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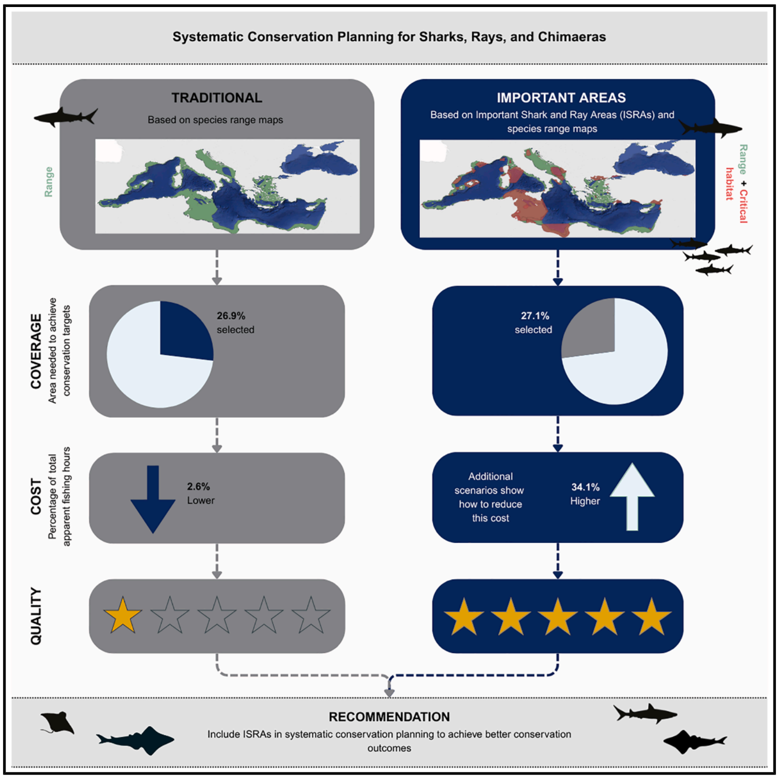
Important Shark and Ray Areas can inform conservation planning in the Mediterranean and Black Seas

Graphical abstract



Highlights

- Important Areas are tools to support effective marine conservation planning
- Adding critical habitats to range maps enhances systematic conservation solutions
- Including critical habitats in solutions can cover a similar area but differ in cost
- Considering Important Areas will enhance outcomes for threatened species protection

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In brief

Marine organism; Nature conservation; Aquatic science; Zoology; Ichthyology; Aquatic biology

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Important Shark and Ray Areas can inform conservation planning in the Mediterranean and Black Seas

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SUMMARY

The designation of protected areas needs to accelerate rapidly to achieve Target 3 of the Global Biodiversity Framework (GBF), raising concerns that protected area quality will be overlooked. Rather than basing systematic conservation planning primarily on species ranges, critical habitats for life history functions should be prioritized to enhance conservation outcomes. Such critical habitats are being identified as "Important Areas," including Important Shark and Ray Areas (ISRA) for chondrichthyans. Solutions from systematic conservation planning scenarios with 73 chondrichthyan species in the Mediterranean and Black Seas greatly differed between approaches that ignore or include ISRAs. Including ISRAs led to higher costs for fisheries but protected a similar surface area (∼27% in both scenarios), while achieving better conservation outcomes. We highlight ways of reducing fishing costs while maintaining ISRA-based solutions. Systematic conservation planning using Important Areas gives decision makers a tool to balance cost with improved conservation quality, ultimately enhancing protected area network effectiveness by prioritizing critical habitats.

INTRODUCTION

The Kunming-Montreal Global Biodiversity Framework (GBF) specifies global targets to address biodiversity loss, including increasing coverage of protected land, water, and sea areas.[1] Parties to the Convention on Biological Diversity (CBD) have committed to four goals and 23 targets, including an increase in protected areas to 30% of the world's surface by 2030 ("30 by 30"; Target 3) and a 90% reduction in the extinction rate of species by 2050 (Target 4).[1] This commitment to safeguard nature was hailed as a major conservation success.[2] More than 1 million species are already threatened with extinction[3] and only 16.3% of the land and 8.4% of the oceans of the globe are within protected or conserved areas.[4]

The aim to rapidly expand the network of protected areas has raised concerns that habitat quality[5,6] and representativeness will be overlooked.[7] This is despite Target 3 specifically noting that areas important for biodiversity and for ecosystem function and services should be prioritized for protection in ecologically representative networks.[1] The CBD 2010 Aichi target contained similar language, but an analysis of protected area coverage indicated that many were delineated without effectively considering biodiversity coverage.[5] The pressing timeline of Target 3 further increases the risk that quantity will be prioritized over quality.[8] To achieve Target 3, protected area coverage on land needs to almost double by 2030, and in the ocean, it needs to almost quadruple while also balancing food security, marine renewable energy development, and sustainable blue economy objectives.[9] It is therefore now crucial and timely to inform resource managers and decision makers about how to maximize the quality of protected areas while achieving 30 by 30.[5]

Sharks, rays, and chimaeras (chondrichthyans) are a diverse and highly threatened group comprising ~1,260 species distributed globally.[10] They play key ecosystem roles as top or mesopredators that exert top-down pressure, and thus can influence the abundance, distribution, and behavior of smaller species.[11,12] Chondrichthyans are the second-most threatened group of vertebrates globally after amphibians, with over a third of species threatened with extinction.[13] A range of chondrichthyans have suffered severe global population declines, including oceanic,[14] coral reef associated,[15] and deepwater species.[16] Chondrichthyans are characterized broadly by slow growth rates, late maturity, and low fecundity, rendering them vulnerable to human pressures.[13,17–20] Their primary threat is direct and incidental fishery mortality.[13,14,16] Although some species are wide-ranging, migratory, or have large home ranges, not all parts of their range are equally important for their life history, and thus for area-based protection. Focusing on these important areas will substantially improve the benefit chondrichthyans gain from additional and/or an expansion of protected areas in aquatic ecosystems under Target 3. Important areas may be outside Exclusive Economic Zones (EEZs) requiring the establishment of protected areas in the high seas as stipulated in the United Nations High Seas Treaty (Biodiversity Beyond National Jurisdiction [BBNJ]; www.un.org/bbnj). The benefit for chondrichthyans afforded by additional protected areas assumes they are effectively managed and can stop or substantially reduce fisheries induced mortality.[6]

Designing protected areas for chondrichthyans has growing support and is urgently needed to reverse their declines and improve their high extinction risk status.[21–24] Designating protected areas for these species will also have widespread ecosystem benefits due to their key ecosystem roles, by avoiding cascading effects from predator declines to lower trophic levels and habitats.[11,25] Limiting fishing in these key areas will also benefit the many other marine species impacted by fishing through direct catch, accidental catch (i.e., bycatch), and habitat modification.[26] However, chondrichthyans have often been overlooked in the design of protected areas.[21,25,27] A recent review of Marine Protected Area (MPA) governance in the Central and South American Pacific found that only 11% of MPAs ($n = 182$) mentioned chondrichthyans as a Conservation Value.[28] Similarly, in South Africa, chondrichthyans are mentioned in the published gazettes of only 12% of MPAs ($n = 41$).[29] While a lack of political will likely plays a role in this underrepresentation, spatial data on critical areas for chondrichthyan conservation are often unavailable when MPAs are designed[25,29] or implemented.[30]

Systematic conservation planning is a structured, science-driven approach to designing networks of protected areas that effectively conserve biodiversity.[31] Unlike ad-hoc or opportunistic methods, this approach integrates ecological and economic considerations to identify and prioritize areas for protection. In systematic conservation planning, prioritization tools are employed to optimize the selection of conservation areas (i.e., the solution), balancing biodiversity conservation goals with economic efficiency. The first main objective of protected areas is representativeness, meaning that protected areas need to represent the full spectrum of biodiversity.[32] In conservation planning, this is usually achieved by including a percentage of the geographical range of each conservation target in the protected area design. The second main objective of protected areas is persistence, meaning that the area needs to ensure the long-term survival of species, primarily through separating them from threatening processes.[32] The traditional approach of using species range maps in systematic conservation planning fulfills the first objective, but this approach may not maximize species persistence, primarily because not all areas in species' ranges are equally important[33] and some species may need more attention than others (e.g., rare, threatened, or endemic species).[21,34] In the marine environment, species often have a broad range but important life history functions such as feeding or reproduction may be concentrated in smaller areas with specific characteristics. For example, the Vulnerable Lemon Shark *Negaprion brevirostris* has a large coastal distribution in the Western Atlantic and small nursery areas, such as in Bimini, The Bahamas, to which females regularly return to pup.[35] Preferentially protecting important life-history sites is therefore likely to have a larger positive impact on a species' persistence than simply selecting a percentage of its range.[36]

To increase the likelihood of species persistence in protected areas, efforts to highlight important areas at the taxon level have been initiated.[36–38] The goal of such initiatives is to inform area-based conservation efforts with data from taxa that were previously underrepresented in systematic conservation planning. The Important Shark and Ray Areas (ISRA) project by the

International Union for Conservation of Nature (IUCN) Species Survival Commission (SSC) Shark Specialist Group is filling this gap for chondrichthyans by identifying areas that are important for this taxon based on a set of criteria.[36,39] ISRA Criteria, developed through a series of workshops with experts on the taxon,[36] were designed to consider the biology and life-history of chondrichthyans. All delineated ISRAs require contemporary evidence (<15 years old) of the regular and predictable occurrence of a species/criterion combination.[36,39] Evidence can include a wide range of data types, including fishery-dependent studies from recreational, artisanal, or industrial fisheries, fishery-independent surveys, and citizen science observations. ISRAs include reproductive areas, feeding grounds, resting areas, migration routes, areas with particularly high densities of a range-restricted species, or areas supporting a high number of species.[36]

Here, we illustrate how ISRAs in the Mediterranean and Black Seas region can contribute to the systematic conservation planning of chondrichthyans. We first investigate the existing protection afforded by the MPA network in the region, assessing the overlap between ISRAs and existing MPAs. We only consider no-take MPAs as likely affording protection to chondrichthyans because overfishing (target and incidental catch) is the main threat to chondrichthyans.[13] We then examine the difference in systematic conservation plans that ignore or include ISRAs, highlighting differences in area and cost. Finally, we identify the most important ISRAs for achieving conservation targets whilst minimizing impacts on fishing. Since in practice it is unlikely that all ISRAs are converted to MPAs at the same time, this approach highlights the priority areas that managers could consider first. We believe that our approach illustrated here for including ISRAs in MPA networks is broadly applicable to other Important Area approaches, such as Key Biodiversity Areas (KBAs)[40] or Important Marine Mammal Areas (IMMAs).[37]

RESULTS

Methods summary

We identified Important Shark and Ray Areas (ISRAs) in the Mediterranean and Black Seas region through a workshop with regional experts.[41] ISRAs are identified using a set of criteria, including species' vulnerability; range-restricted species; key life-history characteristics, such as reproduction, feeding, resting, movement, and aggregations; as well as distinctive attributes and diversity.[36] We then compared area and cost of conservation solutions for chondrichthyans from spatial prioritization based on species' range maps with two key scenarios: (1) ignoring ISRAs, and (2) including ISRAs (see Table S1), using the *prioritizr* package.[42] Conservation targets based on the IUCN Red List of Threatened Species status of 73 chondrichthyan species had to be achieved while minimizing the cost, for which we used fishing effort data from Global Fishing Watch. To explore ways of reducing the cost when including ISRAs, we added two further scenarios: (3) only locking-in ISRAs with a low cost-importance ratio (n = 21), and (4) excluding ISRAs delineated based on Sub-criterion D2 (Diversity, n = 2) and C4 (Movement , n = 4) because these are often large (see Table S1).

Current area-based protection for chondrichthyans in the Mediterranean and Black Seas

There are 57 designated no-take MPAs in the Mediterranean and Black Seas, ranging from 0.0004 to 896.3 km^2 (Figure 1A). Most are relatively small, and combined span 3,742 km^2, covering only 0.14% of the planning region. No-take MPAs overlapped with 10 ISRAs (out of 65). Just over one-third (37.1%) of the no-take MPA area overlapped with ISRAs. However, the total area of ISRAs covered 16.2% of the planning region, with only 0.3% of their coverage being strictly protected in a no-take MPA (Figure 1A). No chondrichthyan species had >2% of their distribution in planning units covered by a no-take MPA.

Species richness of chondrichthyans per 86.6 km^2 hexagonal planning unit ranged from 1 to 61 species (Figure 1B). Richness was highest in coastal and shelf areas, with up to 84% of the 73 species occurring within a planning unit. Mean species richness was 19.2, although species richness was low in the Black Sea (mean = 2.7; Figure 1B). Mean species richness in planning units that overlapped ISRAs was significantly higher (35.3) than in planning units outside ISRA boundaries (mean = 15.5; $t = -96.4$, df = 8,086.1, $p < 0.001$). Although ISRAs are generally in areas with high species richness, some areas with high species richness did not overlap with ISRAs, such as in the central Adriatic, in coastal areas of the Aegean Sea, or off the North African coast of the Alboran Sea. Planning units inside ISRA boundaries were shallower (461.7 ± 562.0 m) than those outside ISRA boundaries (1,653.4 ± 1,178.9 m; $t = -115.0$, df = 19,092, $p < 0.001$), demonstrating that ISRAs were mostly delineated closer to the coast (Figure 1D). Similarly, planning units overlapping with ISRAs also had a higher cost (mean = 2,006.4 apparent fishing hours) than those outside ISRA boundaries (mean = 900.8; $t = -16.4$, df = 7,178.2, $p < 0.001$). Areas with high cost values that were not in ISRAs were mainly found in coastal areas of Spain, France, Italy, and Greece (Figure 1C). Finally, species richness correlated positively with cost (Pearson's r = 0.40, F = 6,040, df = 31,799, $p < 0.001$).

Important Shark and Ray Areas substantially changed conservation plans

The two scenarios, which either ignored or included ISRAs, showed starkly contrasting results. This was despite them having the same targets, fishing cost layer, boundary penalty, and locked-in no-take MPAs.

Scenario 1 ignoring ISRAs selected 26.9% of the planning region for conservation, with many of these off North Africa, Greece, and in the Tyrrhenian and Balearic seas (Figure 2A). Although this scenario ignored ISRAs, the solution had almost half of the selected planning units (43.7%) inside ISRAs. These included 42.0% of the area of the largest ISRA, located in the Strait of Sicily, which covers 7.7% of the planning region and was delineated based on ISRA Sub-criterion D2 (Diversity). It also included 40.9% of the Balearic Islands ISRA that was the second ISRA delineated based on the diversity criterion.

Scenario 2, which locked in all ISRAs so that they had to be part of the solution, had a solution that selected only a slightly larger area of the planning region (27.1%; Figure 2B). The solution included fewer areas in the Aegean, Levantine, and Black seas, but added areas in the Adriatic, Tyrrhenian, and Balearic

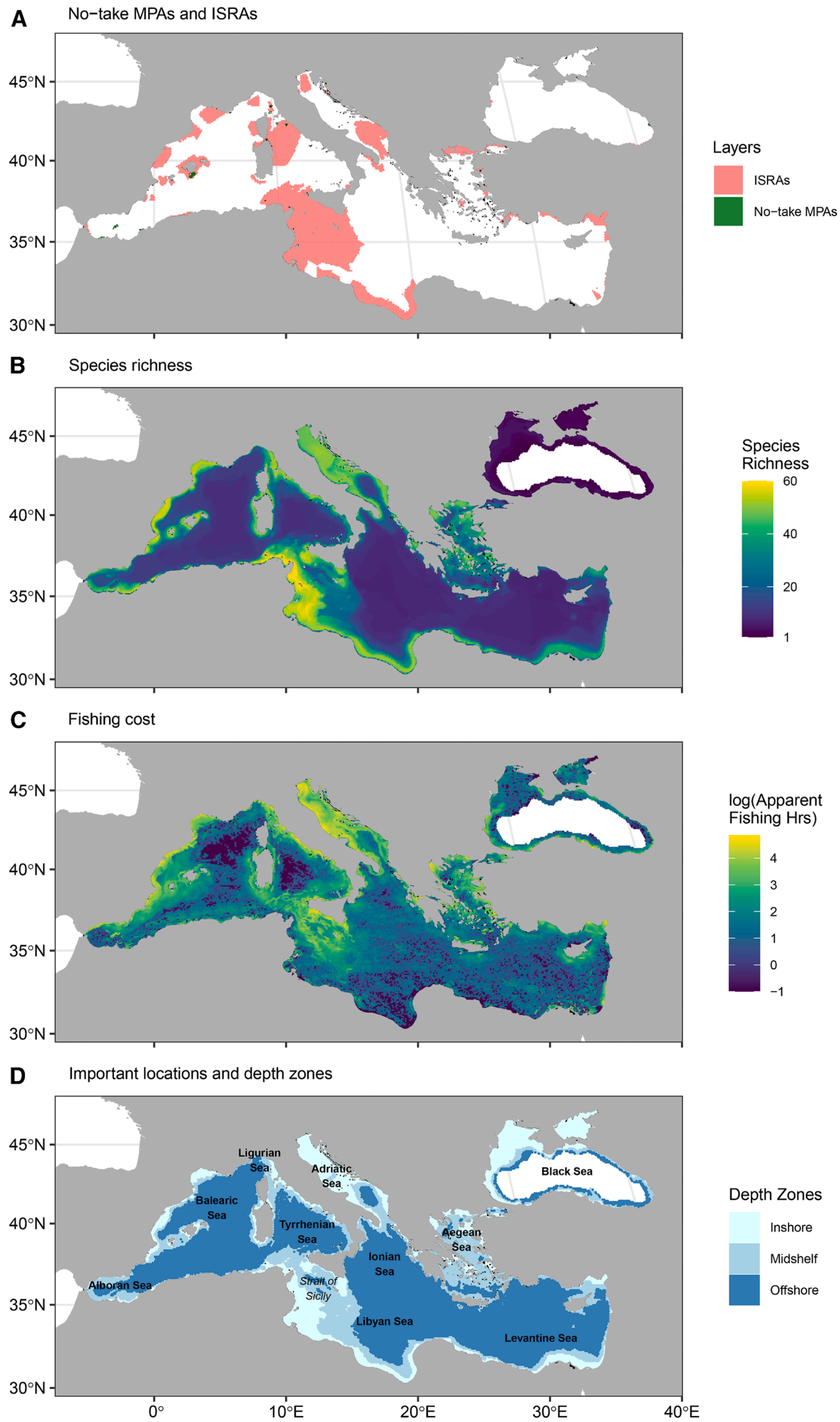

Figure 1. Key datasets in the study region

(A) All no-take MPAs (green; n = 57; combined area = 3,742 km^2 or 0.14% of planning region) and ISRAs (coral red; n = 65; combined area = 444,674 km^2 or 16.2% of planning region) in the Mediterranean and Black Seas.

(B) Species richness of chondrichthyans per 86.6 km^2 hexagonal planning unit.

(C) Cost layer based on fishing effort (apparent fishing hours) from Global Fishing Watch AIS and satellite data. See also Figure S1.

(D) Important locations and depth zones: inshore (0–200 m), midshelf (200–1,000 m), and offshore (>1,000 m), all including the benthos within their depth range.

seas, and in the Strait of Sicily (Figure 2C). The two solutions were quite different, with a Cohen's Kappa correlation coefficient of 0.45 indicating only moderate agreement. Planning units selected in both scenarios comprised 16.2% of the planning region.

The maps of importance scores showed that in Scenario 1, ignoring ISRAs, areas in the southern Strait of Sicily were most important to achieving the solution, followed by coastal areas of the southern Libyan and Alboran seas (Figure 3A). Areas with high importance scores partly overlapped with high species richness, although the Adriatic Sea, western and northern Balearic Sea, and northeastern Tyrrhenian Sea had high species richness but also high cost, resulting in low importance scores. In Scenario 2, including ISRAs, the southern and central Strait of Sicily was the most important, followed by coastal areas of the southern Libyan Sea, and the western and northern Balearic Sea (Figure 3B). Even when ISRAs were not explicitly considered in the prioritization (Scenario 1), planning units that overlap with ISRAs had high importance scores. This was reinforced in Scenario 2, where planning units inside ISRAs had higher importance scores (0.00096) than those outside ISRAs (0.000043; $t = -135.3$, $df = 6188.9$, $p < 0.001$). This indicates that ISRAs contain high-value habitat for the conservation features being targeted, regardless of whether they are deliberately prioritized in the solution. ISRAs with the highest mean importance score that were also larger than 1,000 km^2 were Jerba-Zarzis (0.0015 Importance Score/PU), followed by Tripolitania (0.0012), Kerkennah (0.0012), and Sirt Gulf (0.0012), all located in coastal waters of the southern Libyan Sea. These ISRAs were based on reproductive areas for angel sharks *Squatina* spp., Common Guitarfish *Rhinobatos rhinobatos*, Blackchin Guitarfish *Glaucostegus cemiculus*, smoothhounds *Mustelus* spp., and on range-restricted species. However, they also overlapped with areas of high species richness (Figure 1B).

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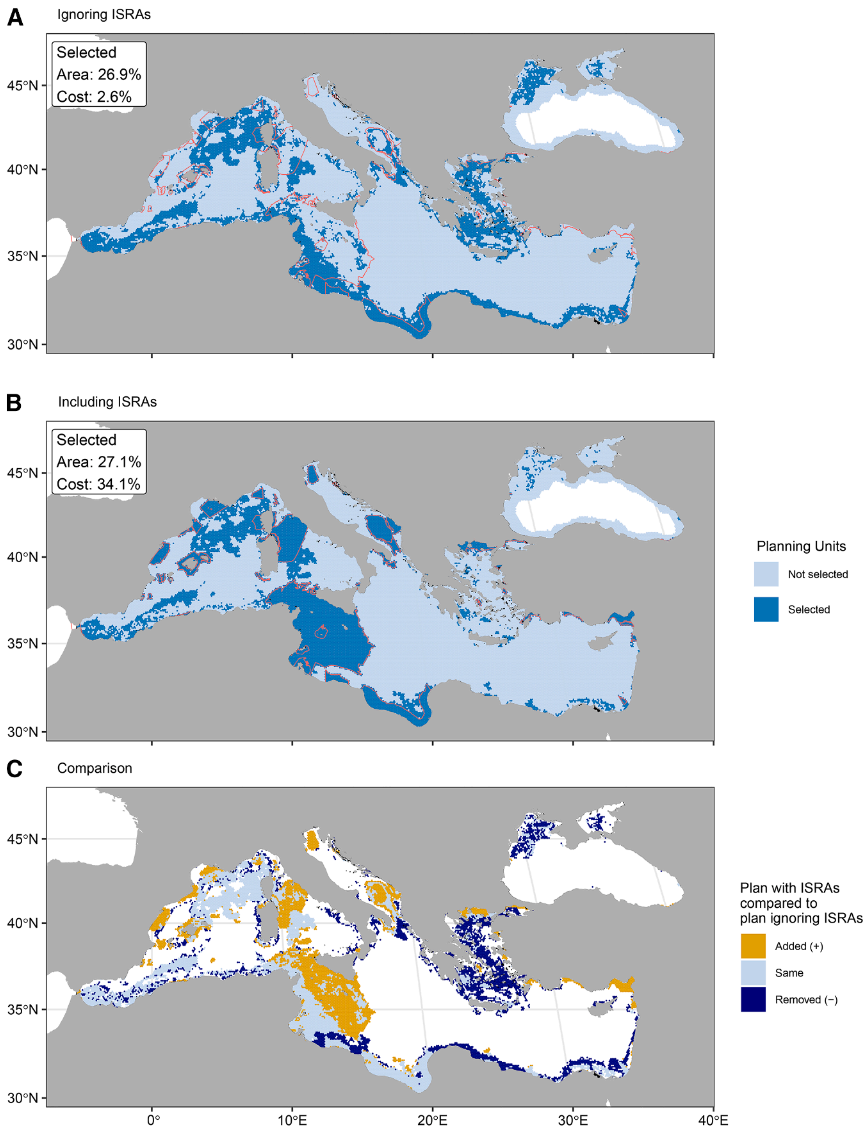

Figure 2. Prioritization solutions

(A–C) Solutions from (A) Scenario 1 - ignoring ISRAs, (B) Scenario 2 - including ISRAs, and (C) the difference between these solutions. In coral red in (A) and (B) are the ISRA outlines.

Using the minimum set objective in the prioritization ensures that all conservation targets (i.e., the proportion of a species' range that is selected for conservation based on the IUCN Red List status of each species) are met or exceeded (Figure 4A, also see Figure S2). Species that highly exceeded their target generally had a small range and a low target (Figure 4A). For example, the Spotted Skate *Raja montagui* had a range of 77,856 km^2, a target of 25% for a Least Concern (LC) species, and an area selected of 73.1% and 84.3% in Scenarios 1 and 2, respectively. By contrast, species that only marginally exceeded the target generally had a wide range and a high target. For example, the Smooth Hammerhead *Sphyrna zygaena* had a range of 1,762,015 km^2, a target for Critically Endangered (CR) species adjusted for its wide range to 32%, and an area selected of 33.3% and 34.7% in Scenarios 1 and 2, respectively (see Figure S2). Non-threatened species exceeded their lower targets by a higher percentage than threatened species exceeded their higher targets (Figure 4A).

The second solution, including ISRAs, resulted in 63 species (86.3% of the total) having a larger area selected than in Scenario 1, ignoring ISRAs. For example, the Endangered (EN) Dusky Shark *Carcharhinus obscurus* (target = 45%) just met the target in Scenario 1 compared to an area selected of 69.9% in Scenario 2, including ISRAs (see Figure S2). This difference was despite the first solution (26.9%) covering a similar amount of the planning area as the second solution (27.1%). Threatened species had a higher mean area selected when including ISRAs (48.3 ± 10.3%) compared to when ignoring them (42.7 ± 7.8%; t = −3.11, df = 91.7, p = 0.003). Non-threatened species had no difference. Non-threatened species had a lower target, but a greater excess of the area selected above the target value compared to threatened species (Figure 4B). However, the excess of the area selected above the target was higher in Scenario 2 including ISRAs compared to when ignoring ISRAs for threatened species only and not for non-threatened species (Figure 4B).

Cost of including Important Shark and Ray Areas

At the basin scale, including ISRAs in conservation planning selected only a slightly larger area in the solution (27.1% of total area) than Scenario 1, which ignored ISRAs (26.9%); however, the cost was higher when including ISRAs. Scenario 1, ignoring ISRAs, had a total cost of 903,208 apparent fishing hours over 10 years, equivalent to 2.6% of the total cost of the entire study region. This would leave 97.4% of the apparent fishing hours to continue to be fished. By contrast, Scenario 2, including ISRAs, had a cost equivalent to 34.1% of the total cost, leaving the area representing 65.9% of the cost to continue to be fished.

The Strait of Sicily and Tunisian Plateau ISRA was the most expensive ISRA, with a total cost of 4,356,812 apparent fishing hours (12.4% of total), more than four times as much as the entire solution under Scenario 1. This was also by far the largest ISRA (2,663 planning units). However, on a per-area basis, the Strait of Sicily and Tunisian Plateau ISRA fell just under the median cost for the area of ISRAs, with a mean cost of 1,636 h per planning unit. As the mean cost per planning unit was low and the mean

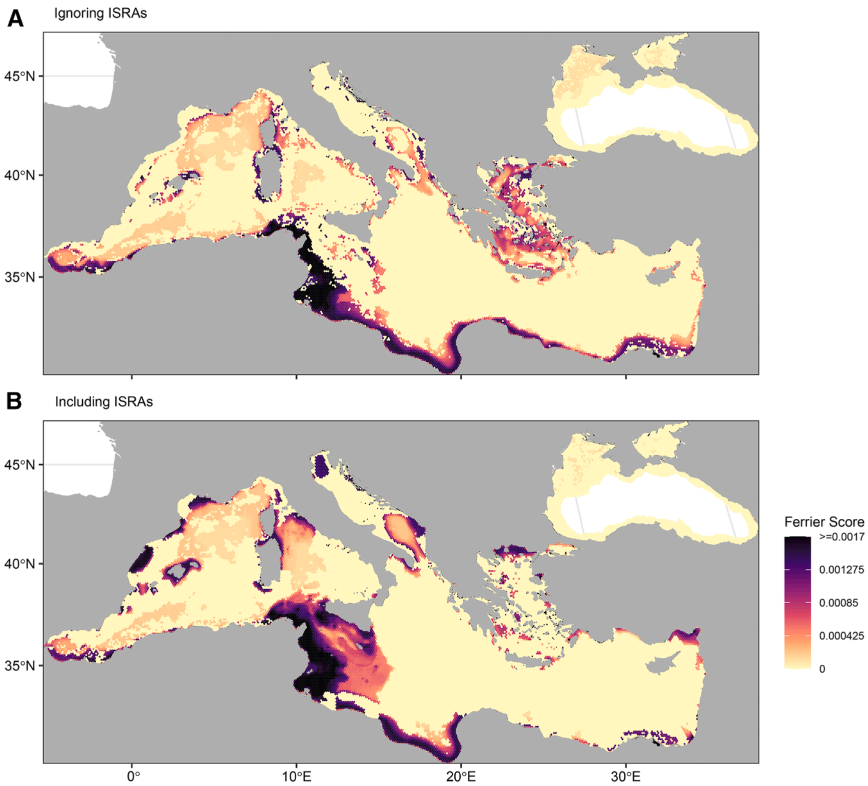

Figure 3. The relative importance of each planning unit to the final solutions of Scenarios 1 and 2

(A and B) The importance score for (A) the solution ignoring ISRAs (Scenario 1) and (B) including ISRAs (Scenario 2).

importance score was high, this ISRA was among those with the best cost-importance ratio (Figure 5). Others in that group included Sirt Gulf, Tripolitania, Lagoon of Bizerte, and Jerba-Zarzis ISRAs off Libya and Tunisia, and Amvrakikos Gulf ISRA in Greece (Figure 5). By contrast, some ISRAs had a high cost but a low importance score, including Strait of Messina ISRA in Italy, Northwest Adriatic ISRA in Italy and Croatia, or Danny Reef Palmahim ISRA in Israel (Figure 5).

To examine ways of reducing the cost of the conservation solution when including ISRAs compared to when ignoring ISRAs, we ran Scenario 3 that only locked-in ISRAs that had a low cost-importance ratio (top-left corner in Figure 5; n = 21 of 65 ISRAs). The locked-in percentage was reduced to 12.2% of all planning units in the study region. The solution selected an area of 27.3% of the total area, comparable to the 27.1% of the area including all ISRAs (see Figure S3). The cost was reduced from 34.1% when including all ISRAs to 15.6% of the total cost for the study region, meaning 84.4% of all fishing hours remained.

As an alternative, we also ran Scenario 4 that included all ISRAs, except those that were delineated based on Sub-criterion D2 (Diversity; n = 2) and Sub-criterion C4 (Movement; n = 4). These types of ISRAs are typically large and may, in some cases, be impractical to include in their entirety in conservation solutions. Excluding them meant that we reduced the locked-in area to 9.9% for the subset of ISRAs. The number of planning units selected in this solution (26.9% of total area) was comparable to the previous scenarios, ignoring or including all ISRAs. The cost was reduced from 34.1% when including all ISRAs, to 20.4% when locking in the subset of ISRAs, meaning 79.6% of all fishing hours remained.

Region-specific conservation planning

When adding the restriction that each target for each feature had to be met in each Marine Ecoregion of the World bioregion (MEOW[43]), scenarios ignoring or including ISRAs were different from the overall solutions without MEOWs (kappa = 0.03 and 0.05, respectively).

Comparing the two solutions when targets had to be achieved in each MEOW, the solution ignoring ISRAs selected 31.9% of planning units for conservation, with a cost equivalent to 8.8% of the cost of the entire planning region (see Figure S5). By contrast, the solution including ISRAs selected more planning units (36.2%) and was more expensive, with 37.1% of the total cost (see Figure S5). The percentage of the area selected for protection varied widely among different MEOWs, and only the Levantine Sea and Ionian Sea MEOWs had <30% of their areas selected (Figure 6). For example, the Adriatic Sea and the Alboran Sea MEOWs would need to have >40% of their areas protected to reach the conservation targets in both scenarios. Interestingly, the Tunisian Plateau/Gulf of Sidra MEOW had 34% of the area selected when ignoring ISRAs compared to 52% of the area selected, and with a higher cost, when including ISRAs (Figure 6).

There were also regional differences in the cost of these solutions. The overall cost was highest in the Western Mediterranean MEOW when including ISRAs, at least partly because it also had the most planning units selected for conservation. The Adriatic Sea MEOW had more planning units selected when including ISRAs (n = 840), than when ignoring ISRAs (n = 645). The mean cost per planning unit also increased when including ISRAs and was the highest of all MEOWs (Figure 6).

DISCUSSION

The Mediterranean and Black Seas region is a global hotspot of high extinction risk for chondrichthyans.[44] To halt and reverse steep population declines of chondrichthyans in this region, conservation planning needs to consider and prioritize these species. Our findings confirm that only a small fraction of this region is fully protected,[45] with 0.14% designated as no-take MPAs. None of the chondrichthyan species in this region had >2% of their range overlapping with no-take MPAs, showing that the current no-take MPA

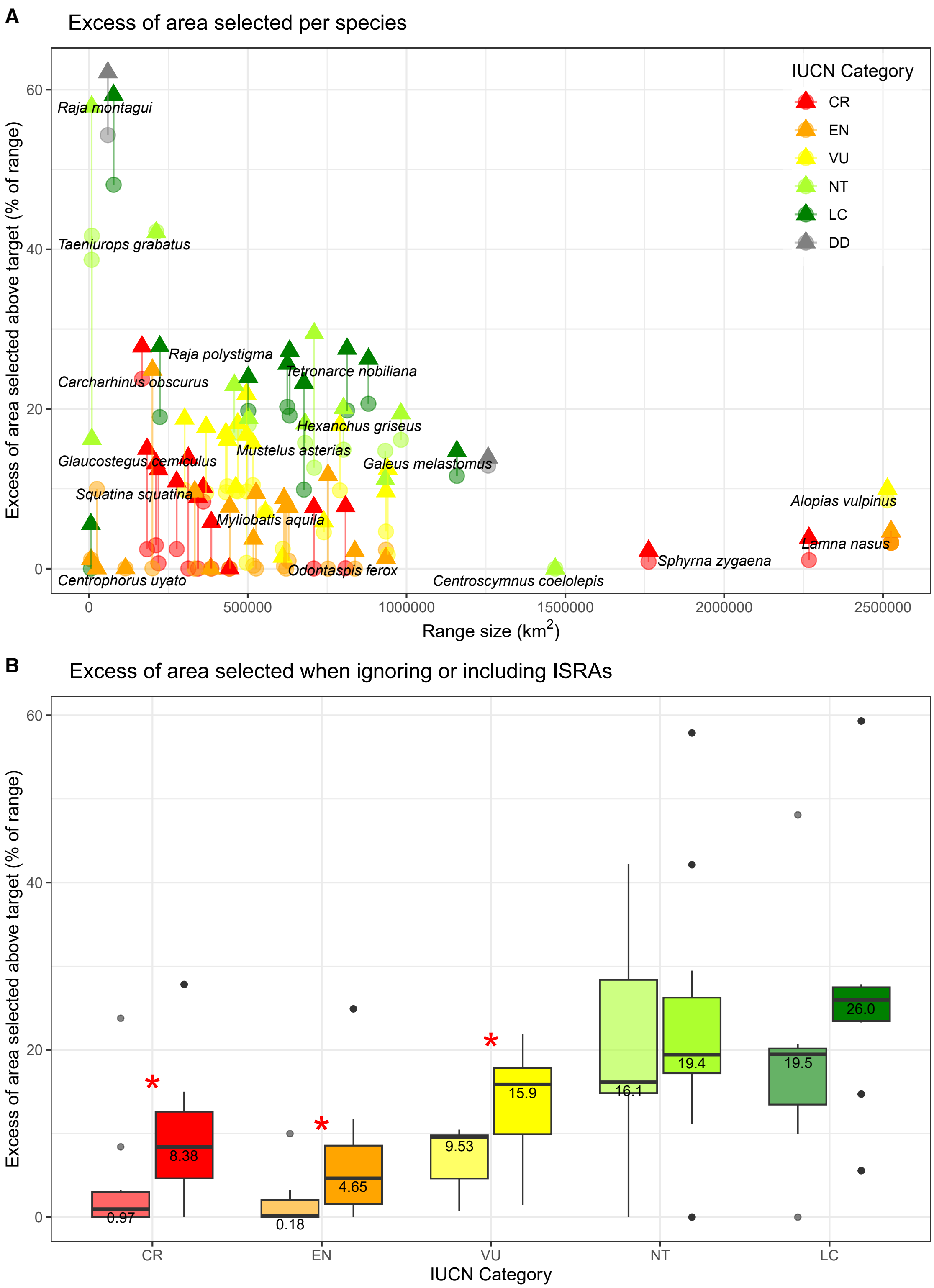

Figure 4. Representation in the final solutions

(A and B) The excess of the area selected above the target value by Scenario (A) grouped by species and plotted against their range size (Scenario 1 ignoring ISRAs = circle, Scenario 2 including ISRAs = triangle), and (B) grouped by IUCN category (CR = Critically Endangered; EN = Endangered;

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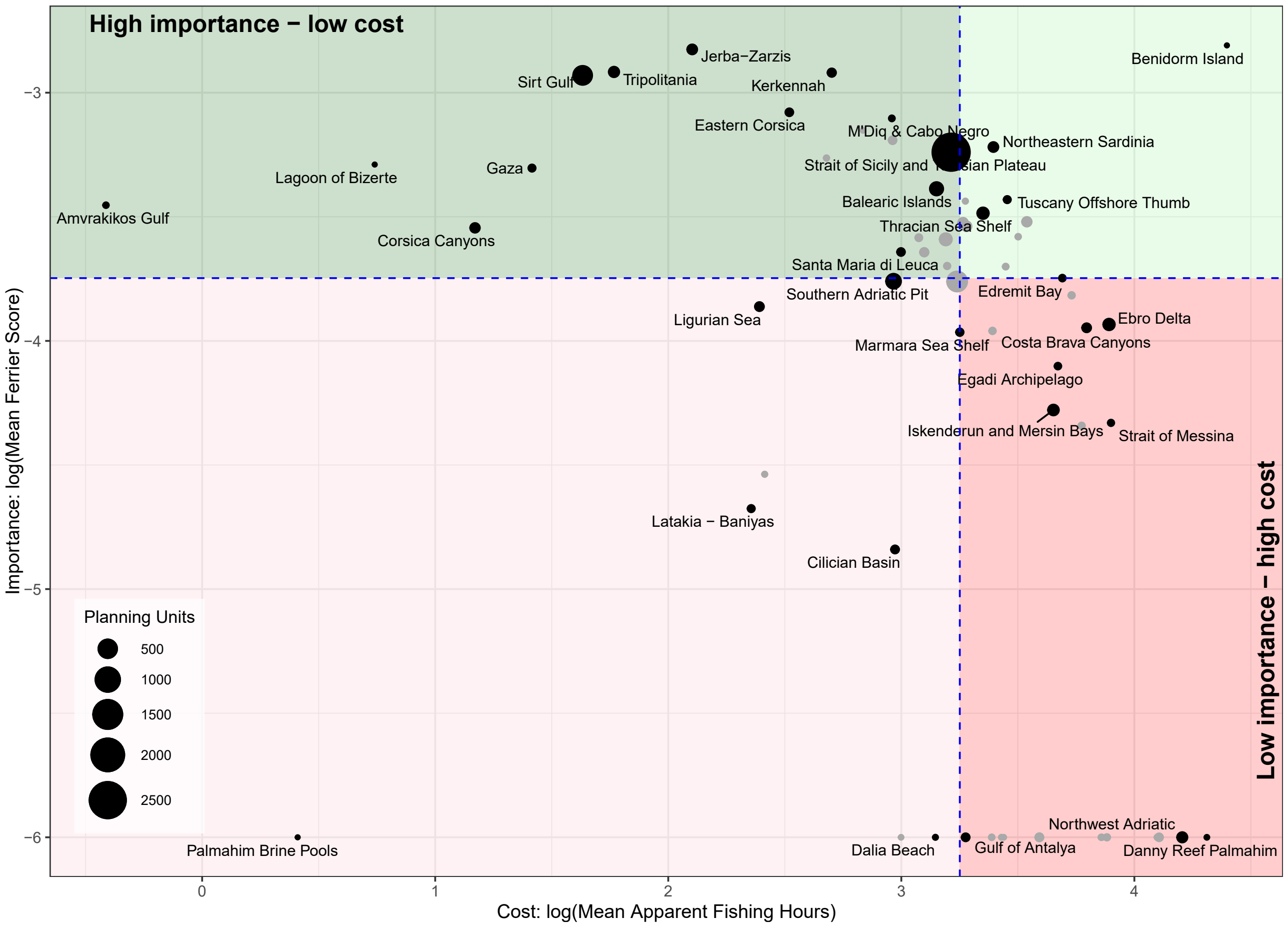

Figure 5. A cost-importance plot for ISRAs based on the solution from Scenario 2 including ISRAs, highlighting key ISRAs that might be prioritized for initial protection

The mean apparent fishing hours per planning unit (log) is the cost, and the mean importance score per planning unit (log) is the importance score. Quadrants are delineated by medians in the plot. Dark-green indicates high importance and low cost, while dark-red indicates low importance and high cost. Each dot represents an ISRA, labeled ISRAs are black and unlabeled ISRAs gray. See also Figure S3.

network affords poor protection to chondrichthyans in the Mediterranean and Black Seas. Although there are additional forms of management, designing no-take MPAs for chondrichthyans is key and urgently needed.[21–23] We show how ISRAs can inform systematic conservation planning and ensure areas important for critical life-history processes are included in the design of protected area networks. The 65 ISRAs delineated in this region[41] cover 16.2% of the planning region. Conservation solutions were markedly different when either ignoring or including ISRAs in the analyses. Despite the differences in the location of selected areas, the two scenarios selected a similar area size (∼27% of the study region; below the 30% of GBF Target 3). This suggests there is little drawback to including ISRAs in terms of protected area size and that it will likely provide benefits for the broader regional marine biodiversity. However, we found a substantial cost increase when including ISRAs, largely due to their overlap with areas of high fishing effort. We highlight several ways of reducing the cost while still focusing MPA design on ISRAs. We argue that the benefit of selecting important areas under the various scenarios, including ISRAs, outweighs their cost, as ISRAs are very likely to markedly improve the quality of the habitat protected for chondrichthyans and their likely conservation effectiveness, compared with solutions solely based on species range maps.

Benefits of using Important Shark and Ray Areas in systematic conservation planning

Many conservation planning approaches use species range maps, making the implicit assumption that all parts of a species'

VU = Vulnerable; NT = Near Threatened; LC = Least Concern) with Scenario 1 in light colors (left) and Scenario 2 in dark colors (right). In panel b, boxplots show median (center line), first and third quartiles (box edges), 1.5× interquartile range (whiskers), and outliers (individual points beyond whiskers). * indicates a significant difference ($p < 0.05$) between the scenarios using Welch's t-test. Data Deficient species were excluded due to small sample size ($n = 2$). See also Figure S2.

Figure 6. Differences in the solutions - ignoring and including ISRAs - among MEOW ecoregions

Differences in the percentage of planning units selected and the cost per planning unit when ignoring (solid circles) or including (triangles) ISRAs for each MEOW (excluding the Saharan Upwelling with only 3 planning units). The size of the symbols is relative to the number of planning units in each MEOW and the green horizontal line indicates 30% of the area. See also Figure S5.

range have the same importance to the species and its persistence.[46] However, this assumption does not hold true for most species, including many chondrichthyans that have broad ranges but use small, specific areas for important life history functions e.g., Refs. 47 and 48. Conservation solutions based on ranges for such taxa do not always select these important areas that are critical to the persistence and recovery of species (e.g., Scenario 1 ignoring ISRAs). Important sites may include reproductive areas, feeding grounds, stop-over points along migration routes, or areas with particularly high densities of a range-restricted species.[36] These key sites supporting life-history processes are often relatively small compared to species ranges.[41,49,50] For example, Blue Sharks *Prionace glauca* range widely in the Mediterranean Sea, but mating and nursery activities occur in small, coastal areas in the Gulf of Lions.[49] Similarly, threatened and wide-ranging species are most susceptible to further population decline at aggregation sites, such as at offshore seamounts, where threats such as fishing can target and impact the high density of otherwise solitary individuals.[51] Conservation plans that ignore these important aggregation sites could achieve little for the conservation of these species. Additionally, protecting areas important for species with a small range is important because habitat destruction or disturbance can exacerbate fishing pressure, and overharvesting can put these species at risk of extinction.[13,52] The underrepresentation of chondrichthyans in conservation planning to date[25,29] is partly because of a lack of centralized information on critical habitats. The ISRA approach addresses this gap directly and identifies these important areas through a wide-ranging expert consultation and an independent review process, following clear guidelines and a data-driven approach to delineate boundaries. This approach therefore represents the best-available knowledge for these taxa[36] and helps inform conservation planning.

Beyond the key representation of critical habitats, the solution with ISRAs covered a similar amount of the total area to that ignoring ISRAs (26.9% and 27.1%), providing higher quality for the same quantity. Both values are also under the 30% goal under Target 3,[1] despite our ambitious targets for the 73 species.

Broadly, this means that including ISRAs in systematic conservation planning for chondrichthyans in this region does not necessarily lead to unrealistic solutions that require more area for conservation than the global target percentage suggests. This is, in part, a direct consequence of the size of ISRAs, which span ∼16.2% of the total area in this planning region. A key component in the delineation of ISRAs is that they have the potential to be managed for conservation.[36] As such, boundaries are drawn around the most important areas to ensure the size of ISRAs is within dimensions that allow them to be used in spatial planning. It is thus possible to include ISRAs in systematic conservation planning and greatly enhance conservation outcomes, without exceeding area budgets.

Another major benefit of including ISRAs in conservation planning is that threatened species can achieve better protection. In our example from the Mediterranean and Black Seas, threatened species had a larger area protected in Scenario 2, including ISRAs, compared to when ISRAs were ignored. A larger area protected means that more of the range of each species is selected for protection in the solution, in addition to selecting the important areas, which can be crucial for threatened species that require urgent conservation intervention to halt and reverse population declines.[53] Although targets were the same, and were achieved in both scenarios, the solution including ISRAs exceeded the target more than when ISRAs were ignored. An ISRA criterion exists for threatened species, but it does not trigger an ISRA alone – instead, a threatened species also has to meet one of the other criteria.[36] It is also likely that threatened species were included in more ISRAs because fishing has reduced their broad range to remnant populations in areas that had enough data to support an ISRA. By contrast, there was no difference in the area selected for non-threatened species whether ISRAs were included or ignored.

Costs of using Important Shark and Ray Areas in systematic conservation planning

Historically, protected areas have been placed in areas that minimize conflict with human needs and thus minimise the cost, but there is often a trade-off between meeting conservation objectives and minimizing the cost to industry.[54] The GBF Target 3 now specifically commits governments to protect areas that optimize biodiversity conservation and ecosystem function.[1] This approach of considering quality and not just quantity of protected areas likely increases their cost.[5,6,54] Our study shows that, although the solution when locking-in ISRAs affords the greatest protection for chondrichthyans and is likely to maximize their persistence, it was also more expensive. Scenario 1, including all ISRAs, left ∼66% of hours available for fishing and was ∼13 times more expensive than the scenario ignoring ISRAs. The major contributor to this difference in cost is that more ISRAs were delineated in coastal areas that have much higher fishing costs. In practice, when other taxa, not just chondrichthyans, and even other Important Areas are included as features in a systematic conservation plan, coastal areas will still often be important to achieving the solution. For example, almost all marine Key Biodiversity Areas (KBAs) are in coastal waters in the Mediterranean and Black Seas (median depth = 76 m).[55] Solutions from these planning problems will therefore likely have a similar or higher cost than our Scenario 1, ignoring ISRAs based on chondrichthyans only. The additional cost of including ISRAs in a more comprehensive analysis would then be much smaller. Our example highlights the general trade-off between higher cost and better quality of protected areas to achieve conservation goals under the GBF.[5,6] However, we note that even the solution ignoring ISRAs had almost half of the selected planning units (43.7%) inside ISRAs. This is likely to be a consequence of the positive correlation between species richness and ISRAs ($r = 0.52$) and highlights the importance of considering these areas for the conservation of chondrichthyans.

We explored several ways to reduce the cost but still have a solution focused on ISRAs. First, we considered ISRA size, as establishing large protected areas can be difficult to balance with human needs near the coast, and can be ineffective and impractical to implement in remote areas.[54,56] We can thus exclude large ISRAs from locking in, particularly those that are movement areas (delineated under ISRA Sub-criterion C4). In our study region, examples include the Eastern Gulf of Lions and the Costa Brava Canyons ISRAs for Blue Shark movements. Although there were few and relatively small movement areas in this region, compared to other ISRA regions, removing these from the locked-in areas could help reduce the area or the cost of a solution based on ISRAs. Similarly, although highly diverse areas can be selected for protection to more rapidly reach the area target for many species,[57] these areas, here delineated under ISRA Sub-criterion D2, can also be large, expensive, and impractical to include in their entirety (e.g., Strait of Sicily and Tunisian Plateau ISRA). Not locking in ISRAs triggered by Sub-criteria C4 and D2 in our study region almost halved the cost of the solution, from 34.1% to 20.4% of the total area cost. In cases where individual ISRAs may be too large to be included in area-based protection, other conservation measures, such as fishing gear restrictions or temporal closures, can be explored. These can also provide benefits to chondrichthyans, particularly in combination with protected areas.[24]

Second, we propose a data-driven approach to identify priority ISRAs based on a cost-importance analysis that could help to better balance the trade-off between conservation and fishing in practice. Instead of basing selection on the type or characteristics of Important Areas (i.e., the ISRA Criteria applied),[58,59] we only locked in ISRAs with a favorable ratio of low cost and high importance score. This approach reduced the cost of the solution from 34.1% to 15.6% of the total cost of the study region. An alternative approach may be to exclude ISRAs in the worst cost-importance quadrant from locking in to also get a cheaper solution, or to set a percentage target for these areas rather than using a binary approach.[60]

Mediterranean and Black Seas

Ambitious targets are needed for chondrichthyans in the Mediterranean and Black Seas because many populations are severely depleted.[44,61] Further, the number of threatened chondrichthyans species has gradually increased, making this a hotspot of extinction risk.[44,62,63] Our analyses showed that ambitious targets, ranging from 19 to 45% of species' ranges, and relative to their IUCN Red List status and the distribution for wide-ranging species, can be achieved by protecting <30% of the area. However, there were differences between the scenarios in the location of areas selected for protection that complicate achieving a region-wide solution. In the overall solutions, ignoring or including ISRAs, large shelf areas of the southern Strait of Sicily and Libyan Sea were consistently selected, while other areas, including much of the Black Sea or the central Adriatic were ignored. Although a conservation solution for the entire region would be the most efficient,[64,65] it will be difficult to implement as countries individually strive to increase protection in their waters. For example, protecting most of the coastal waters of Tunisia is impractical, as some areas will need to continue to be available for fishing, despite the region-wide analyses suggesting it is important to achieve the solutions. Similarly, protecting a small amount of Croatian waters in the Adriatic Sea, as suggested by the region-wide analyses, will not help this country substantially strive for increased protection.

Since EEZs have not been consistently declared in the region,[66] we used Marine Ecoregions of the World instead to further examine region-specific differences. The inclusion of MEOWs in conservation planning improves the effectiveness and representativeness of protected areas[43] but can also increase the area and cost of a solution. The solutions from our analyses with MEOWs ignoring and including ISRAs covered a larger combined area (31.9% and 35.8%, respectively) than solutions from a basin-scale analysis, and including MEOWs resulted in more expensive solutions (8.6% and 36.4% of total cost, respectively). This shows that systematic conservation plans on a smaller scale may need to reduce the targets to achieve a practical solution. Individually, most MEOWs exceeded 30% of the area selected, including the Alboran Sea with 45% selected in both scenarios. The largest increase in area selected under Scenario 6, including ISRAs, was in the Tunisian Plateau/Gulf of Sidra and the Adriatic Sea MEOWs. There were also differences in cost, with the highest mean cost per planning unit in the Adriatic Sea MEOW in both scenarios. The Alboran Sea, Ionian Sea, and the Western Mediterranean MEOWs were also expensive to protect. Smaller-scale systematic conservation planning may benefit from a minimum shortfall approach that can set the total amount of area to be selected for conservation,[42] instead of the minimum set objective used here that balances the cost with achieving defined targets for each species.

Limitations of the study

The goal of this study was to illustrate how Important Areas (e.g., ISRAs) can be used in systematic conservation planning and how they can influence the solutions and improve the conservation of chondrichthyans. As such, this is a theoretical, large-scale study that has not been an iterative process involving a broad set of stakeholders and is thus not meant to be prescriptive in terms of where to place protected areas. There are several ways to improve systematic conservation planning solutions based in part on Important Areas, all largely reliant on better available data when planning a smaller area in more detail.

The Important Areas used here represent the best available data on the taxon; however, identifying additional Important Areas will enhance conservation outcomes.[8,67] In our study region, information from deep-sea and offshore areas, particularly in the eastern Mediterranean Sea, was largely lacking, resulting in few ISRAs delineated there. Further studies and data collection from fisheries in these areas could lead to the delineation of additional ISRAs and improve the conservation of underrepresented species.[16] The conservation plans here also do not include other potential conservation features, such as teleost fishes, marine reptiles, marine mammals, or habitats such as seagrass meadows. The ambitious targets in our analyses, with the protection of up to 45% of the range for CR and EN species, resulted in <30% of the study area selected for protection. However, when additional conservation features are included alongside chondrichthyans in an analysis (e.g., other key taxa groups), targets might need to be lower to achieve a solution that selects a realistic amount of area for protection.

A major limitation is the relatively simple cost layer. We used apparent fishing hours as the only cost because fishing is the most pertinent threat to chondrichthyans in general. Our fishing cost layer was derived from the Global Fishing Watch data, mainly using the AIS data and supplementing it with satellite data where no AIS data were available.[68] The GFW algorithm performs well when classifying fishing methods used by large vessels (e.g., trawls, longlines), but can overestimate their fishing duration,[69] and it yields poorer results for methods used by smaller vessels, such as gillnets.[70] The conversion from satellite data to apparent fishing hours has the limitation that there were areas, particularly off North Africa, with no AIS data to input into the calculation. This means that if the boat size or the number of boats is different here, the conversion might not accurately reflect the fishing pressure. Aside from the conversion, the apparent hours fished ignores the tonnage and value of fish caught and are thus only a coarse proxy for the revenue from fishing. More detailed prioritisation analyses may be able to use more realistic fishing costs in terms of value. Also, other zones apart from MPAs can impact fishing, such as offshore wind farms, which are expanding rapidly, especially in Europe, and often prohibit fishing activities,[71,72] however, it will also be important to further examine any potential negative effects they could have on chondrichthyans.[71] Finally, setting areas aside for conservation can also impact other human uses of the marine environment (e.g., shipping, mining, oil and gas, marine renewable energy, aggregate extraction, tourism), and these costs could also be taken into consideration in more detailed prioritization exercises.

Our fishing cost layer also does not include all types of fishing. Small-scale or artisanal fishing is widespread in the study region, comprising 82% of fishing vessels, 15.4% of landings, and 26% of fisheries revenue,[73] and also threatens chondrichthyan populations.[30,62] However, it is more difficult to track, and spatial data of small-scale fisheries at the regional scale are lacking, as they remain mostly untracked[74] and largely unmanaged.[75,76] These fisheries constitute a vital source of food, income, and culture for coastal communities, especially in southern Mediterranean countries.[77] Costs to livelihood dependency and food security were not considered in this study, as broad-scale spatial data are lacking, but should be included in more detailed conservation planning analyses. A lack of data on small-scale fisheries also meant that some of the ISRAs with a low cost-importance ratio, based on our cost layer, have some of the most important artisanal shark and ray fishing. The redistribution of fishing effort after implementing no-take MPAs, and thus how the future cost will change, was not considered. This response is likely to vary by fishery type. A broad stakeholder consultation process will be crucial to secure equitable and participatory marine protected area design and management.[78,79]

Functional groups of chondrichthyans have specific vulnerabilities to certain fishing gear types.[80,81] Specific plans for each group with the relevant fishing cost layer (e.g., trawlers for benthic species vs. longliners and purse seiners for pelagic species) would improve conservation while also reducing the cost of the solution. For our region-wide analyses, these specific data were not consistently available, mainly because the satellite-derived GFW data do not allow distinction between gear types, but they may be used when planning protected area networks in smaller areas or sub-regions.

Including Important Areas in systematic conservation planning and future research

The approach shown here for chondrichthyans also broadly applies to Important Areas developed to delineate areas for the life history functions of other taxa or for biodiversity (e.g., IMMAs,[37] IMTAs,[38] or KBAs[58]). These Important Areas are not legislative and do not directly invoke protection for delineated areas. However, they provide spatial planners with a tool that can be used to effectively manage and conserve critical habitats for a range of biodiversity.[82] Important Areas are not yet consistently used in systematic conservation planning but offer a great advantage over range-based approaches that ignore the benefits of Important Areas to the species.[58,83] While we focus here on area-based protection, Important Areas can also be used when developing Other Effective Area-based Conservation Measures (OECMs). This is a key consideration since OECMs offer one approach to achieving large scale conservation targets while mitigating biodiversity loss (e.g., Targets 3 and 4).[84] We also highlight that a broad stakeholder involvement will be required when taking this theoretical work to an applied systematic conservation planning process. Visualizing results from a variety of scenarios (e.g., with different taxa/habitats to protect, different conservation targets, different parameterizations), such as with a Shiny App or other interactive dashboard, will help decision makers to compare solutions and make informed choices.[85]

The nuances of how these Important Areas can be incorporated into systematic conservation planning may vary with taxa, but the overall framework will be similar. When Important Areas cover a relatively small part of the planning area, planning units that overlap with them can be locked in in prioritization analyses so that they have to be selected in the solution. ISRAs cover ∼16.2% of this planning region and we thus argue that all ISRAs are important to protect and therefore locked them in. For simplicity and to focus on the potential inclusion of ISRAs in MPA networks, we did not consider any forms of connectivity - including dispersal of spawning products, movement of megafauna, or climate connectivity - in the analyses. However, there are also other approaches that warrant further investigation. First, it is also possible to select only certain Important Areas based on the criteria they were delineated for or on an importance-cost ratio. For example, large movement areas or areas with a high cost-importance ratio could be excluded from locking-in, or only areas delineated for the reproduction of chondrichthyans could be selected for locking-in. This may be particularly applicable to Important Areas approaches that delineate areas with different levels of importance.[58] Second, Important Areas could be given a target rather than locking them in as a whole; for example, a target of 50% for each ISRA would ensure at least half of each Important Area is selected in the solution. This approach would further reduce cost, as high-cost areas within ISRAs could be excluded from the solution. We avoided this scenario to highlight that the whole area of ISRAs is considered critical habitat and has important protection value. However, such an approach is likely a necessary step, particularly for large ISRAs, when balancing stakeholders' interests and designing a network of protected areas on a smaller scale. Nevertheless, further subdivision of ISRAs would likely be detrimental to the conservation outcomes for the species in that area and may require more detailed investigation of the spatial aspect of important life history functions within ISRAs to ensure that selected areas do provide protection for these critical habitats. It would also be part of tradeoffs negotiated by stakeholders. Third, the vertical dimension of ISRAs could be used to reduce the protected volume, as not all ISRAs extend from the surface to the seafloor, while also considering the fishing methods used in the area. When detailed AIS data are available throughout the study region, the *prior3D* package[86] could be valuable for additional analyses when different depth layers could have different costs depending on the fishing gear used, allowing better depth-specific conservation plans. There are several subsurface ISRAs that extend from between 100 and 1,150 m depth and are benthic or benthic and pelagic (e.g., Ibiza Channel Slope, Otranto Channel, Cilician Basin ISRAs). Vertically zoned protected areas could be designated,[87] which means that these areas could be fished in the water column above, while bottom trawlers or deep-water longliners are excluded. However, allowing pelagic fishing in a benthic ISRA might be problematic if there is strong vertical connectivity of ocean communities through active (e.g., vertical migration)[88] and passive (sinking)[89] transport. Similarly, an area overlapping with an ISRA delineated for a seasonal aggregation of a species could still be fished outside of that season, again reducing the cost while still improving protection for that species. Such seasonal closures may qualify as OECMs, but might need further examination, as they can have opposing effects on abundance in a multi-species fishery[90] and achieve little for benthic communities.[91] Finally, a more practical approach for a smaller-scale systematic conservation planning exercise would be to consider management zones instead of the binary selected/not selected approach used here. Such work would require more detailed data on how an area is used, particularly on costs from stakeholders other than industrial fisheries (e.g., artisanal fishers, offshore energy) to balance interests. For example, management zones could define what fishing gears can be used to achieve effective chondrichthyan protection outside of strict no-take zones. Overall, for chondrichthyans, we stress the benefit of selecting areas under the ISRAs scenario as this approach can improve the quality of the protected area network, and ultimately, its conservation effectiveness.

RESOURCE AVAILABILITY

Lead contact

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Materials availability

This study did not generate new unique materials.

Data and code availability

- Data: Links to data repositories are in the key resources table. Additionally, all updated species range map shapefiles from the regions are available upon request.
- Code: All original code has been deposited on GitHub and is publicly available at https://github.com/SpatialPlanning/ISRA_Systematic-Conservation-Planning as of the date of publication.
- Other Items: Any additional information required to reanalyze the data reported in this article is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

C.A.R., A.J.R., and R.W.J. designed the study. C.A.R., E.G.R., R.C., A.B.M., J.B., T.L.M., G.N.d.S., A.O.A., R.B., A.B., M.B., N.B., C.B., I.Ć., I.G., J.G., M.M., G.M., R.N.A.S., S.M., F.S., E.S., A.S., and R.W.J collected data. C.A.R., A.J.R., J.D.E., and T.L.M. analyzed the data. C.A.R., R.W.J., and A.J.R. drafted the article. All authors contributed to the interpretation of results and edited the article.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- QUANTIFICATION AND STATISTICAL ANALYSIS
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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Important Shark and Ray Areas (ISRA) shapefiles are publicly available for download.	Important Shark and Ray Areas eAtlas	https://sharkrayareas.org/e-atlas
IUCN species range maps are available for download.	The International Union for Conservation of Nature (IUCN) Red List of Threatened Species	https://www.iucnredlist.org/
Global Fishing Watch data are available for download.	Global Fishing Watch (GFW)	https://globalfishingwatch.org
MAPAMED data are available for download.	MAPAMED, the database of MArine Protected Areas in the MEDiterranean	https://www.mapamed.org/
Protected Planet data are available for download.	Protected Planet	https://www.protectedplanet.net/
Software and algorithms		
R version 4.4.2	R Core Team[92]	https://www.R-project.org/
prioritizr R package	Systematic Conservation Prioritization in R	https://prioritizr.net/
Data analysis R scripts	This paper	https://github.com/SpatialPlanning/ISRA_Systematic-Conservation-Planning

METHOD DETAILS

Important Shark and Ray Areas

ISRAs are 'discrete three-dimensional portions of habitat that are critical for the survival of one or more shark, ray, or chimaera species and have the potential to be managed for conservation'. The IUCN SSC Shark Specialist Group leads the delineation of ISRAs by developing proposals for candidate ISRAs in collaboration with regional experts. An independent review panel critically assesses whether there is sufficient supporting evidence and if the ISRA Criteria are applied correctly before ISRAs are delineated. ISRA Criteria were designed to consider the biology and life-history of chondrichthyans and all delineated ISRAs require evidence of the regular and predictable occurrence of a species/criterion combination.[36,39] Briefly, these criteria include: (A) Vulnerability, as many chondrichthyans have a high risk of extinction, and protecting areas that are important to these threatened species is needed to reduce biodiversity loss. (B) Range Restricted, used for species with restricted geographic ranges, broadly defined as occurring in up to two adjoining Large Marine Ecosystems.[93] (C1) Reproductive Areas, applies to areas that are important for courtship, mating, gestation, egg deposition, pupping, and for early life stages. (C2) Feeding Areas, applies to important areas for chondrichthyans to derive nutrition. (C3) Resting Areas, applies to areas used in a species' daily activity cycle to conserve energy. (C4) Movement, applies to areas that are important for migrations of species. (C5) Undefined Aggregations, applies to areas where chondrichthyans aggregate predictably but the driver of the aggregation is unknown. (D1) Distinctiveness, is used for areas where chondrichthyans display distinct characteristics. Identifying these areas can ensure the persistence of unique behavioural or ecological adaptations in sub-populations. (D2) Diversity, which refers to areas that support a relatively high number of species.

All ISRA maps and factsheets are publicly available on the ISRA eAtlas (https://sharkrayareas.org/e-atlas). In May 2023, a workshop was held in Thessaloniki, Greece, in which 173 contributors from 21 countries collated information on chondrichthyans in the region and applied the ISRA Criteria.[41] For this region, the threshold for the ISRA Diversity Sub-criterion (D2) was set at 19 species (26% of total).[94]

QUANTIFICATION AND STATISTICAL ANALYSIS

Prioritisation

We compared conservation solutions from spatial prioritisation based on species range maps of chondrichthyans based on two scenarios: 1) ignoring ISRAs and 2) including ISRAs (see Table S1). The conservation problem had several inputs: *features* (e.g., species or habitats) to be conserved by selecting *planning units* (spatial units within the planning region) to achieve a *target* (the amount of each feature to conserve) while minimising the *cost* (usually the cost to industry - typically fishing - of protecting certain areas).[31] In our case, chondrichthyans were the features and targets were percentages of their ranges. Targets were set based on the extinction risk status of each species from the IUCN Red List of Threatened Species (IUCN Red List) so that more of a species' range would be selected for more threatened species. The cost was based on a high-resolution fishing effort spatial layer from Global Fishing Watch data (https://globalfishingwatch.org), because fishing is generally the largest threat to chondrichthyans. We compared the similarity of the two solutions (ignoring and including ISRAs) with the Cohen's Kappa pairwise correlation coefficient *r* that measures agreement beyond what can be expected by chance.

The R package 'prioritizr' version 8.0.3[42] was used to run spatial prioritisations. We used the Coin or Branch and Cut (CBC) solver with an optimality gap of 0.001 (the proximity to the optimal solution) and a binary decision (an entire planning unit is either included or excluded from selection in a protected area) in all analyses. We used the minimum set objective, which meets all conservation targets whilst minimising the cost of the MPA network.[42] The planning region was the Mediterranean and Black Seas ISRA region,[39] but we excluded areas where our species range maps suggest no presence (in the central Black Sea). This resulted in a planning region covering an area of 2,751,147 km^2 and including coastlines from 28 jurisdictions. We divided this area into 31,801 equal-area hexagonal planning units (86.6 km^2) with a centre-to-centre distance of 10 km.

Conservation features

Conservation features in our systematic conservation plans were species of sharks, rays, and chimaeras based on their range maps. To create these range maps, shapefiles were downloaded from the IUCN Red List database in November 2022.[10] We updated species ranges for species: 1) that did not have their range corrected for the bathymetry of their global depth range, as this was not part of the mapping process for assessments published prior to 2018; and 2) with more recent literature. For example, the IUCN Red List range of the Dusky Shark *Carcharhinus obscurus* does not include the Mediterranean Sea,[95] but more recent work confirms that they are found there[96–98] and we thus included it. Vagrant or locally extinct species were excluded, leaving 73 species that regularly occur in our planning region, including 40 shark, 31 ray, and 2 chimaera species. Species richness was calculated as the number of species per planning unit whose range covered at least half of the planning unit's surface area. More than half (47 of 73) of these species had sufficient information to apply at least one of the ISRA Criteria and delineate ISRAs.[41] To assess the vertical occurrence of conservation features, we used the global depth range of each species from the IUCN Red List, and updated it where newer records were available.[99,100]

Targets

Two-thirds of the species in the region (68.5%) are threatened with extinction on the IUCN Red List (i.e., Critically Endangered [CR], Endangered [EN], or Vulnerable [VU]).[10] For each conservation feature (i.e., chondrichthyan species), we assigned targets on the basis of the global IUCN Red List category, unless the region-specific assessment listed the species more than one category above the global level (n = 6 species).[101] For example, the White Shark *Carcharodon carcharias* is VU on a global level but CR within this region and we thus considered it CR for our analyses. Targets used in the prioritisation were set based on extinction risk status because threatened species require greater protection to halt and reverse population declines. We followed Faure-Beaulieu et al.[29] to set targets and adjusted them to achieve a practical solution of <30% of the area selected. Species considered CR and EN were given the highest target of 45% of their range in selected protection areas in the solution, while VU (35%), Near Threatened (NT; 30%), and Least Concern (LC; 25%) species were given lower targets. Following Faure-Beaulieu et al.,[13] Data Deficient (DD) species were assigned same protection (30%) as NT species, considering that many may be threatened but have insufficient available data to be assessed. Eleven species had a wide distribution >1,000,000 km^2 and we reduced their target by scaling the IUCN-based target by species' range size.[102] For example, the Shortfin Mako *Isurus oxyrinchus* is EN (target=45%) but is also widely distributed (2,525,503 km^2) and has a target multiplier of 0.54 resulting in a target of 24%.

Cost

We use a proxy of fishing effort as the cost layer, considering that fishing is the largest threat to chondrichthyans.[13] We express the cost of a solution as the percentage of the total cost, i.e., how many apparent fishing hours would be removed from the total fishing effort. Cost was the sum of apparent fishing hours in each planning unit, based on Global Fishing Watch automatic identification system (AIS) data.[103] These were annual data from 2013–2023 with a 0.01° spatial resolution. Although cost information is needed in every planning unit, AIS data were only available for 76.2% of planning units, as not all fishing effort is recorded with AIS data.[68] We thus used vessel detection from Sentinel-1 SAR satellite data to estimate the fishing cost in planning units with no AIS data available (see Figure S1). We used monthly vessel detection data from January 2017 to April 2024 and summed the number of vessels that were fishing in each planning unit. Fishing was defined as vessel/location combinations that had a fishing probability index of 0.9 or more.[68] We then used planning units that had information from both datasets (67.1%) to predict apparent fishing hours from the number of fishing vessels, using a linear model of log-log data (r=0.44, F=11,270, df=21,350, p < 0.001). Finally, all planning units with <0.1 apparent fishing hours (n=214, 0.7% of total area) and with no data (n=1,974, 6.2%) were given a cost of 0.1 to avoid some cells being completely 'free' to select in solutions. The median cost per cell was 38.5 apparent fishing hours with a range of 0.1–72,450. Although the considerable missing data for planning units based on the Global Fishing Watch was far from ideal, we considered this dataset more appropriate than other large-scale fisheries datasets such as from Sea Around Us, which is older and less spatially resolved.[104] We have focused on the surface-to-seafloor analysis in the main text and included the 3-D prioritisation analysis in the Supplementary because there was insufficient cost data by depth for a robust 3-D prioritisation (see the discussion for more information).

Locked-in areas and importance scores

The MAPAMED database[105] for the Mediterranean Sea basin and the Protected Planet database[106] for the Black Sea were used to determine areas already designated as strictly protected; these were locked-in in the prioritisation analyses. We only included areas with an IUCN Category Ia, Ib, II, or III ('strictly protected' henceforth). These are the categories that represent no-take zones where no fishing should be allowed[107] and can thus be considered effective for chondrichthyan protection if appropriately implemented and enforced. These were locked-in in all scenarios, i.e., the planning units overlapping with no-take MPAs had to be selected in the solution. Although much of the region is under some form of management, the legal and policy framework for spatial management is highly complex in this region,[108] including for chondrichthyans,[109] and MPAs often lack a management plan or effective implementation[110] We acknowledge that there are other areas in the region with specific fishing management rules or protected areas with management plans that may also protect species from some forms of fishing, however, analysing the fishing threat to chondrichthyans in each of those was outside the scope of this study.

To compare the influence of ISRAs on conservation plans, we then also locked-in planning units that overlap with ISRAs in Scenario 2. A total of 65 ISRAs were delineated in the Mediterranean and Black Seas. The horizontal extent of these ISRAs ranged from 0.1 to 219,913 km^2, with a median of 994 km^2 and covering a combined 444,674 km^2 (16.2% of the planning region). We used the ISRA spatial data layers available at https://sharkrayareas.org/e-atlas/.

The importance score reflects the contribution of each planning unit to achieving the overall solution. We used the Ferrier Score as a measure of the importance score; it is calculated for each feature per planning unit and then summed.[111] We extracted the importance scores from Scenario 1 for planning units located within ISRA boundaries to examine the importance of areas where ISRAs were placed, based on species range maps only. These importance scores do not quantify the importance of an ISRA itself, but rather their importance in achieving the overall conservation solution. As such, they calculate the irreplaceability of the area to achieving the solution, which can be driven by various factors, including complementarity with other selected areas, species richness, or species with small, isolated ranges. We compared the excess of the area selected above the target value between Scenarios 1 and 2 grouped by IUCN Red List category using Welch's t-test.

To explore ways of reducing the cost when including ISRAs, we added two further scenarios. We only locked-in ISRAs with a low cost-importance ratio (n=21) that had an above-median importance score to achieving the solution, and a below-median cost per planning unit (Scenario 3). Then, we excluded ISRAs delineated based on Sub-criterion D2 (Diversity, n=2; Strait of Sicily and Tunisian Plateau, and Balearic Islands ISRAs) and C4 (Movement, n=4; Strait of Gibraltar, Eastern Gulf of Lion, Costa Brava Canyons, and Strait of Messina ISRAs) because these are often large, and locked in the remaining ISRAs (Scenario 4; see Table S1).

Boundary penalty

The boundary penalty determines the balance between a cheaper more fragmented MPA network and a more clumped but expensive one.[31] We balanced this trade-off by visually assessing a suite of candidate solutions for different boundary penalties and choosing a boundary penalty that penalised fragmented MPA networks but was not too restrictive[31] (see Figure S9). For the overall scenarios, the boundary penalty was set at 0.005 and it was adapted based on individual tests of candidate penalty values for other analyses that included depth layers or Marine Ecoregions of the World (MEOW)[43] in the problem.

Inclusion of ecoregions

To maximise the likelihood of long-term persistence of conservation features, it is important to ensure features are protected in multiple separate patches, spaced apart. This replication of features spreads risk against damaging events and long-term change affecting individual MPAs, and ensures that natural variation in the feature is covered (either at a genetic species level or within habitat types).[31] EEZs have not been consistently declared in this region[66,112,113] and we therefore used MEOWs as biologically-relevant sub-regions in a further analysis (Scenarios 5 & 6; Table S1). These MEOWs are a biogeographic classification of coastal and shelf waters. We excluded the three planning units in the Saharan Upwelling MEOW in this analysis, leaving eight MEOWs in our study region (see Figure S4). We then used the same targets as in the overall approach, but in this scenario the targets had to be met inside each MEOW. The boundary penalty was visually assessed and set at 1e-09 for this analysis.