

MARINE CONSERVATION

At-risk marine biodiversity faces extensive, expanding, and intensifying human impacts

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Human activities and climate change threaten marine biodiversity worldwide, though sensitivity to these stressors varies considerably by species and taxonomic group. Mapping the spatial distribution of 14 anthropogenic stressors from 2003 to 2013 onto the ranges of 1271 at-risk marine species sensitive to them, we found that, on average, species faced potential impacts across 57% of their ranges, that this footprint expanded over time, and that the impacts intensified across 37% of their ranges. Although fishing activity dominated the footprint of impacts in national waters, climate stressors drove the expansion and intensification of impacts. Mitigating impacts on at-risk biodiversity is critical to supporting resilient marine ecosystems, and identifying the co-occurrence of impacts across multiple taxonomic groups highlights opportunities to amplify the benefits of conservation management.

The impact on the world's oceans of human activities, including fishing (1), land-based development and runoff (2), and ship strikes (3), coupled with the accelerating effects of climate change (4), are pervasive and increasing (5). Impacts from these anthropogenic stressors threaten marine species across taxa, driving thousands toward extinction (6, 7) and jeopardizing the sustainability of coastal social-ecological systems (7, 8).

Species respond differently to stressors, and multiple stressors can have cumulative impacts on threatened marine species (9). Efforts to assess cumulative human impacts on marine species have been single snapshots in time limited to a few specific taxa and stressors [e.g., (10–13)], leaving most species unassessed. A recent comprehensive, species-level assessment of cumulative impacts on at-risk terrestrial vertebrates (14) did not include marine species and did not capture changes in impact over time. Assessments of the distribution and rate of change of cumulative human impacts on global marine habitats (5, 15) provide valuable insights into ecosystem-level concerns, but habitat-focused assessments do not capture the heterogeneity of species' vulnerability (4, 11), which is crucial for designing conservation strategies.

Here, we present a global assessment of cumulative human impacts on at-risk marine species and changes in those impacts over a recent time period. For each of 1271 threatened and near-threatened marine species comprehensively assessed and mapped for the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (16) (hereafter “at-risk species”), we identified sen-

sitivity to 14 anthropogenic stressors. We then intersected species range maps with relevant maps of annual stressor intensity from 2003 to 2013 to determine the extent of potential impacts [as in (17); hereafter simply “impacts”] across species' ranges, as well as how rapidly these impacts have been expanding in extent and increasing in intensity.

Mapping potential impacts to at-risk species requires understanding which stressors threaten the species (sensitivity) and where those stressors overlap the species' range (exposure) (17). We identified sensitivity to various stressors

for each at-risk species based on threat information from IUCN Red List assessments (16). Of the 1271 marine species identified as at risk, 1036 (82%) are sensitive to one or more of our suite of 14 anthropogenic stressors (tables S1 and S2), with 865 species (68%) being sensitive to multiple stressors (Fig. 1). The remaining 235 species (18%) are not classified as sensitive to these stressors, but rather as either sensitive to others (e.g., invasive species, terrestrial hunting) or having insufficient information to determine sensitivity. The greatest proportion of at-risk species are sensitive to artisanal fishing (59%), direct human disturbance (e.g., trampling or coastal development, 46%), and sea surface temperature extremes (42%). Overall, 70% of at-risk species are sensitive to one or more fishing stressors (Fig. 1).

We then assessed where the range for each at-risk species intersected with the spatial extent of stressors to which it is sensitive (i.e., the footprint of potential impacts on species range, hereafter “affected range”) and found highly heterogeneous patterns, with a much higher number of affected species occurring in the Central Indo-Pacific and Coral Triangle regions (Fig. 2A). This result agrees with general understandings of global marine species richness (18) and patterns of threatened status of marine species (19). Adjusting for local richness of at-risk species (fig. S1), we found additional areas with a high proportion of affected species

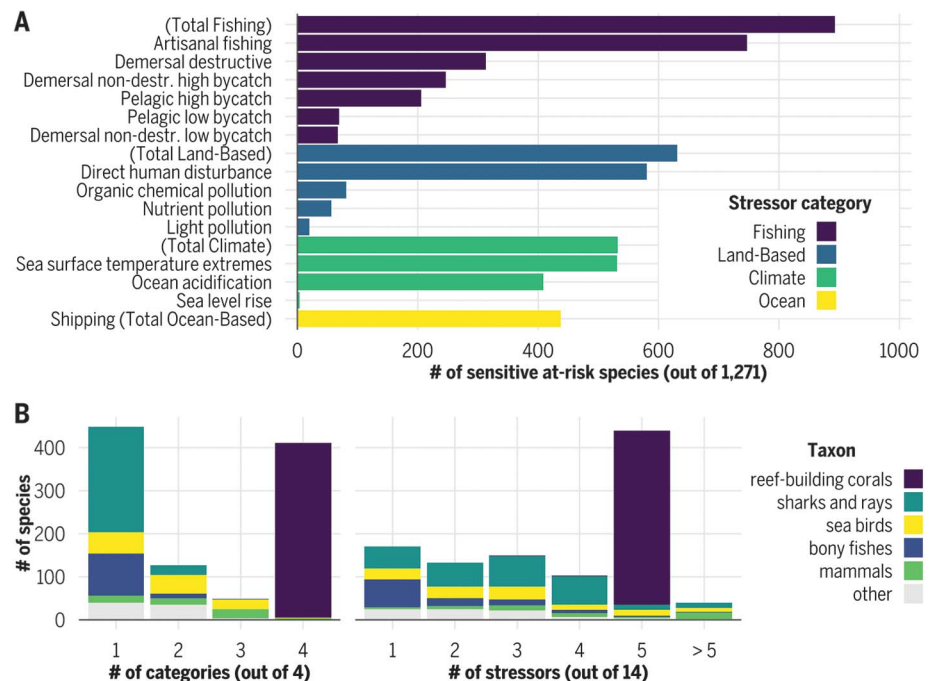


Fig. 1. Number of stressors and stressor categories (fishing, ocean, land-based, and climate) affecting at-risk species. (A) Counts of species classified as sensitive to each anthropogenic stressor or category; category totals count species sensitive to one or more stressors in the category. **(B)** Counts of species by number of stressor categories (left) or stressors (right) to which each is sensitive; the five largest taxa are highlighted.

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in the North Atlantic, North Sea, and Baltic Sea; international waters in the eastern Atlantic; and the western Pacific and tropical Indo-Pacific (Fig. 2B).

Areas with a high proportion of affected at-risk species ($\geq 50\%$ of species present in a cell were affected) cover 22% of the global ocean, whereas areas with a low proportion of impacts ($\leq 10\%$ of species affected) cover 26% (Fig. 2B). These regions represent areas of particularly high concern and potentially lower concern, respectively, for managing at-risk species. In 14% of the ocean, including some high-biodiversity areas in Australia's northern waters, no at-risk species are affected (Fig. 2B), highlighting potential refugia. Fishing stressors dominate impact footprints in most national exclusive economic zones (EEZs); however, there are areas where this pattern is reversed and low fishing effort within certain EEZs gives way to unrestricted effort in areas beyond national jurisdiction (fig. S3A). The footprint of climate stressors on at-risk species range is particularly notable in temperate and polar regions, as well as in the Coral Triangle region (fig. S3B).

Human impacts on at-risk species are changing over time. From 2003 to 2013, impacts were intensifying (i.e., one or more stressors significantly increasing in intensity faster than 0.1% per year) for at least one at-risk species in 70% of the global ocean, and in 4% of the ocean, a high proportion ($>50\%$) of species were experiencing intensifying impacts (Fig. 2C and figs. S2 and S4 by stressor group). Only 4% of the ocean had areas where impacts were abating for at least one at-risk species, and a high proportion of abatement occurred in only 0.5% of the ocean (Fig. 2C and fig. S2).

The footprint of impacts on species ranges was extensive and varied considerably by taxonomic group (fig. S5). In the most recent year of assessment (2013), impacts occurred across $57 \pm 42\%$ (mean \pm SD; median 73%) of the total range of at-risk marine species, with a mean of $19 \pm 35\%$ of range affected by two or more stressors (Fig. 3A). Impacts exceeded half the total range for 59% ($n = 744$) of at-risk species and 90% of the total range for 42% ($n = 540$) of species; the entire range was affected for 7% ($n = 92$) of species. Corals and mangroves bore the largest cumulative impact footprints ($99 \pm 2\%$ and $89 \pm 18\%$ of range, respectively).

Because greater exposure to pressures likely increases extinction risk, there is an expectation that the percentage of range affected should correlate positively with IUCN risk category. Such a relationship was evident for small-ranged species (i.e., those with range areas in the bottom quartile, $<113,000 \text{ km}^2$) (fig. S6A). However, this correlation broke down for middle-ranged species (second quartile), and for large-ranged species, the

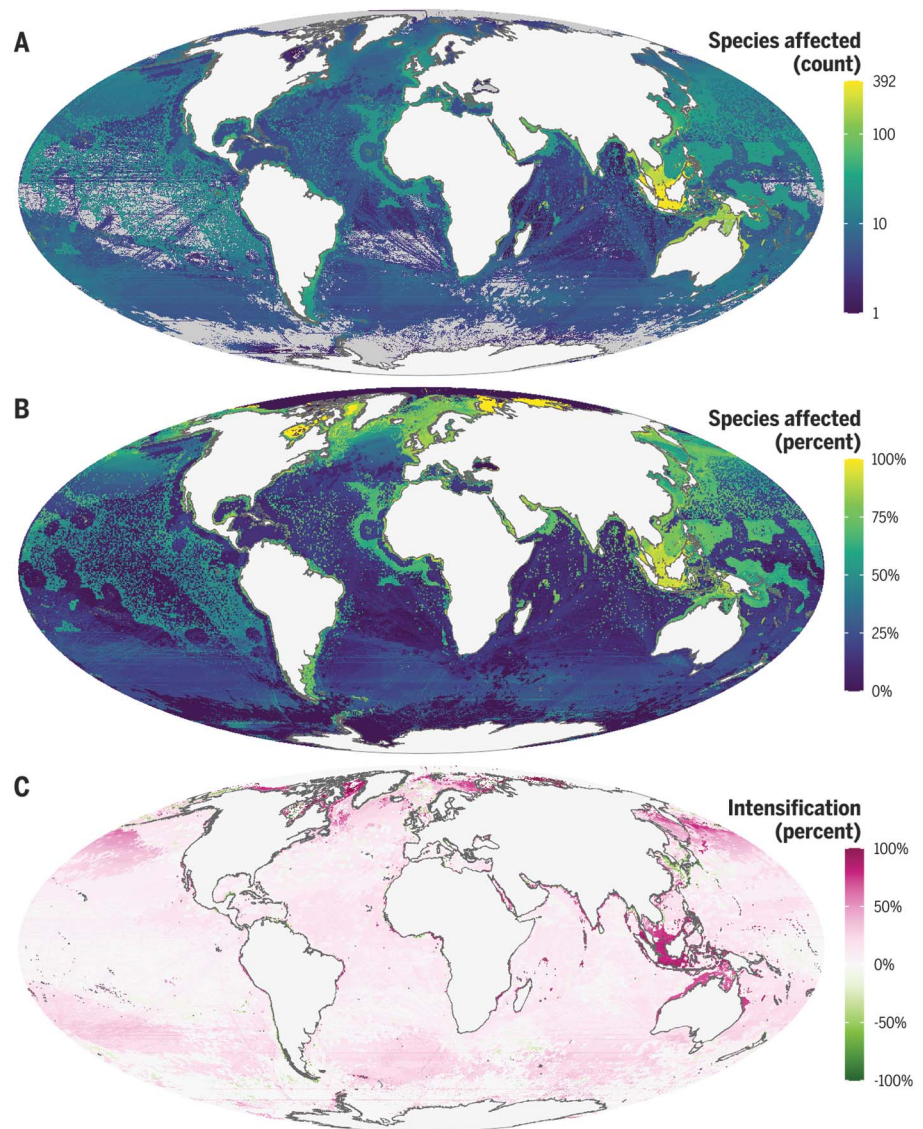


Fig. 2. Proportion of species affected and with intensifying impacts. (A) Number of threatened species affected by one or more stressors in 2013, the most recent year of assessment; gray indicates no affected species. (B) Proportion of threatened species relative to at-risk species richness affected by one or more stressors. (C) Net proportion of affected at-risk species in which stressors intensified at a rate $\geq 0.1\%$ per year over the period 2003 to 2013. See fig. S2 for insets highlighting areas of high intensification and abatement.

affected range ostensibly correlated negatively with extinction risk. A likely driver of these results is that, as range size increases, extinction risk becomes predicted less by overall impact footprint and more by impacts on critical habitats or life stages (20, 21), particularly as stressors and species are concentrated in coastal areas. Focusing on species-stressor interactions in neritic waters, the results for small-ranged species were essentially unchanged, but the counterintuitive patterns for larger-ranged species were subdued (fig. S6B). Large-ranged species at lower extinction risk were dominated by coast-

hugging corals, which were widely affected by the stressors included in this assessment, whereas large-ranged Endangered and Critically Endangered species included a higher proportion of pelagic-ranging turtles and sea birds harmed by terrestrial threats, e.g., hunting and invasive species, which are not assessed here (fig. S6C).

Across all included species, the average impact footprint increased over time, from $53 \pm 41\%$ in 2003 to $57 \pm 42\%$ in 2013 (Fig. 3A) but varied substantially among taxonomic groups. Mangroves (impact footprint +53%), marine reptiles (+18%), and bony fishes (+8%) showed

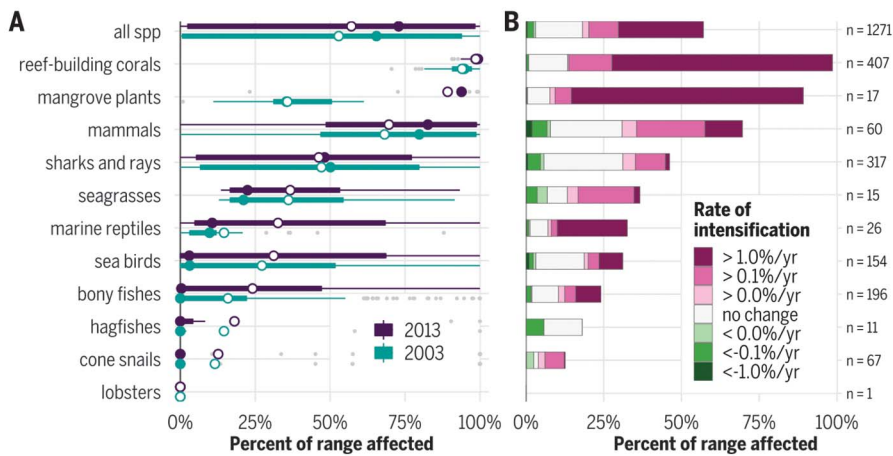


Fig. 3. Proportion of range affected, including intensifying and abating impacts, by taxonomic group. (A) Boxplots of affected range and expansion per taxon for 2003 and 2013. Hollow point is mean, solid point is median, thick line spans the interquartile range (IQR), and thin lines extend to the last observation within $1.5 \times$ IQR. Gray points represent outliers. (B) Taxon-level mean affected range (2013) and average portion of that range intensifying or abating.

marked expansion of the mean impact footprint from 2003 to 2013; the mean impact footprint for mammals, seagrasses, cone snails, and hagfishes did not significantly change. The impact footprint of sharks and rays showed a mild contraction over time, driven by shifting patterns of fishing pressure.

On average, the impacts experienced by at-risk species intensified faster than 0.1% per year in $37 \pm 39\%$ of their ranges and faster than 1% per year in $27 \pm 35\%$ of their ranges. Overall, only $2 \pm 6\%$ of species' ranges experienced abating impacts and only $1 \pm 2\%$ abated rapidly (Fig. 3B). Mangrove plants and corals in particular experienced intensifying impacts across their ranges ($80 \pm 16\%$ and $85 \pm 11\%$, respectively), largely driven by climate stressors. Although the impact footprint on sharks and rays contracted by a small amount overall (Fig. 3A), impacts intensified over $11 \pm 15\%$ of their ranges (Fig. 3B), particularly from small-scale fishing. On average, the intensifying range exceeded the abating range by a factor of 15.

Although species ranges are dictated by ecological boundaries, effective management of activities that affect those species is dictated by political boundaries. At-risk species in the eight most-affected EEZs on average suffered impacts across 88% of their ranges within those EEZs. In the largest EEZs, the mean impact footprint varied considerably, e.g., Indonesia (84%) versus French Polynesia (12%). Uninhabited or sparsely inhabited islands made up the regions with the smallest mean footprint; within the eight least-affected EEZs, species were on average affected across 8% of their ranges (Fig. 4 and table S3).

Fishing activity, because of its broad reach (fig. S3) and preponderance of sensitive species (Fig. 1), was the dominant contributor to cumulative impact to species' ranges in most EEZs, with some notable exceptions (e.g., Jordan and Australia; Fig. 4). Climate impacts were the second-largest contributor, followed by ocean-based impacts. Land-based impacts were the most extreme in very small EEZs (e.g., Jordan, Singapore, Oecussi Ambeno, and Bosnia-Herzegovina; Fig. 4) but in general were the smallest contributors to species range impacts because they were limited to coastal areas and absent for uninhabited islands.

IUCN Red List assessments (16) have long provided critical information on the status and key threats to at-risk species. Leveraging that work and recent advancements in mapping the location and pace of change of human-induced stressors to the oceans (5), we show where species are being affected and how the impacts are changing in intensity over time. This spatially and temporally resolved information helps to inform conservation strategies aimed at species and locations with the greatest conservation need. It can also inform



Fig. 4. Mean footprint of impacts on at-risk species ranges by EEZ. Each panel shows the area-weighted mean proportion of species range affected within each EEZ by stressor category. Yellow and green bars indicate the eight EEZs with the highest and lowest mean cumulative impact footprint, respectively. Purple bars indicate the eight largest EEZs by area, which do not coincide with the eight highest- or lowest-scoring EEZs. Narrow gray bars indicate other EEZs within each geographic region.

effective ecosystem-based management strategies such as protections for flagship or keystone species or taxa-specific mandates such as the Marine Mammal Protection Act of the United States, which leverage particular species to benefit the ecosystem more broadly. Co-occurrence analysis of taxa-level impacts highlights where such species-based strategies potentially confer co-benefits broadly across the ecosystem. For example, conservation efforts to reduce pressures on corals can simultaneously generate considerable benefits for marine mammals, bony fishes, sharks, seabirds, and marine reptiles (fig. S7 and table S4). Additionally, by assessing at-risk marine species across all comprehensively assessed taxa, our approach provides a window into broader ecosystem health with greater resolution into impacts across ecosystem structure complementary to impacts mapped onto representative habitats. Stressors that selectively affect some species over others potentially disrupt the “biostructure” of an ecosystem (22), resulting in reductions in the biomass of exploited species (23), reduced ecosystem functioning (22, 24), and general loss of resilience (25) that can lead to ecosystem collapse to an undesirable stable state (25–27).

Reactive conservation measures are urgent where impacts on at-risk species are pervasive and intensifying (28) to allow for ecosystem recovery (29). Of particular concern is the tropical Indo-Pacific, where accelerating climate impacts are exacerbated by intensifying fishing, shipping, and land-based stressors affecting most species (fig. S4). Areas of low and/or abating impacts may indicate opportunities for proactive conservation to maintain existing patterns and trends (28); e.g., the legal designation of the Phoenix Islands Protected Area in 2008 locked in already low impacts to species and enabled further reductions in impacts over time.

Because most marine species ranges cross international boundaries (30), effective conservation in one country may be undone by ineffective management in the next, and the fate of an at-risk species depends on managing impacts throughout its range. For example, despite low fishing pressure in Jordan's waters (mean impact range due to fishing, 18%; Fig. 4), higher fishing pressures in bordering Egypt (32%), Israel (68%), and Saudi Arabia (82%) (table S3) may reduce the capacity of at-risk populations to rebuild after a regional disturbance. Quantifying the effects of marine, land-based, and climate change stressors helps to link drivers of impacts to the management

actions best suited to address them (31, 32). Because climate impacts do not respect political boundaries, it is especially important to manage those impacts that can respond to localized policy, e.g., marine protected areas or fisheries management, to improve the resilience of at-risk species and populations to climate change (33).

Within the 1271 species included in our study, marine vertebrates are well represented, and this includes most large marine predators (e.g., sharks, cetaceans), which are widely considered as useful proxies for ecosystem health (34) (table S5). Habitat-building species are also well represented, including reef-building corals, seagrasses, and mangroves (table S5). Sharks and rays ($n = 312$) and corals ($n = 407$) together represent 56% of the at-risk species included. Although range maps and occurrence data exist for many more marine species than are included here, our dataset is limited by current state of knowledge of threatened species and species-specific sensitivity to anthropogenic stressors. Whereas frameworks have been developed to estimate species sensitivity to climate stressors [e.g., (4, 17)], a general framework for estimating species sensitivity to a comprehensive set of stressors that is based on physiological and life history traits would enable a thorough global assessment across many more species and taxonomic groups.

Our analysis reveals that human activity and climate change are affecting at-risk marine species within most of the global ocean and across most of their ranges, and these impacts are expanding and increasing in intensity for most species. However, areas of the ocean remain that harbor at-risk species free of impacts, including areas rich in biodiversity. If we hope to reverse the course of species extinction and recover populations of at-risk species, then we need to know where species are exposed to the threats to which they are sensitive and how those threats are changing. Our results provide that information and can be embedded within a wide range of management and conservation strategies, including marine protected areas, fisheries reform, land-sea conservation, and climate change mitigation efforts.

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- Code and results from data analysis for: C. C. O'Hara, M. Frazier, B. S. Halpern, At-risk marine biodiversity faces extensive, expanding, and intensifying human impacts, Knowledge Network for Biocomplexity (2020); <https://knb.econinformatics.org/view/doi:10.5063/SJ1J03>.

ACKNOWLEDGMENTS

We thank the National Center for Ecological Analysis and Synthesis (NCEAS) for computational support. **Funding:** We gratefully acknowledge financial support from NCEAS, the National Philanthropic Trust, and a fellowship from the Bren School of Environmental Science and Management. **Author contributions:** All authors conceptualized the study goals and methodology. C.C.O. performed the analysis, software coding, data curation, and visualization. B.S.H. provided supervision. C.C.O. wrote the initial draft, and all authors contributed to reviewing and editing the manuscript. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** All raw data are freely available from the original sources. All code and results from this analysis are available at the Knowledge Network for Biocomplexity (35).

SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/372/6537/84/suppl/DC1
Materials and Methods
Tables S1 to S5
Figs. S1 to S7
References (36–46)
MDAR Reproducibility Checklist

8 September 2020; accepted 3 March 2021
10.1126/science.abe6731