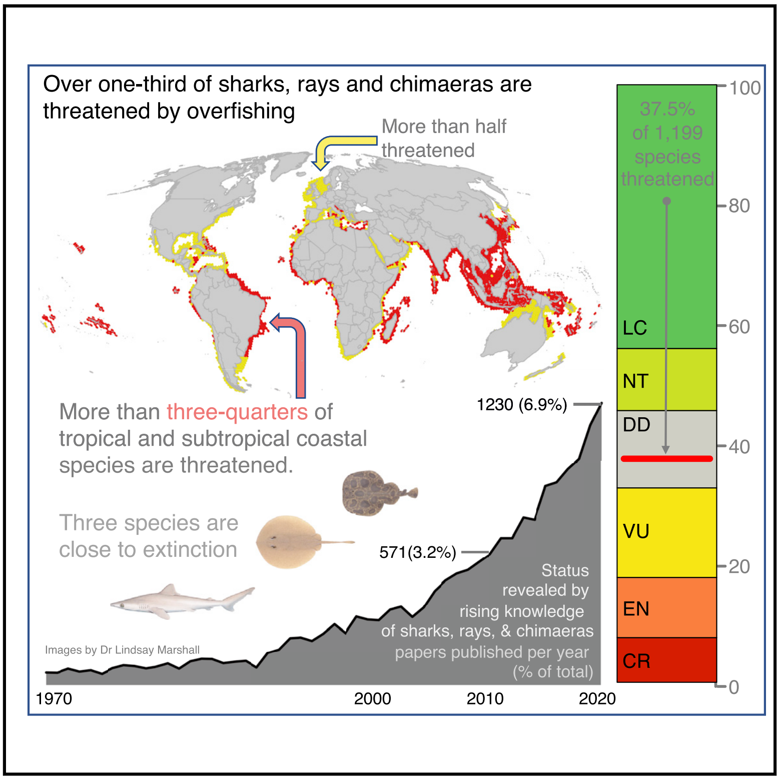
Article

Current Biology

Overfishing drives over one-third of all sharks and rays toward a global extinction crisis

Graphical Abstract



Highlights

- More than one-third of chondrichthyan fish species are threatened by overfishing
- Disproportionate threat in tropics risk loss of ecosystem functions and services
- Three species not seen in >80 years are Critically Endangered (Possibly Extinct)
- The depletion of these species has been driven by continuing demand for human food

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In brief

The IUCN Red List of Threatened Species is increasingly used to reveal the health of ocean biodiversity. Dulvy et al. assess 1,199 chondrichthyans and demonstrate the need for fishing limits on target and incidental catch and spatial protection to avoid further extinctions and allow for food security and ecosystem functions.

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Overfishing drives over one-third of all sharks and rays toward a global extinction crisis

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SUMMARY

The scale and drivers of marine biodiversity loss are being revealed by the International Union for Conservation of Nature (IUCN) Red List assessment process. We present the first global reassessment of 1,199 species in Class Chondrichthyes—sharks, rays, and chimeras. The first global assessment (in 2014) concluded that one-quarter (24%) of species were threatened. Now, 391 (32.6%) species are threatened with extinction. When this percentage of threat is applied to Data Deficient species, more than one-third (37.5%) of chondrichthyans are estimated to be threatened, with much of this change resulting from new information. Three species are Critically Endangered (Possibly Extinct), representing possibly the first global marine fish extinctions due to overfishing. Consequently, the chondrichthyan extinction rate is potentially 25 extinctions per million species years, comparable to that of terrestrial vertebrates. Overfishing is the universal threat affecting all 391 threatened species and is the sole threat for 67.3% of species and interacts with three other threats for the remaining third: loss and degradation of habitat (31.2% of threatened species), climate change (10.2%), and pollution (6.9%). Species are disproportionately threatened in tropical and subtropical coastal waters. Science-based limits on fishing, effective marine protected areas, and approaches that reduce or eliminate fishing mortality are urgently needed to minimize mortality of threatened species and ensure sustainable catch and trade of others. Immediate action is essential to prevent further extinctions and protect the potential for food security and ecosystem functions provided by this iconic lineage of predators.

INTRODUCTION

Human activity has affected the ocean for centuries, directly through fishing and hunting, and indirectly by habitat modification and climate change.[1–3] These effects, coupled with those on land, have heralded a new geological epoch—the Anthropocene—characterized by rapid environmental transitions driven by humanity.[4] On land, the Anthropocene has seen

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increased extinctions, with some postulating life on earth is facing its sixth mass extinction.[5] In the ocean, the extinction risk has increased most recently over the past century with the growth of human populations and associated intensification of industrial fishing and technological efficiency, and the rapid development of coastlines.[6–8] While the recent effects of human pressures have been well documented for coral reefs,[9,10] much of our understanding of fishery impact is heavily biased toward the most data-rich target species in the developed world.[11] However, statistical predictions, based on life histories, catch, and fisheries development, warn that the unassessed data-poor fisheries, particularly for sharks, may be highly unsustainable.[12]

The Class Chondrichthyes (sharks, rays, and chimeras) is one of the three lineages of fishes, and the most evolutionary distinct radiation of vertebrates.[13] It has survived at least five mass extinctions in its 420 million year history[14,15] and has radiated throughout the major marine (and some freshwater) habitats, dominating upper trophic levels and imposing predation risk in many food webs.[16,17] Chondrichthyans are one of the first major marine fish lineages for which extinction risk has been determined for the entire clade. The first global IUCN Red List of Threatened Species assessment reported at least 17.4% of 1,041 species were threatened, while a trait-based model predicted one-quarter of all species were threatened.[18] That assessment also revealed almost half (46.8%) of species were Data Deficient (DD), meaning a lack of information inhibited a full grasp of their extinction risk. As our understanding of this crisis has become clearer, regulatory frameworks and commitments to halt depletion have evolved. Fishing limits and restrictions on trade have increasingly been imposed for both target and incidentally caught species.[19–23] To date, these actions cover a small fraction of chondrichthyans, are applied unevenly across species' ranges, frequently fall short of scientific advice, and are often inadequate.[23,24]

Reassessment of the extinction risk faced by chondrichthyans provides a refined understanding of this group's trajectory and how individual species are responding to management action or inaction. More broadly, their distribution across marine habitats and a range of higher trophic levels means reassessment enables tracking progress toward broad indicators of the state of the world's oceans (e.g., biodiversity targets, Sustainable Development Goals).[25] Here, we report on the first full reassessment of chondrichthyans almost 10 years after the completion of the first global assessment.[18] From 2013 to 2021, we assessed 1,199 chondrichthyans through 17 workshops resulting in published Red List global-scale assessments co-authored by 322 Assessors.

RESULTS

Overall number and percent threatened

We estimate over one-third of chondrichthyans are threatened with extinction globally, based on the observed number of threatened species combined with the estimated number of DD species that are likely to be threatened (Figure 1A). Of 1,199 species assessed, 391 (32.6%) are threatened, with 180 (15%) Vulnerable (VU), 121 (10.1%) Endangered (EN), and 90 (7.5%) Critically Endangered (CR; Table 1). A further 124 species (10.4%) are classified as Near Threatened (NT) and less than half (44.1%, n = 529) are considered Least Concern (LC). Rays are more threatened than previously estimated, with 36.0% (n = 220 of 611) of species now threatened, compared to sharks (31.2%, n = 167 of 536) and chimeras (7.7%, n = 4 of 52) (Table 1).

Updated threat status compared to the 2014 assessment

The current observed number of threatened species is more than twice (391 of 1,199) that of the first global assessment in 2014, which reported 181 of 1,041 species were threatened[18] (Figure 1A). If we assume that DD species are threatened in proportion to the other species, then over one-third (37.5%) of chondrichthyans are threatened, with a lower estimate of 32.6% (assuming DD species are all LC or NT) and an upper estimate of 45.5% (assuming all DD species are threatened; Figure 1A). In 2014, based on the observed but uncertain threat level, predictions of the true threat level were made using two methods. First, using a trait-based model (similar to the models used in Figure 4) one-quarter (23.9%; n = 249) of chondrichthyans were predicted to be threatened. Second, using the method recommended by IUCN,[26] which assumes that DD species are threatened in the same proportion as non-DD species, 33% of species were predicted to be threatened (n = 340; range 17.4%–64.2%). In 2014, this simple IUCN DD calculation successfully forewarned of the likely high threat level, albeit with a high degree of uncertainty; the current estimate based on the less uncertain 2021 assessments is 37.5% threatened species (n = 449, range 32.6%–45.5%).

A key question is whether species have genuinely worsened in status since the last assessment or whether we now have a more accurate assessment of status. The reality is that it is a combination of both; nevertheless, there are now twice as many threatened species to recover. Next, we consider how the increase in threatened species arose from reduction in data deficiency and *genuine* (an improvement or worsening of the rate of decline, or population size, or range size, or habitat) and *non-genuine* changes (arising from one or a combination of six reasons; see STAR Methods for further details).

Reduction of data deficiency and *non-genuine* change due to new knowledge

The previous global assessment had a very high level of data deficiency, with nearly half (46.8%, 487 of 1,041) of species classified as DD. Due to taxonomic changes, this new assessment retrospectively finds that 454 of the current species list were DD in 2014, compared to 155 of 1,199 (12.9%) in 2021, i.e., DD has been reduced by approximately one-third (34.1%, 155/454 species). Indeed, we find that, of the species previously categorized as DD, nearly a quarter (23.4%, n = 106 of 454) are now placed in one of the three threatened categories (CR, n = 19; EN, n = 24; VU, n= 63), whereas just under half (44.5%, n = 202) are now LC, and 106 remain DD (Figure 1A). The spatial patterning of DD is striking: formerly there were up to 55 DD species per hexagon grid cell (23,322 km^2; see Figure 7B in Dulvy et al.[18]) and now there are fewer than 10 DD species per hexagon grid cell (Figure 1B). The current spatial pattern shows high data deficiency in species-rich countries with considerable scientific capacity to discover new species that might be listed as DD

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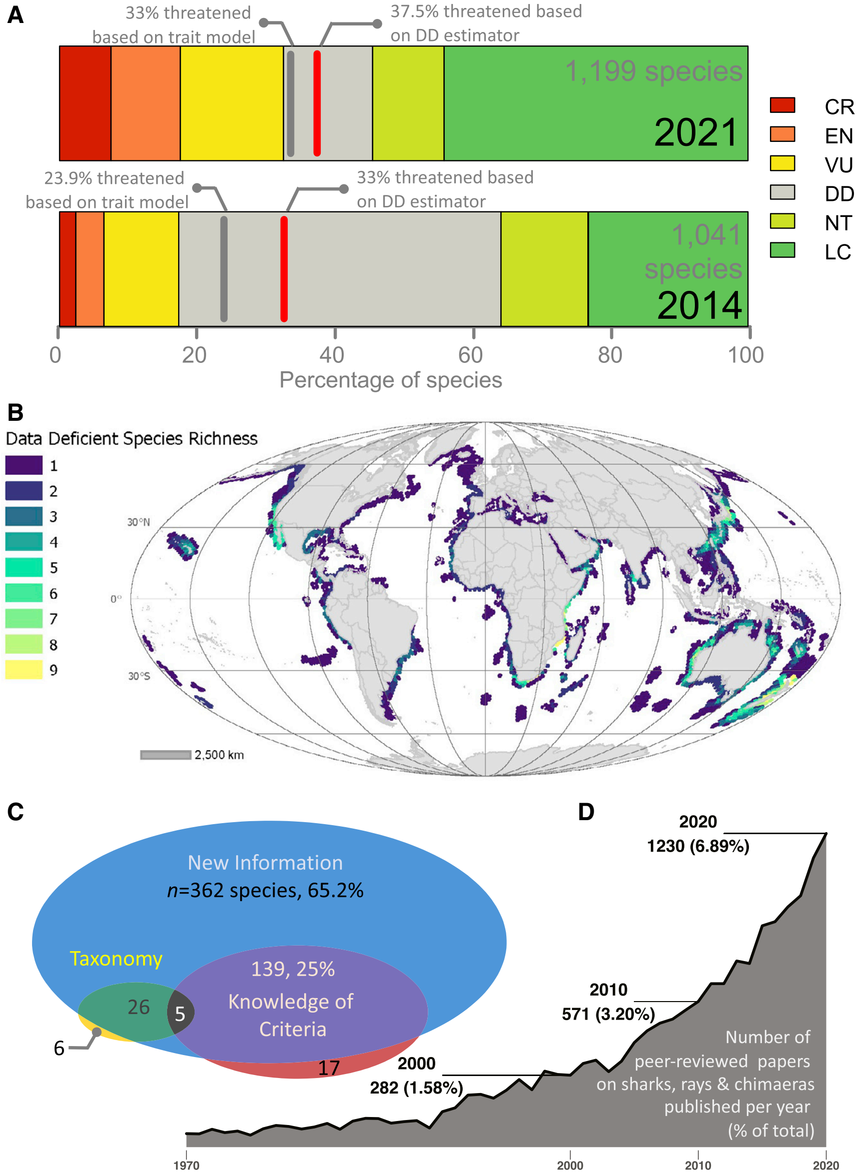

Figure 1. Currently, over one-third of chondrichthyans are threatened

(A) Difference in IUCN Red List status between 2021 (upper bar) and the first assessment (lower bar, 2014). This current threat is much greater (37.5%, estimated range 32.6%–45.6%, red line in upper bar), based on the observed number of threatened species combined with the estimated number of Data Deficient (DD) species that are likely to be threatened, than the 24% estimated using a trait-based model in 2014 (gray line in lower bar) and more similar to the estimate from the IUCN DD estimator (red line in lower bar, 33%, range 17%–64%).

(B) The spatial pattern of data deficiency (scale bar, 2,500 km).

(C) Euler diagram of three main reasons for *non-genuine* change: new information, knowledge of criteria, and taxonomy.

(D) Half a century of exponential growth in peer-reviewed scientific literature on sharks, rays, and chimeras indexed on the Web of Science. CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient.

(New Zealand, Australia, Taiwan, and Japan), as well as areas with a high degree of endemicity where research is particularly needed: the Western Indian Ocean, southern Brazil, the Pacific coast of Nicaragua, and the Gulf of California[13,27,28] (Figure 1B). Next, we consider how the increase in threat level and number of LC species in this reassessment is due to the reduction in DD species through *non-genuine* changes.

Excluding the previously Not Evaluated (NE) species, just under half (43.6%, n = 448) of chondrichthyan species have not changed status since 2014, and just over half (55%, n = 565) have undergone some form of *non-genuine* status change (Figure 1C). Much of the *non-genuine* change can be attributed to three main reasons: new information (94.2% of *non-genuine* changes), improved application of the criteria (28.5%), and improved taxonomic resolution (6.5%, Figure 1C; see STAR Methods for details). The last decade has seen major improvements in information and taxonomy, notably with the publication of major field guides for sharks[29] and rays[30] resulting in 171 NE species assessed for the first time and 50 revised taxonomic concepts. The volume of peer-reviewed chondrichthyan research is growing exponentially with the number of scientific papers published doubling each decade (Figure 1D). In addition, a concerted effort to compile time series of relative abundances, combined with decision-support Bayesian state-space methods has improved population reduction estimates.[31–34] These approaches were applied to 111 (9.3%) assessments. Prior to this development, the calculation of population reduction of relatively data-rich species was controversial (1) because of the challenge of choosing among multiple, potentially contradictory time series, and (2) because the focal species was a target or significant incidental catch of commercial fisheries.[33] Further, new space-for-time approaches were applied to extensive baited remote underwater video abundance estimates for nine wide-ranging coral reef species[35] (STAR Methods).

A *genuine* status change was recorded for only 15 species (1.6%, seven sharks and eight rays): twelve species have worsened (i.e., moved to a higher threat category) and three skate species have improved (i.e., moved to a lower category). These *genuine* improvements demonstrate the promise of fishery management for addressing declines. The New Zealand Smooth Skate (*Dipturus innominatus*) moved from NT to LC due to population increases attributed to the implementation of

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Table 1. Observed number and percent of chondrichthyan species in IUCN Red List categories

	Species number (% of 1,199)	Number threatened (% of 391)	Number threatened (% of group)	CR (%)	EN (%)	VU (%)	NT (%)	LC (%)	DD (%)
Taxon									
Rays[a]	611 (51.0)	220/391 (56.3)	220/611 (36.0)	55 (9.0)	65 (10.6)	100 (16.4)	70 (11.5)	246 (40.3)	75 (12.3)
Sharks	536 (44.7)	167/391 (42.7)	167/536 (31.2)	37 (6.9)	54 (10.1)	76 (14.2)	49 (9.1)	248 (46.3)	72 (13.4)
Chimeras	52 (4.3)	4/391 (1.0)	4/52 (7.7)	0 (0.0)	0 (0.0)	4 (7.7)	4 (7.7)	35 (67.3)	9 (17.3)
Total	1,199		391 (32.6)	92 (7.7)	119 (9.9)	180 (15.0)	123 (10.3)	529 (44.1)	156 (13.0)
Habitat									
Coastal	582 (48.5)	296/391 (75.7)	296/582 (50.9)	77 (13.2)	81 (13.9)	138 (23.7)	75 (12.9)	161 (27.2)	50 (8.5)
Deepwater	572 (47.7)	65/391 (16.6)	65/572 (11.3)	11 (1.9)	20 (3.5)	34 (5.9)	47 (8.2)	355 (62.1)	105 (18.4)
Pelagic and mesopelagic	38 (3.2)	23/391 (5.9)	23/38 (62.2)	3 (7.9)	13 (34.1)	8 (21.1)	1 (2.6)	13 (34.2)	0 (0.0)
Freshwater[a]	7 (0.6)	6/391 (1.5)	6/7 (85.7)	1 (14.3)	5 (71.4)	0 (0.0)	0 (0.0)	0 (0.0)	1 (14.3)

Separated for the three main extant lineages—rays (Subclass Batoidea), sharks (Subclass Selachimorpha), and chimeras (Suborder Holocephali)—and for the four main habitats. CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient. Number threatened is the sum of CR, EN, and VU. Species number and number threatened are expressed as percentage of the total species number (1,199) and total number threatened (391), respectively. The percent of each species in IUCN Red List categories is expressed relative to the total number of species in the group (taxon or habitat).

[a] Excluding South American freshwater stingrays

science-based catch quotas since 2003.[36] Two other large skates from the Northwest Atlantic shelf seas have recovered from severe depletion: Barndoor Skate (*D. laevis*) and Smooth Skate (*Malacoraja senta*). While the reasons are not fully understood, recovery is partially due to closure of the targeted skate fishery in Canada and landing prohibitions in the USA.[37,38] The smooth skate improved from EN to VU due to increases in abundance indices in the southern part of its range in the USA and the eastern Grand Banks in Canadian waters while the barndoor skate improved from EN to LC based on recovery since the mid-1990s; the population index has exceeded 1965 abundance levels for almost a decade.[37]

Emergence of extinctions most likely due to overfishing

Three species are now likely to be extinct, and there are at least eight cases of local extinction. Based on comparison across all of the CR and EN species and the application of a new methodology, three species were classified as Critically Endangered (Possibly Extinct) (CR(PE))[39,40] (Figure 2). Both the Lost Shark (*Carcharhinus obsoletus*) and the Java Stingaree (*Urolophus javanicus*) were estimated to have extinction probabilities $p_{extinct}$ of ~0.77 and 0.84, meeting the threshold for CR(PE) ($p_{extinct}$ between 0.5 and 0.9). The Pondicherry Shark (*Carcharhinus hemiodon*), which has not been seen for 30 years, had a $p_{extinct}$ of 0.464, which is just below the CR(PE) threshold and thus listed as CR.[41–43] The Red Sea Torpedo (*Torpedo suessi*) was assessed as CR(PE) in 2017 prior to the development of the latest criteria. These probabilities are in part based on a lack of sightings for nearly a century despite considerable passive surveillance and recent directed surveys, but more directed surveys are needed to definitively conclude extinction.[39,40] The Java Stingaree has not been recorded since 1868, the Red Sea Torpedo since 1898, and the lost shark since 1934.[41,42,44,45] These CR(PE) species are poorly known to science with few confirmed specimens collected from limited localities. Yet there are numerous other poorly known species assessed as LC or DD, e.g., the Papuan Guitarfish (*Rhinobatos manai*) and the Pocket Sharks (*Mollisquama* spp.). These species are known from only one specimen, and all were assessed as LC based on their low likelihood of capture by fisheries.

These are the first reports of likely global extinctions of chondrichthyans and overexploitation is the most parsimonious explanation for the cause of these disappearances.[46] We attribute cause to overfishing for three main reasons: (1) as we show next, all threatened species are imperiled by overexploitation; (2) we considered all 11 major threats in the IUCN threat classification scheme for each threatened species; and (3) these species are all distributed in the northern Indian Ocean and more than 75% of species in any map cell are threatened through this region (Figures 6C and S2). The Lost Shark and the Java Stingaree both occurred in the heavily fished waters of Southeast Asia, while the Red Sea torpedo was known only from a small section of the Red Sea (Figure 2B). The Java Stingaree and Red Sea Torpedo likely had small ranges that might have increased their sensitivity to extinction risk. Three local extinctions notably occurred in the northern Indian Ocean (Tentacled Butterfly Ray, *Gymnura tentaculata*; Indian Sharpnose Ray, *Telatrygon crozieri*; and Ganges Shark, *Glyphis gangeticus*; Figure 2C). We have not included further local extinctions that are more recently mapped and extensively documented for sawfishes and Northeast Atlantic angel sharks. These eight species are locally and regionally extinct, on average, from more than half of their former ranges[47,48]

Overfishing is the key threat driven by use and trade

Of the 1,093 species, 99.6% were threatened by overfishing mainly due to unintentional catch (often referred to as bycatch). Overfishing is the main threat for all 391 threatened species (Figure 3A) and is the sole threat for two-thirds of species (67.3%, n = 263; Figure 3A). Large-scale (industrial) fisheries are the key threat, either on their own as a unique threat

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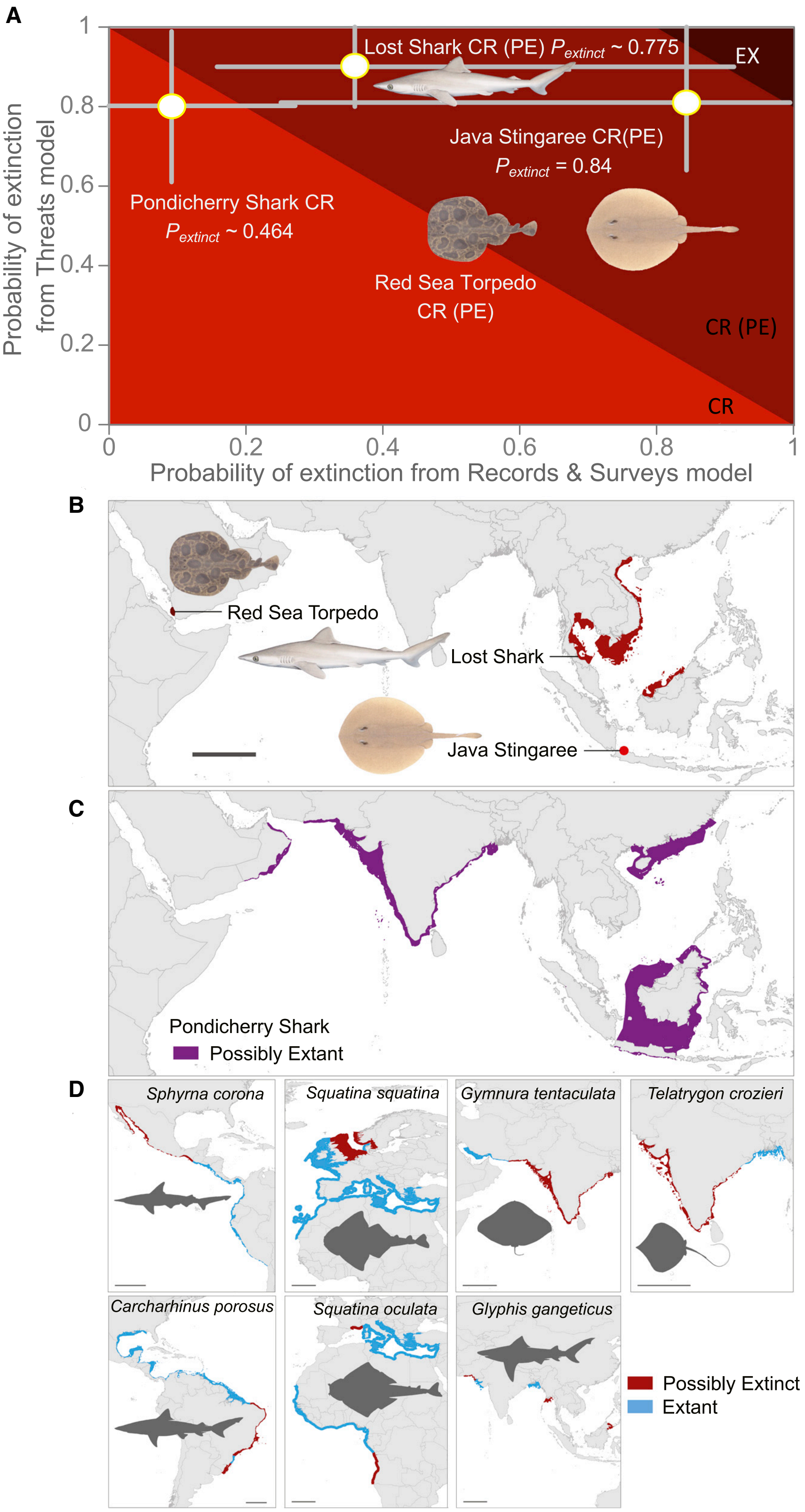

Figure 2. Global and local extinctions of sharks and rays

(A) Two rays and one shark are now Critically Endangered (Possibly Extinct) (CR(PE)). The probability that local threats are high and span the range of both the Lost Shark and Java Stingaree resulting in a high and relatively certain threat probability (y axis). However, the low level of passive surveillance and directed surveys mean the probability of extinction estimated using the record and survey model is lower and less certain (x axis). The Red Sea Torpedo was evaluated as CR(PE) in 2017 prior to the development of the guidance on the application of the Records & Survey Model and the Threats Model and does not have an extinction probability.

(B) The former geographic range of the three CR(PE) species (scale bar, 1,000 km).

(C) Former range of the CR Pondicherry Shark based on the Country of Occurrence (COO) classification of "Possibly Extant."

(D) Local extinctions of seven species based on the COO classification of "Possibly Extinct." Images were drawn by Dr. Lindsay Gutteridge.

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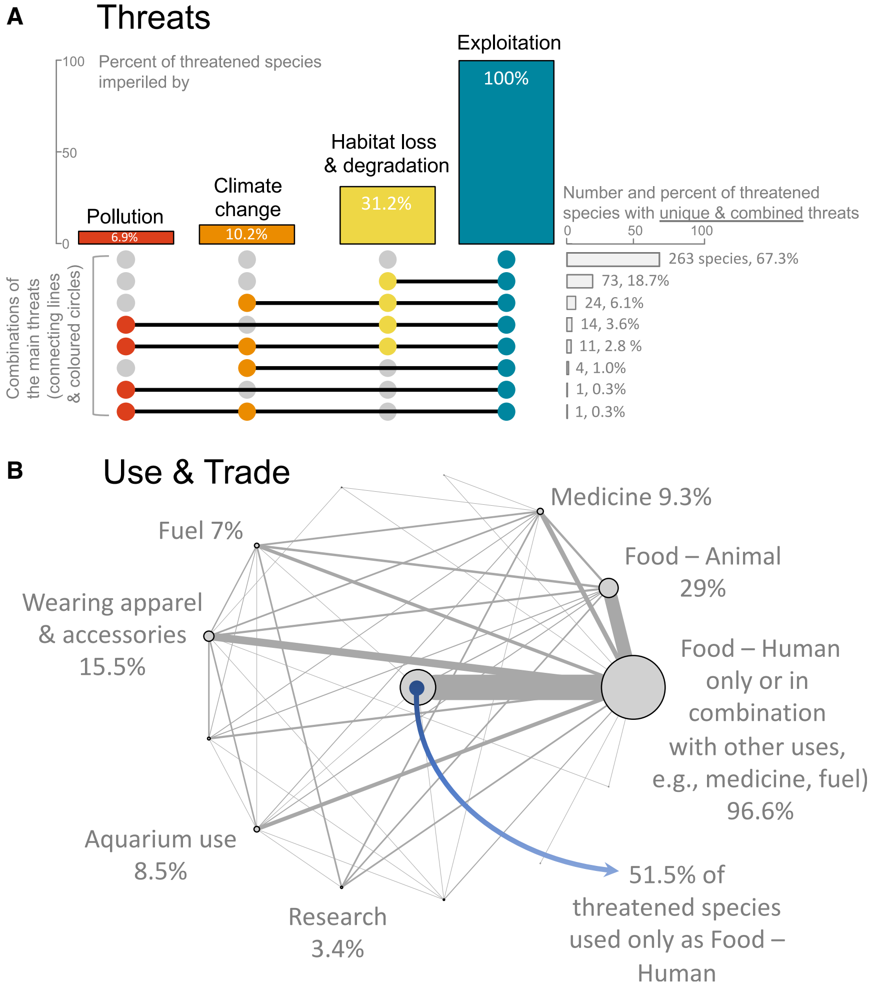

Figure 3. Threats to chondrichthyans and the use and trade of the species threatened by overexploitation

(A) An "upset plot" of species threats and threat combinations following the IUCN Red List threat classification scheme. The upper bar chart represents the percentage of species for which each threat was reported. The bar chart on the right represents the number of species threatened only by exploitation (upper righthand bar) or combination of threats (shown by the combination of colored circles and connecting lines in each row). The gray circles denote the threat is not included in the combination.

(B) Interaction web of the uses and trade. The predominant use is food for human consumption, alone or in combination with others—as shown by connecting lines to other uses.

See also Table S1.

(36.5%; Table S1) or in combination with other fisheries (96% of species; Table S1). Large-scale fisheries are often compounded by incidental catch in small-scale fisheries (62.3%; Table S1). Almost all species of chondrichthyan are taken unintentionally in fisheries (99%, 1,082 of 1,093; Table S1). While the catch may be incidental, chondrichthyans are, with few exceptions, retained for food and animal feed and indeed may be the unofficial target species in many fisheries.

Most fished species have multiple uses and are often fully utilized. Most threatened species are utilized (90.7%, 355 of 391); the remainder are likely discarded, which still results in some mortality. When retained, most threatened species are used for food consumption by humans (96.6%, n = 343 of the 355; Figure 3B). Half of threatened species are consumed only as food by humans (51.5%; Figure 3B). The remainder are also used for a range of purposes, including animal feeds (29%), and skins and other body parts are fashioned into apparel/accessories (15.5%). Further, 16.3% of species, predominantly threatened deepwater and coastal Squaliformes, are retained for their liver oil, which is used in pharmaceuticals (e.g., health supplements and as vaccine adjuvant, 9.3%) and as biodiesel fuel (7%; Figure 3B). Chondrichthyans are also removed from the wild for aquarium use (8.5%) and scientific research (3.4%; Figure 3B).

Overfishing is compounded by habitat loss, climate change, and pollution

Three additional main threats were identified that act in combination with exploitation. Habitat loss and degradation compound overfishing for nearly one-fifth (18.7%, n = 73) of threatened species (Figure 3A). Habitat loss and degradation take the form of seven sub-threat classes dominated by residential and commercial development (25.8%, n = 101), agriculture and aquaculture operations (mainly mangrove loss and degradation, 9.5%, n = 37), natural system modifications (4.6%, n = 18), human intrusions and disturbance (2.6%, n = 10), energy production and mining (1.5%, n = 6), invasive and other problematic species (0.8%, n = 3), and transportation and service corridors (0.8%, n = 3).

Climate change is a rapidly emerging concern for threatened chondrichthyans (10.2%, n = 40) and compounds the effects of overfishing and habitat loss for 6.1% of species (n = 24; Figure 3A, row 3 horizontal barchart). Climate change threatens via two main pathways. First, the loss and degradation of habitat from the reduction of coral cover due to bleaching and disease risks affecting the health of coral reef-associated species, such as the walking sharks (Hemiscylliidae).[49] Second, some temperate species are declining at their equatorward boundary where rising water temperature makes their native habitat less suitable.[50,51] For example, the Thorny Skate (*Amblyraja radiata*) population has declined by more than 80% over the past three generations in the southern parts of its North Atlantic range, yet is increasing further north.[52]

Pollution is typically a non-lethal stressor affecting 6.9% (n = 27) of threatened chondrichthyans. All four main threats, together, affect 2.8% (n = 11) of threatened species (Figure 3A, row 5).

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Which species, habitats, and places are most threatened?

The probability that a chondrichthyan species is threatened can be broadly predicted by body size and median depth. Larger-bodied species are more likely to be threatened than smaller species (Figures 4A and 4B). The level of threat to chondrichthyans is so high that even medium-sized species (>150 cm), such as the Yellownose Skate (*Dipturus chilensis*), have a high likelihood (probability > 0.5) of being threatened (Figure 4A). Species with a shallower median depth are more likely to be threatened than deeper-dwelling species (Figures 4A and 4B). For example, Broadnose Skate (*Bathyraja brachyurops*) has a median depth of 316 m and is NT, whereas Spotback Skate (*Atlantoraja castelnaui*) has a median depth of 110 m and is CR (Figure 4A). This pattern holds across all species, and in sharks and rays separately (Table S2). Geographic range has limited explanatory power and there is little evidence that species with a larger range have relatively lower extinction risk (Table S3). In fact, rays with larger geographic ranges are at greater risk than those with smaller geographic ranges (Figure 4B). The categorical trait-based predictive models revealed that 15 of 141 DD species could be threatened (all VU), yielding a total of 406 (34%) threatened species, comparable to the IUCN estimate of 37.5% (Data S1; Figure S1). Our interpretation is that relatively larger-bodied species have lower maximum population growth rates and are less able to replace the numbers removed by overfishing, compared to smaller species.[53–55] Further, unlike shallow species, deeper-dwelling species have refuge from mortality if a significant fraction of their depth range is beyond the reach of fisheries.[18,55]

The global spatial pattern of threatened species closely tracks species richness, but areas of disproportionately high risk can be identified throughout the tropical and subtropical coastal seas (Figure S2). Regions with higher richness have greater numbers of threatened species (Figures 5A and 5B), with proportionally more threatened species in the tropics and subtropics (Figure 5C). The greatest richness occurs in the coastal shelf waters of the tropics and particularly at the boundary with subtropical ecosystems, e.g., Brazil, South Africa, Australia, and Taiwan (Figure 6A). Threat is greatest in coastal shelf waters with 75.7% (n = 296 of 391) of threatened species occurring there compared to deepwater (16.6%) and the pelagic ocean (5.9%; Table 1). The greatest richness occurs in the coastal waters of northeast Taiwan and the greatest threat is also found there, with 105 threatened species in a single 23,322 km^2 hexagonal grid cell resulting from high levels of overfishing of both coastal and deepwater species (Figures 6A, 6B, 6D, and 6E). Coastal threat is disproportionately high in the tropics and subtropics where more than three-quarters of species are threatened, particularly in the waters of the longest standing and most intensive chondrichthyan fisheries in the world, including the northern Indian Ocean and Western Central and Northwest Pacific Oceans, from Pakistan to Japan and as far east as the Wallace Line (between Bali and Lombok; Figures 6B, 6C, and S2). This disproportionately high level of threat in the Indo-Pacific Ocean risks overshadowing high levels of threat throughout the coastal waters of South America, particularly Brazil and Uruguay and the Mediterranean Sea, as well as West and East Africa, including Madagascar (Figures 6B and 6C). The threat to deepwater species is somewhat decoupled from the global richness pattern due to the patchiness of these fisheries. Deepwater richness is greatest in subtropical boundaries, but with notable tropical richness in the Caribbean and temperate richness in the Northeast and Eastern Central Atlantic Oceans, Japan, Taiwan, southeastern Australia, and New Zealand (Figure 6D). Deepwater threat is disproportionately high in the Southwest Atlantic, Northeast Atlantic Ocean and Mediterranean Sea, southern India and Sri Lanka, southern Java (Indonesia), and the Northwest Pacific (Figures 6E and 6F). Richness and threat of pelagic and mesopelagic species are similar and centered on the tropical and subtropical oceans with greatest concentration along the continental and insular shelf breaks (Figures 6G and 6H). The Atlantic Ocean has the greatest proportion of threatened pelagic and mesopelagic species, particularly in the Gulf of Mexico and along the east coast of the USA, and Northeast Atlantic Ocean and Mediterranean Sea (Figures 6H and 6I).

The combination of body size, depth refuge from fishing, and the high intensity of threat in the tropics and subtropical waters is reflected in the pattern of threat across families. Pelagic eagle rays and devil rays join the giant guitarfishes, sawfishes, wedgefishes, hammerhead sharks, and angel sharks as the most threatened families .[47,48,56] Further, many highly threatened families include some of the most speciose mainstays of tropical coastal landing sites, where catches were historically dominated by stingrays, requiem sharks, guitarfishes, eagle rays, and weasel sharks (Table S4). Finally, the high level of threat in the gulper shark reflects the expansion of deepwater fisheries (Table S4).

DISCUSSION

This first global reassessment of the Class Chondrichthyes yielded more than double the number of threatened species, which means the conservation challenge is now at least twice as great as previously thought in 2014. Accounting for the 12.9% of DD species, the proportion threatened is now 37.5% based on IUCN criteria and is at least 34% based on the trait-based model (Data S1; Figure S1). While it is difficult to understand the true level of *genuine* change since the first assessment, this will eventually become clearer when we calculate the Red List Index (RLI) for all chondrichthyans, but RLIs for species subsets already indicate very significant *genuine* change over time.[32,56,57] After the amphibians, chondrichthyans are the most threatened vertebrate Class assessed to date.[58] More than 75% of species are threatened throughout tropical and subtropical coastal and pelagic waters, warning of widespread loss of ecological function and services.

For the first time, three species are listed as CR(PE). These were formerly assessed as DD, suggesting a high likelihood that species losses are going largely unnoticed or unreported.[59] Emerging large-scale local chondrichthyan extinctions and the three CR(PE) species forewarn that overfishing is sufficiently intense and widespread to cause significant irreversible biodiversity loss in tropical coastal seas, particularly off Mexico, Brazil, and throughout the northern Indian and Western Central Pacific Oceans (Figure 2). At least four species are close to global extinction; extensive caveats are detailed in the Red List assessments. In the case of the Lost Shark, there are three

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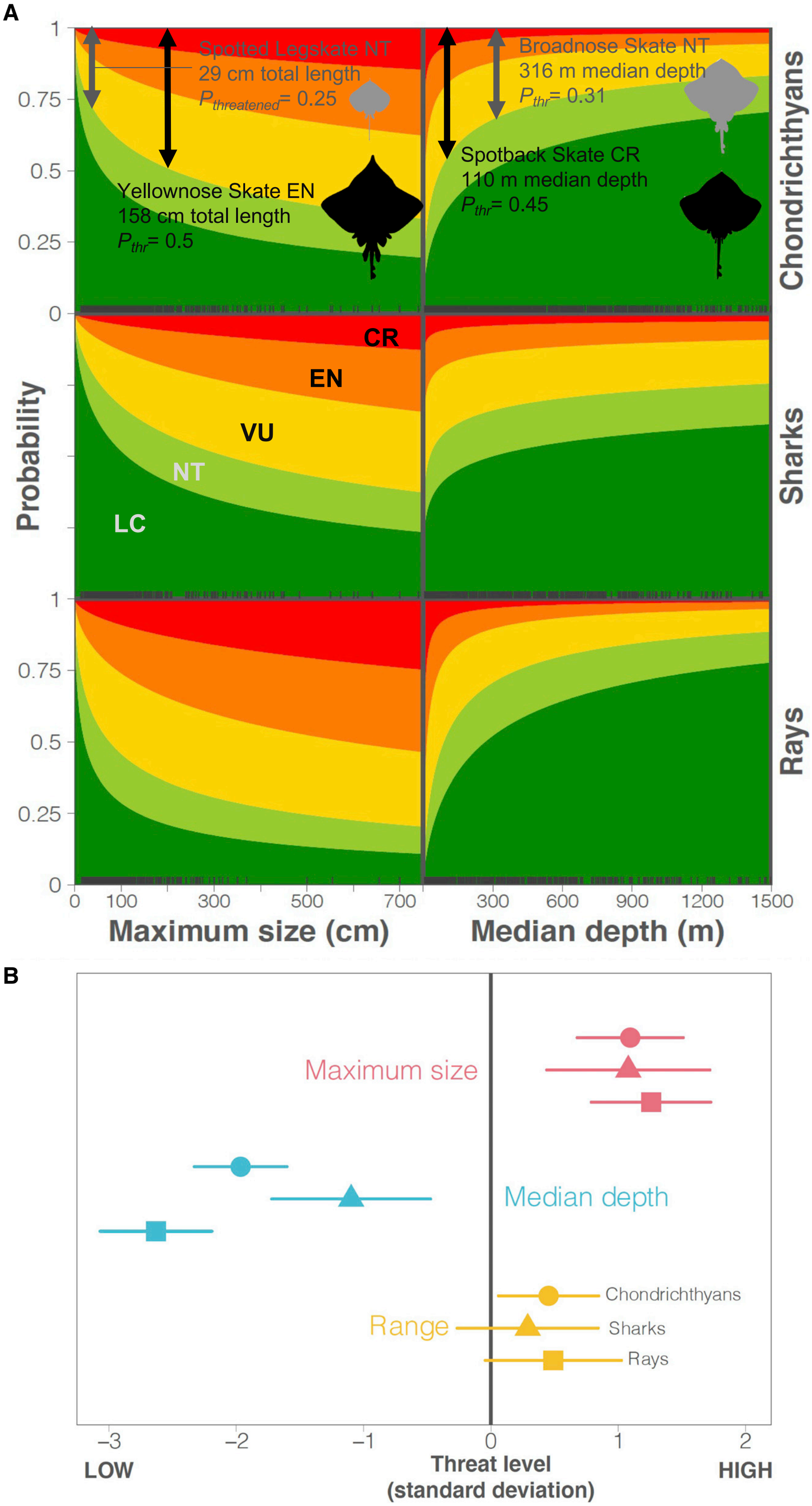

Figure 4. Global trait models of chondrichthyan extinction risk

(A) The effects of maximum body size, median depth, and geographic range size on the probability that a data-sufficient chondrichthyan (upper row), shark (middle row), or ray (lower row) is listed as either Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), or Least Concern (LC) based on cumulative link mixed-effects models. The black/gray vertical arrows indicate the probability that a skate was categorized as threatened (i.e., VU, EN, or CR). South American skates offer a range of depths and body sizes matched for phylogeny and geography. We contrast the small-bodied Spotted Legskate (29 cm total length, TL) with the large-bodied Yellownose Skate (158 cm TL, upper left panel), and the shallow dwelling Spotback Skate (110 m median depth) with the deep-dwelling Broadnose Skate (315 m median depth, upper right panel). Maximum size was measured as maximum linear dimension for chondrichthyans (i.e., TL or disc width, DW), whereas maximum size for sharks and some rays was defined as maximum TL and as DW for some rays. Median depth (m) was calculated as the midpoint between upper and lower depth as documented in the Red List assessment (Figures S1 and S2; Tables S3–S5).

(B) Standardized effect sizes (with standard error) of trait-based models of extinction risk of data-sufficient chondrichthyans (n = 1,178 species), sharks (n = 528), and rays (n = 598).

See also Table S2 and Data S1.

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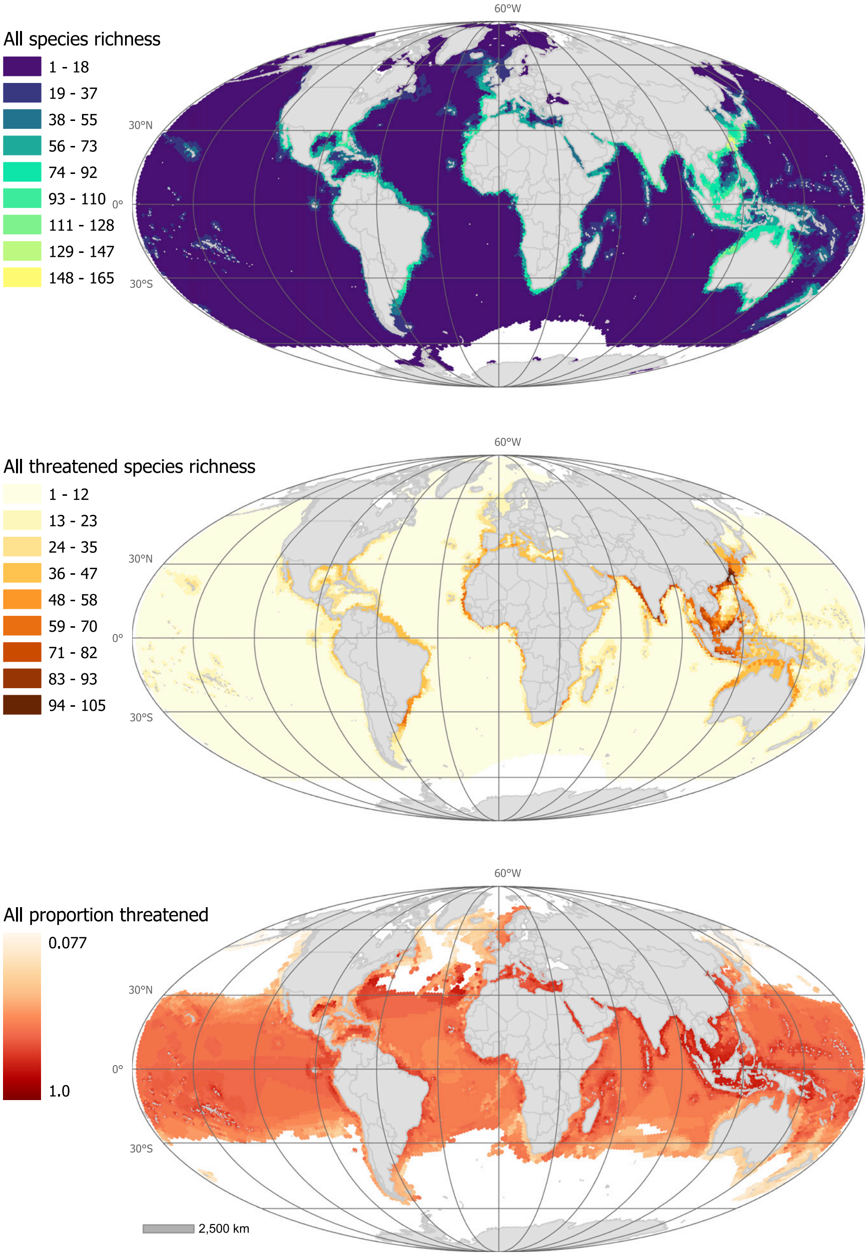

Figure 5. Global chondrichthyan richness and threat

(A) Species richness as the number of species per hexagonal cell.

(B) Number of threatened species per cell.

(C) Proportion of species that are threatened only for cells with more than 10 species (see Figure S2 for disproportionate threat). Scale bar, 2,500 km.

See also Table S4.

lines of evidence in support of extinction and here we summarize the three against extinction: (1) it does not have any ecological specialization that might predispose it to extinction (though both rays may well have had small geographic ranges), (2) as a small requiem shark it can be difficult to differentiate from other similar species and could go unnoticed among catches of other carcharhinids, and (3) the recent rediscovery of two other "lost" carcharhinid species cautions that further specimens of the lost shark might be found in the future with more directed surveys.[41,60,61] As a further cautionary note, the Tentacled Butterfly Ray was regionally assessed as CR(PE) in the 2017 Arabian Sea and adjacent waters. More recent surveys revealed the existence of this species in Iranian waters despite no records for several decades across its remaining known range.[62] Consequently, this species was assessed globally as CR in 2021.[42] Even with increased research on chondrichthyans (Figure 1D), the likelihood of rediscoveries and downlisting is lower for the three species assessed using the threat modeling approach. Nevertheless, there remains a dim possibility that further searches will find additional specimens. Furthermore, the increased number of CR species suggests that this number of CR(PE) will grow unless urgent action is taken to dramatically reduce or eliminate fishing mortality, possible through strict species protection and large-scale marine protected areas.

Notwithstanding these caveats, which would also apply to terrestrial CR(PE) species, we provide the first chondrichthyan extinction rate of potentially 25 extinctions per million species years (E/MSY), assuming three of 1,199 species have been driven toward extinction in the past 100 years. This rate is similar to that of terrestrial vertebrates, which is 33.6 E/MSY based on 519 of 30,873 bird, mammal, reptile, and amphibian species listed as Extinct, Extinct in the Wild, or CR(PE) over the past 500 years.[63] As with terrestrial vertebrates, the chondrichthyan extinction rate exceeds the proposed target rate of less than 10 E/MSY over the next century.[63] Even if only two species were CR(PE), this yields 16.7 E/MSY, which is 17–170 times greater than the background extinction rate in the fossil record (0.1–1 E/MSY).

The urgent challenge is to halt and reverse population declines and minimize extinction risk in order to bend back the marine biodiversity loss curve.[64] This requires immediate policy actions bolstered by targeted enforcement and educational programs. The killing and landing of chondrichthyans listed as CR or EN (collectively referred to as endangered) should be strictly prohibited wherever possible. In some cases, countries have already pledged and/or have treaty obligations to do this, but enforcement remains inadequate.[23] However, in others, especially developing countries throughout the global tropics where small-scale and subsistence fisheries are common, these

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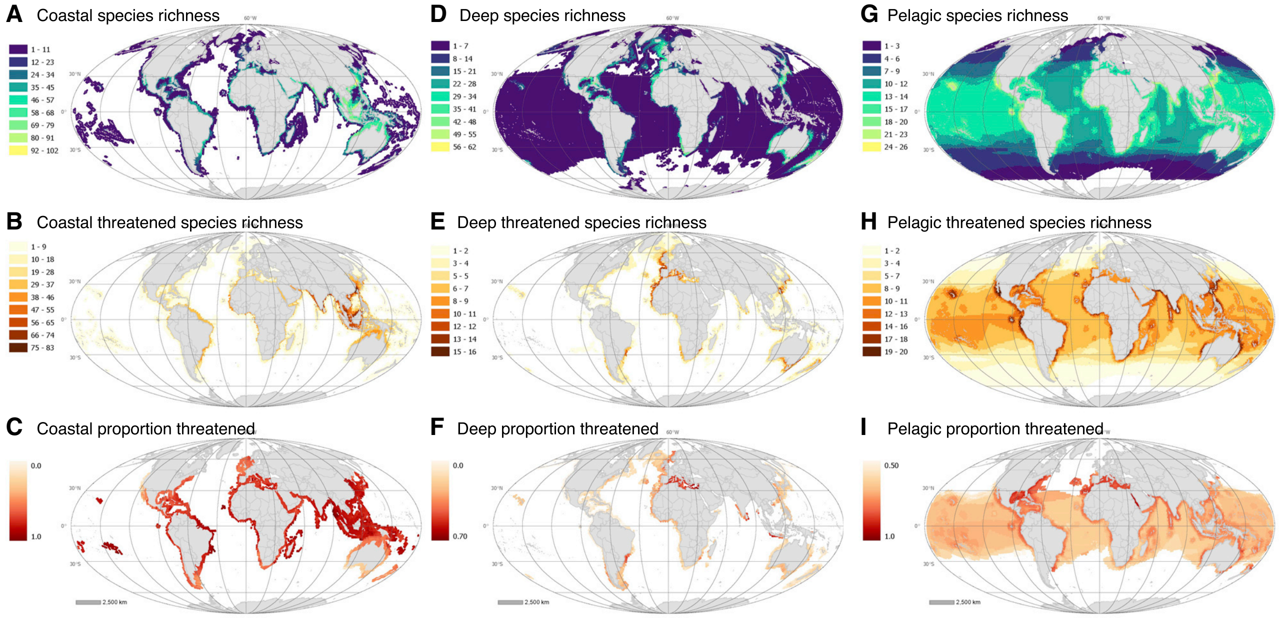

Figure 6. Global chondrichthyan species richness, threat, and proportion threatened by habitat

(A, D, and G) Chondrichthyans species richness by habitat.

(D, E, and H) Number of threatened chondrichthyans by habitat.

(C, F, and I) Threatened species as proportion of total richness (for cells with >10 species) by habitat.

(A–C) Coastal species (<200 depth), (D–F) deepwater species (>200 depth), and (G–I) pelagic and mesopelagic species found in the open ocean. Scale bar, 2,500 km.

species play important roles in food security and livelihoods that make strict protections difficult to implement and enforce.[65] In these situations, novel management approaches that transform markets and providing alternate livelihood options may provide a way forward that takes account of the needs of fishing communities.[66] Other approaches, such as effective marine protected areas,[67,68] conservation engineering,[69] trade regulations (e.g., appendix listings on the Convention on International Trade in Endangered Species of Flora and Fauna),[22] and initiatives that reduce the incentives of retaining catches,[70] are among a range of tools that can be implemented to reduce mortality of endangered species, arresting declines, and enabling recovery.

To prevent VU, NT, and LC species from becoming endangered, fisheries must be managed for sustainability through fishing limits based on scientific advice and/or the precautionary principle. The issue of incidental capture is central to chondrichthyan conservation, but definitions and perceptions vary quite widely, from catch that is discarded to that which is retained for consumption and sale, alongside the focal or target species of the fishery.[20,71] IUCN data reflect whether catch is intentional or unintentional, but in reality, this aspect is difficult to ascertain and can change from day to day, depending on availability and markets. Too often, bycatch is incorrectly perceived as unavoidable and labeling catch as such can inhibit management attention. Depleted species may be exceptionally valuable and welcomed as catch, but simply insufficiently plentiful to be a true target of fishing operations and management attention.[72] Ultimately, it is the mortality that matters, regardless of fishers' intentionality. Excessive fishing mortality has resulted in the serial depletion and local extinction of numerous chondrichthyan populations to the point where they contribute to the global extinction risk of wide-ranging species, such as angel sharks, sawfishes, and many rhino rays.[47,48,56]

Governments worldwide have committed to address these threats repeatedly over several decades through the FAO Code of Conduct for Responsible Fisheries and the International Plan of Action for Conservation and Management of Sharks, as well as numerous international biodiversity and fishery treaties and UN Sustainable Development Goals (e.g., Fischer et al.[73]). The high and rising chondrichthyan extinction risk shows that management measures undertaken to date have been seriously insufficient, have low compliance rates, and/or have not been implemented and are thus failing to reverse the decline for almost all species.[23,24] Some of the most recent policy actions may not have had sufficient time to stem declines, taking into account the generally low reproductive rates of this taxon.[23,54] Fisheries management measures, primarily catch limits, have succeeded in the rebuilding and sustainable exploitation of several chondrichthyan populations and species in the USA, Canada, Europe, Australia, and New Zealand,[21] and the improvement of two Endangered species (Barndoor Skate and Smooth Skate). It is important to note that many developed countries have some form of chondrichthyan catch limit for both endangered and target species and extending these successes to countries with lower fisheries management capacity and food security crises is a key challenge.[65,66] Considerable effort has already been deployed to address this challenge,[74] but much remains to be done given the diversity of species at risk and the wide range of socio-economic conditions in which the fisheries that catch sharks operate.

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A brighter future for chondrichthyans depends urgently on enacting effective fisheries regulations that focus on reducing catches to sustainable levels and, wherever possible, strictly protecting endangered species. These actions should be bolstered by well-enforced measures to minimize incidental mortality, including bycatch mitigation technologies, best practices for handling and release, and effective marine protected areas that can provide species with refuge from fishing throughout a meaningful fraction of their range. The increasing likelihood of extinction in the marine realm suggests that chondrichthyans may face a future similar to that of biodiversity on land, where human pressures have led to the loss of numerous species and possibly triggered a sixth mass extinction.[7,59,75] Immediate, global implementation of sound fisheries management measures is also an adaptation to climate change and is essential to avoiding this fate and allowing for sustainable chondrichthyan fishing over the long term.

STAR★METHODS

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

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2021.08.062.

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AUTHOR CONTRIBUTIONS

N.K.D. and C.A.S. conceived the idea and coordinated the Global Shark Trends Project. C.L.R., R.A.P., R.W.J., D.A.E., B.F., C.S.S., W.J.V., J.M.L., R.H.L.W., J.K.C., P.C., K.K.B., D.F., N.K.D., and C.A.S. planned and coordinated workshops and collected the Red List data. C.M.P. and C.H.-T. trained key staff and reviewed the Red List data. K.B.H., D.H.D., G.M.R., and J.C. collected and quality controlled the map data. C.L.R., B.F., J.K.C., C.S.S., N.K.D., and C.A.S. classified habitat data and collected traits. C.A.S., W.J.V., and N.K.D. collected and analyzed the scientific publication data. N.P., R.H.L.W., J.H.M., J.C., C.M.P., and N.K.D. analyzed the Red List and map data. N.K.D. and C.A.S. led the writing of the manuscript and all authors contributed critically to the drafting.

DECLARATION OF INTERESTS

The authors declare no competing interests. Most authors are or have been volunteer members of an International Union for the Conservation of Nature Species Survival Commission Specialist Group.

INCLUSION AND DIVERSITY

One or more of the authors of this paper self-identifies as an underrepresented ethnic minority in science. While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list. The author list of this paper includes contributors from the location where the research was conducted who participated in the data collection, design, analysis, and/or interpretation of the work.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Red List assessments and maps	IUCN Red List of Threatened Species	https://www.iucnredlist.org/
Population time-series	Global Shark Trends project	https://www.sharkipedia.org/trends
Baited Remote Underwater Video Survey data	Global FinPrint Project	https://globalfinprint.org
Software and algorithms		
R statistical environment (open-source software)	The Comprehensive R Archive Network	https://cran.r-project.org
R package ordinal version 3.5.2.	[76]	https://cran.r-project.org/web/packages/ordinal/index.html
R package ROCR version 1.0-11	[77]	https://cran.r-project.org/web/packages/ROCR/index.html
Rmarkdown analysis browser	This paper	https://github.com/NickDulvy/SharkReassessment
Custom R code used to analyze time-series	JARA: Just Another Red List Assessment	https://github.com/Henning-Winker/JARA

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Nicholas Dulvy (dulvy@sfu.ca).

Materials availability

IUCN Red List assessment data have been deposited at https://www.iucnredlist.org/ and are publicly available as of the date of publication, a list of species and their urls can be found in Data S3.

Data and code availability

This paper analyzes publicly available data published on the IUCN Red List version (https://www.iucnredlist.org/); Red List Assessment URLs are listed in Data S3. A browsable RMarkdown html document summarizing the analysis is available at https://github.com/NickDulvy/SharkReassessment.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

For our analyses we used the databases listed in the key resources table: IUCN Red List of Threatened Species, which in turn used the Global Shark Trends Project and Global FinPrint Project.

METHOD DETAILS

We first describe the collation of information and the assessment process, including the taxonomic and geographic scope. Next, we summarize the International Union for Conservation of Nature’s Red List of Threatened Species assessment approach, including transfer of category, generation lengths, estimation of population reduction from time-series and space-for-time methods, and attitude to risk and uncertainty. Finally, we summarize threats, habitat classification schemes, the mapping of species distributions, and the statistical analyses used.

Collating information and the assessment process

The Red List assessment and mapping process was conducted through the IUCN Species Survival Commission (SSC) Shark Specialist Group (IUCN SSC SSG; https://www.iucnssg.org/) for which NKD and CAS were Co-Chairs for the duration of

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this project. We conducted a total of 17 workshops, with the Northeast Pacific workshop spanning 1.5 days but all other workshops spanning 4–5 days (Table S5). These workshops were attended by a total of 353 individuals and 244 unique experts and/or members of the IUCN SSC SSG from 71 countries and territories (Table S6). Fifteen of the workshops were in-person, but due to the global COVID-19 pandemic, the final two regional workshops in Southeast Asia and West Africa were conducted through weekly two-h sessions via video conference (Table S5). All workshops were conducted in English, with Spanish and Portuguese translation for the South and Central American workshops (provided by PC), and parallel French language sessions for the West Africa online workshops (provided by RWJ, NP, and Sarah M. Gravel).

Participant lists were developed first by project staff and Red List Authority Coordinators, and reviewed by the Co-chairs, based on the regional membership in consultation with Regional Vice-Chairs and the local organizers, following five considerations: (1) the taxonomic and geographic scope of the assessment process; (2) knowledge of population trend information and threatening processes; (3) Red List assessment training and experience; (4) diversity and representation of government agencies, non-governmental organizations, academia, countries, and demography; and (5) logistical constraints of budget, timing, and location.

The IUCN Red List Categories and Criteria (Version 3.1) were applied following the Guidelines for Using the IUCN Red List Categories and Criteria.[40] We evaluated geographic distribution, occurrence, population, habitats and ecology, use and trade, threats, and conservation actions through literature searches of field guides, primary and gray literature, and through expert consultation at the workshops.

Draft assessments were prepared in the IUCN Species Information Service (SIS) online database and following consultation and consensus of all assessors, the completed assessments underwent a three-stage review process. Each assessment was peer-reviewed by at least two reviewers, at least one of which was trained in the application of the IUCN Red List Categories and Criteria and the other was chosen for expertise in the ecology and interaction with fisheries of the focal species. A summary of the assessments was also circulated to the entire 170+ person membership of the IUCN SSC SSG for their input over a two-week-long consultation period. Assessments were then submitted to the IUCN Red List Unit (Cambridge, UK) where they underwent further review and quality checks before being accepted for publication on the IUCN Red List of Threatened Species.[40] The Red List assessments were completed with a total 322 Assessors and 363 Contributors, and were checked by 118 Reviewers, through workshop processes managed by 24 Facilitators (Data S2). These Red List assessments cite an average of 17.8 sources per assessment and, overall, more than 5,200 unique sources including: books, conference papers and proceedings, electronic databases, journal articles, magazine articles and reports. Unpublished data and anecdotal evidence contributed by Assessors and Contributors during workshops were also frequently incorporated into assessments and subject to review by the workshop participants.

Taxonomic scope

The nomenclature and authorities used for chondrichthyans follow those of the online electronic version of the Catalog of Fishes[78] and Sharks of the World[29,79] for sharks, and Rays of the World for rays,[30,80,81] supplemented by more recent taxonomic papers, e.g., Notarbartolo di Sciara et al.[82] and personal databases for chimeras (D.A. Ebert, unpublished data). Tracking chondrichthyan taxonomy is challenging as there are more than 20 new species descriptions each year and much consolidation to eliminate synonymy.[83] At the start of this assessment process, there were 1,185 recognized species in 2012,[83] 1,188 species in 2015[84] and 1,176 species in 2017, but the total current count is estimated to be around 1,250 species.[79] Species lists for each workshop were developed by project staff and the Red List Authority Coordinators (Peter M. Kyne, RAP, CLR, and RHW), working with the Vice-Chair of Taxonomy (DAE) and previously William T. White. The final taxonomy refinements were made to the underlying IUCN Species Information Service (SIS) database on 31st March 2021. At this point in time, we consider 1,199 species valid for this assessment and exclude but recognize the ongoing assessments of at least 36 South American freshwater stingrays (subfamily: Potamotrygoninae). We caution that these numbers will differ slightly from those reported on the IUCN Red List website due to the older freshwater stingray assessments. We also note that four other species will be present in the 2021-2 Red List update, but we do not include them here, as they are either recently considered to be invalid or are now recognized as junior synonyms of other species. These issues will take slightly longer to fix in the SIS database as reassessment of the new taxonomic concepts is necessary. In this paper, we recognize that *Mustelus walkeri* is invalid and is part of the taxonomic concept of Gummy Shark *Mustelus antarcticus* Günther 1870.[85] Second, *Amblyraja badia* and *Amblyraja robertsi* are currently on the IUCN Red List but are junior synonyms of Arctic Skate *A. hyperborea* (Collett 1879).[86] Third, the Zanzibar Guitarfish (*Acroteriobatus zanzibarensis*) is currently on the IUCN Red List, but the validity of this species is under review.[87] We also recognize the ongoing work to resolve species complexes, such as the radiation of micro-endemic guitarfishes (*Acroteriobatus* spp.) and maskrays in the genus *Neotrygon*.[30,87] All species assessments have been reviewed and published online on the IUCN Red List of Threatened Species (https://www.iucnredlist.org/; IUCN release 2021-2). A total of 171 species were assessed for the first time and a further 50 species underwent a change in species concept, so while the name appeared previously on the Red List because the concept changed technically these could be considered as NE prior to this assessment (Table S7). However, because many of these species are widely known we have not considered them as part of the 171 new species concepts assessed for the first time. For example, with the resurrection of the Pacific Smalltail Shark *Carcharhinus cerdale*, which is restricted to the eastern Pacific Ocean, the Smalltail Shark *C. porosus* is now restricted to the western Atlantic Ocean.[88] For this analysis *C. cerdale* is considered part of the 171 NE, whereas we classify *C. porosus* as one of the 50 species with a changed taxonomic concept.

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Geographic scope

Nearly all assessments were undertaken at the global level, i.e., for the entire global population of each species. This was possible at the workshops focusing on subsets based on taxonomy (e.g., Sawfishes, Devil rays, Chimeras) or habitat (coastal, pelagic, deepwater).[32,89–91] However, six skate species were assessed at the regional level in the Northeast Atlantic and Mediterranean and Black Seas (Blonde Skate *Raja brachyura*, Thornback Skate *R. clavata*, Smalleyed Skate *R. microocellata*, Spotted Skate *R. montagui*, Undulate Skate *R. undulata* and White Skate *Rostroraja alba*). This is because the West Africa workshops confirmed that these species have only a small fraction of their range in West African waters and are rarely captured in fisheries there. Hence, these interactions are unlikely to have influenced the published Red List Status.

The regional workshops assessed endemic species and gathered region-specific information on the wider-ranging species. For example, the regional context of the wide-ranging pelagic and deepwater species was documented at the Northeast Pacific, European, and Australian workshops before global scale assessments were compiled at the pelagic and deepwater workshops. Similarly, the wide-ranging coastal species, consisting mainly of carcharhinids, were completed at the Southeast Asia workshop by CLR drawing upon regional workshop assessments and through email consultation. Individual species assessments of wide-ranging species, notably the manta rays (Giant Manta Ray *Mobula birostris* and Reef Manta Ray *M. alfredi*) were originally conducted in 2011 following a taxonomic revision and then revised at the pelagic workshop (Table S5). The Whale Shark (*Rhincodon typus*) assessment was conducted outside the workshop process through correspondence.[92]

Training and application of the IUCN red list categories and criteria

Workshops and the Red List training were organized and conducted by project staff certified as IUCN Red List Trainers who had successfully completed all nine modules of the online IUCN Red List training course (https://www.iucnredlist.org/resources/online), and the IUCN Red List Trainer course led by CMP and CHT. Since 2017, all workshop participants were requested to complete Modules 1–4 of the online IUCN Red List Training material, spanning: (1) What the IUCN Red List is and how it is used?, (2) The Red List assessment process, (3) How to apply the IUCN Red List Categories and Criteria, and (4) What supporting information is required for Red List assessments? Most of the project staff involved in the previous assessment were certified IUCN Red List Trainers (NKD, JML, RHW, and Peter M. Kyne).

Species were classified into six of the eight IUCN Red List Categories: Extinct (EX), Extinct in the Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), and Data Deficient (DD).[40,93] None of the species were considered to be EX or EW, however we did evaluate a number of species as Critically Endangered (Possibly Extinct) (CR(PE)). The Possibly Extinct tag was "developed to identify those Critically Endangered species that are, on the balance of evidence, likely to be extinct, but for which there is a small chance that they may be extant."[39,40,94] A species is considered EX "when there is no reasonable doubt that the last individual has died"; EW "when it is known only to survive in cultivation, in captivity or as a naturalised population (or populations) well outside the past range"; CR, EN, and VU species are considered to be facing an extremely high, very high, or high risk of extinction in the wild, respectively, and together are known as the threatened categories. NT species do not "qualify for CR, EN, or VU now, but are close to qualifying for or are likely to qualify for a threatened category in the near future." LC species do not qualify for CR, EN, VU, or NT. Finally, DD species have "inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status, and it is not clear to assessors whether the species is LC, CR, or in any of the other extant categories."[40]

To list a species in a threatened category (CR, EN, VU) on the Red List, expert assessors consider the risks associated with both the declining population paradigm and the small-population paradigm[95] using five assessment criteria (A to E): A – Population size reduction; B – Geographic range; C – Small population size and decline; D – Very small or restricted population; and, E – Quantitative analysis.[40,93] To qualify for one of the three threatened categories, a species must meet a quantitative threshold for that category in any of the five criteria listed above (A–E). Most threatened species (98.5%, n = 385) were assessed with the A and B criteria, with the C and D criteria applied to only 1.5% (n = 6) of cases and no cases of the E criterion being used.

Criterion A is based on quantitative thresholds of reduction, which is the reduction in population size scaled over a period of the greater of 10 years or three generation lengths (3GL).[40,93] Where time-series were available, these were combined using a Bayesian population state–space model for averaging relative abundance indices designed as a decision support tool for IUCN Red List assessments (Just Another Red List Assessment, JARA).[32–34] This method was applied to 111 species of mainly temperate wide-ranging species, such as Tope (*Galeorhinus galeus*) or Smooth Skate (*Malacoraja senta*). Most threatened species were assessed under criterion A (95.4%, n = 373). The A2 criterion was used because we found no species for which the causes of population reduction were (i) reversible, (ii) understood, and (iii) had ceased, and hence the A2 criterion thresholds of ≥30% (VU), ≥50% (EN) and ≥80% (CR) were used instead of the higher A1 thresholds. A total of 12 species (3.1%) were assessed based on criterion B, based on restricted geographic range and continuing decline. Criterion C, based on small population size and continuing decline, was applied in only six cases (Ganges Shark, *Glyphis gangeticus*; Northern River Shark, *G. garricki*; Speartooth Shark *G. glyphis*; Pondicherry Shark *Carcharhinus hemiodon,* Colclough's Shark *Brachaelurus colcloughi*; and Sharpfin Houndshark, *Triakis acutipinna*), and criterion D, for very small or restricted populations, was applied to two species [Lost Shark, *Carcharhinus obsoletus* and Java Stingaree, *Urolophus javanicus*, both assessed as CR(PE)].

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Transfer of category and changing status since the first assessment

A change in Red List Category can be classified as a *genuine* or *non-genuine* change. A *genuine* change is where the change in category is genuinely due to an improvement or worsening of the rate of decline, population size or range size or habitat.[40] Whereas a *non-genuine* change can arise from one or a combination of six reasons: Criteria revision, New Information, Taxonomy, Knowledge of the criteria (i.e., a mistake in the interpretation of criteria), Incorrect data used previously, and Other. The IUCN Guidelines state, ''determining the appropriate reasons for change often requires careful consideration'' and ''many category changes result from some combination of improved knowledge and some element of genuine deterioration and improvement in status.'' In such cases, *genuine* change should only be assigned if the amount of genuine change is sufficient on its own to cross the relevant Red List Category threshold.''[40]

While most of the 15 *genuine* changes were a worsening of status, two species have recovered enough to now be LC (New Zealand Smooth Skate, *Dipturus innominatus* and Barndoor Skate, *Dipturus laevis*), and the population of one species (Smooth Skate, *Malacoraja senta*) has increased enough to move from EN to VU. As recommended by IUCN, a five-year rule was applied to ensure that species were only transferred to a lower category when the data show the species no longer met the previous criteria for the category it was listed under for a minimum of five years.[40] Since assessments have been conducted using the 2001 Categories and Criteria there are five reasons for *non-genuine* change: New Information, Taxonomy, Mistake, Incorrect data, or Other.[40] There were five cases when species changed due to *Incorrect data* and three cases when the reason given was *Other.*

The reassessment of many species previously listed as DD into a threatened category dramatically reduced the proportion of DD species, revealing the high level of uncertainty due to data deficiency in the previous assessment that masked the full extent of the extinction crisis facing chondrichthyans. This reduction in DD species was achieved largely through the creation of more knowledge (Figure 1D). In part, this results from the exponential increase in shark research,[83] but also a concerted effort to improve fisheries stock assessments[21,32] and the development of new analysis techniques.[33,34] Unlocking these data was made possible by working closely with local researchers in regional assessment workshops.

Assessments of not evaluated species

A total of 171 (14.3%) species, previously considered Not Evaluated (NE), were assessed for the first time. Most new assessments of Not Evaluated (NE) species result from the discovery and description of formerly unknown species, such as chimeras (Seafarer's Ghostshark *Chimera willwatchi*, Falkor Chimera *Chimera didierae*, and Robin's Ghostshark *Hydrolagus erithacus*, all DD).[91] While others result from the splitting of species, such as the separation of Flapper Skate (*Dipturus intermedius*, CR) from Common Blue Skate (*D. batis,* CR).[96] We find that, of the NE species assessed for the first time, more than one-quarter (26.3%, n = 45 of 171) are threatened, whereas roughly one-third (38.6%, n = 66) are LC, 11.7% (n = 20) are NT, and one-quarter are DD (23.4%, n = 40). We also note there are an additional 50 species for which the species concept was revised substantially to the point where the revised concept could previously be considered NE (Table S7).

Generation lengths

The estimation of population size reduction requires an observed, estimated, inferred, or suspected generation length. The Red List Guidelines[40] offer several demographic approaches for calculating generation length, but most require age-structured vital rates which are available for relatively few sharks and rays. Therefore, we used a simple measure of generation length (GL) that could be consistently calculated across a wide range of species and which requires only female age-at-maturity (A_{mat}) and maximum age (A_{max}): GL = $A_{mat} + ([A_{max} - A_{mat}]z)$. The constant z depends on the mortality rate of adults and is typically around 0.3 for mammals.[97] We assumed a more conservative value of $z = 0.5$ to account for the likelihood that the age structure had been truncated by overexploitation by the time it was measured[98] and due to concerns of systematic underestimation of chondrichthyan ages.[99] When a generation length was not available for the focal species, we inferred a generation length based on the nearest relative matched by body size and temperature (i.e., selecting related species found in similar latitudes and depth ranges). Generation lengths were compiled from the primary published peer-reviewed literature and gray literature, including government reports, and we only recorded data from individuals where both the female age at which 50% of the population is mature (A_{mat}) and the maximum age A_{max} were measured. This dataset was originally compiled and made available by PM Kyne and Rhian Evans and augmented with additional estimates over time by Assessors. Generation lengths for species for which empirical data were unavailable were estimated by using proxy data from species with empirical data that are closely related, similarly sized, inhabit similar depths and latitudes, and occupy similar habitats. For example, for Giant Guitarfishes and Wedgefishes (Family Glaucostegidae and Rhinidae, respectively), an estimated generation length of 15 years was applied to larger species (> 200 cm total length [TL]) and 10 years for smaller species.[56]

Estimating population reduction using time-series methods

To analyze population time-series data, we used a Bayesian population state-space model designed for IUCN Red List assessments (Just Another Red List Assessment),[34] which builds on the Bayesian state-space tool for averaging relative abundance indices[100] and is available open-source on GitHub (https://www.github.com/henning-winker/JARA). Each relative abundance index (or time-series) was assumed to follow an exponential growth defined through the state process equation:

$$\mu_{t+1} = \mu_t + r_t$$

where μ_t is the logarithm of the expected abundance in year t, and r_t is the normally distributed annual rate of change with mean $\hat{r}$, the estimable mean rate of change for a time-series, and process variance σ^2. We linked the logarithm of the observed relative abundance indices to the logarithm of the true expected population trend using the observation equation:

$$\log(y_t) = \mu_t + \varepsilon_t$$

where y_t denotes the abundance value for year t, ε_t is observation residual for year t, which is assumed to be normally distributed on log-scale $\varepsilon \sim N(0, \sigma_\varepsilon^2)$ as a function of the observation variance σ_ε^2. We used vague normal prior for $\hat{r} \sim N(0, 1000)$ and vague inverse-gamma prior for the process variance $\sigma^2 = IG(0.001, 0.001)$.

The model for analyzing multiple relative abundance indices in a single run builds on the approach in JABBA for averaging relative abundance indices and assumes that the mean underlying abundance trend is an unobservable state variable.[100]

JARA is run from the statistical environment R[101] and analyses were done between 2018 and 2020 using v3.5.0 to v4.0.3 and executed in JAGS ('Just Another Gibbs Sampler' v4.3.0),[102] using a wrapper function from the R library 'r2jags' library v0.5-7).[103] The Bayesian posterior distributions are estimated by means of Markov Chain Monte Carlo (MCMC) simulation. Three Monte Carlo Markov chains were run for each dataset with different initial values. Each Markov chain was initiated by assuming an initial population size in the first year drawn in log-space from a normal distribution with the mean equal to the log of the first available count (y_1) and a standard deviation of 1000. JARA provides a range of contemporary diagnostic tests and graphics to evaluate fits to the data, residual patterns, potential model misspecification of variance parameters, data conflicts, model convergence, as well as retrospective and forecast bias (see Supplemental Material of the relevant Red List Assessments, e.g., *Malacoraja senta* or *Amblyraja radiata* for details). Unless otherwise specified, JARA reports medians and the Highest Density Interval as the estimator of 95% credible intervals.

A posterior probability for the percentage change (C%) associated with each abundance index can be conveniently calculated from the posteriors of y_t, the model predicted population trajectory. If y_t represents a longer time span than the assumed 3GL, C % is automatically calculated as the difference between the median of three years around the final observed data point T, and a three-year median around the year corresponding to T-(3GL[1]). The year T+1 is always projected to obtain a three-year average around T to reduce the influence of short-term fluctuations.[104] When the span of y_t is < 3GL, JARA projects forward, by passing the number of desired future years without observations to the state-space model until y_t > (3GL)+2.

Estimating population reduction using space-for-time substitution

For nine species resident on coral reefs, changes in species abundance relative to pre-exploitation levels were estimated using a space-for-time approach from Baited Remote Underwater Video Systems (BRUVS). The nine species comprised six sharks (Grey Reef Shark *Carcharhinus amblyrhynchos,* Blacktip Reef Shark, *C. melanopterus,* Caribbean Reef Shark *C. perezi,* Whitetip Reef Shark *Triaenodon obesus,* Nurse Shark *Ginglymostoma cirratum,* Lemon shark *Negaprion brevirostris*) and three rays (Bluespotted Lagoon Ray *Taeniura lymma,* Southern Stingray *Hypanus americanus,* and Yellow Stingray *Urobatis jamaicensis*). We estimated status using MaxN data derived from videos collected from 391 coral reefs in 66 nations as part of the Global Finprint Project.[35] The historical occurrence of each species at each reef was determined from literature and expert knowledge, and the assessment for each species restricted to those from which they were known to occur. For each reef within the species' known range, the mean MaxN value was estimated. Since there are large differences in the potential carrying capacity of individual reefs for sharks,[105] we used the median of all positive MaxN values as the reference level for no depletion (i.e., if a reef's estimated mean MaxN value from the model was > the median of non-zero mean MaxN values then depletion was assumed to be zero). This is a conservative measure, and it likely under-estimates levels of depletion. For rays, it has been demonstrated that abundance can increase at reefs with low levels of shark abundance,[106] so we accounted for possible increases in abundance by selecting reefs with known healthy populations of Caribbean Reef Shark (*Carcharhinus perezi*) (Atlantic species - Bahamas, Turks and Caicos, Pedro Bank (Jamaica) and the Colombian islands) or Grey Reef Shark (*C. amblyrhynchos*) (Indo-Pacific species – Australia and Papua New Guinea) as a reference for natural ray populations. The population level of rays relative to the no depletion reference level for each reef was calculated as: reef MaxN/(reference MaxN for reefs with undepleted reef shark populations). Reef population levels greater than one indicated possible increases, while those levels of less than one indicated possible depletion.

The level of depletion of sharks (scale 0-1) for each reef was calculated as: 1-[reef MaxN/reference MaxN for no depletion]. For sharks, reef depletion levels greater than one were converted to one. Depletion levels by jurisdiction were calculated by taking the mean of all reefs within that jurisdiction. Standard error of the means was also calculated and used to produce confidence intervals for depletion levels. To estimate an overall global depletion level by species, we weighted the jurisdictional values by the percentage of the world's coral reefs in their waters and produced a weighted mean depletion. Percentages of coral reefs by jurisdiction were taken from the "World Atlas of Coral Reefs."[107]

The extinction risk for each species at the global level was assessed by applying IUCN Red List Criterion A (population size reduction) over the past three generation lengths. The depletion estimates did not provide time frames, however, pressure on most shark and ray populations increased from approximately 1980 when demand for shark fins increased.[108] Of the nine species for which the space-for-time approach was used, four had 3 generation length periods that extended to before 1980 (*Ginglymostoma cirratum, Carcharhinus melanopterus, C. amblyrhynchos,* and *Negaprion brevirostris*), and the remaining species had 3 generation lengths that extended to between 1983 and 1991. Thus, we assumed that most of the declines described here have occurred during the past three generation lengths of each species.

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Attitude to risk and classification of uncertainty

The application of the IUCN Red List Categories and Criteria has improved in this assessment because of (i) broad application of the precautionary mindset to risk assessment, (ii) avoiding the inclusion of 'downstream consequences' for status assessment, (iii) better understanding of the alignment between fisheries assessment and IUCN Red List Criteria, and (iv) the use of JARA as a decision support tool to minimize conflict over the choice of models and time-series.

First, the guidelines on the application of the criteria explicitly caution that the risk tolerance of the assessor used to evaluate information can fall along an axis of *evidentiary* (high risk tolerance) to *precautionary* (low risk tolerance). An evidentiary attitude will classify a species as threatened only when there is strong evidence (i.e., numeric data) to support a threatened classification. The revised guidance states that global assessments should adopt a *precautionary* but realistic attitude and resist an *evidentiary* attitude, see section 3.2.3, p. 23 of the IUCN Red List Guidelines.[40]

Second, IUCN guidelines recommend assessors should not consider 'downstream' consequences of a listing, and this issue was directly addressed in workshop training sessions. Three examples of a downstream consequence are (1) a species being listed in one of the threatened categories that might lead to strict protection curbing fisheries operations, (2) the listing of a species as DD might incentivise greater research funding, or (3) downlisting might lead to the removal of prohibition on retention of the species, see section 3.2.3, p. 23 of the IUCN Red List Guidelines.[40] While difficult to quantify, previous assessments were highly evidentiary and were concerned for 'downstream' consequences, particularly for target species and the bycatch of commercially important species.

Third, the previously evidentiary attitude arose from early concerns over the applicability of extinction risk criteria, generally, and IUCN Red List Categories and Criteria, specifically, to wide-ranging exploited marine fishes.[109,110] These early concerns have not been borne out.[111] Since then, a large body of empirical meta-analysis and simulation analyses demonstrated strong alignment between the fisheries status of species and the Red List status, including for chondrichthyans.[21,112] Further the accumulation of evidence has confirmed the dire status of many species previously listed as CR, such as the sawfishes.[48,113]

Fourth, the early application of the JARA analyses to available time-series, mainly from South Africa, USA, Canada, and Australia, has eliminated three previous sources of conflict: the choice of which time-series to include (JARA can cope with multiple different time-series), choice of model (linear, log linear, or more complex models), and the selection of outliers for sensitivity testing. Further, the approach allows for the inclusion of population abundance and geographic area weightings to scale regional population reduction to the global scale and the results are straightforward to communicate.[33]

Finally, there were no cases where data were available throughout the range of a species and the lack of high quality comprehensive information should not be a barrier to assessment. We used the standard IUCN terms of estimated, inferred, and suspected to classify data uncertainty. Where time-series of catch-per-unit-effort (CPUE) data were available for the focal species from surveys, the assessments were classified as 'estimated'.[32,33] Population reduction was 'inferred' when CPUE data were available from reconstructed catches[3] or comparisons of landings composition at two different time periods.[114] Finally, population reduction was 'suspected' based on rates of habitat loss or from declines in a related species.

Major threats and species habitat classifications

Each species was coded according to the IUCN Major Habitats, Threats and Stresses, General Use and Trade, and Conservation Actions Classification schemes (https://www.iucnredlist.org/resources/classification-schemes).[115] Overall, 1,097 species face some form of threat and 102 species are not facing any threats (80 LC species) or not known to be facing any threats (22 DD species).

We assigned chondrichthyans to four habitat categories (coastal, deepwater, pelagic and mesopelagic, and freshwater). Some species range across habitats and for these species, a primary and secondary habitat were assigned with the primary habitat defined as that in which the species spends most of its life cycle. We analyzed all species considering the primary habitat only. Coastal species occur on continental and insular shelves in waters less than 200 m depth and include species found in euryhaline habitats. Deepwater species were those found on continental slopes and abyssal plains at depths greater than 200 m. For species straddling the shelf edge and upper slope we used additional literature to determine the habitat the species predominantly occurred in. Pelagic species include those found mainly in the upper 200 m of the open ocean and mesopelagic species found deeper in midwater.[18,32] However, this group also includes species that spend a significant portion of their life cycle in coastal waters, such as the hammerheads (family Sphyrnidae) which give birth in coastal embayments, the White Shark (*Carcharodon carcharias*) which aggregates around marine mammal haul-out sites, and the Devil Rays; some of which spend a considerable period of their life in coastal neritic waters. The seven freshwater obligate chondrichthyans comprised a single West African species (Smooth Stingray *Fontitrygon garouensis*) and six Southeast Asian species (Roughback Whipray *Fluvitrygon kittipongi*, Marbled Whipray *F. oxyrhynchus*, White-edge Whipray *F. signifer*, Mekong Stingray *Hemitrygon laosensis*, Chindwin Cowtail Ray *Makararaja chindwinensis*, and Giant Freshwater Whipray *Urogymnus polylepis*). Species habitats were assigned based on depth range, position in the water column, and life cycle based on the previous classification,[18] updated with information elicited from workshop participants as well as primary literature including annotated checklists and guides (e.g., Ebert et al.,[29] Last et al.,[30] and Weigmann[84]). There were 11 species with an unknown depth range. Where possible, these were assigned a potential habitat based on the original taxonomic descriptions of their occurrences and the habitat of regional congeners.

Distribution mapping

A global distribution range map was generated for each species. For reassessments, these built upon the previous assessment maps primarily following the geographic ranges in field guides,[29,30] with modifications based on new records revealed in the workshop

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processes. All maps were prepared using ArcMap 10.4–10.6.[116–118] For new species, the formal range description was mapped from the primary taxonomic references and in consultation with taxonomists. The geographic ranges were clipped to the minimum and maximum depth of demersal species, and for those species without known depth ranges, these were mostly set to the maximum confirmed depths of the family. Eleven species could not be mapped because they were known from a single depth or the depth was unknown and could not be inferred based on family, such as the Simushir Skate (*Arctoraja sexoculata*), Kwangtung Skate (*Dipturus kwangtungensis*), Starrynose Cowtail Ray (*Pastinachus stellurostris*), Java Stingaree, and Chilean Round Ray (*Urobatis marmoratus*). Species presences in the Country Of Occurrence and FAO Major Fishing Areas were coded according to the four classes used in the IUCN Mapping Standards: Extant, Possibly Extant, Possibly Extinct, and Presence Uncertain. Presence was generally coded only at the country level, except for Australia, Brazil, and USA, where we also coded occurrence at the state level. Generally, only the Extant range was mapped except for some pelagic species, such as the Devil Rays and White Shark, for which we also classified and mapped parts of the range as Possibly Extant, based on a high likelihood of occurrence but an absence of confirmed records. The Pondicherry Shark was mapped as Possibly Extant because of the lack of confirmed sightings for over 30 years. For the obligate freshwater rays, we mapped three parts of the range classification: the Extant range, Possibly Extant, as well as Presence Uncertain. (See also Data S1 and S3.)

QUANTIFICATION AND STATISTICAL ANALYSIS

The statistics for all 1,199 species presented in this manuscript were obtained from the Red List assessments already published on the IUCN Red List and assessments accepted for publication in the 2021-2 Red List update scheduled for the 4th September 2021 (See Data S3). The information within the Red List assessments was downloaded from the IUCN SIS database then merged and summarized using R (v4.1.0).[119] Co-authors assessed and reviewed the statistics in an RMarkdown document.

Increase in peer-reviewed chondrichthyan science 1970–2020

To determine the number of peer-reviewed scientific papers published on chondrichthyans, we used the topic search with Boolean operators on the Clarviate/ISI Web of Science database. We topic searched for the following eight terms: ‘shark’ OR ‘sawfish’ OR ‘stingray’ OR ‘wedgefish’ OR ‘elasmobranch’ OR ‘chondrichthyes’, OR ‘chimera’ OR ‘skate’, while simultaneously excluding unrelated terms using the Boolean operator, i.e., NOT ’shark bay’ NOT ‘skating’.

Global mapping analysis

To determine global patterns of biodiversity, species richness maps were produced for all species combined and for the three main habitats: coastal, deepwater, and pelagic and mesopelagic. All maps were prepared using ArcGIS Pro 2.7.0.[120] We spatially joined the polygons representing species ranges to a hexagonal grid of individual units (cells) that retain their shape and area ($\sim$23,322 km^2) throughout the globe to generate a species count in each cell. We used the geodesic discrete global grid system, defined on an icosahedron and projected to the sphere using the inverse Icosahedral Snyder Equal Area (ISEA).[121,122] The proportion of threatened species was calculated only for map cells with greater than 10 species, to avoid directing attention to high latitude seas with few species, e.g., Baltic Sea.

Biological and ecological trait-based threat modeling

We tested the relationship between threat status and biological and ecological traits of assessed species based on the knowledge that vulnerability is a product of a species’ intrinsic biology (slow life history) coupled with the degree of exposure to a threatening activity (overfishing).[18,123,124] We modeled risk using cumulative link mixed effect models (CLMM) using the clmm2 function from the package ordinal[76] in R version 3.5.2 with threat status as the response and three fixed effects: maximum body size (in cm, Total Length for sharks, skates, rhino rays, and chimeras; Disc Width for rays), median depth (m), and geographic range (km^2). Maximum size is an accessible measure of intrinsic sensitivity[125,126] and median depth is the measure of exposure to depth reach of fishing activity in the absence of fishing mortality estimates.[18,55] We also included taxonomic family as a random effect to account for phylogenetic covariation. This CLMM approach maintains the hierarchy of the IUCN categories while preventing the loss of information that inevitably occurs when grouping the categories as threatened or non-threatened.[55,127] As there are no known Extinct chondrichthyans, the categorical models scored the five relevant IUCN categories as follows: Least Concern = 1, Near Threatened, = 2, Vulnerable = 3, Endangered = 4, and Critically Endangered [including C R(PE) = 5 (i.e., excluding Data Deficient species). All data were compiled from the most recent global IUCN Red List assessments (IUCN 2021) and all fixed effects were centered and scaled by two standard deviations to normalize the data distribution. Median depth was calculated as the midpoint between minimum and maximum depth as reported in the Red List assessments, hence combining minimum depth and depth range to account for exclusively shallow or deep species’ distributions, while also avoiding having two highly correlated fixed effects within the model. Any species for which these trait data were unavailable were excluded from the models (n = 21, leaving n = 1,178 species to be tested). We used the Akaike Information Criterion (AIC) and ranked models according to their delta AIC (zero is the highest ranked model with any model two or fewer AIC units away from zero not significantly different from the best).[128] We tested for pairwise collinearity between variables with the Pearson correlation coefficient using the cor function in R version 3.5.2 (R Core Team 2021) and all variables had acceptable levels of correlation (i.e., < 0.6).

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Predicting the status of Data Deficient species using trait-based and IUCN methods

Predictive power of the CLMMs was first tested by excluding the DD species (n = 141 excluding 14 DD species for which trait data were unavailable) from the dataset then dropping one species at a time from the model to predict its IUCN status and cross validating each predicted status with the known assessed status (i.e., n = 1,036 versus 1, after removing all DD species and those lacking the relevant trait data). Predictive accuracy was evaluated using the Area Under the Curve (AUC) measure from Receiver Operating Characteristic curves, which is the proportion of species statuses that the model was able to predict accurately.[77] Model performance was evaluated using the ROCR package in R.[77] The AUC measure only works for binary classification, so we tested the predictive accuracy for each category by scoring them as one and comparing them with all four remaining categories scored as zero.[77] The model with the highest average AUC across all five categories was used to predict the statuses of the DD species. The models give five probabilities, one for each category, which add up to one for each species. The IUCN categorization was chosen using a 50% cut-off point.[55]

In 2014, the IUCN estimate of the number of DD species likely to be threatened was not considered credible for chondrichthyans for two reasons: (1) many of the DD species were found in deepwater and were thought likely to be beyond the reach of fishing activity, and (2) the majority of authorship team took an evidentiary perspective toward extinction risk and viewed the lower trait-based estimate as more credible. The new threat level revealed by the second assessment demonstrates the IUCN DD calculation provides a good estimate of threat when the distribution of traits (body size and depth range) is similar between DD and data-sufficient species, however, the trait-based method may perform better when the distribution of traits differs between DD and data-sufficient species.[55]