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Conserving threatened marine species and biodiversity requires 40% ocean protection

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ABSTRACT

Global prioritisation of where to locate Marine Protected Areas (MPA) has not considered both a comprehensive range of measures of biodiversity as well as threatened species distributions. Using maps of 974 threatened species ranges, we found that areas of high threatened species richness are distributed throughout the world's coastal and continental shelf areas as well as in offshore regions and well-known biodiversity hotpots. We then assessed whether Representative Biodiversity Areas (RBAs), the top 30% of the global ocean prioritised based on holistic measures of biodiversity from genes to ecosystems, adequately cover the ranges of threatened species. Implementing RBAs could protect a minimum of 30% of most threatened species ranges, but 26 threatened species have distributions in areas with poor overlap with biodiversity priorities.

Using decision support software we found that a minimum of 40% of the ocean is required to adequately protect over 68% of all aspects of biodiversity and 30% of IUCN Red List threatened species ranges. Priority areas outside Exclusive Economic Zones (39%) demonstrate the importance of the High Seas (59% of the global oceans) to biodiversity conservation. Recognising the uncertainties inherent in our approach due to the limited proportion of taxa assessed by the IUCN Red List, we used an uncertainty analysis to support our findings. We found that currently, only 2.5% of priority areas are within marine reserves, highlighting the urgent need for increased protection of important areas for biodiversity and threatened species across EEZs and the High Seas.

1. Introduction

Marine biodiversity has declined substantially over the last half-century due to fishing, pollution, climate change and a myriad of other anthropogenic impacts (Halpern et al., 2015; McCauley et al., 2015). To arrest recent declines in species abundance and diversity and sustain the ecosystem services that humans depend on, member countries committed to The Convention on Biological Diversity's (CBD) Aichi Target 11, to include 10% of the ocean in protected areas by 2020 (Convention on Biological Diversity, 2010). The World Parks Congress and the IUCN World Conservation Congress further called for the full protection of at least 30% of the global ocean, a target supported by scientific evidence needed to effectively conserve marine biodiversity (World Parks World Parks Congress, 2014; IUCN, 2016a; O'Leary et al., 2016). Marine Protected Areas (MPAs) currently cover 6.4% of the global ocean, but the level of protection provided by many MPAs is unknown and over 90% allow fishing (Costello and Ballantine, 2015; Marine Conservation Institute, 2021). Furthermore, partially protected MPAs are no more effective than unprotected areas at benefiting biodiversity (Aburto-Oropeza et al., 2011; Costello, 2014; Turnbull et al., 2021). In contrast, no-take MPAs, hereafter called marine reserves, are effective at restoring and preserving biodiversity while benefiting ecosystem resilience (Costello, 2014; Roberts et al., 2017; Sala and Giakoumi, 2018; Bates et al., 2019). Marine reserves currently cover 2.7% of the global ocean, but such limited ocean protection is insufficient to achieving global ecological and economic targets (Lindegren et al., 2018; Roberts et al., 2020; Marine Conservation Institute, 2021). There is increasing support for ocean protection, and globally, the public expect and desire a greatly expanded, effective network of protected areas (Hawkins et al., 2016; Lotze et al., 2018). Given the slow

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progress towards achieving protection targets and the ongoing decline of marine biodiversity, identifying priority areas for marine protection has been promoted in order to target resources and conservation efforts where they are most required (Jefferson and Costello, 2020).

Marine conservation prioritisation has identified areas with high species richness, endemism and threats. Yet, rarely are threatened species considered with such importance, even though they represent those most likely to become extinct (Roberts et al., 2002; Trebilco et al., 2011; Stuart-Smith et al., 2013; Selig et al., 2014; Klein et al., 2015; Davies et al., 2017; Ramírez et al., 2017). Protecting threatened species is a key tenet of the CBD targets, as per Aichi Target 12 “By 2020 the extinction of known threatened species has been prevented and their conservation status, particularly of those most in decline, has been improved and sustained” (Convention on Biological Diversity, 2010). Prioritisation approaches from Selig et al. (2014), Klein et al. (2015), Jenkins and Van Houtan (2016), O'Hara et al. (2019), Visalli et al. (2020), Zhao et al. (2020) and Sala et al. (2021), have provided a global scale analysis of where MPAs should be located to protect biodiversity, but a number of these studies do not specifically consider threatened species. Of those that do, Jenkins and Van Houtan (2016) ranked areas for conservation priority based on the sum of 4352 individual species' ranges within an area relative to threats and existing protection, with summed metrics resulting in priorities biased towards areas with high overlap of species. O'Hara et al. (2019) combined species spatial range and conservation status to map the mean extinction risk of 5291 species assessed by the IUCN Red list including species of ‘Least Concern’. However, by using the mean conservation status in each particular cell (averaging risk across all species) to delineate spatial conservation priorities, this approach did not account for the imperilment of individual species. Visalli et al. (2020) used prioritisation software on species richness weighted for extinction risk, habitat indicators and fishing effort, to propose where best to locate MPAs, but their study scale was limited to the High Seas (also called Areas Beyond National Jurisdiction, ABNJ). Sala et al. (2021) prioritised areas based on food provisioning, carbon storage and biodiversity. Their analysis considered 4242 species distributions and their threat status, as well as functional and evolutionary distinctiveness. While providing a comprehensive analysis, their study was limited to roughly half ($n = 537$) of known threatened marine species and they did not determine the minimum ocean protection needed to protect threatened species or their ranges. As such, determining where conservation efforts should be focussed to provide adequate protection to reduce extinction risk for all known threatened species remains unmapped.

While few prioritisations based on threatened marine species have been undertaken, there have been a number of global studies tasked with prioritising important areas for biodiversity. Selig et al. (2014) used species richness (12,500 species), two measures of endemism (range rarity and proportional range rarity) and cumulative human impacts to identify priority areas. Klein et al. (2015) assessed the overlap of global MPAs with the ranges of 17,348 species, determining priority areas based on the distribution of gap species (those with no protection) and rare species (<2% of range represented). Jenkins and Van Houtan (2016) used an index that considered species vulnerability, coverage by MPAs and human impacts. Apart from Sala et al. (2021), none of these analyses specifically differentiated or included areas of varying species composition, such as areas of high species endemicity, i.e., realms (Spalding et al., 2007; Costello et al., 2017), nor ecosystems, habitats or biomes (Costello et al., 2020). Addressing these gaps, Zhao et al. (2020) quantitatively prioritised the top 30% of the marine environment using seven ecosystems (mapped based on 20 environmental variables), four biomes (seagrass, kelp, mangrove, and shallow water coral reefs), seabed rugosity (as a measure of topographic habitat complexity), and species richness within each biogeographic realm using AquaMaps species range maps of 24,904 species, thereby maximising the representivity of overall biodiversity. This approach provided a comprehensive assessment of where to protect biodiversity, prioritising the 30% of the ocean with 68% of all species and more than 80% of biomes, but did not consider the threat status of species. As the distribution of threatened species does not always coincide with areas of high species richness or endemicity (Asaad et al., 2018), it is important to consider threatened species, as well as biodiversity as a whole, when prioritising areas for protection.

Here we address the shortcomings of marine protection global prioritisations with respect to threatened species conservation. We first compile the most comprehensive database of threatened species distributions to date, determining optimal spatial prioritisations for the protection of threatened marine species. We then assess the efficacy of using Representative Biodiversity Areas (RBAs), as prioritised by Zhao et al. (2020), to protect threatened species. Finally, we determine the most spatially efficient prioritisation to protect both threatened species and biodiversity, and then evaluate the overlap of these areas with the current global marine reserve network.

2. Methods

2.1. Threatened species ranges

Threatened species were defined as per the International Union for Conservation of Nature Red List of Threatened Species (IUCN Red List), the foremost authority on the extinction risk of flora and fauna (Rodrigues et al., 2006; Betts et al., 2020; IUCN, 2020). The current IUCN Red List was searched for: species; marine systems; all marine regions; and only those species in the Red List categories: Critically Endangered (facing an extremely high risk of extinction), Endangered (facing a very high risk of extinction), and Vulnerable (facing a high risk of extinction). In line with previous research, species classed as Data Deficient, which are too poorly known to be included in analyses determining spatial proportions of threatened species or extinction risk, were excluded (Webb and Mindel, 2015; O'Hara et al., 2019; Visalli et al., 2020). The resulting list (as per data downloaded on 19th December 2020) was then refined by further evaluation of all species in the taxonomic rank “Aves” to distinguish marine from terrestrial species. To determine which species within the rank “Aves” to include in this study, the species group ‘seabirds' was used, as defined by BirdLife International and Croxall et al. (2012). Each threatened species name was then checked for nomenclature against the World Register of Marine Species (WoRMS, Horton et al., 2021), the leading authority on marine species taxonomy (Costello et al., 2013a, 2013b; Vandepitte et al., 2018).

Two sources were utilised to acquire species distribution maps: the IUCN Red List (IUCN, 2020) and AquaMaps (Kaschner et al., 2019). Analyses were performed at species level. Thus, any subspecies distributions were merged into a single parent species layer. IUCN Red List species ranges consist of expert drawn, simplified polygons around known occurrence localities (Herkt et al., 2017). Species range polygons (range maps) are categorised under a variety of presence categories (IUCN, 2016b). All polygons with categories indicating uncertain presence (Extinct, Possibly Extinct, Presence Uncertain, Possibly Extant - breeding, Possibly Extant - resident, Probably Extant - seasonality uncertain and Probably Extant - resident) were removed before determining each threatened species extent of occurrence, as per IUCN mapping standards (IUCN, 2016b). Distributions recorded under Vagrant were also excluded. This ensured that any modelling was based on high certainty of spatial occurrence for the threatened species included in our analysis.

AquaMaps generates model-based predictions of species ranges by using estimates of environmental preferences (using depth, water temperature, salinity, primary productivity, and association with sea ice or coastal areas) within FAO areas (large geographical fishing areas designated by the Food and Agriculture Organization of the United Nations), creating environmental envelopes derived from species occurrence data (Kesner-Reyes et al., 2016). These environmental envelopes are then matched against environmental conditions to determine the suitability of an area for a species (Kesner-Reyes et al., 2016). AquaMaps ranges contain a probability of occurrence per cell. In line with previous research, species presence was defined as all cells with a probability threshold above zero, the most comparable to the range maps of maximum extent used by Birdlife International and the IUCN Red List (Selig et al., 2014; Zhao et al., 2020).

Using ArcMap (version 10.6.1) and R (version 3.6.0), IUCN species range maps were converted to a resolution of 0.5-degree latitude – longitude cells. AquaMaps range maps were already at 0.5-degrees. Species with distribution data in both databases (488) were compared with OBIS and GBIF occurrence data, detailed geographic range information from the IUCN Red List website, and recent literature ($\leq$10 years), to determine which range map best represented the species distribution. Threatened species with only IUCN (458) or AquaMaps range maps (28) were automatically included for further analyses, as the data represented the only available distribution data for such species. The inaccuracies of both IUCN and AquaMaps range maps have been noted in previous studies (Herkt et al., 2017; O'Hara et al., 2017; Ramesh et al., 2017; Alhajeri and Fourcade, 2019). While some may be inaccurate at local scale, or not reflect recent changes in species distributions due to human impacts or climate change, they provide the best indicator of where conservation measures may best protect threatened species at a global scale.

In total, AquaMaps and the IUCN Red List provided range maps for 974 threatened species from 19 taxonomic classes. The list of species used, their threat status, global range, and the source of each species range map is provided in the online Supplementary Material. Range maps for 35 threatened species were not available in either database and were excluded from our analysis. The IUCN Red List and AquaMaps provided 78% and 22% of threatened species range maps, respectively (Table 1).

2.2. *Protecting threatened species*

Using R, species richness was summed per 0.5-degree cell for all threatened species. Data were grouped by threat status (Critically Endangered, Endangered and Vulnerable) and by taxonomic rank, birds (Aves), mammals (Mammalia), reptiles (Reptilia), ‘fish’ (which combined Actinopterygii, Elasmobranchii, Holocephali, Coelacanthi and Myxini), ‘corals’ (Anthozoa), ‘invertebrates’ (Bivalvia, Cephalopoda, Gastropoda, Holothuroidea, Hydrozoa, Malacostraca and Merostomata), ‘mangroves and seagrasses’ (Magnoliopsida), and ‘algae’ (Florideophyceae and Phaeophyceae), to highlight important areas for threatened species richness. As mapping species richness is only one method of defining important areas for threatened species, we used the decision-support tool Zonation to identify optimal areas for hypothetical protection of each threatened species range. Zonation is a decision-support software that uses a stepwise algorithm that begins by assuming that the ocean is fully protected, and then progressively identifies and removes cells that contribute the smallest marginal losses in the representation of specified biodiversity features (Moilanen et al., 2005; Moilanen et al., 2009; Moilanen et al., 2011; Moilanen et al., 2014; Lehtomäki and Moilanen, 2013). Zonation also provides a number of cell-removal rules, of which we used the Target Based Function (TBF), as it enables the user to set a target of spatial coverage for each threatened species range.

Species whose range of cell occurrence covered two or less 0.5-degree cells could not be included in the Zonation analysis, namely the cone snails *Conus belairensis, C. decoratus, C. lugubris,* and *Conus tacomae,* and fish *Brachionichthys hirsutus* and *Entomacrodus solus*. Following analysis, these species ranges were individually compared with Zonation results and were nevertheless found to be included in high priority Zonation solutions, due to their spatial overlap with other threatened species ranges. All threatened species range maps were converted to a 360 × 720 grid-cell raster file with a total of 259,200 cells at a resolution of 0.5-degrees, ranging from 90°N to −90°S and −180°W to 180°E. All terrestrial cells were masked using the Natural Earth 10 m Ocean polygon (version 4.1.0, (Natural Earth, 2019)). As all data layers were projected by equal degrees, cells at high latitudes were distorted and smaller than those at the equator. However, few threatened species had ranges in polar or high latitude areas, and all polar species had large geographic ranges, so cell distortion had minimal effect on determining relative protection of each threatened species.

The first Zonation scenario (hereafter Scenario 1) determined the most spatially efficient solution to protecting a minimum of 30% of every threatened species range. As far ranging species such as blue whale (*Balaenoptera musculus*) and sperm whale (*Physeter macrocephalus*) have a near global distribution, a TBF target of 0.3 (30%) was used to ensure the prioritisation of 30% of each threatened species range, in accordance with recent calls for 30% ocean protection (World Parks Congress, 2014; IUCN, 2016a).

2.3. *Does protecting biodiversity protect threatened species?*

Zhao et al. (2020) identified areas that provide a comprehensive marine biodiversity prioritisation for 30% of the global oceans based on

Table 1

The database used, threat status and total number of threatened species per taxonomic class. Empty cells = 0, NA = classes not represented by the database.

Class	IUCN species				AquaMaps species				Total species
	No.	CR	EN	VU	No.	CR	EN	VU	
Actinopterygii	227	16	50	161	81	8	15	58	308
Anthozoa	147	2	22	123	76	1	1	74	223
Aves	100	13	33	54	NA				100
Bivalvia	1	1			NA				1
Cephalopoda	NA				1			1	1
Coelacanthi	NA				1	1			1
Elasmobranchii	160	33	38	89	35	7	13	15	195
Florideophyceae	9	6		3	NA				9
Gastropoda	32	1	11	20	4	1	2	1	36
Holocephali	1			1	NA				1
Holothuroidea	11		5	6	5		2	3	16
Hydrozoa	3	1		2	1		1		4
Magnoliopsida	16	1	5	10	1			1	17
Malacostraca	1	1			1			1	2
Mammalia	28	2	13	13	4		3	1	32
Merostomata	1		1		1			1	2
Myxini	6	1	2	3	3			3	9
Phaeophyceae	6	4	1	1	NA				6
Reptilia	9	4	2	3	2			2	11
Total species	758	86	183	489	216	18	37	161	974

ecosystems, biomes, seabed rugosity and species richness adjusted within areas of endemicity, hereafter "Representative Biodiversity Areas" (RBAs). The efficacy of using RBAs to protect threatened species was then evaluated. The threatened species richness data layers were analysed to determine the highest 30%, 20% and 10% of threatened species richness cells for each grouping. All threatened species richness data layers were then compared with the RBAs in ArcMap to determine the amount of overlapping 0.5-degree cells and the percentage overlap. As the resolution of the RBA data layer was 0.9-degrees, it was resampled in ArcMap to match the resolution of other data used in our analysis (0.5-degrees). The ArcGIS data management tool 'Resample' with the 'Bilinear' resampling technique was used as it provides the most accurate resampling method, calculating the value of each pixel by averaging the values of the surrounding four pixels (weighted for distance). The processing extent (grid size) of the RBA data layer was also increased to match the extent of other data layers.

Whereas Scenario 1 only used threatened species ranges, in Scenario 2 we used Zonation to evaluate the efficacy of using RBAs to protect threatened species ranges. The RBA data layer was used as a mask, allowing Zonation to give highest conservation priority to areas within RBAs. The RBA data layer was prepared for Zonation analysis as per the threatened species range maps in Scenario 1; all other Zonation settings remained the same. For accuracy, all terrestrial cells were masked from the Zonation processing extent of the RBA data layer. Hence, the RBA data layer evaluated here was slightly smaller in total area than that presented by Zhao et al. (2020).

2.4. *Combined priority areas for threatened species and biodiversity*

In Scenario 3, we combined prioritisations from Scenarios 1 and 2 to illustrate multi-objective optimisation for both threatened species and biodiversity. The Zonation result from Scenario 2 was used to quantify the minimum ocean protection required to conserve both 30% of all threatened species ranges and all RBAs. The proportion of ocean protection was increased until 30% of every threatened species range and 100% of RBAs were prioritised, resulting in Combined Priority Areas (CPAs). The percent of CPAs protected by currently implemented marine reserves was then calculated, as per data downloaded on the 21st of January 2021 from MPAtlas. MPAtlas independently evaluate the protection level of protected areas using a scientifically rigorous approach, providing the most accurate depiction of marine protection (Marine Conservation Institute, 2021). All marine reserves classed as unimplemented and those smaller than a single 0.5-degree cell (55 km × 55 km at the equator, $\sim$3000 km^2) were excluded for accuracy, as including such reserves would have led to an overestimation of current protection (as many reserves are considerably smaller than a single cell). Using the ArcGIS spatial analyst tool, 'Extract by Mask', all cells within CPAs overlapping with marine reserve shapefile polygons were identified. Further analysis in R determined the number and percentage of cells within CPAs currently protected by the existing reserve network.

2.5. *Uncertainty analysis*

To account for the deterministic nature of our analysis and investigate the uncertainty of our results, we used a bootstrapping exercise, conducting 100 iterations of our priority analysis. Each iteration contained a random subset of threatened species, equal to 70% of the entire threatened species database ($n = 678$); all other Zonation settings remained the same as those used in Scenario 2. The count of each cell selected by the 100 iterations (with a score of at least 0.6) within the Combined Priority Areas (CPAs) was then summed, providing an irreplaceability score for each cell in our priority solution. The average priority score per cell was also determined from the 100 iterations, providing a sensitivity score for all cells within the CPAs. Results were then mapped to show the probability of cell selection based on irreplaceability scores in which each cell was within the top 60, 70, 80 and 90% of our prioritisation solution (CPAs), and the sensitivity of cells within CPAs based on their average priority score, displayed as percent increase or decrease in average cell score.

The final prioritisation maps provide an index for every 0.5-degree cell and are available as a digital spatial layer on Figshare.

3. Results

3.1. *Protecting threatened species*

The global distribution of threatened species showed higher species occurrence richness in coastal and continental shelf areas, particularly in the tropics and subtropics, as well as around island arcs and oceanic islands (Fig. 1). Threatened species richness was generally higher in known marine biodiversity hotspots such as Australia, southeast Asia to Japan (including the Coral Triangle), southern Asia, southeast Africa, the Red Sea, the Caribbean Sea, the Gulf of Mexico, the eastern U.S.A., the central Pacific and the Galápagos. Vulnerable species (67% of threatened species) had higher richness in the western Pacific and Indonesia (including the Coral Triangle), southern Asia, the Red Sea, southeast Africa and the Galápagos (Fig. 1A). Endangered species (22% of threatened species) had higher richness in similar areas to Vulnerable species, but also showed a more varied, offshore distribution (Fig. 1B). No Endangered species were distributed in the Arctic Ocean. Critically Endangered species (11% of threatened species) were limited to temperate, subtropical and tropical oceans, with no species distributed within the Arctic Ocean and the majority of the Southern Ocean (Fig. 1C). Regardless of threat status, most species occurred in coastal, continental shelf marine environments, with the highest areas of threatened species richness located in Australia, southeast Asia, the Coral Triangle, Japan, the Red Sea and southeast Africa (Fig. 1).

Most of the threatened species for which range maps were available were corals and fish, and thus the overall pattern of richness reflected their distribution (Fig. 2). That pattern also applied to the other invertebrates, as well as mangrove and seagrass richness, which were highest in southeast Asia, the Coral Triangle, Japan and the Yellow Sea. Threatened algae species were only located within the waters of the Galápagos (Fig. 2). However, this overall pattern contrasted with the ranges of birds, mammals and reptiles (Fig. 2). The highest counts of threatened birds were in the South Pacific, South Atlantic and southern Indian Ocean (Fig. 2A). Mammals showed higher threatened richness predominately in northern temperate waters, but also in southeast Asia and southern New Zealand, where they overlapped with areas of high bird richness (Fig. 2B). Higher counts of threatened reptiles were in southeast Asia and the Coral Triangle, southeast U.S.A. and the Gulf of Mexico (Fig. 2D). Areas of overlap between high richness of reptiles, fish and mammals were limited to southeast Asia and eastern North America. Only mammals had threatened species distributions within both polar regions.

Scenario 1 showed the most spatially efficient solution to protect 30% of threatened species ranges (Fig. 3). In the highest prioritised 30% of the global ocean, only the polar bear (*Ursus maritimus*) had less than 30% range protected (9%). However, the polar bear, in contrast to the other marine vertebrates who only come to land to nest or give birth, is arguably more a terrestrial than marine species as it lives on land and ice. Areas of highest prioritised cells (cell rank $\geq$0.95) were located in New Zealand, Australia, the Coral Triangle, Peninsular Malaysia, the South China Sea, south Japan, Sri Lanka, the Chagos Archipelago, the Gulf of Oman, the Red Sea, southeast Africa, South Africa, the Gulf of Guinea, Cape Verde Islands, Madeira, parts of the Mediterranean Sea, eastern Canada, the Gulf of California, the Caribbean Sea, the Gulf of Mexico, southern Brazil, Uruguay, Argentina, the Galápagos, the Hawaiian Islands and numerous other island arcs, oceanic islands and coastal and continental shelf areas. Highly prioritised pelagic areas were located in the South Atlantic, from South America to South Africa. The majority (60%) of prioritised areas (particularly those with a cell

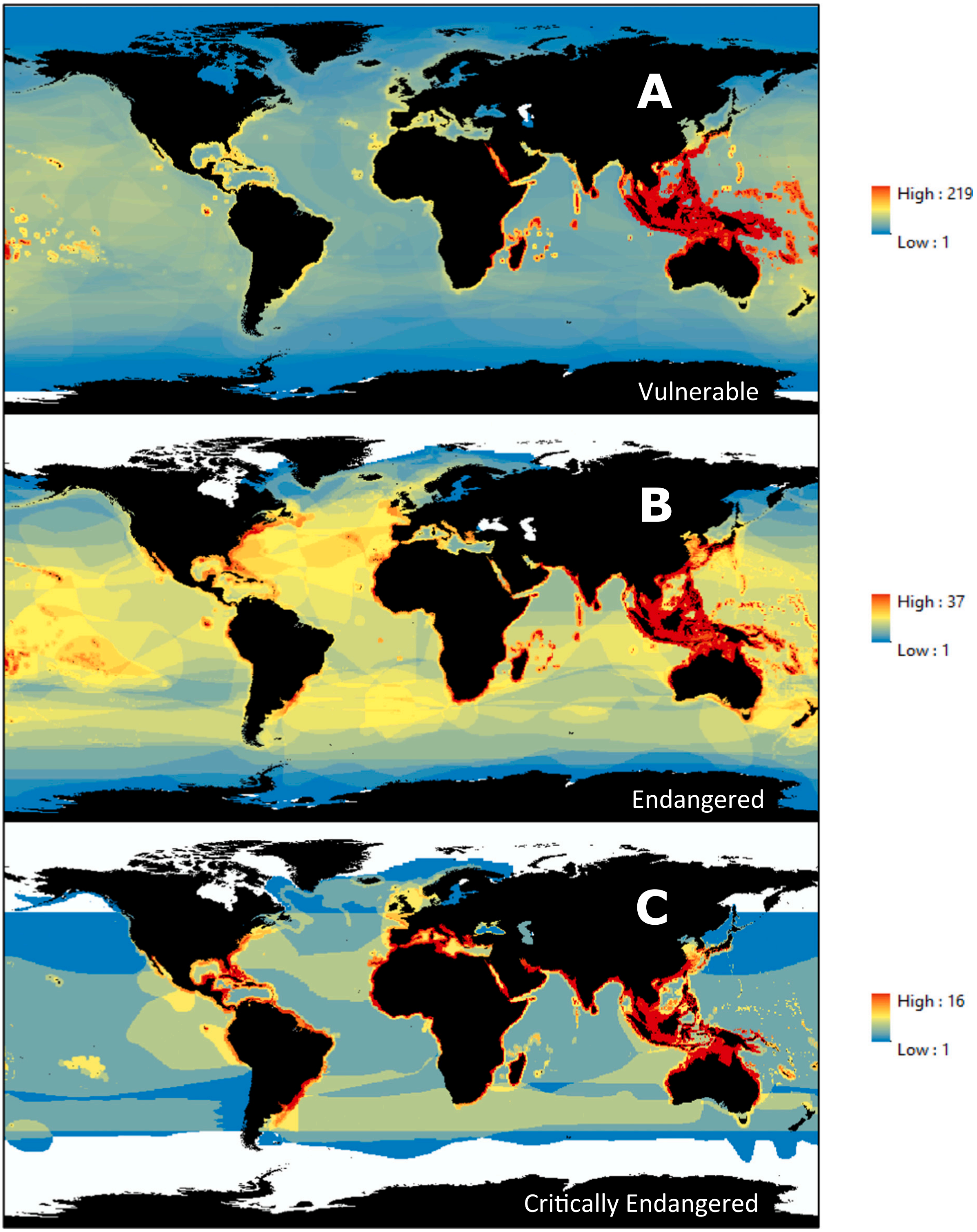

Fig. 1. Species richness maps of threatened species grouped by threat status, per 0.5-degree cell. Colour bar shows high (red) to low (blue) priority; white cells included no threatened species ranges. A, Vulnerable (650 species); B, Endangered (220 species); C, Critically Endangered (104 species). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ranking ≥0.95) were within the Exclusive Economic Zones (EEZs) of coastal nations.

3.2. *Does protecting biodiversity protect threatened species?*

There was high overlap between Representative Biodiversity Areas and threatened species richness (Table 2). There was most overlap with ranges of algae, mangrove and seagrass, coral and other invertebrates, considerable overlap with fish, and least overlap with species in the groups All Threatened, Vulnerable and birds. When comparing the overlap between areas with the 10% highest scoring cells for species richness and RBAs, taxa with wide-ranges, such as birds, mammals and reptiles, were poorly represented, with a combined average of 32% overlap, whereas the combined average of all other groups was 82%.

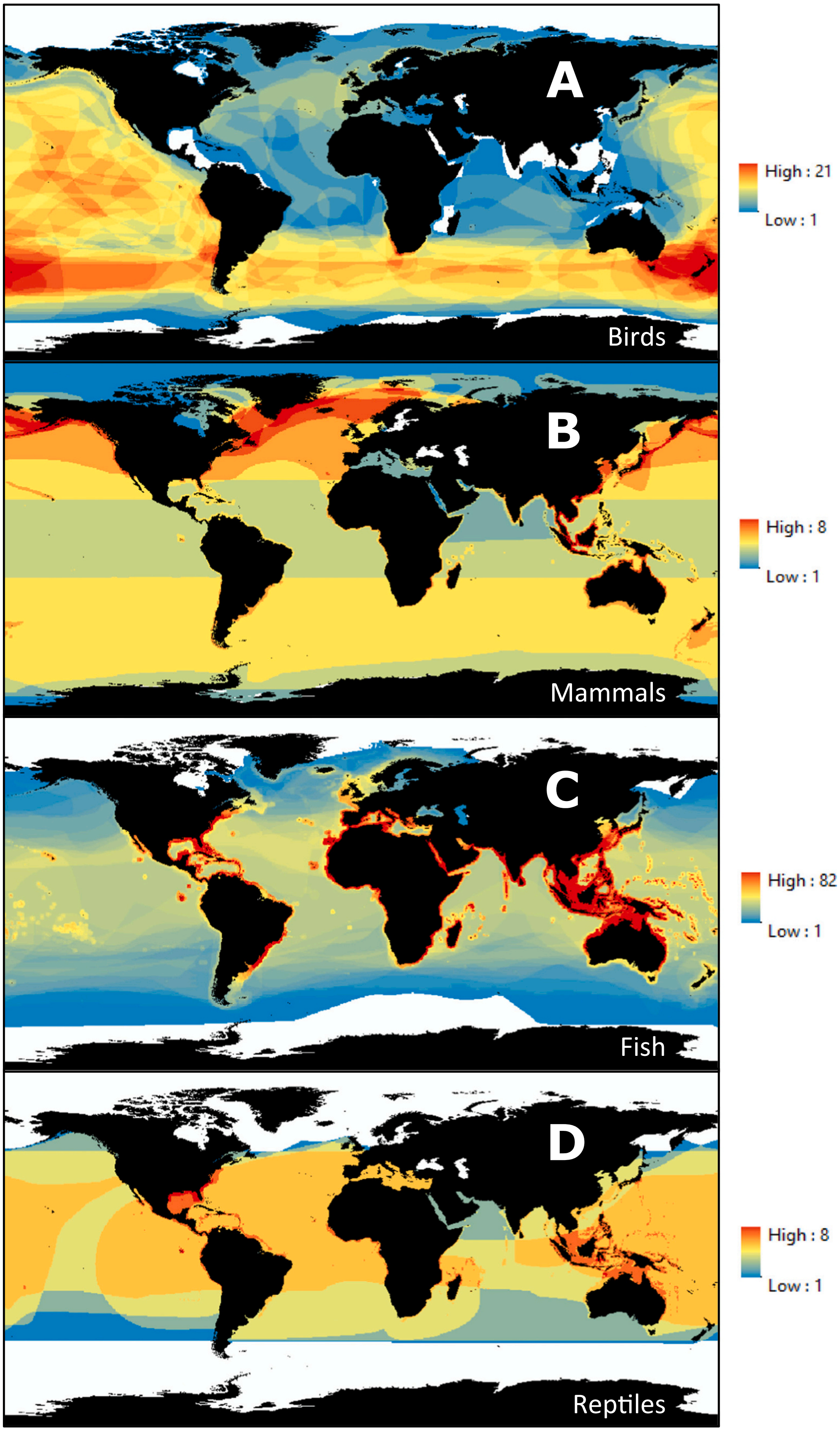

Fig. 2. Species richness maps of threatened species grouped by higher taxa, per 0.5-degree cell. Colour bar shows high (red) to low (blue) priority; white cells included no threatened species ranges. A, birds (100 species); B, mammals (32 species); C, fish (514 species); D, reptiles (11 species); E, corals (223 species); F, invertebrates (58 species); G, mangroves and seagrasses (17 species); H, algae (15 species), all within the waters of the Galápagos. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

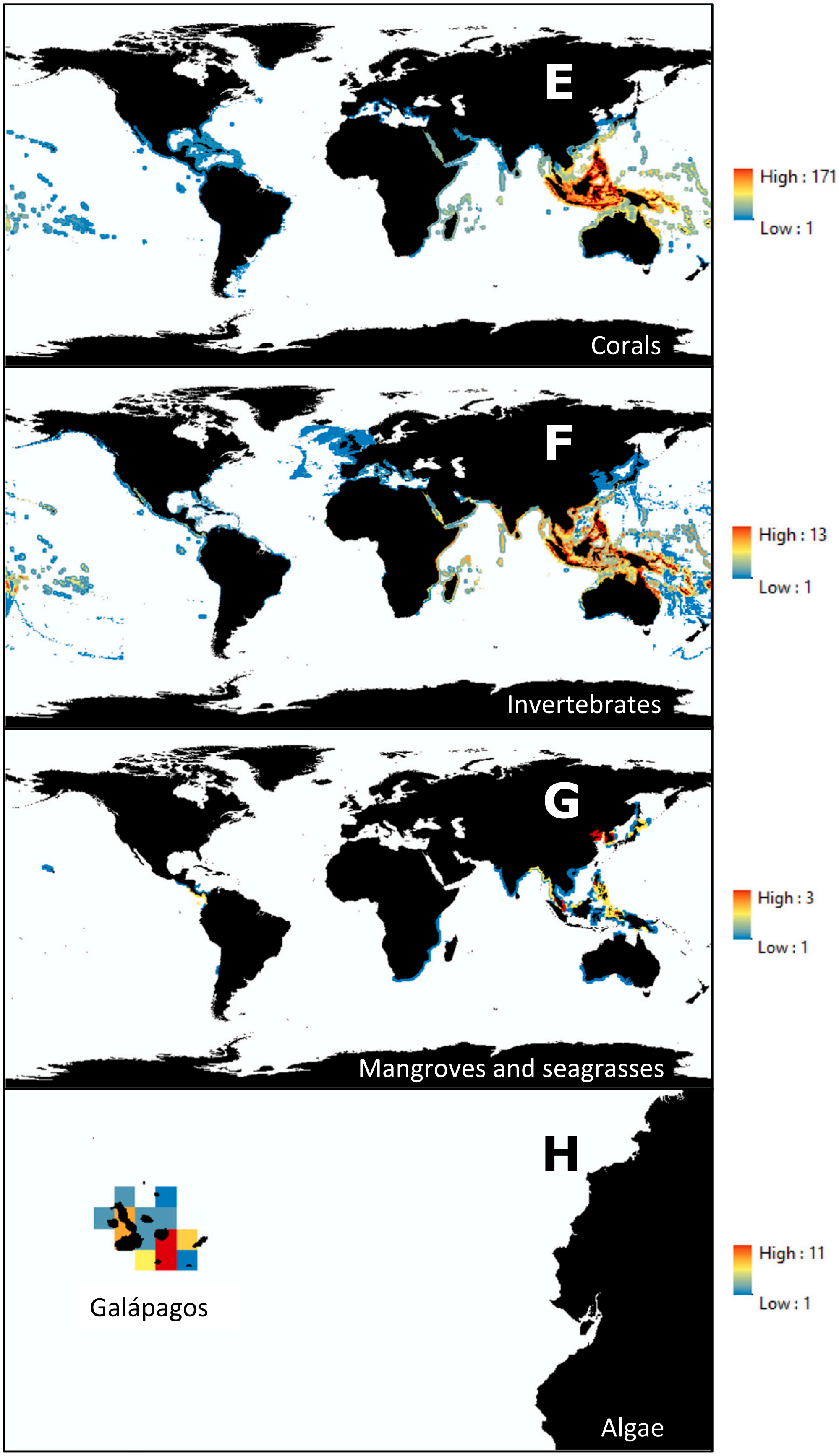

Fig. 2. (*continued*).

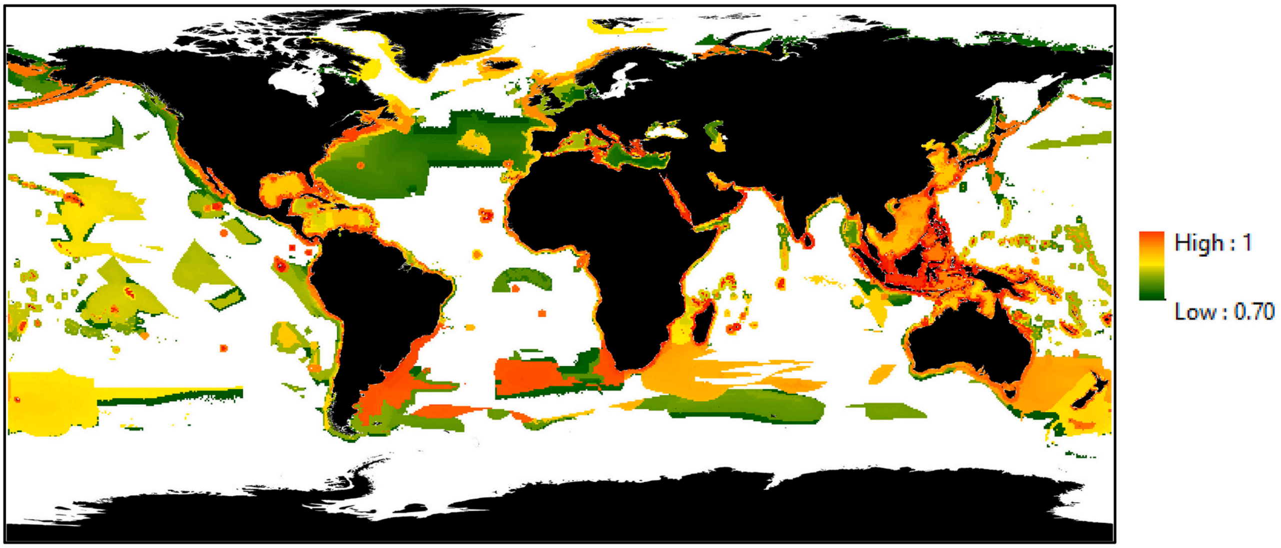

Fig. 3. Scenario 1, prioritising 30% of the ocean for threatened species protection. Colour bar shows high (red) to low (green) priority; white cells were not identified as top priority areas. In combination, all cells displayed are required to efficiently protect threatened species ranges by a minimum of 30% (excluding the polar bear). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Count of threatened species richness per 0.5-degree cell, grouped per threat status and taxon. 'Total cells' is the number of 0.5-degree cells each group is present in, 'Cells in RBAs (%)' is the percent of cells of each group that are within Representative Biodiversity Areas (RBAs). Groupings were subdivided into 10, 20 and 30% highest scoring cells for threatened species richness to determine how effectively RBAs protected the most species rich areas for each grouping. Some groupings had no difference in species richness between the 10, 20 and 30% highest scoring cells.

Threat status	Total cells	Cells in RBAs (%)	Taxon	Total cells	Cells in RBAs (%)
All threatened	201,748	24	Birds	169,244	25
30% highest	60,566	32	30% highest	63,139	25
20% highest	43,714	36	20% highest	34,354	26
10% highest	20,545	61	10% highest	20,334	27
Critically Endangered	119,275	29	Mammals	184,966	25
30% highest	42,425	41	30% highest	96,591	33
20% highest	42,425	41	20% highest	96,591	33
10% highest	16,209	62	10% highest	18,496	39
Endangered	156,775	28	Reptiles	107,368	27
30% highest	57,310	36	30% highest	54,741	30
20% highest	34,903	47	20% highest	54,741	30
10% highest	21,404	58	10% highest	54,741	30
Vulnerable	199,746	24	Fish	138,957	29
30% highest	67,202	29	30% highest	45,940	39
20% highest	45,061	35	20% highest	33,005	47
10% highest	20,924	59	10% highest	14,664	69
			Corals	15,055	68
			30% highest	4568	85
			20% highest	3042	91
			10% highest	1519	95
			Invertebrates	19,803	61
			30% highest	6406	80
			20% highest	5078	82
			10% highest	2338	91
			Mangroves and seagrass	3930	74
			30% highest	1318	72
			20% highest	1318	72
			10% highest	1318	72
			Algae	13	85
			30% highest	13	85
			20% highest	13	85
			10% highest	13	85

The species richness of reptiles, algae and mangroves and seagrasses was the same regardless of the proportion of scoring cells. The threatened species group 'Corals' was the most prioritised by the RBAs, with 95% overlap with the 10% highest cells for threatened coral richness (Table 2). Areas of highest species richness per threat status or group were generally found in coastal and continental shelf areas, places ranked highly as RBAs (Fig. 2). The cells of taxa with wide-ranges, such as birds, mammals and reptiles overlapped less with RBAs, particularly when comparing the highest 10% of cells for species richness for each group.

Zonation analysis of threatened species protection within RBAs (Scenario 2, Fig. 4A) differed substantially from Scenario 1 (Fig. 3). Areas of overlapping, highest prioritised cells (cell rank $\geq$95%) were located in Australia, the Coral Triangle, Peninsular Malaysia, parts of the South China Sea, south Japan, Sri Lanka, the Chagos Archipelago, the Gulf of Oman, the Red Sea, southeast Africa, the Gulf of Guinea, Cape Verde Islands, Madeira, parts of the Mediterranean Sea, eastern Canada, the Gulf of California, the Caribbean Sea, the Gulf of Mexico, southern Brazil, the Galápagos, the Hawaiian Islands, as well as other island arcs, oceanic islands, and coastal and continental shelf areas. Areas of least overlap and largest difference in priority ranking were mostly in offshore, oceanic areas and the polar oceans, which had few threatened species. There was a 56% overlap between the Zonation scenarios (Fig. 4B). Oceanic areas in the Pacific and southern Indian Oceans prioritised by Scenario 1, driven primarily by the distribution of threatened birds (Fig. 2A), were not prioritised in Scenario 2 (Fig. 4B), resulting in lower protection for birds.

In both Zonation scenarios, protecting 30% of the world's oceans was insufficient to protect all threatened species by a minimum of 30% of their range (Table 3). At 30% ocean protection, Scenario 2 had 25 fewer species with 30% of their range protected, compared with Scenario 1 (online Supplementary Material). Of the 26 species with less than 30% range protection, 22 were birds, 2 were mammals (polar bear, northern fur seal) and 2 were fish (Atlantic blue marlin, bigeye tuna). All of these species had either very large ranges or limited overlap with other threatened taxa. Protecting 30% of the ocean using Scenario 1 protected all but one species *U. maritimus* (polar bear) by the minimum 30% range. Protecting 5% of the ocean using Scenario 1 was more efficient for protecting threatened species than protecting 25% of the ocean using RBAs (Scenario 2, Table 3). Despite protecting less species ranges, using RBAs was still effective at protecting 97% of threatened species

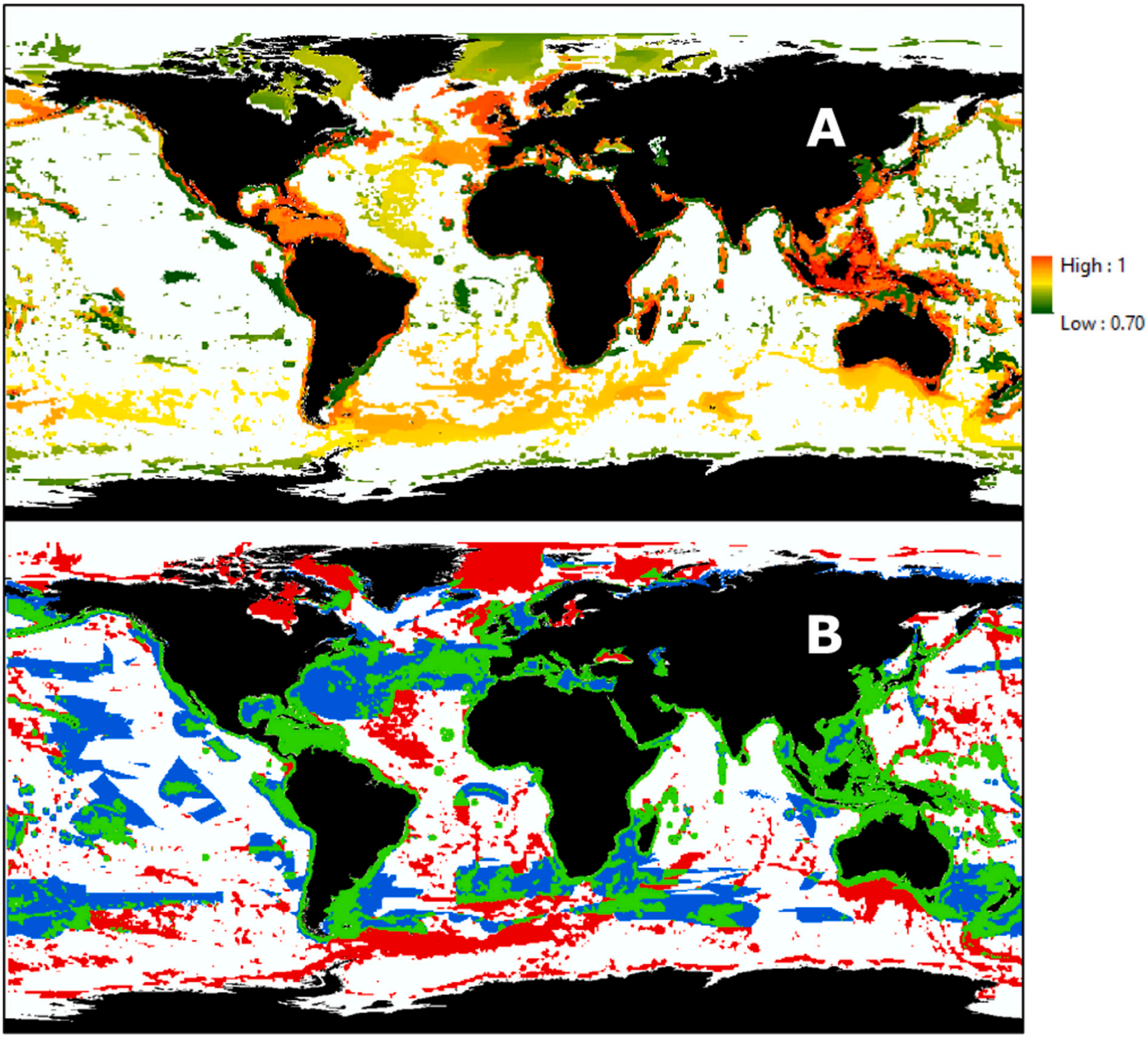

Fig. 4. A, Scenario 2, protecting 30% of threatened species ranges using Representative Biodiversity Areas. Colour bar shows high (red) to low (green) priority; white cells were not identified as priority areas. B, areas of overlap between Scenarios 1 and 2 (green), Scenario 1 alone (blue), Scenario 2 alone (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
The number of threatened species with a minimum of 30% range protection under Zonation Scenario 1 and Scenario 2.

Ocean protected (%)	Number of species (Scenario 1)	Percent of threatened species	Number of species (Scenario 2)	Percent of threatened species
5	830	85.7	775	80.1
10	874	90.3	799	82.5
15	898	92.8	809	83.6
20	926	95.7	823	85.0
25	954	98.6	824	85.1
30	967	99.9	942	97.3

(Table 3).

Though variation existed in the areas prioritised, there was only a small difference in the amount of additional ocean coverage required to protect all Vulnerable species using RBAs (+ 2.7%), when compared with Scenario 1. Protecting 30% of the ocean using RBAs was sufficient to conserve all Critically Endangered species and 97% of all threatened species by a minimum of 30% of their range (Table 3). However, protecting all Critically Endangered species using Scenario 1 required 6% less ocean protection than when using RBAs (Scenario 2). Using RBAs to conserve threatened species required a similarly small increase in ocean protection, whether comparing the number of individual species (Table 3), or species grouped by threat status, when compared with Scenario 1. The ocean protection needed to protect all categories of threatened species using each scenario was the same as that needed to protect all Vulnerable species, as this category contained species with the most extensive or non-overlapping ranges. As such, a key finding was that Scenario 1 required 37% and Scenario 2 required 40% ocean protection to conserve all threatened species by 30% of their range. The proportions for Critically Endangered and Endangered species were 25% and 30%, and 29% and 34%, respectively.

Threatened species with smaller ranges had a greater proportion of their range protected under both scenarios (Fig. 5). Only species with ranges smaller than 10% of the ocean had more than 60% range protected (Fig. 5). At 30% ocean protection, 26 species had less than 30% of their range protected when using RBAs (Scenario 2), whereas Scenario 1 protected all but the polar bear (Fig. 5B). Using RBAs was less effective for protecting seabirds (birds), with 22 species below 30% range protection (Fig. 5). In Scenario 1 seabirds had lower range protection than

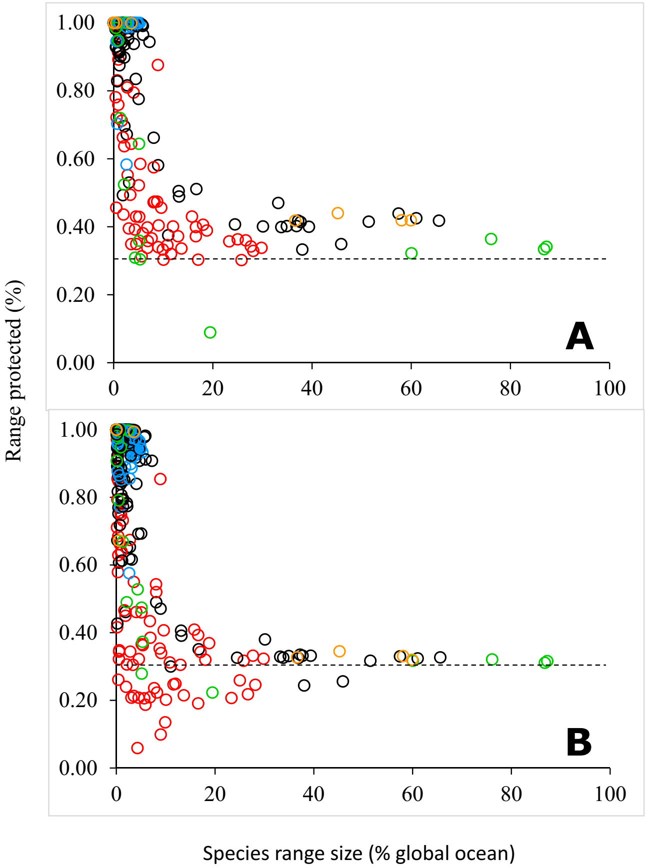

Fig. 5. Threatened species range protected at 30% ocean coverage vs total range size. A, Scenario 1 (only threatened species); B, Scenario 2 (using RBAs). Birds (red), mammals (green), reptiles (orange), fish (black), other classes (blue), 30% range protection (dotted line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

other taxa, although all did have at least 30% range protected (Fig. 5A). Species with smaller ranges had higher protection under Scenario 1, with 864 species receiving between 90 and 100% range protection, compared with 816 in Scenario 2 (Fig. 5).

Scenario 2 determined the efficacy of using RBAs to protect different groups of threatened species (Fig. 6). It resulted in a minimum of 58% range protection per group, and an average of 93% (Fig. 6A), compared with a minimum of 70%, and an average of 94% when using Scenario 1 (Fig. 6B), at 30% ocean coverage. In Scenario 2, the 10% highest priority cells provided an average range cover per class of 64%, with one class below 30% (Malacostraca at 29%). By comparison, Scenario 1 provided an average of 80%, with one class below 30% (Cephalopoda at 17%). The minimum ocean protection needed to conserve an average of 30% range per class was 26% using Scenario 2, and 12% using Scenario 1. A clear inflection point is visible when using Scenario 2 (Fig. 6B). This was because restricting the Zonation prioritisation to RBAs in Scenario 2 was initially effective, but there is a limit to how much protection can be provided to threatened species with RBAs. As the RBAs covered slightly less than 30% of the global ocean due to differences in geographic projection and resolution, there was a marked increase in average coverage per group prior to achieving 30% ocean protection in Scenario 2. Under both scenarios, birds, mammals and reptiles were shown to require the most ocean protection to conserve 30% range, reflecting their far ranging distributions. Overall, the results showed that using RBAs in Scenario 2 to protect threatened species was less efficient than when using Scenario 1, but would nonetheless conserve the ranges of the majority of threatened species.

3.3. *Combined priority areas for threatened species and biodiversity*

Scenario 3 determined Combined Priority Areas (CPAs), created by extending Scenario 2 to cover 40% of the ocean, the minimum ocean coverage required to encompass at least 30% of the range of all 974 threatened species, plus all ocean located within RBAs (Fig. 7). The majority of the prioritised area, 61%, was located within EEZs, with 39% in the High Seas. Protecting CPAs provided an average range protection per threatened species of 95% and only 92 species received less than 90% range protection. The highest prioritised cells within CPAs were located throughout Australia, the Coral Triangle, the Red Sea, the northeast Atlantic and the Caribbean Sea, as well as other oceanic islands and coastal and continental shelf areas. Lower priority cells were predominately in offshore, oceanic regions and in the polar oceans. With the exception of some areas in northern Canada, northern Greenland and northern Russia, CPAs were distributed throughout all coasts.

Current marine reserves cover 2.5% of CPAs (1718 of 69,054 prioritised cells, Fig. S4). The largest areas of overlap were located around Macquarie Island and parts of the Ross Sea, Australia (including the Great Barrier Reef), the Coral Sea, Palau, the Chagos Archipelago, the Seychelles, the French Southern and Antarctic Lands, St Helena, the northern part of the Mid-Atlantic Ridge, the South Georgia and South Sandwich Islands, the Juan Fernández and San Félix and San Ambrosio Islands, the Revillagigedo Archipelago, and numerous islands in the central Pacific, such as the Cook Islands, Fiji, the Phoenix Islands and Hawaii. The majority (66%) of currently implemented marine reserves were located outside CPAs.

3.4. *Uncertainty analysis*

The irreplaceability scores of the bootstrapping analysis indicated that 90% of cells selected within the 100 iterations (with a score of at least 0.6) were within CPAs. Such cells were generally in coastal, continental shelf areas, places with higher threatened species richness, in addition to places included as Representative Biodiversity Areas (red, Fig. S1). The 10% of CPA cells more frequently selected outside the top 40% across all iterations were predominately in the eastern Pacific, as well as the Atlantic and Indian Oceans and northern Russia (dark blue, Fig. S1), all of which were areas with lower threatened species richness, away from RBAs.

The sensitivity analysis showed that across the 100 iterations, 85% of cells within Combined Priority Areas were given an average cell priority score between 0.6 and 1.0 (i.e., within the top 40%), indicating that such places were of low sensitivity to the number of threatened species considered, and were consistently of high conservation value. A number of cells had a higher average priority score from the sensitivity analysis, when compared with the original CPA cell score. Such cells were distributed throughout southern Australia, the central Pacific, the Tasman Sea, the Baltic Sea, along ocean ridges and in Arctic areas (red and brown, Fig. S2). Cells with comparatively minimal changes in cell score were found in the Coral Triangle, the Red Sea, the Mediterranean, the North Sea, the Caribbean and the Antarctic (orange, Fig. S2). Finally, a number of cells had a much lower average priority score from the sensitivity analysis, compared with the original CPA cell score. These were mainly distributed in the eastern Pacific, the central Atlantic, the southern and eastern Indian Ocean and northern Russia, following a similar distribution to those with the lowest irreplaceability scores (dark blue, Fig. S2; dark blue, Fig. S1).

The boxplot analysis of average cell priority score (from the sensitivity analysis) against the original cell value groupings from the CPAs (Fig. S3), showed that within the highest ranking 25% CPA areas, there was low uncertainty in cell score, signified by the small spread and few outliers of the first 5 groupings (100–95, 95–90, 90–85, 85–80 and 80–75, Fig. S3). Larger uncertainty was visible within cells prioritised between 75 and 60 in the CPA analysis, due to the increased range, spread and numbers of outliers (Fig. S3).

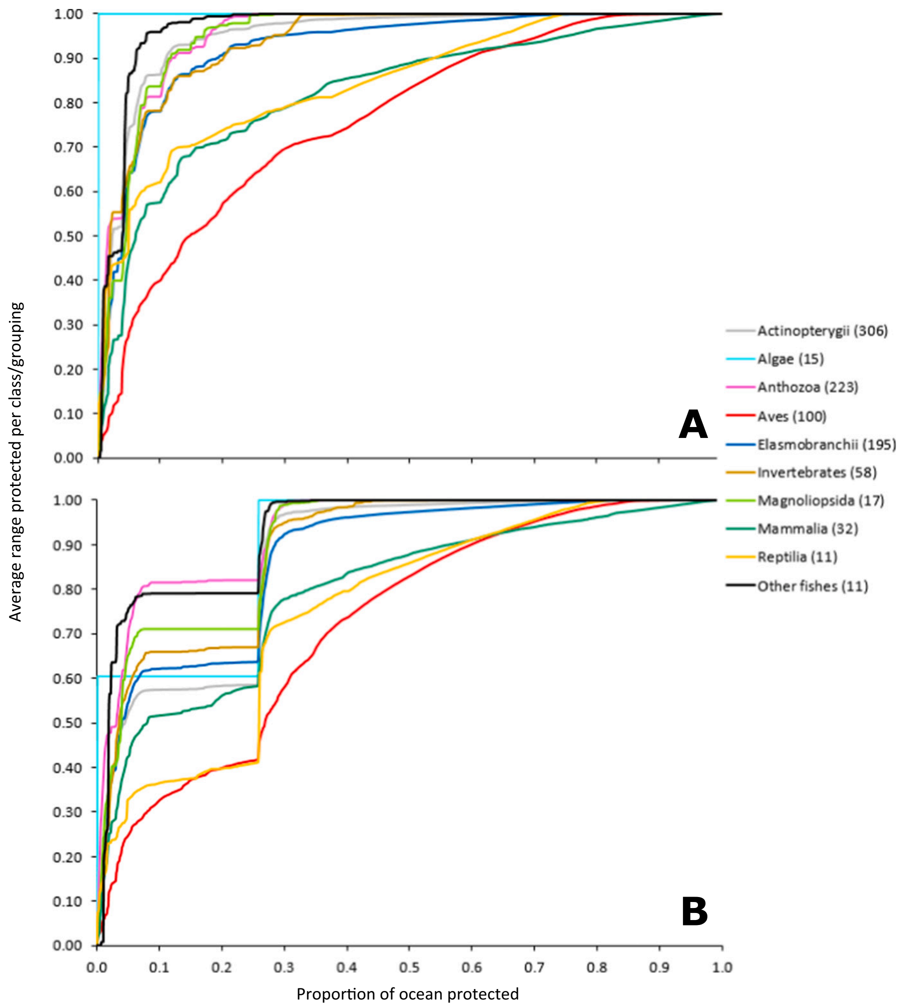

Fig. 6. Ocean protection needed to conserve average range size per group (number of species in brackets). A, Scenario 1; B, Scenario 2. Some classes were combined together for ease of visualization (Algae: Florideophyceae and Phaeophyceae; Invertebrates: Bivalvia, Cephalopoda, Gastropoda, Holothuroidea, Hydrozoa, Malacostraca and Merostomata; Other fishes: Coelacanthi, Holocephali and Myxini).

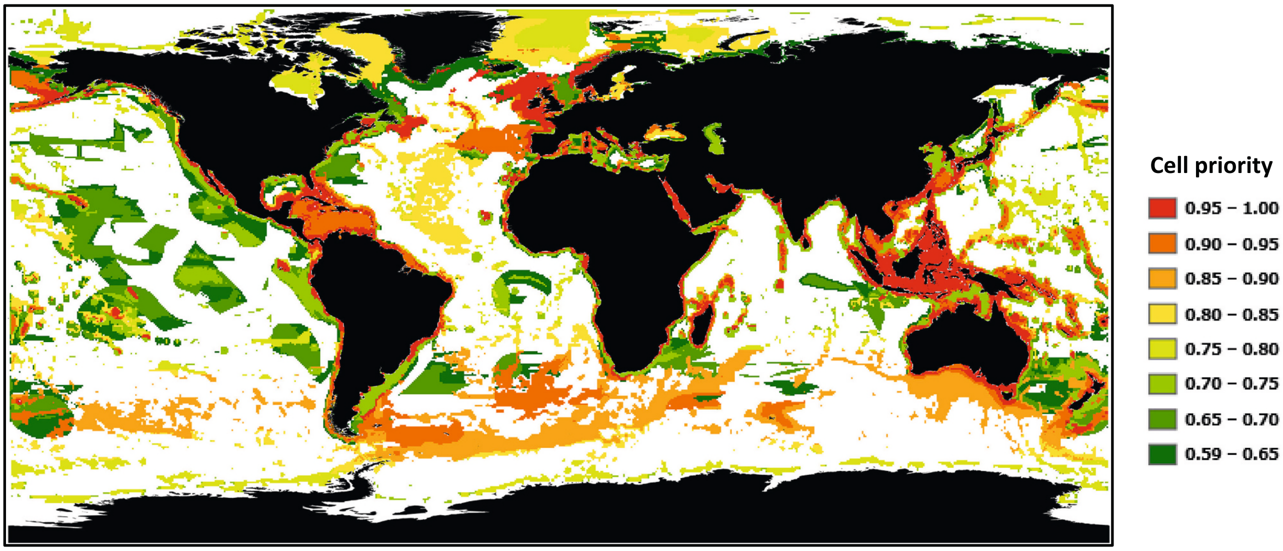

Fig. 7. Scenario 3, Combined Priority Areas. In combination, all identified cells are required to protect at least 30% of every threatened species range and all Representative Biodiversity Areas. Colour bar shows high (red) to low (green) priority; white cells were not identified as top priority areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Threatened species ranges

Our novel assessment of threatened species ranges, using the best of both IUCN and AquaMaps range maps, enabled the most comprehensive assessment of threatened species distributions to date. The highest counts of threatened species follow a similar distribution to recent studies defining marine biodiversity hotspots, with high numbers of threatened species in areas of high species richness (Tittensor et al., 2010; Trebilco et al., 2011; Selig et al., 2014; Jenkins & Van Houtan, 2016; Molinos et al., 2016; Davidson and Dulvy, 2017; Ramírez et al., 2017; Zhao et al., 2020). In line with Jenkins and Van Houtan (2016), we find areas of high conservation importance in the Coral Triangle, western Pacific, western Indian Ocean and Red Sea, but also in the Mediterranean Sea and Caribbean Sea. These areas, well-known for their biological importance, have exceptional species richness and taxonomic uniqueness, and have been ranked as priority areas for conservation in the WWF's Global 200, among others (Olson and Dinerstein, 2002; Jefferson and Costello, 2020). Marine protection should be urgently reviewed in these areas, as they harbour the most threatened species and, crucial to achieving Aichi Target 12, the most Critically Endangered marine taxa.

In addition to these well-known hotspots, we show threatened species are distributed throughout coastal and continental shelf areas, close to human populations where they are subject to over-exploitation and increasing anthropogenic stressors (Petrossian, 2015; Costello et al., 2016; Rhodes et al., 2018; Rodgers et al., 2018; Halpern et al., 2019). However, similar to recent research (O'Hara et al., 2019), we also find high numbers of Endangered species in offshore areas, away from human populations, such as in the central Atlantic and central Pacific Ocean. If we are to protect the biodiversity of our oceans, a proactive approach must be adopted to managing these species in the High Seas before they become further imperilled. Between 48 and 57% of the High Seas are fished annually, yet these areas constitute less than 5% of fishing catch and are not important to global food security (Sala et al., 2018; Schiller et al., 2018). High Seas fishing is mainly by longline fisheries, known for their high bycatch of sharks, seabirds, reptiles and marine mammals, some of which are highly threatened taxa (Lewison et al., 2014; Kroodsma et al., 2018; O'Hara et al., 2019). Protecting the High Seas represents an opportunity to protect many threatened species, at minimal risk to global food security. We find that only the polar oceans have low numbers of threatened species, regardless of threat status, with no Critically Endangered and few Endangered and Vulnerable species. By utilising current understanding of threatened species distributions, we here identify those places in greatest need of protection to avoid species extinction.

4.2. Does protecting biodiversity protect threatened species?

Previous studies serve to prioritise important areas for biodiversity, but few account for the threat status of species, and, of those that do, they combine metrics of threatened species and biodiversity together (Jenkins & Van Houtan, 2016; O'Hara et al., 2019; Sala et al., 2021). Our approach compares the distribution of threatened species and biodiversity, showing that a minority of threatened species have distinct distributions in areas of relatively low biodiversity (Fig. 5). If using biodiversity-centric prioritisation approaches to determine areas for marine protection, such species, the majority of which are seabirds, will require species specific management if they are to avoid extinction. In general, we show that using Representative Biodiversity Areas (RBAs) is an efficient approach to protecting biodiversity and the majority of threatened species, and that the ocean protection required to conserve biodiversity and threatened species is only 2.7% more than to preserve threatened species alone. However, due to their imperilment, threatened species should be specifically accounted for when defining priority areas for marine protection. Due to the spatial resolution of our global analysis, the importance of the spatial distribution of each species range that falls within prioritised areas is not analysed here, but would be valuable to consider at regional and national scales to determine the significance of spawning areas, nursery grounds, migration routes and habitat preferences.

We find that RBAs, which include significant coastal and continental shelf areas, provide an effective conservation strategy for protecting numerous range-restricted and endemic threatened species, but do not protect all threatened species (Fig. 5). The RBAs included here nested richness within areas of high endemicity, and endemic species are at particularly high risk of extinction due to their restricted ranges, and subsequent vulnerability to climate change (Manes et al., 2021). Additionally, species with smaller ranges, and those in coastal areas, generally experience higher anthropogenic pressure when compared to far ranging pelagic or migratory species (Brooks et al., 2006; Halpern et al., 2015). As such, using RBAs to protect threatened species may prioritise those in greatest need of protection, conserving places with high endemism and genetic variability. Where RBAs are less effective is for the protection of far ranging, pelagic and migratory species, such as mammals, birds and reptiles (Fig. 6). Conservation biogeography predicts that species with larger ranges need least protection, but marine defaunation is increasing and the global scale of fisheries means that such species are threatened everywhere (McCauley et al., 2015). Thus, many far ranging species are now among the most threatened due to the diverse anthropogenic pressures they face during their oceanic migrations (Lascelles et al., 2014). In addition to their large ranges, the life history traits of birds, mammals and reptiles means that RBAs are less effective at including these groups. Similar conclusions about priority areas for such taxa were also noted by Jenkins and Van Houtan (2016). Almost all threatened reptiles and birds nest on land and many marine mammals give birth on land (Croxall et al., 2012). Consequently, protecting these species depends on the management of important terrestrial areas, in addition to protecting species' oceanic ranges.

4.3. Combined priority areas and current marine reserve protection

We find that a minimum of 40% ocean protection is required to safeguard against the extinction of all threatened species, while also protecting 94% of coral reefs and mangrove forests, 86% of laminarian kelp forests and seagrass meadows, and 68% of species richness and endemicity (Zhao et al., 2020, (Fig. 7)). This figure exceeds recent calls to fully protect 30% of marine habitats and the wider ocean (World Parks World Parks Congress, 2014; IUCN, 2016a, 2016b), and is close to the average coverage needed to achieve effective ocean protection (37%) proposed by O'Leary et al. (2016). This should be regarded as a minimum target, as below this coverage some threatened species are protected by less than 30% of their range. Some species will require less and others more range protection, depending on their exposure to anthropogenic effects. For example, polar bears may require carbon emissions mitigation rather than spatial protection to ensure their survival (Molnár et al., 2020).

The majority of the 40% area prioritised for both threatened species and biodiversity is located within EEZs (60%), with CPAs identified in the waters of all coastal nations (Fig. 7). Such countries have a responsibility to conserve biodiversity, as well as the ability to unilaterally designate protected areas. EEZs occupy 41% of the global ocean, harbour the majority of CPAs and are subject to high fishing intensity (accounting for ~96% of global marine fishing catch), as such, they have higher relative importance to biodiversity and threatened species conservation when compared to the High Seas (Costello et al., 2010; Schiller et al., 2018). However, due to our comprehensive prioritisation, which results from the inclusion of seven ecosystems, seabed rugosity (including topographic heterogeneity, canyons, seamounts, abyssal hills and areas with hydrothermal vents) and within realm species richness (Zhao et al., 2020), as well as threatened species ranges and their offshore distributions, we prioritise ~40% of CPAs within the High Seas. Thus, our results confirm the importance of the High Seas to biodiversity and threatened species conservation (Olson and Dinerstein, 2002; Selig et al., 2014; Jones et al., 2018; O'Hara et al., 2019; Visalli et al., 2020; Zhao et al., 2020).

Our prioritisation requires that all CPAs be protected to conserve marine biodiversity and threatened species, but when comparing the current marine reserve network with CPAs, many prioritised areas have little or no protection. Moreover, our minimum protection target of 40% dwarfs the size of the current marine reserve network (2.7%) and to date only 2.5% of CPAs are within marine reserves (Fig. S4). Despite a recent increase in reserve establishment, we confirm that current ocean protection is insufficient to achieve conservation objectives. However, our research shows that even a small increase in reserve protection (2.3%) could conserve more than 80% of threatened species and 17% of RBAs (Table 3), if protection is implemented where it is most beneficial. The areas prioritised (CPAs) need urgent protection to halt biodiversity loss and help sustain the ecosystem services vital to human health, particularly as many of the most important areas are within close proximity to human populations. Our research provides a broadscale blueprint of where protection could assist in achieving Aichi Targets 11 and 12, providing a basis from which to conserve marine species and biodiversity for the future.

Exploring the uncertainty of the Combined Priority Areas highlighted that some areas were included in our prioritisation based on the presence of a small number of threatened species ranges (Fig. S1, S2). If targeting the most urgent areas for conservation, these areas, which often had the lowest priority scores within the CPAs (Fig. 7), would be less efficient at conserving multiple threatened taxa and biodiversity. This suggests protecting first and foremost, areas of highest priority and certainty, typically those areas prioritised in the top 30% of CPAs (Figs. 7 & S3). Although this may come at the cost of survival for those species with ranges more isolated from other threatened taxa, areas with fewer threatened species may be indicative of marine environments subject to lower levels of anthropogenic pressure. In such areas, the management of extinction risks, such as restrictions on fishing gear, may prove a more speedy resolution to protecting threatened species than the designation of marine reserves and protected areas. Nevertheless, national and regional priorities may focus on locally threatened species of particular societal or cultural significance, even if not included within the top 30% of our CPAs.

The CPAs we recommend for protection consider all known threatened species ranges, but many species classed as Data Deficient may be reclassified as threatened if additional information becomes available (Dulvy et al., 2014; Bland et al., 2015; Webb and Mindel, 2015; Jenkins & Van Houtan 2016). To date, the IUCN has assessed the extinction risk of 7% of known marine species (IUCN, 2020; Horton et al., 2021). Consequently, a considerable effort is needed to address current knowledge gaps, balance spatial and taxonomic biases and determine the conservation status of the vast majority of marine species. The Combined Priority Areas presented here are designed to guide conservation planning, but assessments are needed to manage threatened species and biodiversity at the local scale and with the consideration of stakeholders. To protect threatened species and biodiversity, the implementation of marine reserves is imperative, and will be most effective when used alongside sustainable fisheries management practices that reduce bycatch, overfishing and habitat destruction (Worm et al., 2009; Weigel et al., 2014; Roos et al., 2020). Determining where and how fisheries should be managed to avoid negative impacts on threatened species, biodiversity and other ecosystem services such as carbon sequestration, is a management priority (Sala et al., 2021).

The Combined Priority Areas, as with the work of Zhao et al. (2020), not only highlight priority areas, but provide a global ocean index of biodiversity importance at a 0.5-degree spatial resolution. This digital map and its constituent layers may be reanalysed with different weightings and combined with additional data. For example, combining the priority areas (CPAs) with human impacts and fishing pressures, may weight prioritisation towards areas more (or less) impacted and in need of management attention to ensure sustainable use and maximise food security.

CRediT authorship contribution statement

Tamlin Jefferson: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data Curation, Writing – Original Draft Preparation, Visualization. **Mark Costello:** Conceptualization, Methodology, Investigation, Writing - Review & Editing, Supervision. **Qianshuo Zhao:** Data Curation, Writing - Review & Editing. **Carolyn Lundquist:** Conceptualization, Methodology, Investigation, Writing - Review & Editing, Supervision.

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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.

Appendix A. Supplementary data

List of all threatened species names (class to species), the source of each species range map (if available), IUCN threat status, global range (in number of 0.5-degree cells), and range protected under each scenario.

Collection of figures resulting from the uncertainty analyses, as well as those displaying current marine protection and current protection of Combined Priority Areas. Supplementary data to this article can be found online at doi: https://doi.org/10.1016/j.biocon.2021.109368.

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