Daly:** Investigation, Writing – review & editing. **Gareth Jordaan:** Investigation, Writing – review & editing. **Sven E. Kerwath:** Investigation, Writing – review & editing. **Alison Kock:** Investigation, Writing – review & editing. **Bruce Q. Mann:** Investigation, Writing – review & editing. **Taryn S. Murray:** Investigation, Writing – review & editing. **Patricia Albano:** Investigation, Writing – review & editing. **Geremy Cliff:** Investigation, Writing – review & editing. **Natalie A. dos Santos:** Investigation, Writing – review & editing. **Enrico Gennari:** Investigation, Writing – review & editing. **Neil Hammerschlag:** Investigation, Writing – review & editing. **Aletta E. Bester-van der Merwe:** Investigation, Writing – review & editing. **Ralph Watson:** Investigation, Writing – review & editing. **Sara Andreotti:** Investigation. **Anthony T.F. Bernard:** Investigation. **Paul D. Cowley:** Investigation. **Lauren De Vos:** Investigation. **Natalia Drobniewska:** Investigation. **Chantel Elston:** Investigation. **Chris Fallows:** Investigation. **Toby D. Rogers:** Investigation. **Michaela van Staden:** Investigation. **Pierre de Villiers:** Investigation. **Timothy Guy Paulet:** Investigation. **Jean Harris:** Supervision, Project administration, Funding acquisition.

Declaration of competing interest

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

Data availability

Raw data will not be available but all products resulting from the data will be upon request or in a specified repository.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110163.

References

Adams, R.J., Kowalski, P., 2021. State of Marine Protected Area Management Effectiveness in South Africa. WWF South Africa.

Adams, K.R., Fetterplace, L.C., Davis, A.R., Taylor, M.D., Knott, N.A., 2018. Sharks, rays and abortion: the prevalence of capture-induced parturition in elasmobranchs. Biol. Conserv. 217, 11–27. https://doi.org/10.1016/j.biocon.2017.10.010.

Agardy, T.S., 1997. Marine Protected Areas and Ocean Conservation. Academic Press.

Albano, P.S., Fallows, C., Fallows, M., Schuitema, O., Bernard, A.T.F., Sedgwick, O., Hammerschlag, N., 2021. Successful parks for sharks: no-take marine reserve provides conservation benefits to endemic and threatened sharks off South Africa. Biol. Conserv. 261, 109302 https://doi.org/10.1016/j.biocon.2021.109302.

Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22 (1), 42–47. https://doi.org/10.1016/j.tree.2006.09.010.

Bansemer, C.S., Bennett, M.B., 2010. Retained fishing gear and associated injuries in the east Australian grey nurse sharks (*Carcharias taurus*): implications for population recovery. Mar. Freshw. Res. 61 (1), 97. https://doi.org/10.1071/MF08362.

Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol. Evol. 3 (2), 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x.

Bond, M., Valentin-Albanese, J., Babcock, E., Abercrombie, D., Lamb, N., Miranda, A., Pikitch, E., Chapman, D., 2017. Abundance and size structure of a reef shark population within a marine reserve has remained stable for more than a decade. Mar. Ecol. Prog. Ser. 576, 1–10. https://doi.org/10.3354/meps12241.

Brill, G., Raemaekers, S., 2013. A decade of illegal fishing in Table Mountain National Park (2000–2009): trends in the illicit harvest of abalone *Haliotis midae* and West Coast rock lobster *Jasus lalandii*. Afr. J. Mar. Sci. 35 (4), 491–500. https://doi.org/10.2989/1814232X.2013.850443.

Chadwick, P., Duncan, J., Tunley, K., 2014. State of Management of South Africa's Marine Protected Areas. WWF South Africa Report Series.

Cliff, G., Dudley, S.F.J., 2011. Reducing the environmental impact of shark-control programs: a case study from KwaZulu-Natal, South Africa. Mar. Freshw. Res. 62 (6), 700. https://doi.org/10.1071/MF10182.

Cliff, G., Olbers, J.M., 2022. The Current Status and Management of South Africa's Chondrichthyan Fisheries. WILDTRUST Special Publication 2, Durban, South Africa, p. 549. https://sharkattackcampaign.co.za/wp-content/uploads/2023/01/2023_01_16_WILDOCEANS-endemic-and-threatened-sharks-species-reports_170822.pdf.

Cortés, E., 2000. Life history patterns and correlations in sharks. Rev. Fish. Sci. 8 (4), 299–344. https://doi.org/10.1080/10408340308951115.

Currie, J.C., Thorson, J.T., Sink, K.J., Atkinson, L.J., Fairweather, T.P., Winker, H., 2019. A novel approach to assess distribution trends from fisheries survey data. Fish. Res. 214, 98–109. https://doi.org/10.1016/j.fishres.2019.02.004.

da Silva, C., Kerwath, S., Attwood, C., Thorstad, E., Cowley, P., Økland, F., Wilke, C., Næsje, T., 2013. Quantifying the degree of protection afforded by a no-take marine reserve on an exploited shark. Afr. J. Mar. Sci. 35 (1), 57–66. https://doi.org/10.2989/1814232X.2013.769911.

da Silva, C., Booth, A., Dudley, S., Kerwath, S., Lamberth, S., Leslie, R., McCord, M., Sauer, W., Zweig, T., 2015. The current status and management of South Africa's chondrichthyan fisheries. Afr. J. Mar. Sci. 37 (2), 233–248. https://doi.org/10.2989/1814232X.2015.1044471.

da Silva, C., Attwood, C.G., Wintner, S.P., Wilke, C.G., Winker, H., Smale, M.J., Kerwath, S.E., 2021. Life history of *Mustelus mustelus* in the Langebaan Lagoon marine protected area. Mar. Freshw. Res. 72 (8), 1142. https://doi.org/10.1071/MF20277.

Daley, R.K., Williams, A., Green, M., Barker, B., Brodie, P., 2015. Can marine reserves conserve vulnerable sharks in the deep sea? A case study of *Centrophorus zeehaani* (Centrophoridae), examined with acoustic telemetry. Deep-Sea Res. II Top. Stud. Oceanogr. 115, 127–136. https://doi.org/10.1016/j.dsr2.2014.05.017.

Daly, R., Smale, M.J., Singh, S., Anders, D., Shivji, M., Daly, K., C. A., Lea, J.S.E., Sousa, L.L., Wetherbee, B.M., Fitzpatrick, R., Clarke, C.R., Sheaves, M., Barnett, A., 2018. Refuges and risks: evaluating the benefits of an expanded MPA network for mobile apex predators. Divers. Distrib. 24 (9), 1217–1230. https://doi.org/10.1111/ddi.12758.

Davidson, L.N.K., Dulvy, N.K., 2017. Global marine protected areas to prevent extinctions. Nat. Ecol. Evol. 1 (2), 0040. https://doi.org/10.1038/s41559-016-0040.

Derrick, D.H., Cheok, J., Dulvy, N.K., 2020. Spatially congruent sites of importance for global shark and ray biodiversity. PLoS ONE 15 (7), e0235559. https://doi.org/10.1371/journal.pone.0235559.

DFFE, 2022a. National Plan of Action for the Conservation and Management of Sharks (NPOA-Sharks II). Department of Forestry, Fisheries and the Environment (Department of Forestry, Fisheries, and the Environment).

DFFE, 2022b. Statement by South Africa's Minister of Forestry, Fisheries and the Environment, Ms Barbara Creecy as South Africa marks World Environment Day 2022. Department of Environmental Affairs. https://www.dffe.gov.za/mediarelease/creecy_wed2022.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36 (1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Dulvy, N.K., Pacoureau, N., Rigby, C.L., Pollom, R.A., Jabado, R.W., Ebert, D.A., Finucci, B., Pollock, C.M., Cheok, J., Derrick, D.H., Herman, K.B., Sherman, C.S., VanderWright, W.J., Lawson, J.M., Walls, R.H.L., Carlson, J.K., Charvet, P., Bineesh, K.K., Fernando, D., Simpfendorfer, C.A., 2021. Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. Curr. Biol. 31 (21), 4773–4787.e8. https://doi.org/10.1016/j.cub.2021.08.062.

Ebert, D.A., Wintner, S.P., Kyne, P.M., 2021. An annotated checklist of the chondrichthyans of South Africa. Zootaxa 4947 (1), 1–127. https://doi.org/10.11646/zootaxa.4947.1.1.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S. J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Thomson, R.J., 2014. Global conservation outcomes depend on marine protected areas with five key features. Nature 506 (7487), 7487. https://doi.org/10.1038/nature13022.

Ellis, J.R., McCully Phillips, S.R., Poisson, F., 2017. A review of capture and post-release mortality of elasmobranchs: capture mortality of elasmobranchs. J. Fish Biol. 90 (3), 653–722. https://doi.org/10.1111/jfb.13197.

Findlay, K., 2018. Operation Phakisa and unlocking South Africa's ocean economy. J. Indian Ocean Reg. 14 (2), 248–254. https://doi.org/10.1080/19480881.2018.1475857.

Finucci, B., Cheok, J., Ebert, D.A., Herman, K., Kyne, P.M., Dulvy, N.K., 2021. Ghosts of the deep – biodiversity, fisheries, and extinction risk of ghost sharks. Fish Fish. 22 (2), 391–412. https://doi.org/10.1111/faf.12526.

Fitzpatrick, M.C., Lachmuth, S., Haydt, N.T., 2021. The ODMAP protocol: a new tool for standardized reporting that could revolutionize species distribution modeling. Ecography 44 (7), 1067–1070. https://doi.org/10.1111/ecog.05700.

Giménez, J., Cardador, L., Mazor, T., Kark, S., Bellido, J.M., Coll, M., Navarro, J., 2020. Marine protected areas for demersal elasmobranchs in highly exploited Mediterranean ecosystems. Mar. Environ. Res. 160, 105033 https://doi.org/10.1016/j.marenvres.2020.105033.

Hanson, J.O., Schuster, R., Morrell, N., Strimas-Mackey, M., Watts, M.E., Arcese, P., Bennett, J., Possingham, H.P., 2021. Prioritizr: systematic conservation prioritization in R. https://CRAN.R-project.org/package=prioritizr.

Harris, L., Holness, S.D., Kirkman, S.P., Sink, K.J., Majiedt, P., Driver, A., 2022. National Coastal and Marine Spatial Biodiversity Plan, Version 1.2 (Released 12-04-2022): Technical Report. Nelson Mandela University, Department of Forestry, Fisheries and the Environment, and South African National Biodiversity Institute, South Africa (280 pp.).

Haupt, P.W., Lombard, A.T., Goodman, P.S., Harris, J.M., 2017. Accounting for spatiotemporal dynamics in conservation planning for coastal fish in KwaZulu-Natal, South Africa. Biol. Conserv. 209, 289–303. https://doi.org/10.1016/j.biocon.2017.02.009.

Henderson, Aaron C., Jourdan, A., Bell, K., 2016. Assessing the incidental value of a marine reserve to a lemon shark *Negaprion brevirostris* nursery: Bell Sound Nature Reserve. Aquat. Conserv. Mar. Freshwat. Ecosyst. 26 (3), 482–491. https://doi.org/10.1002/aqc.2627.

Hyde, C.A., Notarbartolo di Sciara, G., Sorrentino, L., Boyd, C., Finucci, B., Fowler, S.L., Kyne, P.M., Leurs, G., Simpfendorfer, C.A., Tetley, M.J., Womersley, F., Jabado, R. W., 2022. Putting sharks on the map: a global standard for improving shark area-based conservation. Front. Mar. Sci. 9. https://www.frontiersin.org/articles/10.3389/fmars.2022.968853.

Kerwath, S.E., Thorstad, E.B., Næsje, T.F., Cowley, P.D., Økland, F., Wilke, C., Attwood, C.G., 2009. Crossing invisible boundaries: the effectiveness of the Langebaan Lagoon marine protected area as a harvest refuge for a migratory fish species in South Africa. Conserv. Biol. 23 (3), 653–661. https://doi.org/10.1111/j.1523-1739.2008.01135.x.

Kirkman, S., Mann, B., Sink, K., Adams, R., Livingstone, T.-C., Mann-Lang, J., Pfaff, M., Samaai, T., van der Bank, M., Williams, L., Branch, G., 2021. Evaluating the evidence for ecological effectiveness of South Africa's marine protected areas. Afr. J. Mar. Sci. 43 (3), 389–412. https://doi.org/10.2989/1814232X.2021.1962975.

Kock, A.A., Lombard, A.T., Daly, R., Goodall, V., Meÿer, M., Johnson, R., Fischer, C., Koen, P., Irion, D., Gennari, E., Towner, A., Jewell, O.J.D., da Silva, C., Dicken, M.L., Smale, M.J., Photopoulou, T., 2022. Sex and size influence the spatiotemporal distribution of white sharks, with implications for interactions with fisheries and spatial management in the Southwest Indian Ocean. Front. Mar. Sci. 9. https://www.frontiersin.org/articles/10.3389/fmars.2022.811985.

Liu, C., White, M., Newell, G., 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. J. Biogeogr. 40 (4), 778–789. https://doi.org/10.1111/jbi.12058.

MacNeil, M.A., Chapman, D.D., Heupel, M., Simpfendorfer, C.A., Heithaus, M., Meekan, M., Harvey, E., Goetze, J., Kiszka, J., Bond, M.E., Currey-Randall, L.M., Speed, C.W., Sherman, C.S., Rees, M.J., Udyawer, V., Flowers, K.I., Clementi, G., Valentin-Albanese, J., Gorham, T., Cinner, J.E., 2020. Global status and conservation potential of reef sharks. Nature 583 (7818), 801–806. https://doi.org/10.1038/s41586-020-2519-y.

Mann, B.Q., Cowley, P.D., Dunlop, S.W., Potts, W.M., 2018. Is catch-and-release shore angling compatible with the conservation goals of T marine protected areas? A case study from the iSimangaliso Wetland Park in South Africa. Fish. Res. 10.

Mann-Lang, J., Branch, G., Mann, B., Sink, K., Kirkman, S., Adams, R., 2021. Social and economic effects of marine protected areas in South Africa, with recommendations for future assessments. Afr. J. Mar. Sci. 43 (3), 367–387. https://doi.org/10.2989/1814232X.2021.1961166.

Margules, C.R., Pressey, R.L., 2000. Systematic Conservation Planning, vol. 405, p. 11.

O'Brien, S.M., Gallucci, V.F., Hauser, L., 2013. Effects of species biology on the historical demography of sharks and their implications for likely consequences of contemporary climate change. Conserv. Genet. 14 (1), 125–144. https://doi.org/10.1007/s10592-012-0437-8.

Operation Phakisa, 2014. Phakisa: Fast-tracking Ocean Protection in South Africa, Initiative 8, Establishment of an Effective and Representative MPA Network (Technical Report (2014).

Pebesma, E., 2018. Simple features for R: standardized support for spatial vector data. R J. 10 (1), 439–446. https://doi.org/10.32614/RJ-2018-009.

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol. Appl. 19 (1), 181–197. https://doi.org/10.1890/07-2153.1.

Queiroz, N., Humphries, N.E., Couto, A., Vedor, M., da Costa, I., Sequeira, A.M.M., Mucientes, G., Santos, A.M., Abascal, F.J., Abercrombie, D.L., Abrantes, K., Acuña-Marrero, D., Afonso, A.S., Afonso, P., Anders, D., Araujo, G., Arauz, R., Bach, P., Barnett, A., Sims, D.W., 2019. Global spatial risk assessment of sharks under the footprint of fisheries. Nature 572 (7770), 7770. https://doi.org/10.1038/s41586-019-1444-4.

R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. https://www.R-project.org/.

RSA, 2004. No. 57 of 2003: National Environmental Management: Protected Areas Act, 2003. Government Gazette, Republic of South Africa.

RSA, 2019. RSA Government Gazette (No. 647).

RStudio Team, 2022. RStudio: Integrated Development Environment for R. RStudio, PBC. http://www.rstudio.com/.

Schlaff, A.M., Heupel, M.R., Simpfendorfer, C.A., 2014. Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. Rev. Fish Biol. Fish. 24 (4), 1089–1103. https://doi.org/10.1007/s11160-014-9364-8.

Sherman, C.S., Simpfendorfer, C.A., Pacoureau, N., Matsushiba, J.H., Yan, H.F., Walls, R. H.L., Rigby, C.L., VanderWright, W.J., Jabado, R.W., Pollom, R.A., Carlson, J.K., Charvet, P., Bin Ali, A., Fahmi, Cheok, J., Derrick, D.H., Herman, K.B., Finucci, B., Eddy, T.D., Dulvy, N.K., 2023. Half a century of rising extinction risk of coral reef

sharks and rays. Nat. Commun. 14 (1), 1 https://doi.org/10.1038/s41467-022-35091-x.
Shiffman, D.S., Hammerschlag, N., 2016. Shark conservation and management policy: a review and primer for non-specialists. Anim. Conserv. 19 (5), 401–412. https://doi.org/10.1111/acv.12265.
Simpendorfer, C., Cook, J., 2019. A Practical Guide to Effective Design and Management of MPAs for Sharks and Rays. WWF, Gland, Switzerland, p. 64.
Sink, K.J., van der Bank, Megan, Majiedt, Prideel, Harris, Linda, Atkinson, Lara, Kirkman, Stephen, Karenyi, Natasha, 2019. South African National Biodiversity Assessment 2018 Technical Report Volume 4: Marine Realm. South African National Biodiversity Institute, Pretoria, South Africa, p. 597. http://hdl.handle.net/20.500.12143/6372.
Smith, J.A., Tommasi, D., Welch, H., Hazen, E.L., Sweeney, J., Brodie, S., Muhling, B., Stohs, S.M., Jacox, M.G., 2021. Comparing dynamic and static time-area closures for bycatch mitigation: a management strategy evaluation of a swordfish fishery. Front. Mar. Sci. 8. https://www.frontiersin.org/articles/10.3389/fmars.2021.630607.
Steen, V.A., Tingley, M.W., Paton, P.W.C., Elphick, C.S., 2021. Spatial thinning and class balancing: key choices lead to variation in the performance of species distribution models with citizen science data. Methods Ecol. Evol. 12 (2), 216–226. https://doi.org/10.1111/2041-210X.13525.
Thuiller, W., Georges, D., Gueguen, M., Engler, R., Breiner, F., 2021. biomod2: ensemble platform for species distribution modeling. https://CRAN.R-project.org/package=biomod2.
Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., Clerck, O.D., 2012. Bio-ORACLE: a global environmental dataset for marine species distribution modelling. Glob. Ecol. Biogeogr. 21 (2), 272–281. https://doi.org/10.1111/j.1466-8238.2011.00656.x.
van Zinnicq Bergmann, M.P.M., Guttridge, T.L., Smukall, M.J., Adams, V.M., Bond, M.E., Burke, P.J., Fuentes, M.M.P.B., Heinrich, D.D.U., Huveneers, C., Gruber, S.H., Papastamatiou, Y.P., 2022. Using movement models and systematic conservation planning to inform marine protected area design for a multi-species predator community. Biol. Conserv. 266, 109469 https://doi.org/10.1016/j.biocon.2022.109469.
Ward-Paige, C.A., Worm, B., 2017. Global evaluation of shark sanctuaries. Glob. Environ. Chang. 47, 174–189. https://doi.org/10.1016/j.gloenvcha.2017.09.005.
White, E.R., Myers, M.C., Flemming, J.M., Baum, J.K., 2015. Shifting elasmobranch community assemblage at Cocos Island—an isolated marine protected area. Conserv. Biol. 29 (4), 1186–1197. https://doi.org/10.1111/cobi.12478.
Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Yutani, H., 2019. Welcome to the tidyverse. J. Open Source Softw. 4 (43), 1686. https://doi.org/10.21105/joss.01686.
Zurell, D., Franklin, J., König, C., Bouchet, P.J., Dormann, C.F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A., Lahoz-Monfort, J.J., Leitão, P.J., Park, D.S., Peterson, A.T., Rapacciuolo, G., Schmatz, D.R., Schröder, B., Serra-Diaz, J.M., Thuiller, W., Merow, C., 2020. A standard protocol for reporting species distribution models. Ecography 43 (9), 1261–1277. https://doi.org/10.1111/ecog.04960.