Half a century of global decline in oceanic sharks and rays

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Overfishing is the primary cause of marine defaunation, yet declines in and increasing extinction risks of individual species are difficult to measure, particularly for the largest predators found in the high seas¹⁻³. Here we calculate two well-established indicators to track progress towards Aichi Biodiversity Targets and Sustainable Development Goals^{4,5}: the Living Planet Index (a measure of changes in abundance aggregated from 57 abundance time-series datasets for 18 oceanic shark and ray species) and the Red List Index (a measure of change in extinction risk calculated for all 31 oceanic species of sharks and rays). We find that, since 1970, the global abundance of oceanic sharks and rays has declined by 71% owing to an 18-fold increase in relative fishing pressure. This depletion has increased the global extinction risk to the point at which three-quarters of the species comprising this functionally important assemblage are threatened with extinction. Strict prohibitions and precautionary science-based catch limits are urgently needed to avert population collapse^{6,7}, avoid the disruption of ecological functions and promote species recovery^{8,9}.

Over the United Nations 'Decade of Biodiversity' from 2011 to 2020, governments committed to improve human wellbeing and food security by safeguarding ecosystem services and halting biodiversity loss¹⁰. The Sustainable Development Goals, adopted by all member states of the United Nations, and the 20 Aichi Biodiversity Targets of the Convention on Biological Diversity provide a framework to track progress towards the 2020 deadline^{4,5,10}. Seafood sustainability is an integral part of these commitments, and wild-capture fisheries are essential nutritional and economic resources for millions of people globally^{11,12}. However, it is difficult to assess changes in the state of biodiversity and ecosystem structure, function and services beneath the ocean surface¹³.

Elasmobranchs (sharks and rays, hereafter 'sharks') offer a unique window into the state of the oceans. Sharks are one of the most evolutionarily distinct and functionally diverse vertebrate radiations^{14,15}. The first global assessment of the International Union for Conservation of Nature (IUCN) estimated that one-quarter of sharks were threatened with extinction (classified as critically endangered, endangered or vulnerable according to the criteria of the IUCN Red List of Threatened Species)¹⁶, making sharks the most threatened vertebrate lineage after amphibians^{16–18}. The long generation times and low intrinsic population

growth rates of many sharks make them inherently susceptible to overexploitation^{1,7,19}. Globally, sharks are landed for their meat, fins, gill plates and liver oil^{20,21} and catches increased to an estimated peak of 63–273 million individuals in the early 2000s before declining owing to overfishing⁶. The first warnings of the dire status of sharks were based on boom-and-bust catch patterns and the increasing international trade in shark fins^{22,23}. Subsequently, serious declines in many oceanic and coastal shark populations were documented, both in the Gulf of Mexico and Northwest Atlantic^{24,25}, and also in South Africa²⁶ and Australia²⁷. Shark population assessments for many other regions have since become increasingly robust^{8,28,29}. Until now, however, these have not been synthesized to provide a global perspective on shark population trends.

Here we calculate for oceanic sharks two biodiversity indicators established by the Convention on Biological Diversity: the Living Planet Index (LPI)^{5,30} on global population changes since 1970 and the Red List Index (RLI)^{5,31}, which tracks changes in the relative extinction risk of taxa. These indicators quantify progress towards Aichi Biodiversity Targets 6 (manage marine resources for sustainability) and 12 (prevent extinction), and Sustainable Development Goal 14 (conserve

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and sustainably use the oceans). First, we used a Bayesian state-space framework^{32,33} to estimate trends in the relative abundance of 18 species from 57 time-series datasets compiled and reviewed at an expert workshop convened by the IUCN Species Survival Commission's Shark Specialist Group (IUCN SSC SSG). Using these trends, we calculated the global LPI for oceanic sharks from the reference year 1970 (which was set at 1) to 2018-and then extrapolated each time-series to 2020 to encompass the Aichi Biodiversity Target assessment year-by hierarchically aggregating the annual rates of change from each time-series for a species by region, then globally (Extended Data Figs. 1, 2a). Second, we combined a retrospective Red List assessment (1980) with two recent assessments (around 2005 and 2018) from the IUCN Red List for all 31 species of oceanic sharks to build the RLI (Extended Data Fig. 1). The RLI provides standardized assessments of the extinction risk of each species, which are comparable across taxa, and is particularly useful when robust trend data are missing. Comparing the RLI over time, among different taxa, reveals the common trends in extinction risk among groups, despite differences in habitat, life history and threats. Such cross-taxon comparisons are useful to ensure the appropriate allocation of global conservation resources across terrestrial, freshwater and marine biomes.

Finally, we develop three lines of evidence to attribute the decreasing abundance (shown by the LPI) and increasing extinction risk (shown by the RLI) of oceanic sharks to overfishing: (1) increasing relative fishing pressure (RFP) over time (measured as changes in catch rates relative to the changes in the LPI); (2) an increasing proportion, over time, of oceanic sharks that are overfished and below biomass or abundance levels that could produce the maximum sustainable yield (the equilibrium state of the exploited population sustaining the greatest yield (that is, catch rate) over long time periods³⁴); and (3) the near-absence of important threats other than fishing reported in the IUCN Red List assessment of each species.

Declining abundance index

We find that, globally, the abundance of oceanic sharks declined by 71.1% (95% credible interval, 63.2–78.4%) (Fig. 1) from 1970 to 2018, at a steady rate averaging 18.2% per decade (Extended Data Fig. 2c). Over the half-century from 1970 to 2020, the projected LPI estimates that abundance declined by 70.1% (95% credible interval, 62.8–77.2%) (Extended Data Fig. 2b). The declining trend in the LPI trajectory is robust to the exclusion of any individual species (Extended Data Fig. 3). There are three reasons why the true abundance trend index values are likely to be lower (and calculated percentage declines worse) than estimated here (Supplementary Discussion 1): (1) fishing levels were already unsustainable half a century ago; (2) unreported catches (including discards) are not included in our time-series; and (3) traditional stock assessments could underestimate fishing mortality.

The global trend index can be disaggregated into trajectories for each ocean and species, as well as for functional groups with similar ecological or life-history traits. In the Atlantic Ocean, following a long period of decline since 1970, abundances began to stabilize at low levels after 2000 (overall decline of 46.1%; 95% credible interval, 30.7-61.1%) (Fig. 2a). In the Pacific Ocean, abundances decreased steeply before 1990, and then declined at a slower rate (overall decline of 67.0%; 95% credible interval, 53.6-79.4%) (Fig. 2c). In the Indian Ocean, shark abundances have declined steeply since 1970 (overall decline of 84.7%; 95% credible interval, 75.9-92.1%) (Fig. 2b). Despite more resilient life histories, tropical sharks declined more steeply than temperate species (overall declines of 87.8%; 95% credible interval, 79.8-94.3% compared with 40.9%; 95% credible interval, 30.4-50.5%) (Fig. 2d). Overfishing of sharks followed a classic pattern of serial depletion, starting with the largest species, which dropped steeply before the 1980s, followed by declines in medium-sized species and eventually relatively small species (including some devil rays, Mobula spp.) (Fig. 2e). Long-lived,

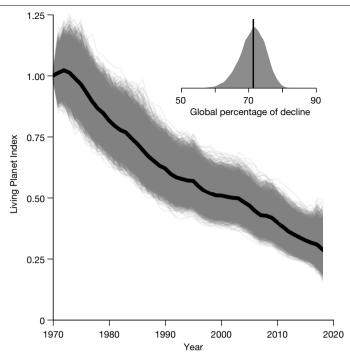


Fig. 1 | **Global LPI for 18 oceanic sharks estimated from 1970 to 2018.** The global percentage of decline was calculated from the posteriors of the LPI around the final assessment year relative to the posteriors for 1970. The black line denotes the mean, the white lines the 95% credible intervals and the grey lines each iteration.

late-maturing species initially declined faster than those with shorter generation times, but two of these species (white shark (*Carcharodon carcharias*) and porbeagle (*Lamna nasus*)) have shown signs of population rebuilding since the early 2000s (Fig. 2f and Extended Data Fig. 7). All species, apart from the smooth hammerhead (*Sphyrna zygaena*), decreased in abundance over the past half-century (Fig. 2g). Devil ray abundance has declined by at least 85% in the past 15 years in the Southwest Indian Ocean (Fig. 2g). Although sparse, the available data for devil rays are representative of the repeated, rapid depletions and local extinctions suspected to have occurred because of overfishing that are driven by target fisheries in many parts of their historical range (Supplementary Discussion 2).

Increasing extinction risk

For all 31 oceanic shark species, the risk of extinction, indicated by IUCN Red List category, has substantially increased since 1980. The RLI declined from a retrospective estimate of 0.86 (range, 0.74-0.90) in 1980 to 0.56 in 2018, comparable to cycads (palm-like plants), the most threatened group of completely assessed species on Earth³⁵ (Fig. 3a). We estimate that in 1980, two-thirds (n = 20) of oceanic shark species fell into the IUCN Red List category of least concern, and only nine were threatened. The basking shark (Cetorhinus maximus) was the only species that was retrospectively classified as endangered. More than three-quarters (n = 24) of these species are threatened now based on steep population reductions (IUCN Red List criterion A). Some formerly abundant, wide-ranging sharks have declined so steeply that they are now classified in the two highest IUCN Red List threatened categories: three are critically endangered (oceanic whitetip shark (Carcharhinus longimanus), scalloped hammerhead (Sphyrna lewini) and great hammerhead (Sphyrna mokarran)), and four are endangered (pelagic thresher (Alopias pelagicus), dusky shark (Carcharhinus obscurus), shortfin mako (Isurus oxyrinchus) and longfin mako (Isurus paucus)) (Fig. 3b). In total, half (16 out of 31) of oceanic shark species are now

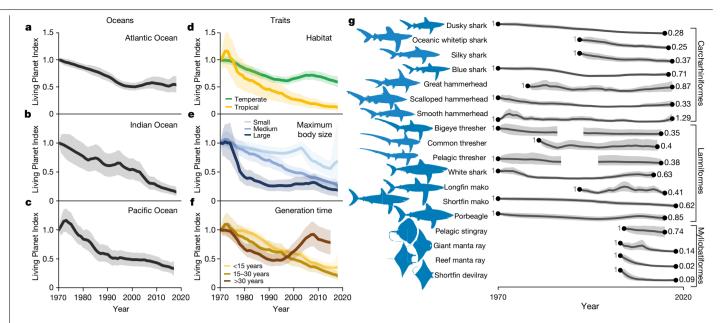


Fig. 2 | LPI for 18 oceanic sharks from 1970 to 2018 disaggregated for each of the oceans and traits. a, Atlantic Ocean; b, Indian Ocean; c, Pacific Ocean; d, geographical zone; e, body size (maximum total length divided into three categories: small, ≤250 cm; medium, 250–500 cm; large, >500 cm); f,

generation time; **g**, species (the time-series for each species are shown in Extended Data Figs. 4–8). Lines denote the mean and shaded regions the 95% credible intervals.

critically endangered (n = 3; $\geq 80\%$ population reduction over three generations) or endangered (n = 13; 50–79% population reduction).

Overfishing is the main threat to oceanic sharks

We attribute the declines in populations and increased extinction risk of oceanic sharks to overfishing based on three lines of evidence. First, there has been a more than twofold increase in fishing with longlines and seine nets, the gears that catch the most oceanic sharks³⁶, during the past half-century (Fig. 4a; data corrected for technological creep, see Supplementary Methods 1). Concomitantly, oceanic shark catch rates have increased threefold since 1970 (Fig. 4a), resulting in an 18-fold increase in RFP (Fig. 4b). This correlation suggests that fishing drove declines in the abundances of sharks with a notable breakpoint in 1990 that we hypothesize coincides with the increasing retention of sharks to meet new market demands (specifically for fins)³⁷ (Fig. 4c). Second, the role of fisheries in driving the declines is thoroughly addressed in the growing number of robust fisheries stock assessments (Extended Data Fig. 9b). The declining LPI is consistent with an increasing proportion of populations and species that have been assessed to be overfished over time (21%) (Fig. 4d); 6 of the 8 assessed species and more than half of the populations (9 of 15) are below the biomass or abundance levels that could produce the maximum sustainable yield (Extended Data Fig. 9c). Third, we compiled the causes of declines reported in the Red List assessments, which are classified into 11 categories ranging from 'human intrusions and disturbance', to 'climate and severe weather'³⁸. Although there are numerous pressures acting on sharks, every Red List assessment for the 31 oceanic sharks concluded that the major

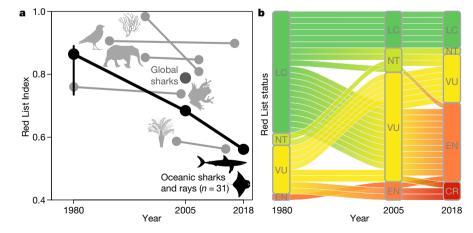


Fig. 3 | **Increase in extinction risk of oceanic sharks. a**, Global RLI for the 31 oceanic shark species (black line) estimated in 1980, 2005 and 2018, and for mammals, birds, amphibians, reef-forming corals and cycads (in grey), and global chondrichthyans (sharks, rays and chimaeras; point labelled 'Global sharks')¹⁶. The error bar denotes the uncertainty around the retrospective 1980 IUCN status (see Methods). A RLI value of 1.0 indicates that all species qualify as

least concern (that is, not expected to become extinct in the near future), whereas a RLI value of 0 indicates that all species have gone extinct. **b**, Change in the Red List status of oceanic sharks from 1980 to 2018. CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; LC, least concern.

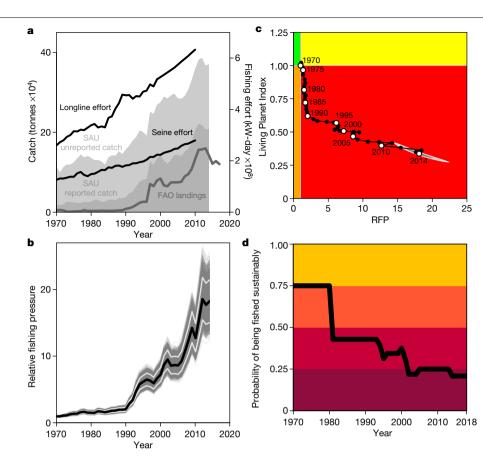


Fig. 4 | **Attributing abundance declines to overfishing. a**, Global catch data of 14 oceanic sharks and fishing effort of longline and seine gears. FAO, Food and Agriculture Organization of the United Nations; SAU, Sea Around Us project. Longline and seine effort are effective corrected fishing effort³⁶. b, Fishing pressure (catch) encountered by oceanic sharks relative to the fishing pressure (catch) in 1970 and to their abundance from 1970 to 2014. The black line denotes the mean, the white lines the 95% credible intervals and the grey

threat was 'biological resource use' and, more specifically, 'fishing and harvesting aquatic resources'. Other threats are reported for only two species (Extended Data Fig. 10).

Discussion

We document an alarming, ongoing, worldwide decline in oceanic shark populations across the world's largest ecosystem over the past half-century, resulting in an unprecedented increase in the risk of extinction of these species. A marked increase in relative fishing pressure is mirrored by the general consistency in the rate and extent of declines across species with differing body sizes and generation times. The low reproductive output of these slow-growing species is clearly no match for the intense fishing pressure that they are currently under.

Overfishing of oceanic shark populations has far outpaced the implementation of fisheries management and trade regulations³⁹. Despite great improvements in conservation commitments in recent decades, relatively few countries impose catch limits specific to oceanic sharks, and fewer still can demonstrate population rebuilding or sustainable fisheries for these species. Obligations under international wildlife treaties⁷ to prohibit retention or restrict international trade of select species have not yet been implemented effectively⁴⁰. The world's four major regional fishery management organizations focused on tunas have, to varying degrees, prohibited the retention of inherently sensitive oceanic shark species that are also of relatively low value to the associated pelagic fisheries. However, tuna regional fishery management

lines each iteration. **c**, LPI as a function of RFP (*n* = 14 species) from 1970 (the initial state for which LPI = 1 and RFP = 1) to 2014 for oceanic sharks (*n* = 18 species). Light-grey, grey and dark-grey polygons denote the 50%, 80% and 95% two-dimensional kernel density estimates of the iterations of LPI versus RFP for the last year (2014). **d**, Proportion over time of oceanic sharks with stock assessments that are at a level of biomass or abundance equal or greater than the levels that would achieve maximum sustainable yield.

organizations fishing limits for more commercially important sharks have been largely inadequate with respect to heeding scientific advice and using ecosystem-based fisheries management^{41,42} (Supplementary Discussion 3).

There are some encouraging findings. We note that the white shark historically declined by an estimated 70% worldwide over the past half-century, but is now recovering in several regions, aided by retention bans⁴³. Hammerhead shark populations are rebuilding in the Northwest Atlantic, owing to strictly enforced quotas throughout their US range. The blue shark has declined less than other species, despite being reported to be at significantly greater risk due to its high distributional overlap with heavily fished areas⁴⁴. This is probably due to its relatively high reproductive rate (compared to other oceanic sharks), but nevertheless its management is warranted on a global scale as market interest and targeted fishing increase. It is possible to reverse shark population declines, even for slow-growing species, if precautionary, science-based management is implemented throughout the range of the species^{8,45} before depletion reaches a point of no return.

We can use IUCN Red List status and trends as a heuristic to guide the conservation priorities of countries with limited capacity to assess, manage and conserve oceanic species. This guidance will be less relevant to nations with the capacity to undertake stock assessments and ensure compliance with management⁸, reflecting the fact that the global Red List status and local status of a species may differ. It has been previously recommended that sharks assessed globally as near threatened or even some assessed as vulnerable may still be able to sustain modest levels of fishing, if managed immediately and carefully throughout their range^{7,16}. Species classified as critically endangered or endangered cannot support fisheries. In these cases, policy recommendations based on stock assessments or on the global Red List status will be congruent⁴⁶; strict measures to prohibit landings and minimize bycatch mortality (by avoiding hotspots, modifying gear and improving release practices) are urgently needed to halt declines and rebuild populations.

The ecosystem consequences of the declines in oceanic shark populations are uncertain because of the complexity and scale of the marine food webs⁴⁷. Nevertheless, the profound effects of depleting predatory species are becoming apparent. For example, the decline in predatory sharks and tunas is associated with increases in mesopredators, including teleosts and smaller-bodied shark species⁴⁸, indicating that fundamental functional changes to these marine food webs are occurring¹⁵. Of further concern is the associated threat to food security and income in many low-income and developing nations⁷, many of which have fished sharks for generations⁴⁹. Alternative livelihood and income options are needed to ease transitions to sustainability.

Conclusion

We demonstrate that—despite ranging farther from land than most species—oceanic sharks are exceptionally threatened by overexploitation. It is clear that the Sustainable Development Goals and specific Aichi Biodiversity Targets (to reverse population declines and use marine resources sustainably) were not met by 2020 for these species. Action is needed immediately to prevent shark population collapses and myriad negative consequences for associated economic and ecological systems. Specifically, there is a clear and urgent need for governments to adopt, implement, and enforce—at domestic and regional levels science-based catch limits for oceanic sharks that are capable of supporting sustainable fisheries, and retention prohibitions, along with bycatch mitigation, for the others^{7.8}. These steps are imperative for long-term sustainability, including potentially increased catch once populations are rebuilt^{9.50}, and a brighter future for some of the most iconic and functionally important animals in our oceans.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-020-03173-9.

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Article Methods

No statistical methods were used to predetermine sample size. The experiments were not randomized and the investigators were not blinded to allocation during experiments and outcome assessment.

Data collection and expert selection of oceanic shark time-series

Time-series data on the relative abundance (n=57) of 18 species (Supplementary Table 1) were gathered from peer-reviewed publications and the grey literature, including government reports. Relative abundance indices, and associated uncertainty estimates when available, included formal stock assessment outputs (trends in biomass), as well as standardized or nominal catch per unit effort (CPUE) or sightings per unit effort (SPUE) from scientific surveys, fisheries data or bather protection nets (Supplementary Table 1 and Extended Data Figs. 4-8). Entry of original time-series (in the database available at https://www.sharkipedia.org/) was conducted by J.S.Y. and N.K.D. and subsequently independently checked by C.L.R. and N.P. All datasets underwent extensive checks before analyses; their reliability was reviewed and assigned to ocean regions (North or South Atlantic Ocean; Indian Ocean; North or South Pacific Ocean) by experts during an IUCN SSC SSG workshop (Dallas, Texas, USA, 5-9 November 2018). Stock assessment outputs were preferred over standardized outputs, then nominal CPUE or SPUE time-series when multiple datasets were available for the same species and region. Stock assessment models integrate the catch history, abundance trends and life-history information to infer population dynamics, whereas CPUE or SPUE represents the trend in relative abundance of the sampled fraction of the population. The details and rationale for the selection of datasets, where pertinent, are presented in the population section of the relevant Red List assessment (https://www.iucnredlist.org/). Two stock assessments were updated^{25,51} after the workshop and are thus included in our analysis.

Data collation and calculation of ecological and life-history traits Estimates of shark age and maximum size can vary regionally, as well as between studies. Where possible, estimates of generation time were based on observed rather than theoretical maximum age. Within regions, preference was given to studies that used: validated ages; the widest size range; and age estimates that included repeat readers, measuring precision and bias. The validated age estimates from the closest region were used in cases for which there was no published age and growth study for a region, or validated ages from a region 52-54. Generation time is defined as the median age of parents in the current cohort⁵⁵. Species- and region-specific generation time (GT) (Supplementary Table 1) were calculated from female median age at maturity (A_{mat}) and maximum age (A_{max}) as $\text{GT} = ((A_{\text{max}} - A_{\text{mat}})z) + A_{\text{mat}}$. The constant z depends on the mortality rate of adults and is typically around 0.3 for mammals^{55,56}. We chose to assume a more conservative value of z = 0.5 to account for the likelihood that the age structure had already been truncated by overfishing by the time it was measured^{26,27} and that ages of sharks have been systematically underestimated⁵⁴. The details of generation time were presented to the workshop for review and the final choices were used in the published IUCN Red List assessments and associated supplementary material for each species (Supplementary Methods 2).

Modelling population dynamics

To analyse oceanic shark trend data, we used a Bayesian population statespace model designed for IUCN Red List assessments (Just Another Red List Assessment (JARA)^{33,57}), which builds on the previously published Bayesian state-space tool for averaging relative abundance indices³² and is available open-source on GitHub (https://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_i is the logarithm of the expected abundance in year t, and r_i 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 $\varepsilon_t \sim N(0, \sigma_{\varepsilon}^2)$ as a function of the observation variance σ_{ε}^2 .

Multiple time-series for a species in the same region (North or South Atlantic Ocean; Indian Ocean; North or South Pacific Ocean) were analysed in a single run and treated as indices following the previously published study³². We used vague normal prior for $\hat{r} \sim N(0, 1000)$ and vague inverse-gamma (IG) prior for the process variance $\sigma^2 \sim IG(0.001, 0.001)$.

For each time-series, we also projected model estimates from the last data point to 2020 to be able to estimate trajectories for the LPI up to the final year of assessment for progress towards the Aichi Targets. These projections were based on the posteriors of the estimated changes across all years in the observed time-series (see ref. ⁵⁷ for details):

$$\overline{r} = \frac{1}{n} \sum_{t=1}^{n} r_t$$

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 1,000. In each chain, the first 5,000 iterations were discarded as burn-in, and of the remaining 50,000 iterations, 10,000 were selected for posterior inference ('thinning rate' = 5). Thus, posterior distributions were estimated from 30,000 iterations. Convergence of each parameter was checked with the Gelman and Rubin diagnostics58. Every model comes with four diagnostic plots: the unscaled input data and uncertainty estimates around each observation in the form 95% confidence intervals, the observed and predicted abundance values for each time-series together with the 95% posterior predictive credibility intervals, individual fits on the log-scale. as well as the 95% Bayesian credible intervals derived from the observation variance, and residual plot (see ref. 57 for detailed description and examples). We conducted posterior predictive checks (drawing simulated values from the joint posterior predictive distribution of replicated data and compare these samples to the observed data) by checking that the credible interval of the fit of the models fell within the posterior predictive distribution limits each time and that the Bayesian P values were around 0.5 (using Pearson residuals)^{59,60}. Analyses were performed using R statistical software v.3.5.2⁶¹ and using the interface from R (R2jags v.0.5-7⁶²) to JAGS ('Just Another Gibbs Sampler' v.4.3.0⁶³). The highest posterior density interval was used as the interval estimator of 95% credible intervals.

Calculation of LPI

The LPI for oceanic sharks is a quantitative mean index of year-to-year rate of change of all species that occur in a given region that is aggregated to a global scale (Extended Data Fig. 1). The annual rate of change d_t for each species in a region is the logarithm of the growth rate of the time-series in a given year t:

$$d_t = \log_{10} \left(\frac{I_t}{I_{t-1}} \right)$$

where I_t denotes the posteriors of the estimated abundance trend in a given year t obtained from the Bayesian state–space model outputs. To calculate the global LPI, the annual rates of change d_t for each species in a region were then aggregated to provide a single annual rate of change for each region (Extended Data Fig. 1a), and the same procedure was applied across regions in the same Ocean (if subdivided in south and north regions), and finally across the three oceans to generate a global year-to-year rate of change. We also computed a global LPI for each species separately, by ocean and by time-series with similar ecological lifestyle or life-history traits: geographical zone (temperate or tropical), body size (maximum total length) and generation time (following the IUCN definition⁵⁵) (Supplementary Table 1). We back-transformed the log-transformed values to a linear scale to generate index values for the range of scales (global, by ocean, by species or trait groupings of the time-series):

$$LPI_t = LPI_{t-1} \times 10^{d_t}$$

where LPI_t is the LPI at a given year t, with LPI_{t=1} = 1.

The global index started in 1970 and was modelled until 2018 using each year-to-year rate of change for the available time-series. In a second step, the global index was extrapolated through to 2020 using each year-to-year rate of change for the available time-series, and their projections after their last data point (Extended Data Fig. 2a).

Although the overall extent of change in the LPI is an indicator of status and trends in biodiversity, the trend may be driven by the data-rich species in our dataset. We evaluated the sensitivity of the LPI to the subset of species, using a jackknife procedure in which we sequentially dropped individual species and recalculated the index (Extended Data Fig. 3).

Calculation of the RFP

To investigate the underlying drivers of the abundance trend decline, we calculated the RFP, the changes in catch from 1970 to 2014 (end of the available data), relative to abundance (LPI) over the same time period, and scaled by the RFP in 1970. First, we extracted the total Sea Around Us project reconstructed reported and reconstructed unreported catch data⁶⁴ by species for 14 of our 18 focal species– catch data were not available for 4 of the species: pelagic thresher (*A. pelagicus*), reef manta ray (*Mobula alfredi*), shortfin devilray (*Mobula kuhlii*) and pelagic stingray (*Pteroplatytrygon violacea*), and these species were therefore not included in this analysis. To account for the disproportionately high catch of some species (for example, blue shark) in the total catch that could affect the overall pattern, we scaled the catch data at the species level (sp) to the first catch value in each time-series before summing across species. The RFP was then calculated as:

$$\mathsf{RFP}_{t} = \frac{\frac{\sum_{\mathsf{sp}} \mathsf{catch}_{t}}{\mathsf{LPI}_{t}}}{\frac{\sum_{\mathsf{sp}} \mathsf{catch}_{t=1970}}{\mathsf{LPI}_{t=1970}}}$$

where LPI_t is the LPI of the 18 oceanic sharks in year *t*. We also calculated the RFP with the LPI_t of only the 14 species for which catch data were available and this was not credibly different from the RFP for all 18 species.

Calculation of RLI

We calculated the RLI based on the proportion of the 31 oceanic shark species in each IUCN Red List category in 1980, 2005 and 2018 (Supplementary Table 2). The categories used in the assessments were critically endangered, endangered, vulnerable, near threatened and least concern. No species of oceanic shark were assessed in the categories extinct, extinct in the wild or not evaluated. The statuses in 2018 were assigned by the IUCN SSC SSG (Dallas, Texas, USA, 5–9 November 2018). For the RLI of 2005, we used the assessments published between 2000 and 2010. Red List assessments for around 2005 and 2018 are published on the IUCN Red List of Threatened Species website⁶⁵. Following the recommended IUCN methodology, species previously assessed as data deficient were retrospectively assigned a data-sufficient category (Supplementary Table 2). No assessment was available in the 1980s and experts involved in the IUCN SSC SSG workshop (Dallas, Texas, USA, 5–9 November 2018) retrospectively determined Red List statuses for 1980, as well as missing statuses in around 2005, as previously described³¹. To account for uncertainty around a retrospective assessment, we used a bootstrap-like method to iteratively resample 10,000 times the status of each species from its retrospective assigned status or one category better, or one category worse, denoted by the error bar (the range of bootstrap-like results) in Fig. 3a around the retrospective RLI in 1980 (black dot).

The RLI value of a particular year (t) is calculated by multiplying the number of species (s) in each Red List category by the category weight (W) (0 for least concern, 1 for near threatened, 2 for vulnerable, 3 for endangered, 4 for critically endangered, and 5 for extinct), then summing the product and dividing by the maximum possible product (number of species (N) multiplied by the maximum weight 5), and subtracted from 1 to have an index between 0 (where all species are extinct (EX)) and 1 (where all species are least concern)³¹:

$$\mathsf{RLI}_t = 1 - \frac{\sum_s W_{c(t,s)}}{W_{\mathsf{EX}}N}$$

The stand-alone point labelled 'Global sharks' in Fig. 3a indicates the starting point for the global chondrichthyan (sharks, rays and chimaeras) RLI calculated from the Red List status as reported in 2006 (the median date of available Red List assessments at this time)¹⁶.

Sustainability of stocks of oceanic sharks

To represent the status of stocks (populations) of oceanic sharks, we compiled total biomass or abundance, relative to the maximum sustainable yield (MSY), provided by authors or extracted from the latest available stock assessment reports (the reference of the source and the trajectory used are provided in Supplementary Table 3). A stock assessment is the process of using statistical models to quantify the population dynamics of a fished stock in response to fishing based on the best available catch, abundance and life-history information. No stock assessment exists for any of the oceanic rays and one of the blue shark stock assessments could not be included because no estimates of MSY-related quantities were available⁶⁶. We therefore used the 8 species (oceanic whitetip shark, dusky shark, shortfin mako, porbeagle, scalloped hammerhead, great hammerhead, smooth hammerhead, and blue shark) with published biomass or abundance trajectories relative to MSY (15 stocks in total) to produce the global proportion-over time-that these species were at levels above the biomass or abundance achieving the MSY (that is, $p(B > B_{MSY})$), and thus were not overfished (Fig. 4d). The biomass or abundance of each stock relative to MSY was transformed into a binary variable, indicating whether the stock was above (1) or below (0) MSY. To represent the status of species with several stocks, we calculated the proportion-over time-of stocks above or below MSY. We then calculated the global proportion-over time-that these species were at levels above the biomass or abundance achieving the MSY by averaging the proportions of the status of each species that were above MSY for each year.

In a stock assessment, scientists attempt to estimate the amount of fishing mortality (F) over time, and the fishing mortality that will achieve MSY (F_{MSY}). Using available stock assessments, we compiled the latest value of fishing mortality relative to the fishing mortality at MSY (F/F_{MSY}) and plotted them against the latest value of biomass or abundance trajectories relative to the MSY, in the 'four quadrant, red-orange-yellow-green' Kobe plot style (Extended Data Fig. 9c).

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

Data are available on https://www.sharkipedia.org/ and at https://doi. org/10.5281/zenodo.4135325. Source data are provided with this paper.

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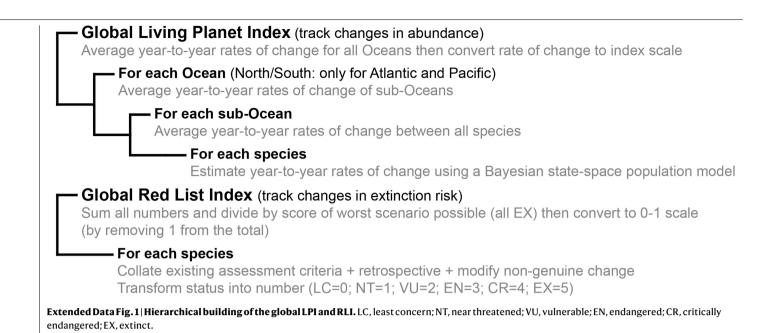
Author contributions C.L.R., P.M.K., R.A.P. and N.K.D. organized and led the workshop investigation of data quality and facilitated the 2018 Red List assessments. N.P., H.K.K. and N.K.D. conceptualized the analysis. J.S.Y., C.L.R., H.K.K., R.B.S., N.P. and N.K.D. compiled and curated the time-series data. J.K.C., A.D.M. and H.W. provided additional time-series data. N.P., R.B.S. and H.W. conducted the statistical analysis. N.P., H.K.K. A.D. visualized the data and wrote the first draft. N.K.D. and H.K.K. acquired the funding. All authors discussed the time-series data, analysis and results, and contributed to writing the manuscript.

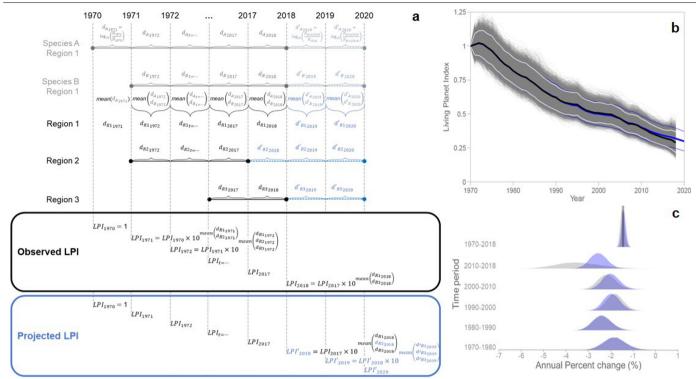
Competing interests The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41586-020-03173-9.

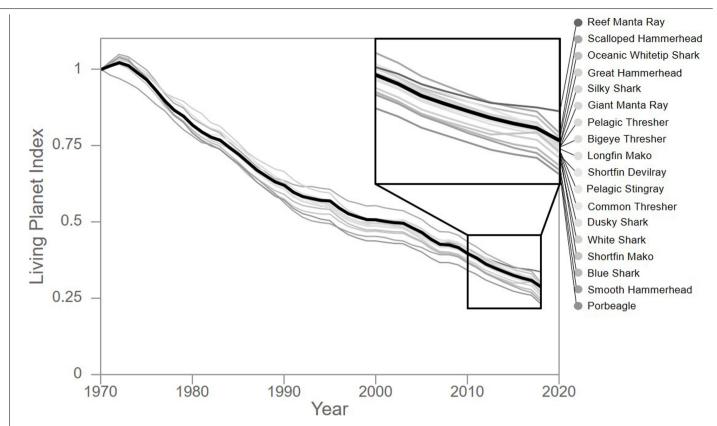
Correspondence and requests for materials should be addressed to N.P. or R.B.S. Peer review information *Nature* thanks Paul Conn, Johann Mourier, Nuno Queiroz and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Reprints and permissions information is available at http://www.nature.com/reprints.



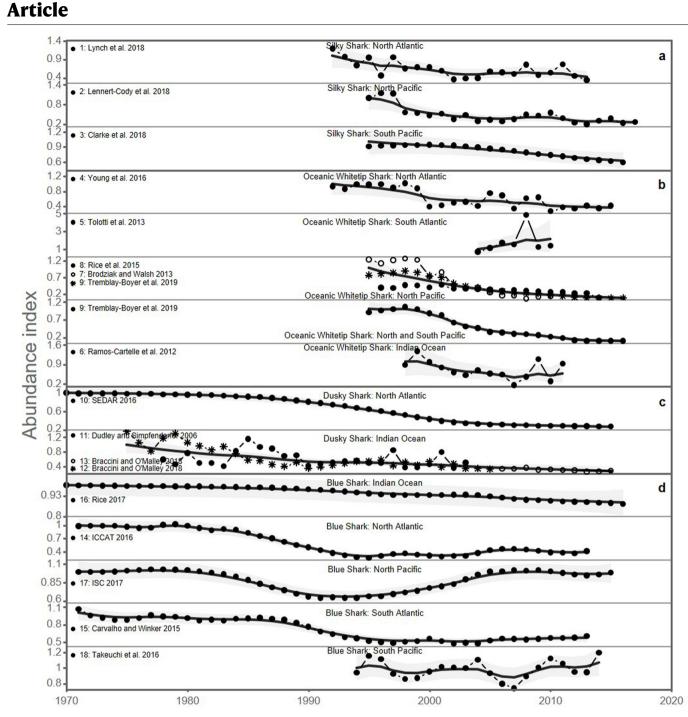


Extended Data Fig. 2 | **Calculation of the LPI. a**, Schematic example of constructing the observed (black) and projected (blue) LPI. First, year-to-year rates of change (yyrc) (d_i) are averaged between species in the same region (for example, in region 1 (R1), species A with d_{A_i} and species B with d_{B_i} averaged in d_{RL_i}). In a second step, yyrc are averaged between regions 1, 2 and 3 to give the global yyrc. The observed LPI builds on the yyrc calculated from the estimated abundance index from the state–space population model. The projected LPI builds on the yyrc calculated abundance index from the state-space population model. The projected LPI builds on the state-space population model. The projected LPI builds on the state-space population model. Projections are from the last data point to 2020. b, Global LPI for oceanic sharks and rays estimated from

1970 to 2018 in black and extrapolated to 2020 in blue. The black and the thick blue lines denote, respectively, the mean of the estimated and extrapolated LPI. The white and thin blues lines denote, respectively, the 95% credible intervals of the estimated and extrapolated LPI and the grey lines denote each iteration of the estimated LPI. **c**, The annual percentage change was calculated from the posteriors of the estimated LPI (grey) and extrapolated LPI (blue) around the final-assessment year relative to the posteriors for 1970. Vertical bars for the 1970–2018 period denote the median of the estimated and extrapolated LPI.

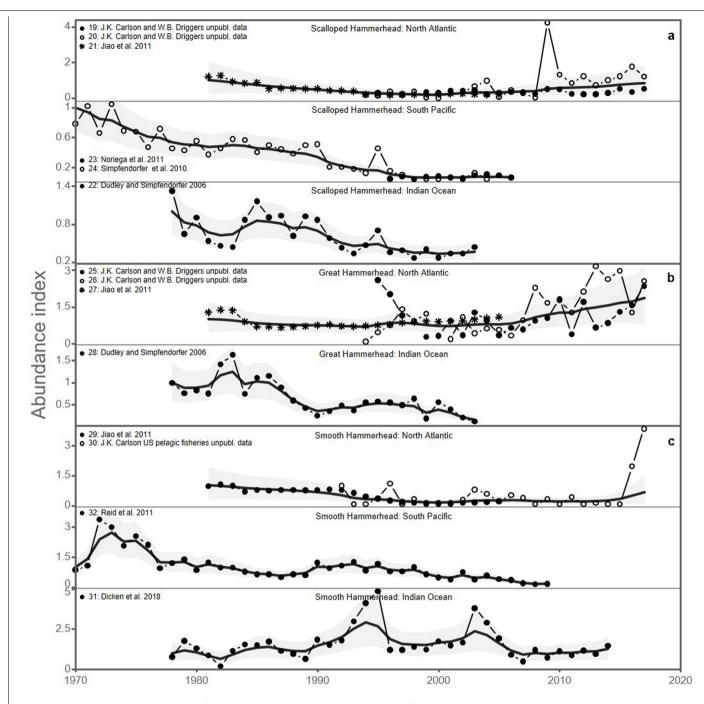


Extended Data Fig. 3 | Global and species-specific LPI for oceanic sharks and rays from 1970 to 2018. Global original LPI is the mean black line. Faint grey lines show the effect of excluding all data for a single species at a time and recalculating the mean global LPI for all other species. No means from jackknife species trends fall outside the 95% credible interval from the run with all of the datasets included, suggesting that our selection of species did not unduly influence the overall LPI result.



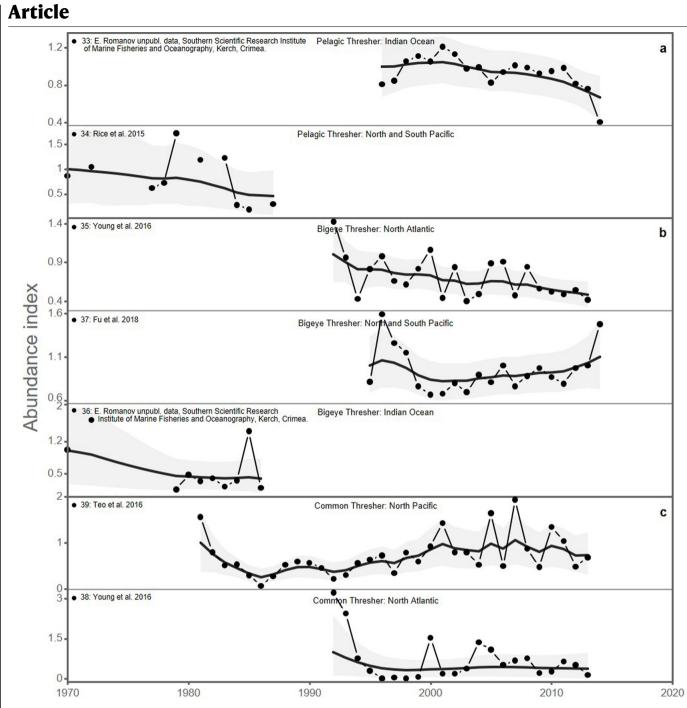
Extended Data Fig. 4 | **Time-series output for Carcharhinidae. a-d**, Observed (black or empty points and stars indicate different time-series) and modelled (black line) abundance indices for silky shark (*Carcharhinus falciformis*) (**a**), oceanic whitetip shark (*C. longimanus*) (**b**), dusky shark

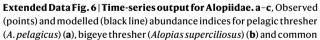
(*C. obscurus*) (**c**) and blue shark (*Prionaceglauca*) (**d**) obtained from the state–space population model. The thick black line denotes the mean of the estimated abundance index and the shaded regions denote 95% credible intervals.



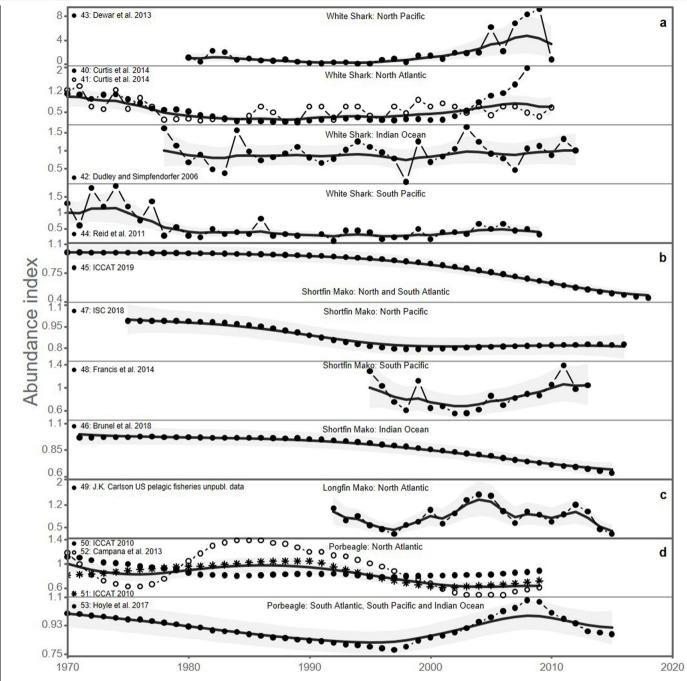
Extended Data Fig. 5 | Time-series output for Sphyrnidae.a-**c**, Observed (black or empty points and stars indicate different time-series) and modelled (black line) abundance indices for scalloped hammerhead (*S. lewini*) (**a**), great hammerhead (*S. mokarran*) (**b**) and smooth hammerhead (*S. zygaena*) (**c**)

obtained from the state-space population model. The thick black line denotes the mean of the estimated abundance index and the shaded regions denote 95% credible intervals.



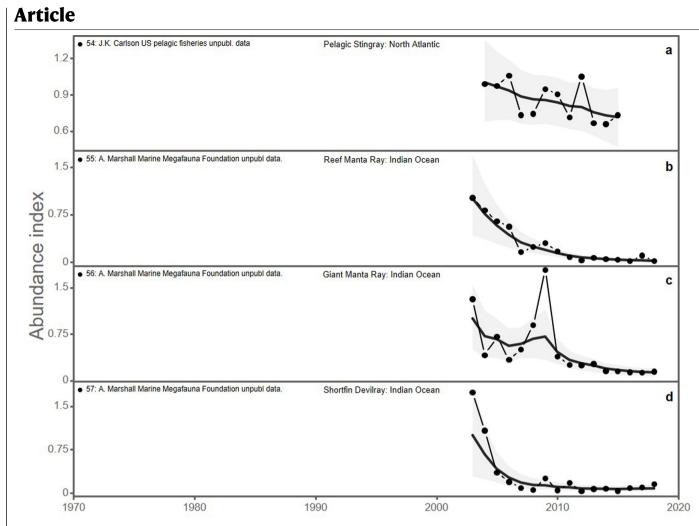


thresher (*Alopias vulpinus*) (**c**) obtained from the state–space population model. The thick black line denotes the mean of the estimated abundance index and the shaded regions denote 95% credible intervals.



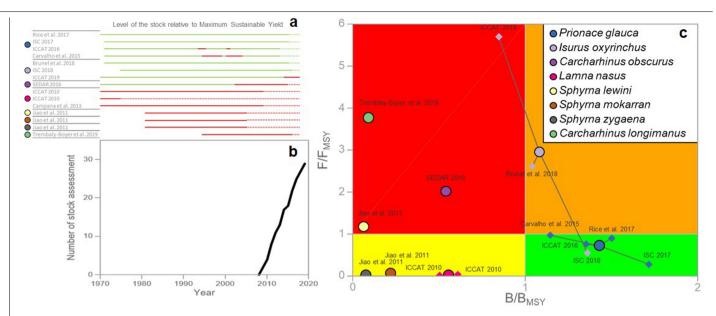
Extended Data Fig. 7 | Time-series output for Lamnidae.a-d, Observed (black or empty points and stars indicate different time-series) and modelled (black line) abundance indices for white shark (*C. carcharias*) (a), shortfin mako (*I. oxyrinchus*) (b), longfin mako (*I. paucus*) (c) and porbeagle (*L. nasus*) (d)

obtained from the state–space population model. The thick black line denotes the mean of the estimated abundance index and the shaded regions denote 95% credible intervals.



Extended Data Fig. 8 | Time-series output for Dasyatidae and Mobulidae. a-d, Observed (points) and modelled (black line) abundance indices for pelagic stingray (*P. violacea*) (a), reef manta ray (*M. alfredi*) (b), giant manta ray (*Mobula birostris*) (c) and shortfin devilray (*M. kuhlii*) (d) obtained from the

state-space population model. The thick black line denotes the mean of the estimated abundance index and the shaded regions denote 95% credible intervals.



Extended Data Fig. 9 | **Stock assessments for oceanic sharks. a**, Oceanic shark stock status—over time—being at levels of biomass or abundance above MSY (green lines) or below MSY (red lines). Data were obtained from refs.^{24,25,28,51}, and refs. 81–84,93,94,96,97 in the Supplementary Information. Dotted lines indicate that a stock is above or below the biomass or abundance levels producing MSY following the last stock assessment value. b, Number of published stock assessments for oceanic sharks and rays over time. **c**, Presentation of 14 stocks of oceanic sharks (no available stock assessments for oceanic rays), status (biomass or abundance over value at MSY) versus pressure (*F*/*F*_{MSY}) in a Kobe plot style, for the last year with available data. Circles represent the unique values of each species if only one stock exists and

represent the mean of the values of the different stocks (diamonds) when the species has multiple stocks. The plot is divided into four panels: the red panel (top left), with four stocks and three species, corresponds to stocks that are being overfished and where overfishing is occurring; the orange panel (top right), with one stock and one species, corresponds to stocks that are not overfished but where overfishing is occurring; the yellow panel (bottom left), with four stocks and three species, corresponds to stocks that are overfished but where overfishing is not occurring; and the green panel (bottom right), with five stocks and one species, corresponds to stocks that are not overfished and where overfishing is not occurring.

	Residential & commercial development
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3%	Energy production & mining
6%	Transportation & service corridors
88%	Biological resource use
3%	Human intrusions & disturbance
Percentage of IUCN threats	Natural system modifications
	Invasive & other problematic species, genes & diseases
	Pollution
	Geological events
	Climate change & severe weather
	Other options

Extended Data Fig. 10 | Percentage of reported threat categories in the 31 oceanic shark IUCN Red List assessments. 'Biological resource use' and, more specifically, 'fishing and harvesting aquatic resources' is the major reported threat.

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Policy information about <u>availability of computer code</u>					
Data collection	WebPlotDigitizer v4.2 (data visualizations to extract the underlying numerical data)				
Data analysis	www.github.com/henning-winker/JARA; Analyses were performed using R Statistical Software v3.5.2 and via the interface from R ('R2jags' package v0.5-7) to JAGS ('Just Another Gibbs Sampler' v4.3.0).				

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Behavioural & social sciences 🛛 🔀 Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see <u>nature.com/documents/nr-reporting-summary-flat.pdf</u>

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	First, we used a Bayesian state-space framework (Winker et al. 2018, Sherley et al. 2020) to estimate trends in relative abundance of 18 species from 57 time-series compiled and reviewed at an expert workshop convened by the IUCN Species Survival Commission's Shark Specialist Group (IUCN SSC SSG). Using these trends, we calculated the global LPI for oceanic sharks from the reference year 1970 (which was set at 1) to 2018 — and then extrapolated each time-series to 2020 to encompass the Aichi Target assessment year — by hierarchically aggregating the annual rates of change from each time-series for a species by region, then globally (see Text box 1 and Extended Data Figure 1a). Second, we combined a retrospective Red List assessment (1980) with two recent assessments (~2005 and 2018) from the IUCN Red List of Threatened Species for all 31 species of oceanic sharks to build the RLI (see Text box 1). Finally, we develop three lines of evidence to attribute decreasing abundance (shown by the LPI) and rising extinction risk (shown by the RLI) for oceanic sharks to overfishing: (i) increasing Relative Fishing Pressure over time (measured as changes in catch relative to the changes in the LPI), (ii) increasing proportion, over time, of oceanic sharks that are overfished below biomass or abundance levels that could produce Maximum Sustainable Yield (MSY, which is the equilibrium state of the exploited population that can sustain the greatest yield [catch] over long time periods Punt and Smith 2001), and (iii) the near-absence of significant threats other than fishing reported in each species' IUCN Red List assessment.			
Research sample	Time-series data on relative abundance (n=57) for 18 species (see Supplementary Table S1) were gathered from peer-reviewed publications and the grey literature, including government reports. Relative abundance indices, and associated uncertainty estimates when available, included formal stock assessment outputs (trends in biomass), as well as standardized or nominal catch per unit effort (CPUE) or sightings per unit effort (SPUE) from scientific surveys, fisheries data, or bather protection nets (see Supplementary Table S1 and EDF 4 to 8).			
Sampling strategy	Time-series data gathered from peer-reviewed publications and the grey literature, including government reports.			
Data collection	Data collection of oceanic shark and ray time-series and expert selection: Time-series data on relative abundance (n=57) for 18 species (see Supplementary Table S1) were gathered from peer-reviewed publications and the grey literature, including government reports. Relative abundance indices, and associated uncertainty estimates when available, included formal stock assessment outputs (trends in biomass), as well as standardized or nominal catch per unit effort (CPUE) or sightings per unit effort (SPUE) from scientific surveys, fisheries data, or bather protection nets (see Supplementary Table S1 and EDF 3 to 7). Entry of original time-series (in the database available at www.sharkipedia.org) was conducted by J.S.Y. and N.K.D. and subsequently independently checked by C.L.R. and N.P. All datasets underwent extensive checks prior to analyses, their reliability was reviewed and assigned to ocean regions (North, South Atlantic Ocean; Indian Ocean; North, South Pacific Ocean) by experts during an IUCN SSC SSG workshop (Dallas, Texas, USA, 5–9 November 2018). Stock assessment outputs were preferred over standardized, then nominal CPUE or SPUE time-series when multiple data sets were available for the same species and region. Stock assessment models integrate the catch history, abundance trends and life-history information to infer population dynamics, whereas CPUE or SPUE represents the trend in relative abundance of the sampled fraction of the population. The details and rationale for the selection of datasets, where pertinent, are presented in the Population section of the conservation of Atlantic Tunas (ICCAT) 2019, Tremblay-Boyer et al. 2019) aafter the workshop and are thus included in our analysis. Data collation and calculation of ecological and life history traits: Estimates of shark age and maximum size can vary regionally, as well as between studies and across regions. Where possible, estimates of generation time (GT) were based on observed rather than theoretical maximum age. Within region			
Timing and spatial scale	Entry of original time-series (in the database available at www.sharkipedia.org) was conducted by J.S.Y. and N.K.D. and subsequently independently checked by C.L.R. and N.P.			
Data exclusions	No data were excluded from the analyses.			
Reproducibility	Code and data are available			
Randomization	Not relevant. No randomization needed.			
Blinding	Entry of original time-series (in the database available at www.sharkipedia.org) was conducted by J.S.Y. and N.K.D. and subsequently independently checked by C.L.R. and N.P.			
Did the study involve field work? 🗌 Yes 🛛 No				

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
\boxtimes	Antibodies
\boxtimes	Eukaryotic cell lines
\boxtimes	Palaeontology and archaeology
\boxtimes	Animals and other organisms
\boxtimes	Human research participants
$\mathbf{\nabla}$	Clinical data

Dual use research of concern

Methods

n/a	Involved in the study
\boxtimes	ChIP-seq
\boxtimes	Flow cytometry

MRI-based neuroimaging