CONSERVATION

# Fishing for oil and meat drives irreversible defaunation of deepwater sharks and rays

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The deep ocean is the last natural biodiversity refuge from the reach of human activities. Deepwater sharks and rays are among the most sensitive marine vertebrates to overexploitation. One-third of threatened deepwater sharks are targeted, and half the species targeted for the international liver-oil trade are threatened with extinction. Steep population declines cannot be easily reversed owing to long generation lengths, low recovery potentials, and the near absence of management. Depth and spatial limits to fishing activity could improve conservation when implemented alongside catch regulations, bycatch mitigation, and international trade regulation. Deepwater sharks and rays require immediate trade and fishing regulations to prevent irreversible defaunation and promote recovery of this threatened megafauna group.

The deep ocean is the largest and one of the most complex ecosystems on the planet, harboring a great diversity of species and the greatest number of individual organisms (*1*). The ocean makes up 71% of Earth's surface, and the deep ocean (beyond depths of 200 m) covers 84% of the ocean area and 98% of its volume (*2*). Unsurprisingly, the deep ocean also remains one of the least-studied environments on Earth (*1*, *2*). Our ever-growing dependence on the deep ocean calls for an improved understanding of biodiversity and ecosystem function (*3*). Governments have agreed to conserve 30% of the world's oceans, and after a decade of negotiations, a globally accepted treaty to manage and conserve the deep ocean in areas beyond national jurisdiction has been finalized (*4*, *5*). Limited sampling of the deep ocean hints at local concerns, yet there are no comprehensive synopses of the state of deepwater biodiversity. Furthermore, there are no policy-relevant indicators to guide global target setting and tracking.

In this work, we calculated global biodiversity change indicators of, status of, and threats to an iconic globally distributed group of deep-ocean megafaunal predators. To do so, we took advantage of the largest and most comprehensive assessment of this group: all 521 species of deepwater sharks and rays. First, we estimated the intrinsic sensitivity of deepwater sharks and rays compared with that of other exploited marine vertebrates (*6*). Second, we analyzed trends in deepwater shark and ray relative abundance using a Bayesian state-space population model (*7*, *8*). Third, we used the latest International Union for Conservation of Nature (IUCN) Red List of Threatened Species Categories and Criteria to estimate global extinction risk, trends in extinction risk from a Red List Index, threats, and the underlying patterns of use and trade (*9*–*11*). Finally, we identify conservation benefits to deepwater sharks and rays from depth and spatial limits to fishing activities and discuss possible trade regulations.

## The intrinsic biological sensitivity of deepwater sharks

Deepwater sharks and rays exhibit some of the slowest vertebrate life histories, with the longest known life spans and very low reproductive outputs (*12*, *13*), which translates into very low maximum intrinsic population growth rates [median $r_{\max}$ = 0.161 year$^{-1}$ (alternative $r_{\max}$ = 0.050 year$^{-1}$)] and long population doubling times extending over 30 years (Fig. 1, A and B, and tables S1 and S2). Deepwater shark and ray maximum population growth rates are, on average, half that of coastal sharks [$r_{\max}$ = 0.296 year$^{-1}$ (alternative $r_{\max}$ = 0.169, 0.183 year$^{-1}$); population doubling time ($T_{\mathrm{d}}$) = 2.6 years] and more similar to threatened pelagic shark maximum population growth rates [$r_{\max}$ = 0.164 year$^{-1}$ (alternative $r_{\max}$ = 0.082, 0.078 year$^{-1}$); $T_{\mathrm{d}}$ = 4.6 years] (*7*). Overall, deepwater shark maximum growth rates are comparable to those of marine mammals that were formerly hunted for their meat, fat, and oil [$r_{\max}$ = 0.065 year$^{-1}$ (alternative $r_{\max}$ = 0.054, 0.051 year$^{-1}$); $T_{\mathrm{d}}$ = 11.0 years]. Some deepwater sharks have the lowest growth rates of all marine vertebrates. For example, Greenland shark population growth rates ($r_{\max}$ = 0.022 year$^{-1}$, $T_{\mathrm{d}}$ = 31.8 years) are comparable to those of dugong [*Dugong dugon*; $r_{\max}$ = 0.029 year$^{-1}$, $T_{\mathrm{d}}$ = 24.4 years) and sperm whale (*Physeter macrocephalus*; $r_{\max}$ = 0.031 year$^{-1}$, $T_{\mathrm{d}}$ = 22.7 years). A more typical deepwater shark, the leafscale gulper



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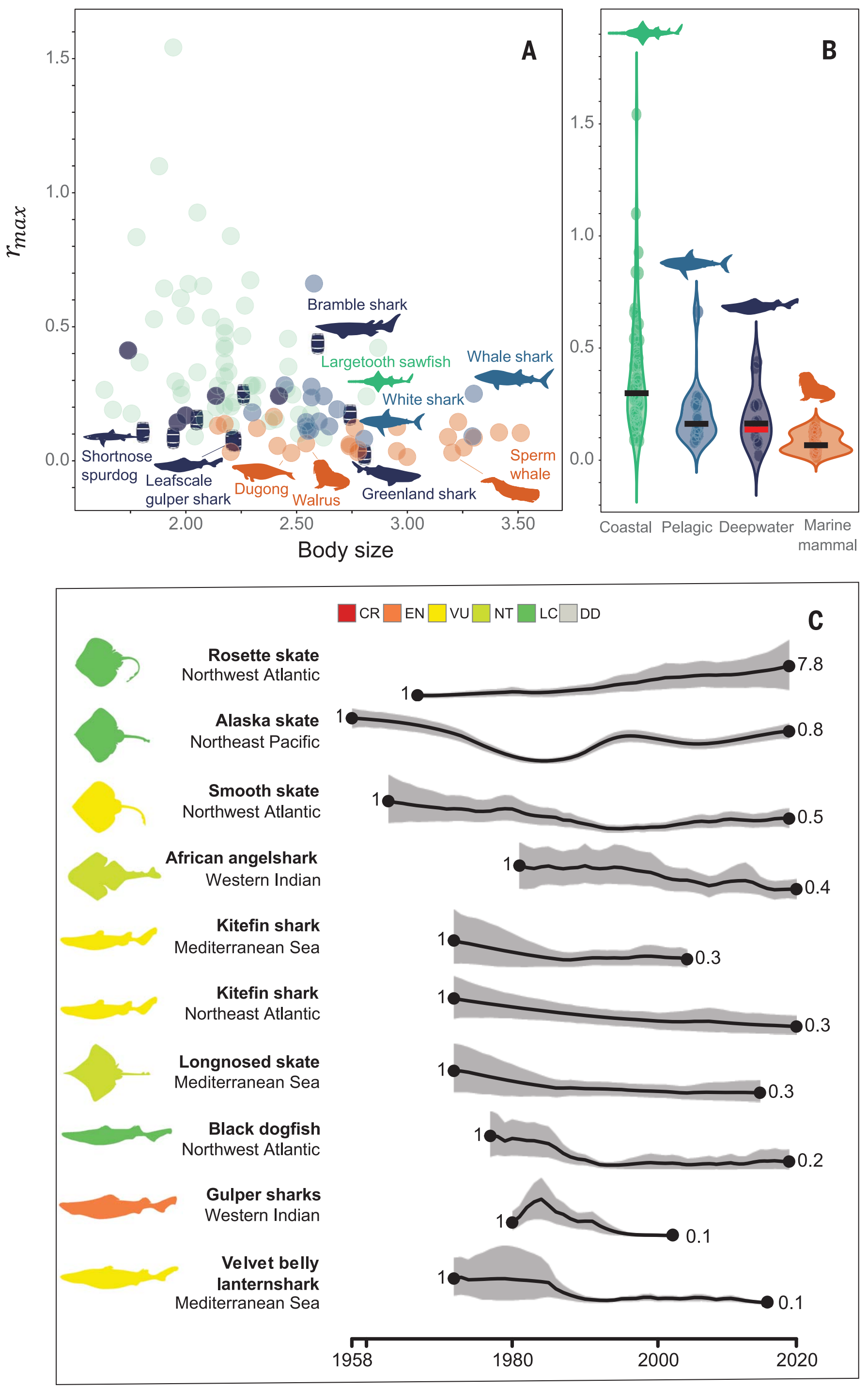


**Fig. 1. Intrinsic population growth rate and population trends of deepwater sharks and rays.** (**A** and **B**) Comparison of maximum intrinsic rate of population increase ($r_{max}$) and body size (where body size is the maximum linear dimension measured as maximum length or maximum disk width, in log scale) for 86 shark and ray species and 22 marine mammal species. Marine mammals are indicated by red, coastal sharks and rays by teal, pelagic sharks and rays by blue, and deepwater sharks and rays by dark blue. Barrels in (A) and the red line in (B) indicate deepwater species identified in the liver-oil trade. In (B), black lines indicate the median, and shaded areas indicate the kernel density estimate. (**C**) Regional population trends for deepwater sharks and rays where data were available from before 1980. Numbers represent changes in the abundance index over the observed time period. Lines denote the mean, and shaded regions indicate the 95% credible intervals. Species are ordered by rate of population change, and species color indicates global Red List status: CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; and DD, Data Deficient.

shark (*Centrophorus squamosus*), has an $r_{max}$ equal to 0.071 year$^{-1}$ ($T_d$ = 10.1 years), which is comparable to that of the walrus (*Odobenus rosmarus*; $r_{max}$ = 0.065 year$^{-1}$, $T_d$ = 11.0 years). Maximum population intrinsic growth rates are equivalent to absolute maximum fishing pressure, beyond which species will be driven to extinction. Fishing limits of Greenland shark and leafscale gulper shark, for example, equate to exploitation limits of no greater than 2.2 and 7.0% per year, respectively, compared with 3.2 and 6.7% per year for sperm whale and walrus, respectively. These limits place deepwater sharks among the most sensitive of all marine vertebrates to overexploitation.

### Estimates of regional population trends

Despite an exhaustive global search yielded 871 population time series for 202 sharks and their relatives (*14*), we found very few population time series that predated the onset of deepwater fishing (1980 or earlier): one genus-level grouping (*Centrophorus* spp.) and nine time series for eight deepwater species (Fig. 1C). Nine of these 10 time series revealed steep declines of >90% reduction in regional populations over time spans equivalent to three generation lengths (table S3). Only one species' population increased: the rosette skate (*Leucoraja garmani*) from the Northwest Atlantic.

### Global extinction risk

Sharks and rays are the most comprehensively assessed and threatened major radiation of the eight major deepwater lineages, totaling 2746 species assessed to date (Fig. 2). We estimate that one in seven (14.1%) deepwater sharks and rays are threatened with an elevated risk of extinction worldwide, on the basis of the observed number of threatened species combined with the estimated number of IUCN Data Deficient species that are likely to be threatened (*10*). Of a total of 521 species of deepwater sharks and rays, there are presently 60 (11.5%) threatened species: nine (1.7%) Critically Endangered, 20 (3.8%) Endangered, and 31 (6.0%) Vulnerable (Fig. 3, A and B). This level of extinction risk is more than twice the number reported from the first global assessment in 2014 [25 of 479 species (5.2%) (*15*)]. Deepwater sharks (15.2%, $n$ = 43 of 283 species) are twice as threatened as deepwater rays (7.1%, $n$ = 17 of 238 species). No species were flagged as Possibly Extinct nor assessed as globally Extinct or Extinct in the Wild; however, gulper sharks often become "commercially extinct" where intensive targeted fishing has occurred (*16*). Almost two-thirds of species (62.0%, $n$ = 323) are assessed as Least Concern and 43 (8.3%) as Near Threatened.

### Trends in extinction risk

Many status changes since 2005 arose from the acquisition of new information combined

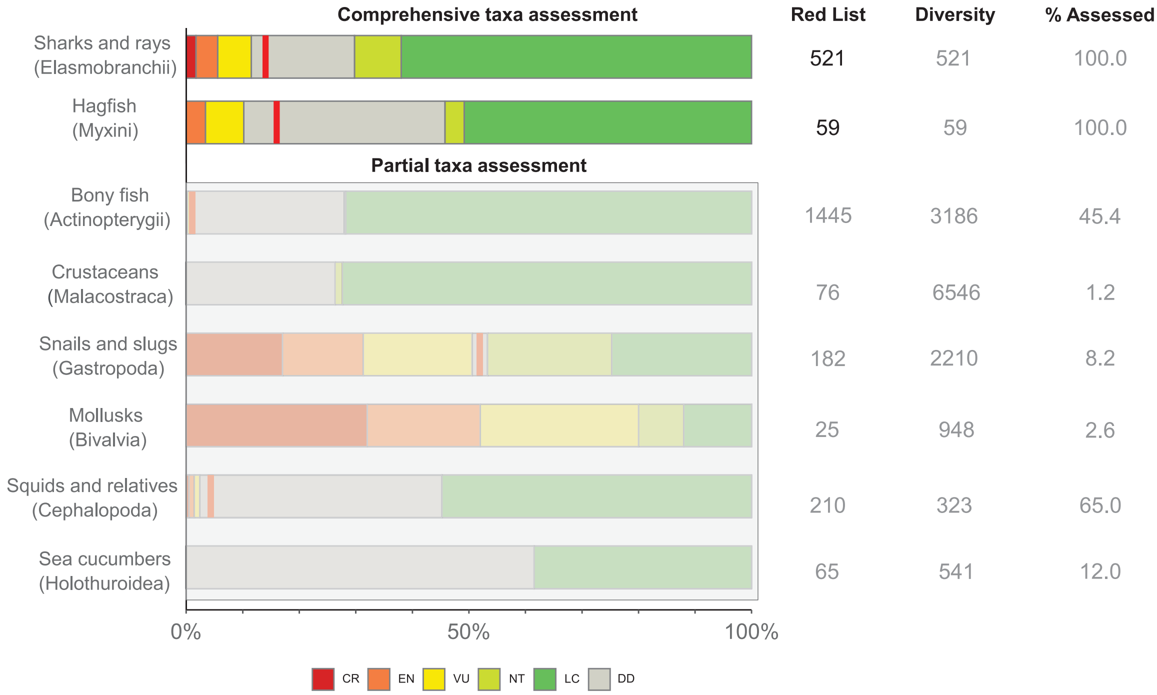


**Fig. 2. Percentage of IUCN Red List categories for other deepwater taxa.** Red lines indicate the best estimate of threatened species if all Data Deficient species faced a similar level of threat to data-sufficient species in the taxa. The shaded box shows groups where not all taxa have been assessed, as indicated by the number of species on the IUCN Red List (Red List), species diversity (Diversity), and percentage of species assessed (% Assessed).

with a more precautionary approach to recent reassessment (*11*). Nevertheless, these changes likely masked considerable, genuine change. We used a back-casting approach to retrospectively infer "genuine" changes that were most likely to have occurred (*10*) and to calculate a Red List Index spanning a half century (1970–2020), where a value of 1 indicates that all species are Least Concern and a value of 0 indicates that species are Extinct. There was very little threat in the deep ocean before 1970, and the Red List Index declined by 7% from a retrospective estimate of 0.98 in 1970 to 0.91 in 2020 (Fig. 3D). The Red List Index for deepwater sharks and rays is comparable to estimates for all fish (sampled $RLI_{2010}$ = 0.91) but worse than for marine fish (sampled $RLI_{2010}$ = 0.97), and deepwater sharks and rays are generally less at risk than members of the class Chondrichthyes ($RLI_{2020}$ = 0.77, $n$ = 1199 species). The Red List Index trends were similar for deepwater sharks and rays, with a faster rate of decline between 1980 and 2005, which coincided with the advent and expansion of most deepwater fishing (*17*). Between 1980 and 2005, the inferred number of threatened species more than doubled from 22 to 57 (i.e., 4.2 to 10.9% of total deepwater diversity; Fig. 3, A and B).

### Overfishing is the main threat to the deep ocean

Overfishing is the primary threat to deepwater sharks and rays. Where threat was assessed, nearly every species (99.3%, $n$ = 435 of 438) is threatened by overfishing (fig. S4). Most (87.7%, $n$ = 384 of 438) deepwater species are taken as incidental catch in trawl, longline, and gillnet fisheries that target groups such as grenadiers (Macrouridae) and hakes (Merlucciidae). One-tenth of deepwater sharks and rays are targeted in fisheries (11.6%, $n$ = 51 of 438 species). Nevertheless, one-third (35%, $n$ = 21 of 60) of threatened species are targeted, primarily from three families: gulper sharks (Centrophoridae; 33.3%, $n$ = 7 of 21), dogfishes (Squalidae; 19.0%, $n$ = 4 of 21), and hardnose skates (Rajidae; 14.3%, $n$ = 3 of 21). Other threats were minor and were identified for only 2.5% of species ($n$ = 11 of 438), including pollution, climate change, and ecosystem modification.

### Shark liver-oil trade as a driver of defaunation and rising extinction risk

The use of sharks for their liver oil dates to ancient civilizations (e.g., for wound healing, heating fuel, or waterproofing boats) (*16*, *18*, *19*), but the globalized expansion of the trade and diversification of use is a relatively new phenomenon (Fig. 3E). International liver-oil trade is now a major driver of targeted fisheries and retention of incidental catch for many deepwater sharks around the world (table S6). Although both coastal and deepwater sharks are used for their liver oil, deepwater shark livers are preferred for their high squalene content (*13*, *16*). Nearly two-thirds of threatened deepwater sharks (58.1%, $n$ = 25 of 43 species) have been used for their liver oil (table S6). Of the 53 species (18.7% of deepwater shark diversity) taken for their liver oil, half (47.1%, $n$ = 25 of 53) are threatened, with 7.5% Critically Endangered ($n$ = 4), 22.6% Endangered ($n$ = 12), and 17.0% Vulnerable ($n$ = 9) (Fig. 3C, fig. S5, and table S6). Specifically, gulper shark liver oil is prized for its very high squalene content, and this family accounts for more than one-fourth of species taken for liver oil (26.4%). Most (93.3%, $n$ = 14 of 15) gulper shark species have been identified in trade or inferred to be traded on the basis of information from regional fisheries that report catch under generic categories (e.g., *Centrophorus* spp.). The mixed end product makes it notably difficult to identify and quantify species composition. Other species identified in the trade include dogfishes (Squalidae; 26.5%, $n$ = 9 of 34 species), sleeper sharks (Somniosidae; 50.0%, $n$ = 8 of 16 species), and cow sharks (Hexanchidae; 100%, $n$ = 4 of 4 species) (fig. S5).

We show that liver-oil fisheries are not sustainable and result in steep population reductions and elevated extinction risk (Figs. 1C and 4). Indeed, these boom-and-bust fisheries are better thought of as nonrenewable mining extractions (*20*), peaking within 2 to 3 years of commencement and collapsing soon after (<20 years; Fig. 4) (*16*, *21*). The shark liver-oil trade has been understudied and overshadowed by the more visible global trades of shark and rhino ray fins, devil ray gill plates, and meat (Fig. 3F). Shark liver oil is among the most widely used shark products (after fins and meat) and is twice as valuable as shark-meat exports in some countries, such as India (*22*). Targeted liver-oil fisheries have occurred in the Northeast and Central Atlantic Ocean, Mozambique,

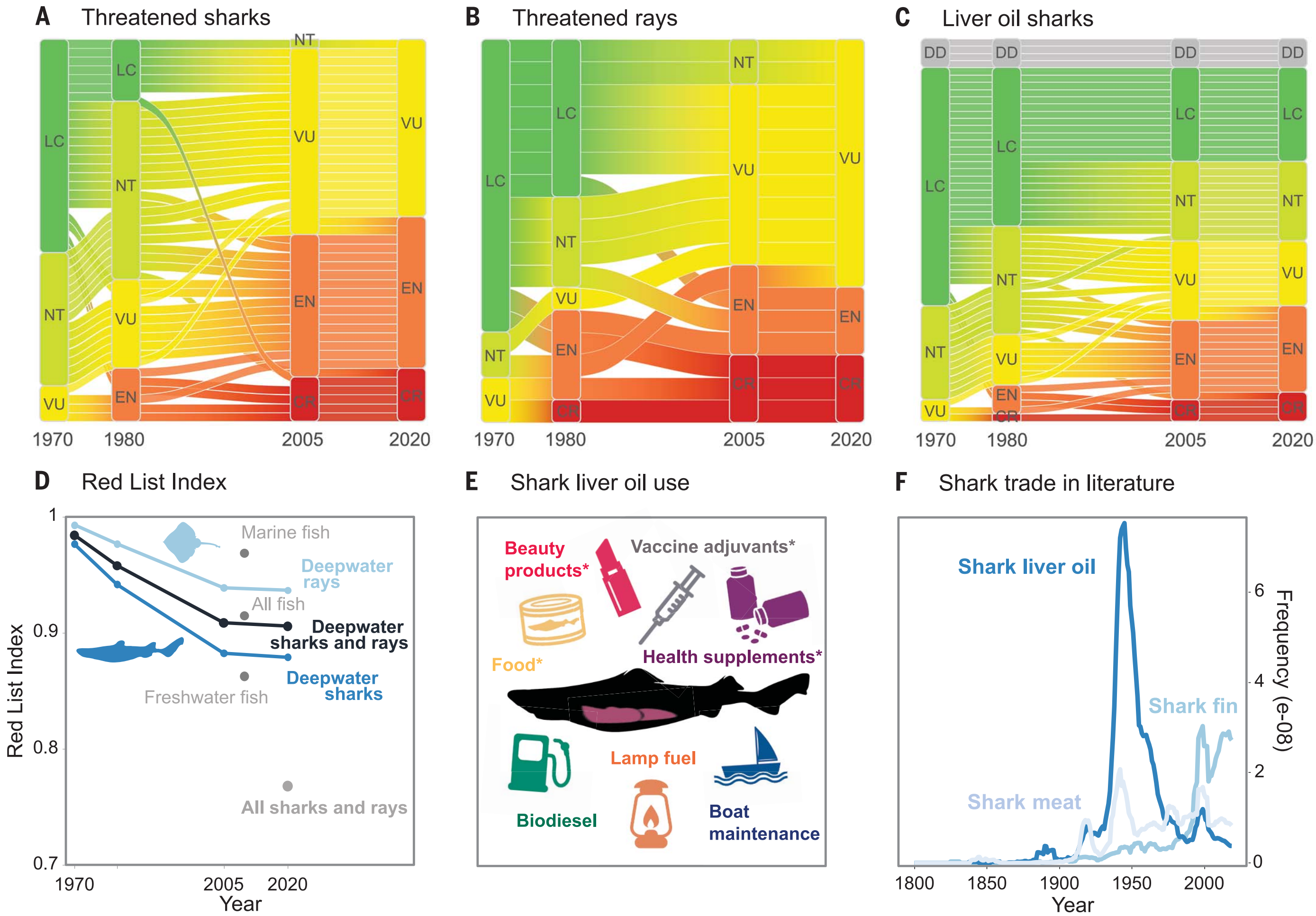


**Fig. 3. Change in Red List status for 521 deepwater shark and ray species from 1970 to 2020, global Red List Index, and shark liver oil–trade knowledge.** (**A** to **C**) Change in Red List status for (A) threatened deepwater sharks, (B) threatened deepwater rays, and (C) deepwater sharks used for their liver oil. (**D**) The Red List Index for sharks and rays combined and each separately, as estimated in 1970, 1980, 2005, and 2020 and compared with the Red List Index for all shark and ray species. The Red List Index for marine fish and freshwater fish combined and each separately, as estimated in 2010, is also shown. A Red List Index value of 1 indicates that all species are Least Concern, and a Red List Index value of 0 indicates that all species are Extinct. (**E**) Specific uses of shark liver oil, where an asterisk denotes contemporary common uses. (**F**) Trends in shark products (fins, meat, liver oil) mentioned in printed sources between 1800 and 2019.

India and Sri Lanka, the Maldives, Indonesia, Japan, and the Southwest Pacific Ocean, where threatened shark richness and the proportion of threatened species is high (Fig. 4 and fig. S6). The only evidence of existence for some historical liver-oil fisheries and associated trade is through liver-oil export records (*16*).

Shark-derived squalene is still in high demand despite readily available plant-based and synthetic alternatives. There is particular interest for its application in cosmetics and human health, including vaccine adjuvants (*23*) (Fig. 3E). Yet the use of liver oil for medical purposes continues despite a failure to evaluate the possible human health risks. The extremely slow life histories and high trophic level of deepwater sharks can result in bioaccumulation of heavy metals and contaminants in the muscle and liver tissues, often in concentrations near or above domestic and international regulatory thresholds (*24*).

### The meat-trade threat

Deepwater sharks and rays are also at risk from demand for meat products. Shark meat is consumed globally and may be a regional delicacy (*19*, *22*). Skate meat is in high demand throughout well-established European markets and demand for fermented skate meat (hongeo-hoe) has risen in the Korean market (*25*). This demand has incentivized skate retention around the world, notably retention of incidental catch in Patagonian toothfish (*Dissostichus eleginoides*) longline fisheries around the Southern Ocean and Chile and in skate fisheries in the Northwest Pacific (Japan, Russia) and off southern South America (Chile, Argentina, Falkland Islands and Malvinas), where the percentage of threatened rays is highest (fig. S6). In Argentina, for example, the reported landings of skates increased from 900 tonnes in 1993 to 28,000 tonnes by 2007 as a response to Korean skate traders providing a market that incentivized fishers to target and retain these species for international trade (*25*, *26*). Of the preferred species identified in this trade, 55.6% ($n$ = 15 of 27 species) are deepwater: Most (66.7%, $n$ = 10 of 15 species) are assessed as Least Concern, four as Near Threatened (26.6%), and one as Endangered [roughskin skate (*Dipturus trachydermus*); table S7]. This suggests that catch levels are not yet causing risk at the global scale for these species. However, half of the preferred

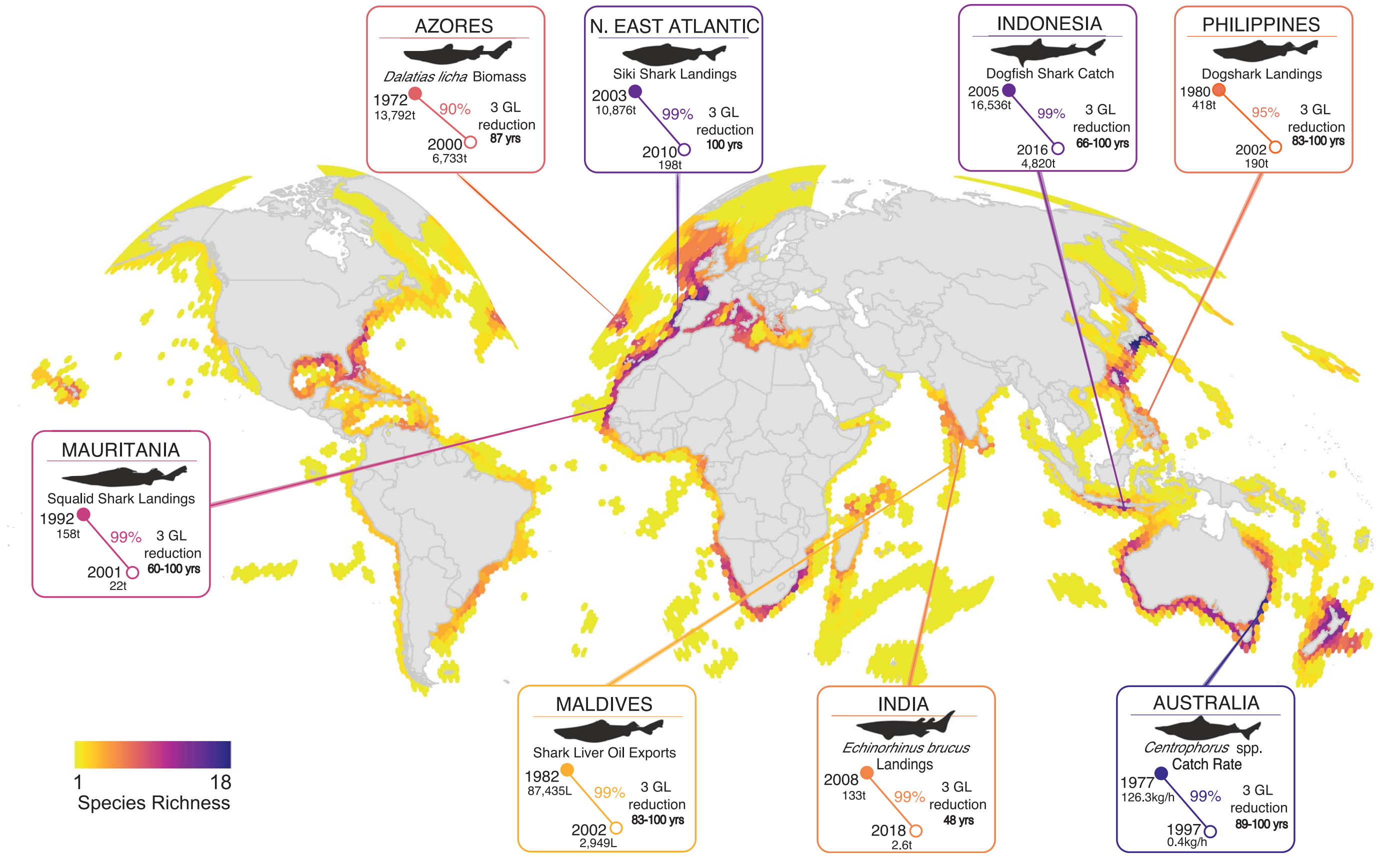


**Fig. 4. Summary of landings and catch-rate data used to infer population reductions in deepwater sharks overlaid on the map of global species richness of deepwater sharks used for their liver oil.** Species are listed by their scientific name or regional generic multispecies reporting code (siki shark, dogshark, dogfish, squalid shark). Box colors highlight regional species richness, which ranges from 1 to 18 species. The estimated population reduction over three generation lengths (GL) is expressed as a percentage. L, liters; t, tonnes.

coastal skate species are threatened ($n$ = 6 of 12), whereas others are fished sustainably in the Northeast Pacific and Northwest Atlantic (*27*). Given the rapidly expanding demand for meat products and the corresponding growth in fishing, the status of skates should be closely monitored and managed to ensure that further increases in extinction risk are avoided.

### Conservation benefits from depth and spatial limits to fishing activity

We considered two approaches to halt and reverse declines of threatened deepwater sharks and rays within the Convention on Biological Diversity's "30 by 30" framework of spatial protection commitments (*5*). The first considers the benefits of setting a worldwide depth limit below which fishing activity would be restricted (vertical refuge), and the second considers the benefit of spatial no-take areas (horizontal refuge). A worldwide prohibition of fishing below 800 m would provide 30% vertical refuge for one-third (27.4%) of threatened species (Fig. 5B and fig. S2), whereas a shallower 500-m no-fishing limit would double the number (60.8%) of species protected (Fig. 5A). Protecting 30% of the deep ocean between 200 and 2000 m would provide ~80% of species with at least partial spatial (horizontal) protection across their range, with the greatest coverage in the Gulf of Mexico and Caribbean Sea, Eastern Pacific (western United States to Peru), Iberian Peninsula and southern Mediterranean Sea, Gulf of Aden, west India and Chagos-Laccadive Ridge, Sea of Japan and Sea of Okhotsk, and the Zealandia continent (Fig. 5D and fig. S3).

### Discussion

We show that deepwater sharks and rays have experienced population decline due to overfishing compounded by highly sensitive life histories, such as those of highly threatened pelagic sharks and formerly exploited, and now highly protected, marine mammals. This combination of life histories, overfishing, and international trade has resulted in a doubling of the number of threatened deepwater shark and ray species in 10 years. Deepwater shark and ray species are often regarded as "welcomed catch" and retained for their liver oil and meat. Focus on their trade has been overshadowed by the challenge of tackling the global fin trade, and trade in deepwater sharks and rays remains difficult to quantify (Fig. 3F). The continued use of the deep ocean for food and increasing interest in resource extraction (e.g., mining for manganese nodules) commit these species to increasing risk. Considering their sensitivity to overexploitation, previous examples of boom-and-bust fisheries, diversifying markets, and a paucity of research and management, threatened deepwater sharks and rays stand little chance of recovery without immediate action. We consider two possible solutions to improve the conservation status of deepwater sharks and rays: (i) spatial closures and (ii) trade and fishing regulations.

Spatial closures that encompass areas that are important to deepwater sharks and rays can provide refuge from fishing and promote recovery and long-term survival. Spatial closures are needed because targeted fishing and retention bans do not prevent the mortality of prohibited species that are brought to the surface from great depths by fishing gear (*28*, *29*). Retention bans have often been introduced as extreme last-resort measures to halt

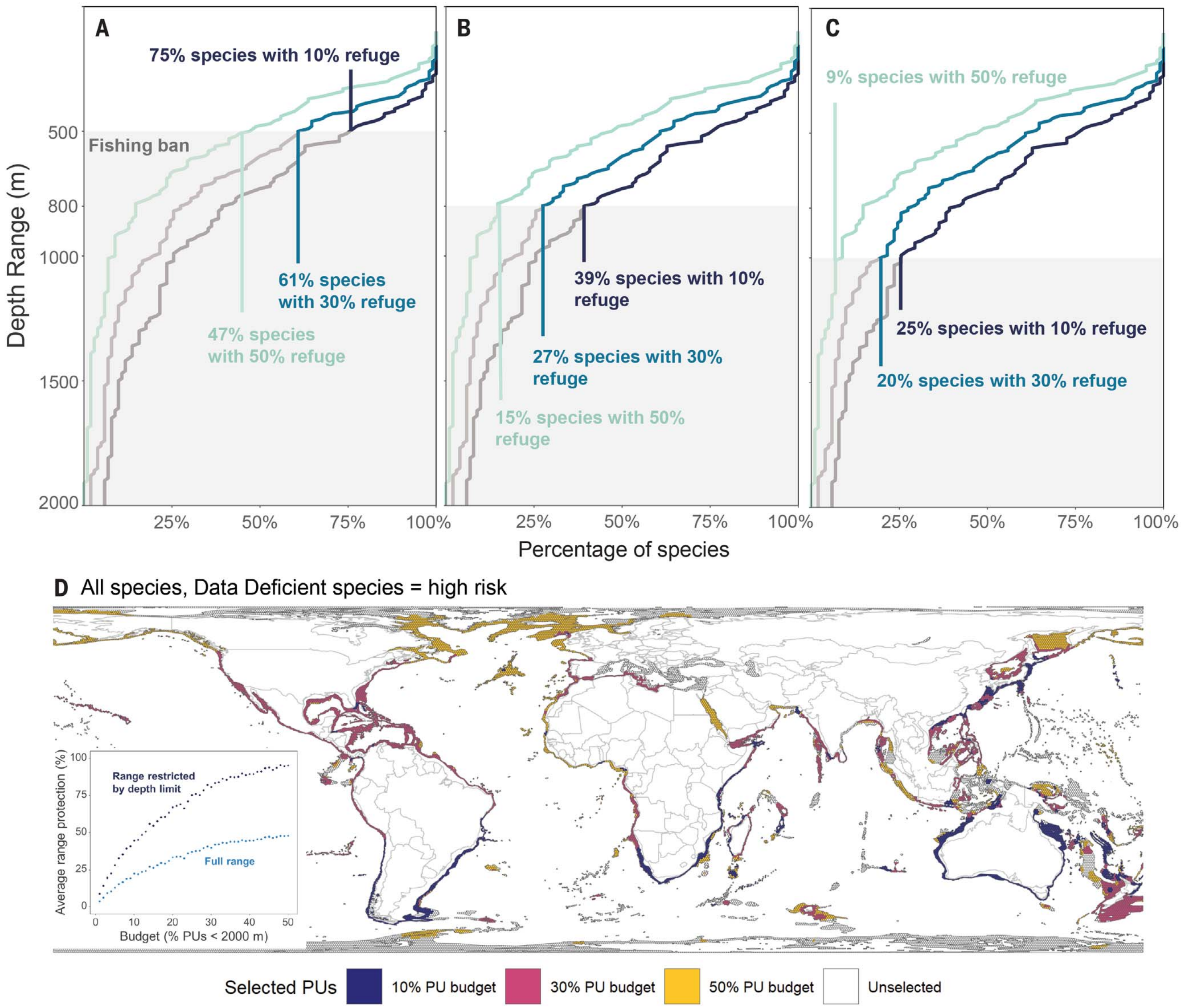


**Fig. 5. The benefits of two complementary conservation strategies for deepwater sharks and rays.** (**A** to **C**) Vertical conservation priorities based on the percentage of threatened deepwater sharks and rays and the average-depth refuge benefit [10% (teal line), 30% (blue line), 50% (purple line)] for fishing prohibitions deeper than (A) 500 m, (B) 800 m, and (C) 1000 m (gray areas). (**D**) Layered spatial conservation priority areas for deepwater sharks and rays for 10% (purple), 30% (pink), and 50% (yellow) of planning units (PUs) within the planning domain (cells between 200 and 2000 m), where Data Deficient species were weighted with high risk. The inset graph is the percentage of spatial protection received for a species' full spatial range (dark blue) and a species' spatial range found within the planning domain (between 200 and 2000 m, light blue) based on the spatial refuge (10 to 50%).

declines after decades of inaction (*30*, *31*). Mitigating capture mortality is becoming increasingly important in high-seas fisheries, where deepwater shark retention bans are established, catch data are limited, and species' risks are uncertain (*32*) (Fig. 5 and fig. S3). Because nearly every deepwater shark is threatened by incidental capture, even low levels of catch can prevent recovery, given their low population growth rates (Fig. 1). Fishing beyond defined depth limits has been banned (*33*, *34*), for example, bottom trawling below 1000 m in the Mediterranean Sea. However, this measure has been ineffective at reducing fishing impacts because deepwater species can be highly threatened by fishing activity in their shallower and highly fishable depth distribution (*2*, *28*). In this work, we show that even a global fishing prohibition below 800 m would still expose most threatened deepwater species to fishing mortality, which would require spatial protection to curb deepwater shark and ray mortality (*35*) (Fig. 5). The best example is off southeast Australia, where a network of targeted spatial closures on the upper slope and seamounts were established to protect 25% of threatened gulper shark core habitat, covering >4738 km$^2$ at a depth between 200 and 650 m (*36*). The design of such closures also needs to consider the management of co-occurring commercial fish species to minimize the trade-off of fishing displaced from new closures having a greater impact on sharks outside the closures. In addition to reducing fishing mortality, habitat protection is needed for recovery and maintaining healthy population levels. Habitat dependence is poorly understood, but some documented examples exist, including deepwater skates using hydrothermal vents to incubate their eggs (*37*). Hydrothermal vents have received global attention for prospective mineral mining operations (*3*), and this provides additional motivation for their protection. Such spatial protection measures have positive impacts, not only on deepwater sharks and rays but on all demersal biodiversity biomass and richness (*38*).

Trade and fishing regulations specific to deepwater sharks and rays are needed to ensure legal, traceable, and sustainable trade and prevent further endangerment. For example, international liver-oil trade regulations could be established to ensure that the trade is not driving extinction risk. At present, there are limited means of determining what species make up internationally traded squalene oil; either the oil may be a by-product of sustainable fisheries or the present lack of regulations could be masking the trade of threatened species (*39*). In the first instance, highly threatened species (e.g., gulper sharks and look-alikes; fig. S5) could be listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) to regulate international trade. There are >145 shark and ray species listed in CITES Appendix II (*40*), but to date, none are deepwater species. National catch regulations, such as landing the shark whole (much like a fins-naturally-attached policy), would improve species identification and fisheries characterization and monitoring and would guide appropriate national-level management, such as catch limits, catch prohibitions, or closed areas. There is also an urgent need to assess the risk to human health and determine the appropriateness of sourcing and using shark squalene for medical applications.

The extinction risk of deepwater sharks and rays is presently much less than that of shallow-water species, but their potential for recovery is low. We have the evidence to act more proactively for the deep ocean and learn from the mistakes that have driven more than half of coastal and pelagic species to be threatened (*11*). Achieving sustainable fisheries for most deepwater sharks and rays would be challenging and require high management capacity, ecological knowledge, and implementation of routine rigorous monitoring. Effective precautionary actions are needed to ensure that the largest ecosystem on the planet maintains its biodiversity and that half of the world's shark and ray species have refuge from the global extinction crisis.

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## SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S6
Tables S1 to S8
References (*42*–*75*)
MDAR Reproducibility Checklist

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