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CONTRIBUTED PAPER

Vulnerability of marine megafauna to global at-sea anthropogenic threats

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Abstract

Marine megafauna species are affected by a wide range of anthropogenic threats. To evaluate the risk of such threats, species' vulnerability to each threat must first be determined. We build on the existing threats classification scheme and ranking system of the International Union for Conservation of Nature (IUCN) Red List of Threatened Species by assessing the vulnerability of 256 marine megafauna species to 23 at-sea threats. The threats we considered included individual fishing gear types, climate-change-related subthreats not previously assessed, and threats associated with coastal impacts and maritime disturbances. Our ratings resulted in 70 species having high vulnerability ($v > 0.778$ out of 1) to at least 1 threat, primarily drifting longlines, temperature extremes, or fixed gear. These 3 threats were also considered to have the most severe effects (i.e., steepest population declines).

Article impact statement: Marine megafauna are highly vulnerable to human activities; industrial longlines, fixed gear, and warming pose the most severe threats.

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Overall, temperature extremes and plastics and other solid waste were rated as affecting the largest proportion of populations. Penguins, pinnipeds, and polar bears had the highest vulnerability to temperature extremes. Bony fishes had the highest vulnerability to drifting longlines and plastics and other solid waste; pelagic cetaceans to 4 maritime disturbance threats; elasmobranchs to 5 fishing threats; and flying birds to drifting longlines and 2 maritime disturbance threats. Sirenians and turtles had the highest vulnerability to at least one threat from all 4 categories. Despite not necessarily having severe effects for most taxonomic groups, temperature extremes were rated among the top threats for all taxa except bony fishes. The vulnerability scores we provide are an important first step in estimating the risk of threats to marine megafauna. Importantly, they help differentiate scope from severity, which is key to identifying threats that should be prioritized for mitigation.

KEYWORDS
anthropogenic threats, climate change, expert elicitation, fishing, marine megafauna, vulnerability

INTRODUCTION

Anthropogenic activities are a widespread and increasing threat to marine biodiversity globally (Dias et al., 2019; Dulvy et al., 2021; O'Hara & Halpern, 2022) and lead to population declines and extirpations worldwide (e.g., Meyer et al., 2017; Nowicki et al., 2019). Across all biodiversity, of particular concern are large marine vertebrates, including those that are highly mobile and typically at (or near) the top of food webs (e.g., large fishes, mammals, seabirds, and reptiles) (henceforth marine megafauna) (Authier et al., 2017). Currently, one third of marine megafauna are globally threatened with extinction (Estes et al., 2016) and listed as vulnerable, endangered, or critically endangered on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (www.iucnredlist.org). These listed species include 31% of seabirds (Dias et al., 2019), 27% of marine mammals (Avila et al., 2018), 37% of elasmobranchs (Dulvy et al., 2021), 32% of scombrids (Juan-Jordá et al., 2011), and 6 of the 7 marine turtle species (despite noted recovery in some populations) (Mazaris et al., 2017). Despite extensive literature describing the effects of anthropogenic activities on marine megafauna (e.g., Clark et al., 2023; Sequeira et al., 2025; Womersley et al., 2022), understanding how these activities affect these species remains a key question in ecology (Hays et al., 2016). Answering this key question is becoming more pressing as anthropogenic threats continue to increase (Halpern et al., 2019), especially because marine megafauna play vital ecological roles in marine ecosystems (Estes et al., 2016), can act as ocean sentinels (Hazen et al., 2019), and are of cultural (Reyes-García et al., 2023) and economic (Hammerschlag et al., 2019) importance globally.

Major at-sea anthropogenic threats to marine megafauna include fishing, climate change, pollution, and shipping (Avila et al., 2018; Braulik et al., 2023; Dulvy et al., 2021). Impacts from fishing stem from directed overexploitation and incidental capture. For example, industrial longline fisheries are responsible for the largest proportion of pelagic shark catches globally (Oliver et al., 2015), and incidental catch in artisanal gillnet and industrial seine and trawl fisheries has resulted in impacts to pinnipeds (Sepúlveda et al., 2023). Entanglement in fixed gear (principally gillnets) is a key threat to cetaceans (Knowlton et al., 2022; Temple et al., 2024) and seabirds (Žydelis et al., 2013). Climate change impacts include ocean warming and acidification and expansion of hypoxic zones, which alter prey abundance and habitat quality (e.g., Krüger et al., 2021; Lenoir et al., 2020). Other climate change impacts include sea level rise, which negatively affects nesting sites for turtles and seabirds (Pike et al., 2015; Rodríguez et al., 2019), altered wind patterns, which influences seabird migrations (Somveille et al., 2020), and elevated UV radiation, which can cause sun damage to whales (Martinez-Levasseur et al., 2011). Pollution, including light (Marangoni et al., 2022) and noise (Duarte et al., 2021) pollution and excess nutrient and organic inputs (Cagnazzi et al., 2020), stems from coastal and maritime sources and can result in negative impacts, such as plastic ingestion (Clark et al., 2023) or entanglement (Jepsen & de Bruyn, 2019). Ship strikes are also a threat for large mobile species, such as whale sharks (*Rhincodon typus*) (Womersley et al., 2022). Land-based threats can also lead to considerable impacts, such as terrestrial invasive species leading to declines of seabird populations (Dias et al., 2019). However, the risk of threats at sea is especially concerning for marine megafauna that travel throughout the high seas, where protection is limited (Conners et al., 2022; Sequeira et al., 2025).

Although identifying the spatial overlap of some marine megafauna species with some of the threats they face has been the focus of recent studies (e.g., Clark et al., 2023; Maxwell et al., 2013; Womersley et al., 2022), to understand risk across multiple species and multiple threats, it is essential to determine each species' vulnerability to each threat. Vulnerability assessments can provide the means with which to assess the spatial risk of threats to marine megafauna based on species distributions and the intensity of each of the threats they experience in different areas of their geographical ranges. A few studies have explored species vulnerability to threats based on species' traits and their environmental tolerances (e.g., Albouy et al., 2020; Butt et al., 2022). However, there is still the need to quantify vulnerability based on the realized (or expected future) impacts (e.g., population declines) of a species' exposure to threats, as has been done by the IUCN.

The IUCN Red List is the leading source for species' extinction risk status and is used to track progress toward global biodiversity targets (Rodrigues et al., 2006). The IUCN developed a globally recognized threats classification scheme, which lists and provides definitions of possible threats to species and a threat ranking system that quantifies the realized or future potential impacts of threats to species (iucnredlist.org/resources/threat-classification-scheme [April 2023]). This ranking system is used to calculate the impact score of threats to individual species based on their timing (period in which impacts occur), scope (proportion of population affected), and severity (resulting degree of population declines) and can be used for direct comparisons across species from diverse taxonomic groups (e.g., Ward et al., 2021). However, incorporating IUCN Red List impact scores in spatial risk assessments for marine megafauna remains challenging because the IUCN Red List threat designations are often provided only for broad categories. For example, although the IUCN generally assesses pollution-related threats at the level appropriate for marine megafauna (i.e., assigns impact scores for each individual relevant pollution source), this fine resolution is missing for climate change and fishing threats. This means that climate change threats, such as sea level rise, coral bleaching, and sea ice loss, are considered a single threat on the IUCN Red List (included in the "habitat shifting & alteration" category under "climate change & severe weather"). Similarly, industrial fishing impacts are delineated based on intentional versus unintentional catch without determination of differences among fishing gears. However, the impact score of each of these finer resolution threats is independently quantifiable and may have different impacts on different marine species (Brierley & Kingsford, 2009).

The vast scope of IUCN assessments, which span species, taxonomic groups, and regions (applied to ∼150,000 species of birds, fishes, fungi, lichen, herpetofauna, invertebrates, and mammals) (iucnredlist.org/ [September 2023]), means that frequent updates are infeasible and may take years to complete (assessments are considered valid for 10 years). This is especially the case for understudied species (Cazalis et al., 2022), including some marine megafauna. A combined ∼20% of fishes, mammals, and turtles (Pimiento et al., 2020) are currently listed as not evaluated or data deficient. Some of the threat-ranking variables (timing, scope, and severity) are listed as unknown for some threats. This leads to serious knowledge gaps in species–threat associations for marine megafauna and hinders the application of the IUCN Red List threat ranking system to marine megafauna globally. Independently considering all threats that can be spatially evaluated across the entire geographical range of a species is a fundamental but missing aspect of conservation planning. For this reason, researchers have developed different threat ranking systems (e.g., Butt et al., 2022; Halpern et al., 2008) or used expert elicitation to rank species-specific threats at different spatial scales (Ward et al., 2021). However, no studies have focused on marine megafauna species and on enhancing the IUCN Red List ranking system to globally assess their vulnerability to the majority of threats they face.

We developed a framework that expands the threats classification scheme and impact ranking system of the IUCN to explicit quantification of current species' vulnerabilities. We applied our framework to the vulnerability of marine megafauna to 23 at-sea anthropogenic threats across the global oceans, including threats at a finer resolution than previously considered by the IUCN, based on spatially explicit data availability for existing threats. Understanding species vulnerability to threats is a key first step in meaningfully defining impacts and spatially evaluating risk. Such assessments will help explain population trends and inform conservation actions to halt biodiversity loss, as mandated by the Kunming–Montreal Global Biodiversity Framework (cbd.int/gbf/targets/).

METHODS

Marine megafauna species selection

We aimed to evaluate as many species as possible that spend a considerable portion of their life cycle in pelagic habitats and make large-scale movements connecting distant or distinct ecosystems. We used the following criteria to determine inclusion in our evaluation of flying birds, fishes, marine mammals, and turtles: listed on the Convention on the Conservation of Migratory Species of Wild Animals Appendix I or II (https://www.cms.int/ [accessed November 2021]) or listed as migratory and using oceanic habitats on the IUCN Red List (iucnredlist.org [accessed November 2021]). This excluded coastal cetaceans heavily affected by entanglement in fishing gears (Temple et al., 2024). However, we included all species of sirenians because of their status as highly functionally unique, specialized, and endangered marine mammals (Pimiento et al., 2020). For some taxa that use terrestrial and marine ecosystems (e.g., penguins and pinnipeds), we included all species because their movements between these ecosystems and their high-latitude habitat use provide functional contributions to marine ecosystems not captured solely by aquatic taxa. Our final list of species was further restricted to species for which we could obtain expert input (detailed below).

We obtained information for 256 species: 21 bony fishes, 57 (predominantly) pelagic cetaceans, 39 elasmobranchs, 77 flying birds, the polar bear (*Ursus maritimus*), and all marine pinnipeds (33), penguins (18), turtles (7), and sirenians (3) (Figure 1a; Appendix S1). These include 14 critically endangered species, 36 endangered, 47 vulnerable, 27 near threatened, 127 least concern, and 5 data-deficient species. Most species had decreasing population trends (113 species), followed by unknown (79), increasing (35), and stable (29) trends. Across the 256 species examined, 48% had an incomplete impact assessment on the IUCN due to unknown threat timing, scope, or severity scores for the threats considered in their assessments (Figure 2).

Anthropogenic threat selection

To complement and build on the existing IUCN Red List assessments, we identified relevant anthropogenic threats by first building a matrix of all at-sea threats listed in the most recent

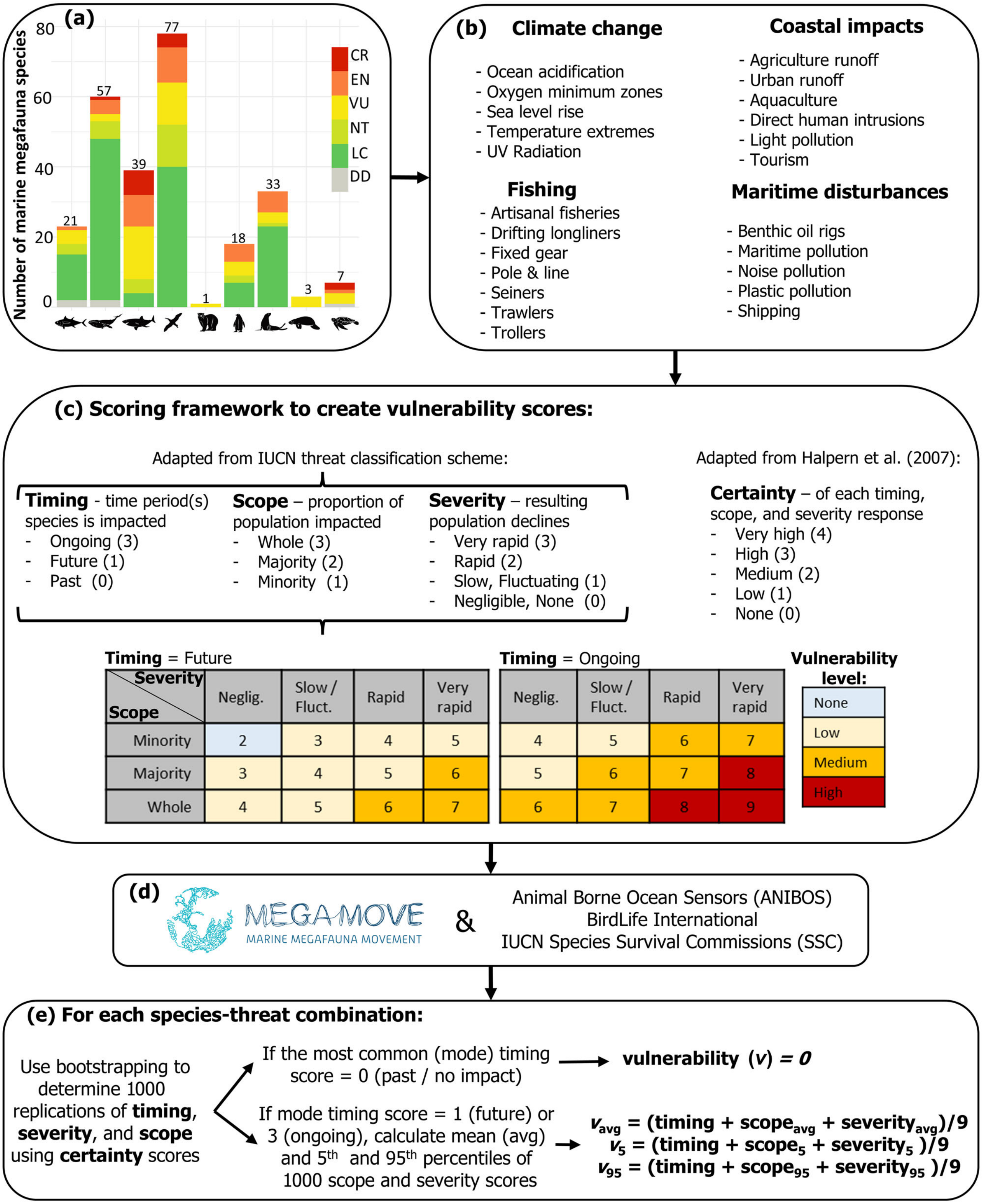

FIGURE 1 Methods used to determine threat vulnerability scores for species–threat combinations: (a) 256 species considered and their extinction risk status according to the IUCN (International Union for Conservation of Nature) Red List (iucnredlist.org) (silhouettes [left to right], bony fishes, cetaceans, elasmobranchs, flying birds, polar bear, penguins, pinnipeds, sirenians, turtles; CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; LC, least concern; DD, data deficient), (b) threats considered based on the IUCN Threats Classification Scheme 3.3 (iucnredlist.org/resources/threat-classification-scheme [accessed April 2023]), (c) framework for expert scoring, (d) networks of experts invited to contribute, and (e) calculation of vulnerability scores.

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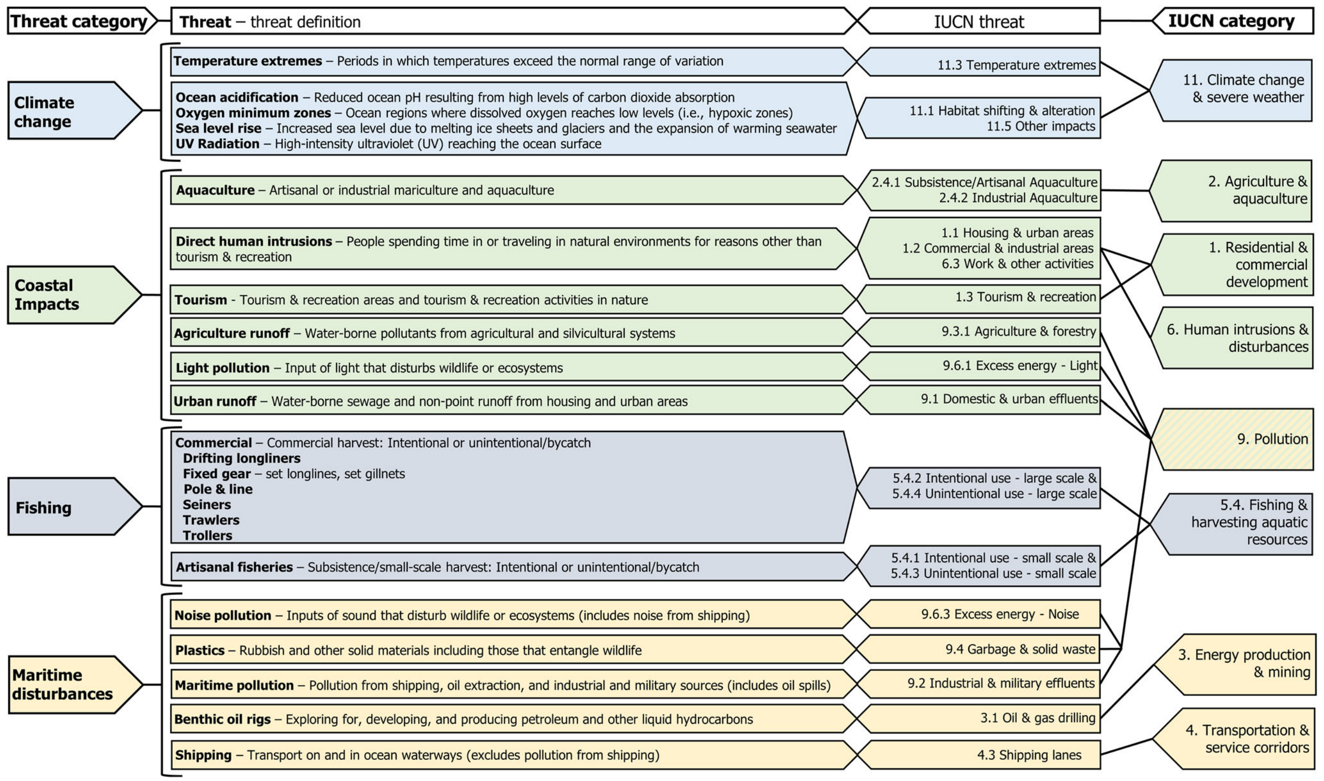

FIGURE 2 Threats and threat categories used in our scoring framework of threats to marine megafauna and the associated IUCN (International Union for Conservation of Nature) Red List of Threatened Species threat and threat categories from which they were derived. Numbers with IUCN threat names correspond to the IUCN Threats Classification Scheme 3.3 (iucnredlist.org/resources/threat-classification-scheme [accessed April 2023]). See Appendix S3 for full definitions of threats.

IUCN global assessments for each species and then cross-referencing these with threats that were also spatially measured across the entire geographic ranges of the species considered (e.g., fishing intensity data from globalfishingwatch.org/). This was done to facilitate future risk assessments based on vulnerability scores and spatially gridded threat datasets. Our resulting list of threats expanded on those already indicated on the IUCN Red List to include 10 additional threats. Additional threats were associated with mechanisms of habitat shifting and alteration from climate change (4 threats) and associated with large-scale fishing (i.e., to include individual fishing gears, 6 threats). We excluded threats based on the same spatially measured data (as O'Hara et al. [2021] did). This was the case for artisanal and industrial aquaculture, which were combined because both are mapped with data from the Food and Agriculture Organization of the United Nations [https://www.fao.org/fishery/statistics-query/en/aquaculture]); for intentional and unintentional artisanal fisheries catches, which were both spatially calculated by Watson (2019); and for 3 direct human intrusions (threats related to human development for which human population density is typically used as a proxy [O'Hara et al., 2021]) (Figure 2). Our final list consisted of 23 anthropogenic threats across the 4 categories of climate change (oxygen minimum zones, sea level rise, temperature extremes, ocean acidification, and UV radiation); coastal impacts (agricultural and urban runoff, direct human intrusions, aquaculture, light pollution, and tourism); fishing (artisanal fisheries [all gear types] and drifting longlines, fixed gear [including set longlines and gillnets], pole and line, seiners, trawlers, trollers); and maritime disturbances (benthic oil rigs, shipping, maritime pollution, noise pollution, and plastics and other solid waste) (listed in Figure 1b and detailed in Appendix S2, including known or proposed associated spatial datasets). The addition of the fine scale threats for fishing and climate change resulted in 2560 new species–threat combinations for which no data were available on the IUCN Red List (Figure 2).

Threat vulnerability framework

We calculated scores for marine megafauna species vulnerability to global anthropogenic threats at sea based on the 3 key variables IUCN uses in their threat ranking system (iucnredlist.org/resources/threat-classification-scheme) (Figure 1c): timing, to indicate the period in which a species was (0 for past), is (3 for present), or will be (1 for future) affected by a threat; scope, to indicate the proportion of a population affected by a threat (1–3); and severity, to indicate the degree of population declines resulting from the threat (0–3). Because we used an expert elicitation approach (detailed below), we added a fourth metric for certainty that had values ranging from 0 (no certainty) to 4 (very high certainty) to account for how confident each expert was in the ranking they provided for each of the 3 variables (following Halpern et al. [2007]). The inclusion of the certainty metric ensured that scores provided for each of the 3 variables were weighted by the expert's level of experience (i.e., perceived confidence in knowledge of relevant literature and direct work with species).

Creating scores for each species–threat combination

We contacted over 600 experts in marine megafauna from networks, including MegaMove (megamove.org), Animal Borne Ocean Sensors (anibos.com), BirdLife International (birdlife.org), and IUCN Species Survival Commission (SSC) specialist groups for cetaceans, marine turtles, penguins, pinnipeds, polar bear, sharks, sirenians, and tunas and billfishes (www.iucn.org/our-union/commissions/group/1445) (Figure 1d). All experts were invited to contribute as coauthors and asked to circulate the invitation through their networks of expert colleagues to identify additional experts who could assist in developing our vulnerability framework. We provided all experts with a document outlining threat definitions (Appendix S2) and asked them to score the timing, scope, and severity of all 23 threats to the species in which they had expertise to provide their certainty on each score assigned (Appendix S3). We also requested that experts list additional threats not included but to which species may have vulnerability, and confirm whether the threats being considered affect species at a local or regional scale rather than globally (i.e., at the entire geographical range of the species). Expert coauthors could assess multiple species and had the option of assigning the same scores to one or more species in the same taxonomic group. Finally, each expert coauthor also provided personal (gender identity, racial background) and professional details (years of experience, primary affiliations) (Appendix S3).

Compiling expert responses and calculating vulnerability scores

With the all-responses dataset (i.e., all the scores combined), we used bootstrapping to determine an average vulnerability score with 5% and 95% confidence intervals for each species–threat combination after removal of scores with no certainty (i.e., certainty = 0 for timing, scope, or severity). To do so, we expanded the datasets for timing per species–threat combination by replicating each expert score according to the associated certainty score provided. For example, for timing, if an expert provided a score of 3 (i.e., present threat) with very high certainty (4), that timing score of 3 was replicated 4 times in the dataset. We did the same for all n timing scores (where n is the number of expert timing scores collected for a given species–threat combination) and then used bootstrapping (with replacement) to get 1000 samples of random timing scores from the full list of replicated timing scores. Each sample contained n scores. We then determined the most common (i.e., mode) timing score for each sample of n scores to generate 1000 timing scores and used the mode of those scores to represent the final timing score for each species–threat combination.

For species–threat combinations where timing was 0 (occurred in the past or not considered a threat), scope and severity were also assigned a 0 because only ongoing or future threats have scope and severity scores as per IUCN's threat scoring system. For species–threat combinations where timing was 1 (future) or 3 (ongoing), we repeated the same bootstrapping procedure for the scope and severity scores but calculated the mean scope and severity scores (instead of mode) for each sample of n scores (repeated analyses calculating the median led to similar results). Using the resulting mean scores per sample (i.e., 1000 sample means) for scope and severity, we calculated the mean scope and severity scores ($scope_{avg}$ and $severity_{avg}$, respectively) across the 1000 sample means and determined the 5th ($scope_5$ and $severity_5$) and 95th ($scope_{95}$ and $severity_{95}$) percentiles. Our final average vulnerability (v) score for each species–threat combination was calculated as per the IUCN threat ranking system, that is, the 3 resulting variables were summed and divided by 9 (which is the maximum possible value for the 3 scores summed as per the IUCN ranking system [Figure 1e]) to rescale scores and obtain values ranging from 0 to 1:

$$v = \left(\text{timing}_{\text{mode}} + \text{scope}_{\text{avg}} + \text{severity}_{\text{avg}}\right)/9. \tag{1}$$

To create confidence intervals for v scores, we calculated vulnerability at the 5% (v_5) and 95% percentile (v_{95}) in a similar way, except that we replaced the average values with the respective percentile values.

To reduce the effect of extreme (and potentially biased) vulnerability scores provided by individual experts, we repeated the above process with a restricted dataset that excluded all species–threat combinations for which we compiled fewer than 3 scores (dataset $R \geq 3$). We further refined the $R \geq 3$ dataset by removing the minimum and maximum scores for timing × certainty, scope × certainty, and severity × certainty from each of the remaining species–threat combinations. Using the $R \geq 3$ dataset, we then identified which threat resulted in the highest vulnerability score for each species and used this value to allocate each species into vulnerability categories. We did the latter by adapting IUCN's threat ranking system. We rescaled scores from 0 to 1, where 1 indicated the threat causes very rapid declines to whole populations), such that vulnerability is considered high for $v > 0.778$ (>7 impact score on IUCN threat ranking system [Figure 1c]), medium for $0.778 \geq v > 0.556$ (6–7), low for $0.556 \geq v > 0.222$ (3–5), and negligible for $v \leq 0.222$ (≤2) (www.iucnredlist.org/resources/threat-classification-scheme). We further summarized the highest vulnerability scores averaged across all species and in each taxonomic group as the single threat with the highest average vulnerability score and all threats with overlapping confidence intervals with this threat. This was also done at a lower taxonomic level for pelagic cetaceans (baleen and toothed whales), elasmobranchs (sharks and rays), and birds (procellariforms and others) to evaluate functionally distinct species groups within a taxon.

RESULTS

Expert responses

We obtained 105,245 individual species–threat timing, scope, and severity scores (Appendix S4), which led to the calculation of vulnerability scores for 5759 species–threat combinations out of the possible 5888 (covering each of the 23 threats for 256 species considered) based on 1694 evaluations provided by 307 marine megafauna experts (coauthors on this article) with affiliations from 51 countries and territories spanning all continents except Antarctica (Appendices S5 & S6). Most evaluations were provided from academics (88.3%) based in Europe (30.7%), North America (26.7%), and Oceania (17.9%) (Appendices S5 & S6), and most (72%) had at least 10 years of working experience with the taxonomic group for which they provided expertise.

At least one set of scores (for all threats to a species) was provided for each of the 256 species, and at least 3 were provided for 190 species (Appendices S7 & S8). Overall, scores for elasmobranchs were completed by the largest number of experts (86), followed by pelagic cetaceans (78) and turtles (49) (Appendix S6). On average, turtles had the most per-species scores (~25, range 12–36), followed by elasmobranchs (~16, 6–28) and the polar bear (8) (Appendix S4). Less than 1% of all 5759 species–threat combinations were rated as only being relevant at local or regional scales (rather than global) (Appendix S4).

Expert certainty

Expert certainty tended to be the highest for fishing threats. Drifting longlines, artisanal fisheries, fixed gear, and trawlers had among the highest average certainties across all 3 variables (timing, scope, and severity) (Figure 3b; Appendix S9). In contrast, climate change threats, including ocean acidification, oxygen minimum zones, and UV radiation, had the lowest average certainties (0.43–0.48). Experts in bony fishes, flying birds, and elasmobranchs had the highest certainty for drifting longlines (average = 0.89, 0.79, and 0.77, respectively). Experts in polar bear, penguins, and pinnipeds had the highest certainty for temperature extremes (0.86, 0.80, and 0.69, respectively). Finally, turtle experts had the highest certainty for light pollution (0.79), sirenian experts for artisanal fisheries (0.73), and pelagic cetacean experts for noise pollution (0.62) (Figure 3b).

Threats to marine megafauna

Across all species–threat combinations for which we received at least one score for all variables (all responses, $n = 5759$ scores for 256 species), we identified 2953 species–threat combinations with at least low vulnerability ($v > 0.222$). Most included species were rated as having at least some vulnerability to temperature extremes (72.7%), followed by plastics and other solid waste (71.9%), maritime pollution (68.4%), and fixed gear (59.1%) (Appendix S1). Most species (~75%) were identified as having vulnerability to at least one threat in each of the 4 threat categories, and 108 species (42.2%) had some vulnerability to at least one threat not included in our list of threats, including diseases and invasive species, offshore windfarms, recreational fishing, extreme weather events, loss of sea ice, predation and resource competition, and harmful algal blooms (Appendix S1). The $R \geq 3$ dataset ($n = 4011$ scores across 190 species) showed that 2223 species–threat combinations indicated species vulnerability (Appendix S7). The largest proportion of species in these datasets was rated as having at least some vulnerability to temperature extremes (91.6%), plastics and other solid waste (91.1%), maritime pollution (78.9%), and drifting longlines (73.2%). Because both datasets yielded similar results (Appendix S10), we focused the remainder of our Results on the most restricted dataset ($R \geq 3$ with 190 species), which included all species of elasmobranchs, sirenians, and turtles considered, polar bears, 51 flying bids, 34 pelagic cetaceans, 23 pinnipeds, 17 bony fishes, and 15 penguins (Appendix S7).

Species and taxa threat timing, scope, and severity scores

Among the 4011 species–threat combinations rated in the $R \geq 3$ dataset, experts rated timing as ongoing for 2004 (~half) and future for 255 combinations (Figure 4b). The largest number of species considered were rated as having ongoing threat vulnerability for plastics and other solid waste, temperature extremes, maritime pollution, drifting longlines, and fixed gear (principally set longlines and gillnets). In contrast, climate change threats, excluding temperature extremes, were among the threats rated as posing ongoing vulnerability to the fewest number of species but had the largest numbers of species with future vulnerability (Figure 4b). For threat scope and severity scores, temperature extremes received the highest scores averaged across all species, overlapping with plastics and other solid waste and maritime pollution for threat scope (i.e., affecting the largest portions of species populations) and drifting longlines and fixed gear for threat severity (i.e., causing the largest population declines) (Figure 4c). On average, experts rated species as having the highest vulnerability to temperature extremes (average = 0.683) and plastics and other solid waste (0.606) (Figure 4a). Although not among the highest scores overall, direct human intrusions (0.426) had the highest average vulnerability scores in the coastal impacts category and drifting longlines (0.515) had the highest average vulnerability scores in the fishing category. Species listed as critically endangered and least concern tended to have the highest and lowest maximum vulnerability scores, respectively, but there was no clear relationship between extinction risk and maximum vulnerability among endangered, vulnerable, and near-threatened species (Figure 5c).

At the taxon level, experts rated temperature extremes as having the highest average threat vulnerability, scope, and severity for polar taxa (i.e., penguins, polar bear, and pinnipeds) (Figure 3a). For turtles, the highest vulnerability scores were for temperature extremes, sea level rise, artisanal fisheries, drift-

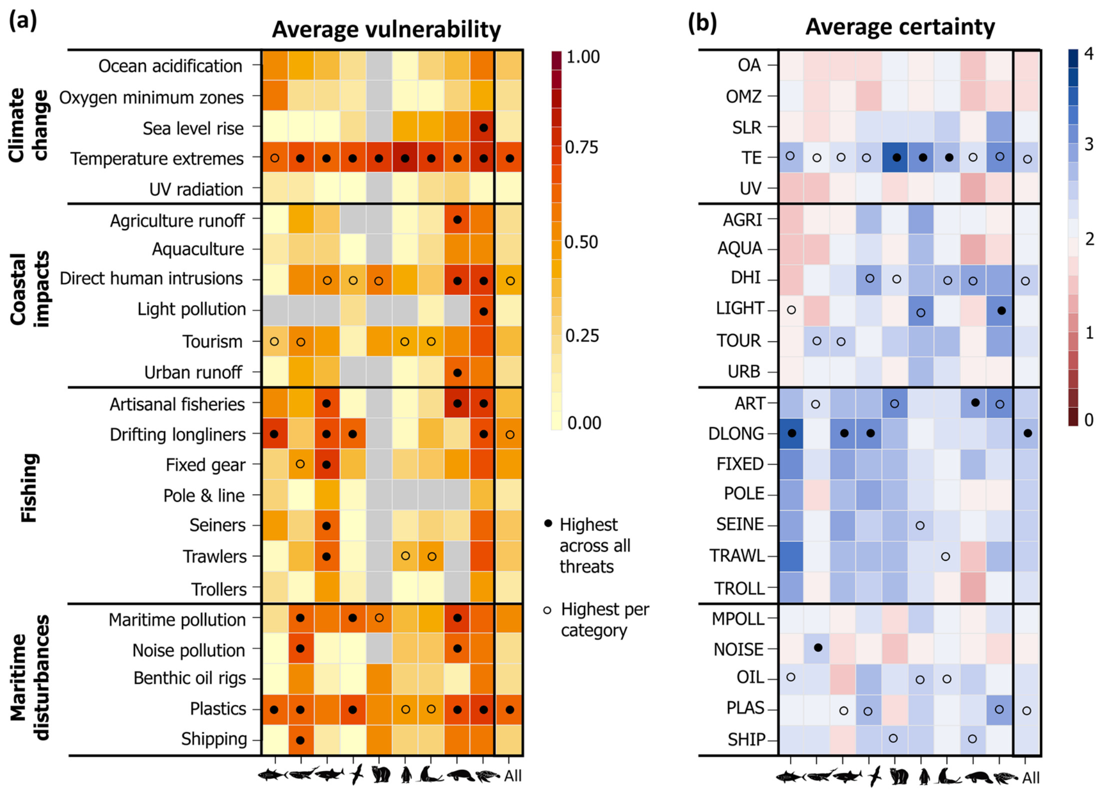

FIGURE 3 (a) Average vulnerability scores per taxa for each threat considered in each category and (b) average certainty of expert timing, scope, and severity scores across all species per taxa for each threat (solid circles, threat with the highest overall average vulnerability or certainty; open circles, highest value per category for categories where no threat is among the highest overall; multiple solid circles for average vulnerability, more than one threat had vulnerability scores with overlapping confidence intervals with the threat that had the highest average vulnerability; gray squares, no species were rated as having vulnerability to that threat in that taxa; silhouettes [left to right], bony fishes, cetaceans, elasmobranchs, flying birds, polar bear, penguins, pinnipeds, sirenians, turtles; all, all species considered).

ing longlines, plastics and other solid waste, direct human intrusions, and light pollution. For flying birds, temperature extremes, maritime pollution, plastics and other solid waste, and drifting longlines resulted in the highest vulnerabilities; the latter was especially pronounced for procellariform species (albatrosses, petrels, and shearwaters) (Appendix S11). Plastics and other solid waste was not among the threats causing the highest severity. Sirenians had the highest average vulnerability to artisanal fisheries and direct human intrusions and also had vulnerability to temperature extremes, agriculture and urban runoff (although only among the highest threat severity scores), plastics and other solid waste, and maritime and noise pollution (although only among the highest threat scope scores). For elasmobranchs, the highest vulnerabilities were to fixed gear, drifting longlines, artisanal fisheries, temperature extremes, seiners, and trawlers, although for the 4 mobulids in this taxon, drifting longlines were not among the highest threats (see Appendix S11). For pelagic cetaceans, the highest vulnerabilities were to noise pollution, shipping, temperature extremes, plastics and other solid waste, and maritime pollution. However, plastics and other solid waste and maritime pollution were only among the highest threat scope scores for cetaceans (i.e., not among the highest severity scores), and maritime pollution vulnerability scores were not among the highest vulnerability scores for the 12 baleen whales considered (Appendix S11). Despite not being among the highest threats to the pelagic cetaceans assessed, fixed gear (a well-known threat to cetaceans [e.g., Temple et al., 2024]) obtained the highest vulnerability scores in the fishing category for this taxon. Finally, the highest threat vulnerability scores for bony fishes were associated with drifting longlines and plastics and other solid waste, and the highest threat severity scores were obtained for oxygen minimum zones, seiners, and temperature extremes (Figure 6).

Species maximum vulnerability scores and categories

We used the maximum threat vulnerability scores per species, which were, on average, 0.757 out of 1 (Appendix S7), to determine species' vulnerability categories. The largest number of these maximum threat vulnerability scores (across species from all vulnerability categories) were obtained for temperature extremes (74), largely due to scope (but also severity for some species, e.g., polar species), followed by drifting longlines (66), plastics and other solid waste (13), and fixed gear and noise pollution (8 each) (Appendix S7).

Almost 40% of species ($n = 70$, 95% CI 28–109) had high vulnerability to at least one threat ($v > 0.778$) (Figure 5b; Appen-

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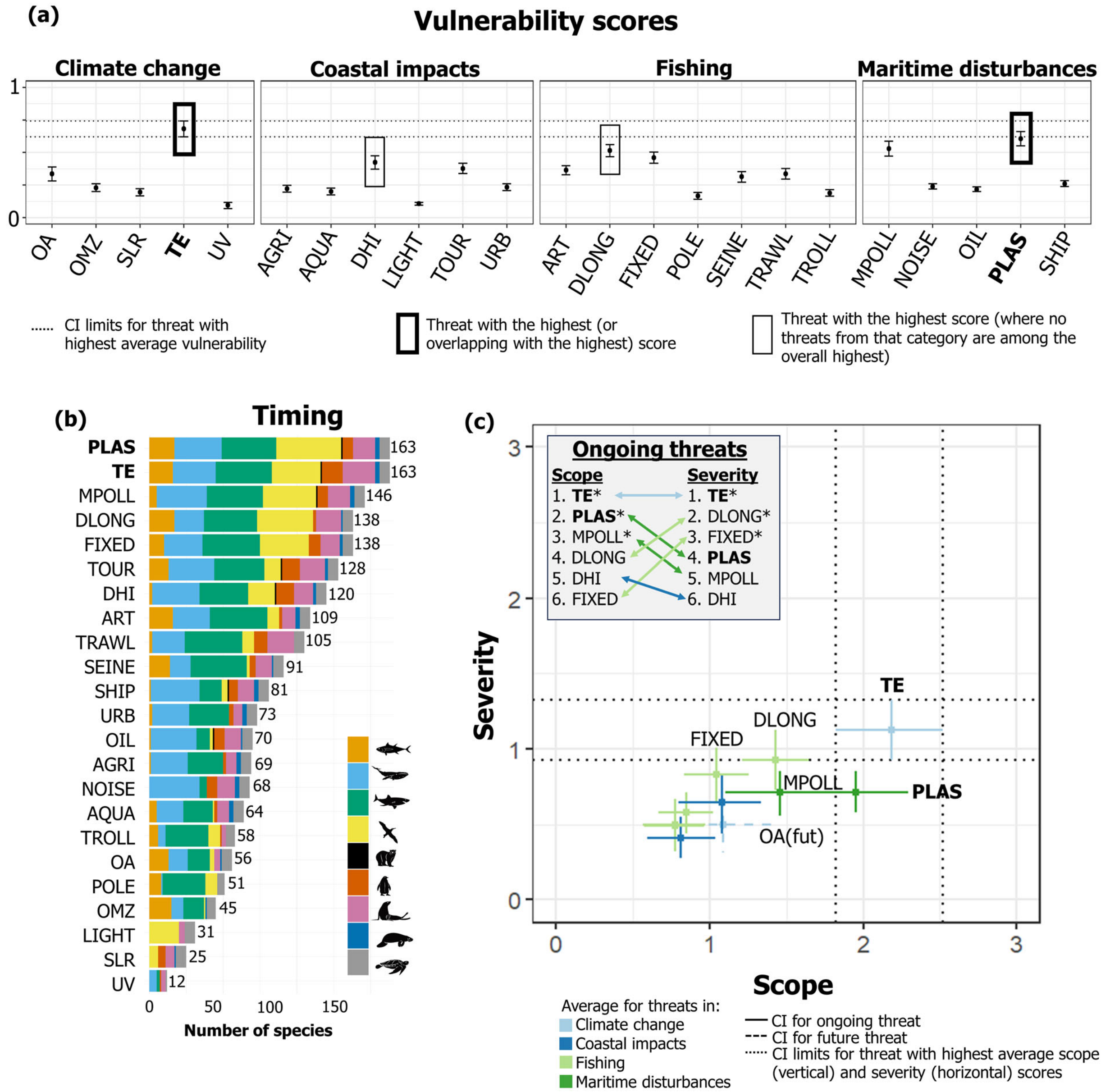

FIGURE 4 (a) Average vulnerability scores across all species (circles) (bars, confidence intervals), (b) per threat the number of species with current vulnerability to a threat (i.e., rated as having ongoing timing by experts), and (c) for threats rated as ongoing or future for the majority of species, average scope (proportion of population affected) and severity (level of population decline) scores (*, highest average scope or severity scores; fut, threat rated as a future threat for the largest number of species; bold, threats with the highest average vulnerability across all species; OA, ocean acidification; OMZ, oxygen minimum zones; UV, ultraviolet radiation; SLR, sea level rise; TE, temperature extremes; AGRI, agricultural runoff; URB, urban runoff; AQUA, aquaculture; TOUR, tourism; DHI, direct human intrusions; LIGHT, light pollution; DLONG, drifting longlines; SEINE, seiners; TRAWL, trawlers; FIXED, fixed gear; TROLL, trollers; POLE, pole and line; ART, artisanal fisheries; SHIP, shipping; OIL, benthic oil rigs; NOIS, noise pollution; PLAS, plastics and other solid waste; MPOLL, maritime pollution).

dices S7 & S8), including 28 flying birds, 22 elasmobranchs, 11 penguins, 6 turtles (all except hawksbill [*Eretmochelys imbricata*], African manatees [*Trichechus senegalensis*], South American fur seals [*Arctocephalus australis*], and sei whales [*Balaenoptera borealis*]) (Figure 5a), of which, 46 were threatened species (Figure 5b). High threat vulnerability scores were obtained for drifting longlines (45 species of elasmobranchs and flying birds), temperature extremes (25) (polar species and turtles), fixed gear (18 elasmobranchs), artisanal fisheries (smalltooth sawfish [*Pristis pectinata*] and African manatees), sea level rise (green [*Chelonia mydas*] and leatherback [*Dermochelys coriacea*] turtles), seiners (African penguins [*Spheniscus demersus*]), trawlers (angelsharks [*Squatina squatina*]), and trollers (smalltooth sand tiger sharks [*Odontaspis ferox*]) (Figure 5a).

The majority of the 190 species (117 species [95% CI 90–149]) (Figure 5b; Appendices S7 & S8) received a maximum of medium threat vulnerability (i.e., $0.556 < v \leq 0.778$) to at least one threat. Pygmy sperm whales (*Kogia breviceps*) received a maximum of low threat vulnerability ($0.222 < v \leq 0.556$) to at least one threat (95% CI 3–12), and 2 petrel species received negli-

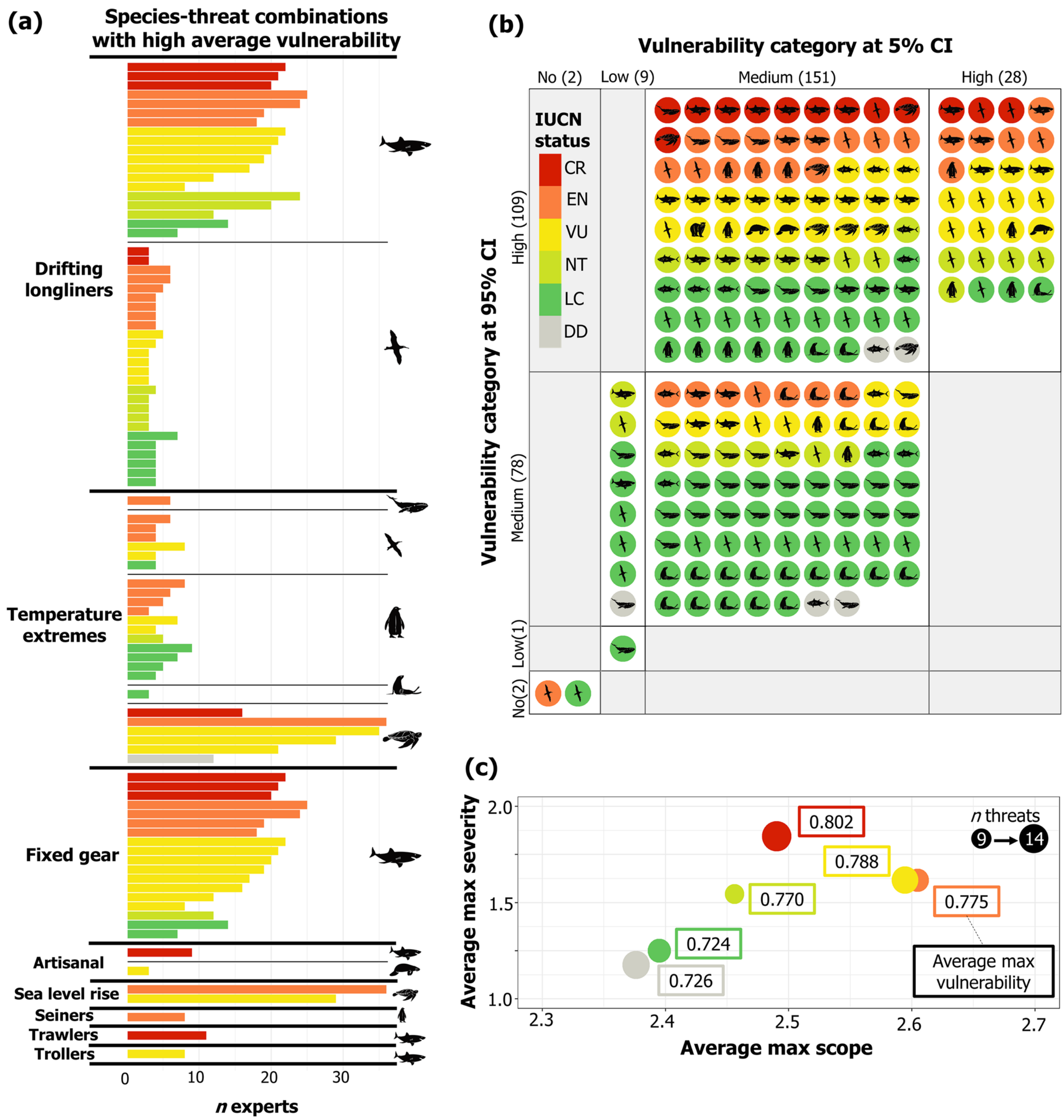

FIGURE 5 (a) Seventy species rated as having high vulnerability to a threat based on average vulnerability scores, threats to which they have high vulnerability, and number of expert opinions received per species, (b) matrix of species ranked as high, medium, or low vulnerability to at least 1 of the 23 threats considered for the vulnerability scores obtained at the 5% and 95% confidence interval (CI) levels (IUCN, International Union for Conservation of Nature; CR, critically endangered; EN, endangered, VU, vulnerable; NT, near threatened; LC, least concern; DD, data deficient [iucnredlist.org; April 2023]), and (c) average maximum threat scope versus average maximum threat severity scores (rectangles, average maximum vulnerability scores; circle size, average number [*n*] of ongoing threats per species per extinction risk category). The IUCN Red List extinction statuses are depicted based on the most recent IUCN species assessments (iucnredlist.org [accessed April 2023]). Silhouettes represent bony fishes, cetaceans, elasmobranchs, flying birds, polar bear, penguins, pinnipeds, sirenians, and turtles.

gible threat vulnerability to all threats considered, including the endangered Henderson petrel (*Pterodroma atrata*) and the least concern Murphy's petrel (*Pterodroma ultima*) (Appendices S7 & S8). However, these 2 petrels received only enough scores for 8 threats (i.e., all other threats were excluded from final analyses) (Appendix S4). The vulnerability categories assigned were higher for 77 species and lower for 4 species than categories based on IUCN Red List assessments (Appendix S12).

DISCUSSION

Our comprehensive species threat vulnerability assessment, based on expert opinion, provides insight into the global risk posed by anthropogenic threats to predominantly pelagic and highly mobile marine megafauna, highlighting the need to prioritize conservation of specific species–threat combinations. Our results showed that species vulnerabilities to a single threat

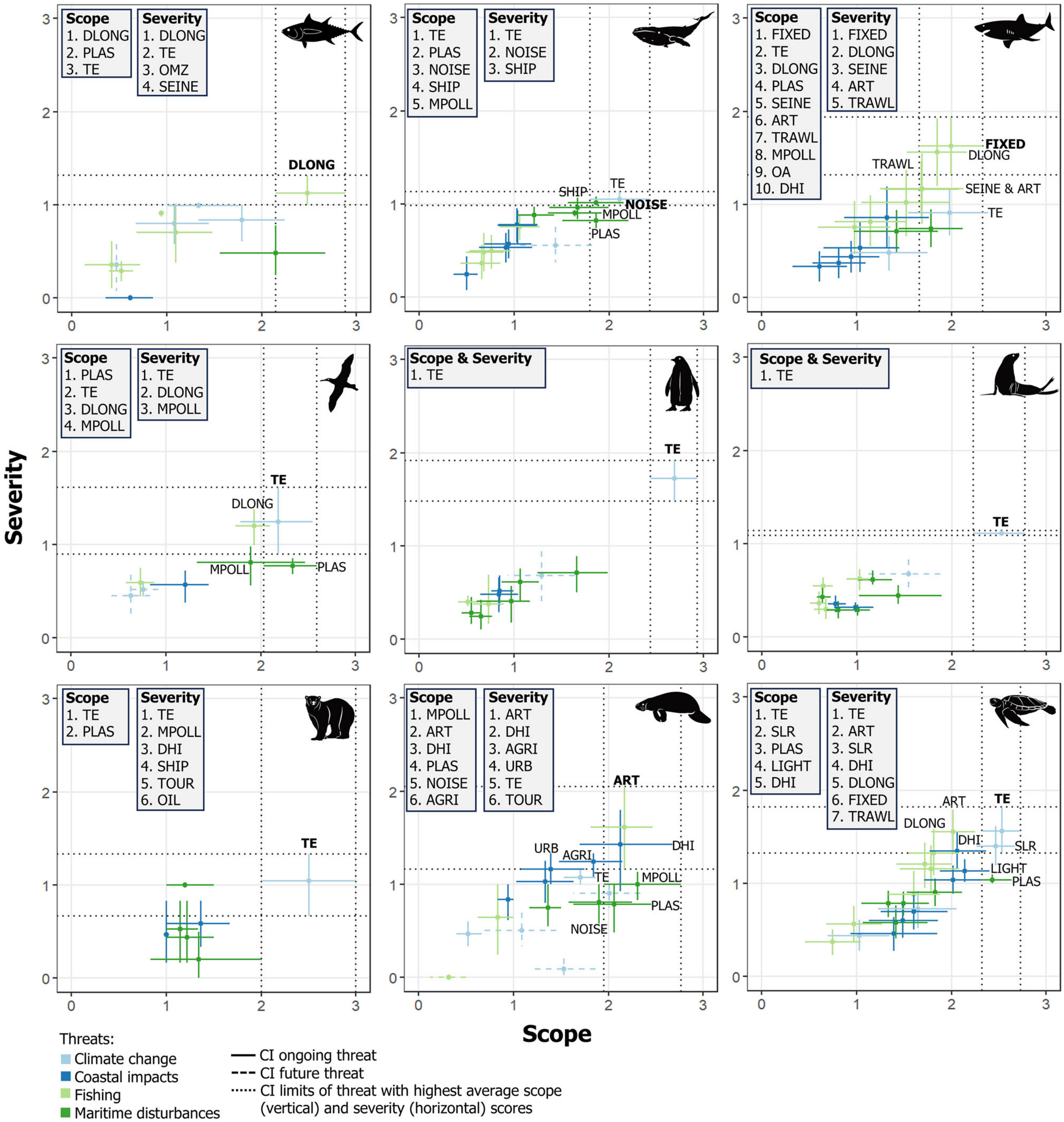

FIGURE 6 Average threat scope and severity scores for threats rated as ongoing or future for the majority of species in each taxonomic group (bony fishes, cetaceans, elasmobranchs, flying birds, polar bear, penguins, pinnipeds, sirenians, and turtles) (bold type, threats with the highest average vulnerability across all species; OA, ocean acidification; OMZ, oxygen minimum zones; SLF, sea level rise; TE, temperature extremes; AGRI, agriculture runoff; URB, urban runoff; TOUR, tourism; DHI, direct human intrusions; LIGHT, light pollution; DLONG drifting longlines; SEINE, seiners; TRAWL, trawlers; FIXED, fixed gear; ART, artisanal fisheries; SHIP, shipping; OIL, benthic oil rigs; NOIS, noise pollution; PLAS, plastics and other solid waste; MPOLL, maritime pollution; dotted lines, range of confidence interval for threat with highest severity and scope for each taxon).

are, on average, 75% of the maximum possible (where the threat is causing very rapid declines to whole populations) and that almost 60% of species have high vulnerability to at least 1 of the 23 threats we considered. Importantly, we provided an assessment of threat scope and severity that showed that high exposure to threats through large threat scope did not necessarily result in population declines (e.g., temperature extremes leading to changes in species distribution), unless there was also high severity of impacts (e.g., fishing leading to direct mortality). Because species across 6 taxonomic groups (and particularly turtles and sirenians) received top vulnerability scores for threats across categories, our results stress the need to address and mitigate multiple anthropogenic threats simultaneously.

Across all taxonomic groups, particularly for polar taxa (pinnipeds, penguins, and polar bear), the highest average vulnerability scores were for temperature extremes. This finding aligns with previous research focused on climate change impacts on marine megafauna (e.g., Grose et al., 2020; Orgeret et al., 2022; Patrício et al., 2021), including the close association between temperature fluctuations and sea ice loss (Olonscheck et al., 2019), which adversely affect the population dynamics of several ice-adapted species from polar regions (Bestley et al., 2020; Laidre et al., 2018). For bony fishes, elasmobranchs, flying birds, and turtles, at least one fishing threat received among the highest vulnerability scores, which is consistent with previous assessments showing that overfishing is the greatest threat to these species (Dias et al., 2019; Dulvy et al., 2021; Senko et al., 2022). As expected, drifting longlines and fixed gear had top severity scores (along with temperature extremes) across all species, underscoring the resulting population declines and urgency in addressing these threats. For sirenians and the pelagic cetaceans included in this study, maritime disturbances (except benthic oil rigs) were of particular concern (in addition to temperature extremes). However, fisheries can lead to more immediate impacts and are expected to be a major threat to marine mammals (Avila et al., 2018), particularly smaller species (Read et al., 2006). Indeed, artisanal fisheries were associated with one of the highest vulnerability scores for sirenians, and although no fishing threats received the highest score for pelagic cetaceans, fixed gear (considered the greatest threat to most cetaceans [Braulik et al., 2023]) had the highest vulnerability score within fishing threats for this taxon. The relatively low estimate we obtained for pelagic cetacean vulnerability to fixed gear is likely due to our focus on highly mobile and wide-ranging species, meaning that most small-bodied threatened cetaceans with relatively small coastal ranges (which are most vulnerable to fixed gear [Temple et al., 2024]) were not included in our analyses.

In the category coastal impacts, direct human intrusion vulnerability scores, on average, were among the highest across all species and were associated with the highest scores for sirenians and turtles. This is in accordance with previous results showing that, for sirenians, in-water construction increases the chance of vessel collisions, entanglement, ingestion of debris, disruptions to migratory pathways, exposure to pollutants, and reductions in food availability (Hieb et al., 2021). For turtles, coastal development is of particular concern because rising sea level pushes nesting beaches closer to urban population centers (Biddiscombe et al., 2020), and for herbivorous species, it may reduce foraging opportunities through reduced plant diversity and abundance (Bastos et al., 2022). At a lower taxonomic level, Mobulidae also had the highest threat vulnerability scores for direct human intrusions and tourism, plastics and solid waste, 2 climate change threats, and 4 fishing threats (the latter is the most significant cause of global ray population declines [Dulvy et al., 2021]). Indeed, mobulids are also well known to inhabit coastal waters (Armstrong et al., 2020) and are affected by tourism activities at aggregation or cleaning station sites (O'Malley et al., 2013). Although we did not assess most coastal and nonmigratory elasmobranchs (representing ∼97% of elasmobranchs), the large number of threats across categories faced by species using coastal habitats underscores the wide range of threats likely to affect all elasmobranchs.

As expected, the majority of species that received high vulnerability scores for at least one threat are listed as vulnerable, endangered, or critically endangered on the IUCN Red List. Our work filled crucial gaps by identifying and quantifying vulnerabilities for 5 marine megafauna currently categorized as data deficient, including the flatback turtle (*Natator depressus*), which had high vulnerability to temperature extremes. Although this species has not been assessed by the IUCN since 1996, recent studies show they are affected by several threats, including marine plastics (Duncan et al., 2021), light pollution (Wilson et al., 2018), and temperature extremes (van Lohuizen et al., 2016). Multiple least concern species with increasing population trends also were assigned high vulnerability to temperature extremes or drifting longlines, specifically. These included great (*Ardenna gravis*) and little (*Puffinus assimilis*) shearwaters, king penguins (*Aptenodytes patagonicus*), and the South American fur seals, for which limited empirical data exist showing any relationship between these species and vulnerability to climate change (e.g., Bost et al., 2015). However, for the latter species, the knowledge that El Niño events affect South American fur seal populations in the Pacific Ocean (Edwards et al., 2021) may have been reflected in expert scoring. In contrast, the endangered Henderson petrel was one of 3 species that scored only low vulnerability to threats. This finding is likely due to the major threat to them being invasive rats at nesting sites (Oppel et al., 2017), a threat that was not included in our assessment given its terrestrial nature. Because terrestrial invasive species are thought to be the greatest threat to seabirds (Dias et al., 2019), the vulnerability scores for these taxa should be used with caution and are likely to underestimate total threat vulnerability. Further, underestimations of vulnerability level are likely for seabirds and pinnipeds given the emerging risk of highly pathogenic avian influenza A (HPAI) H5N1 viruses, which have recently caused widespread mortality to birds globally (e.g., Giralt Paradell et al., 2023).

A small proportion of our threat vulnerability scores, obtained based on the threat timing, scope, and severity variables, differed from expectations or from previous results based only on species traits and environmental tolerances. For example, the sei whale was the only pelagic cetacean included in our study that had high vulnerability to any threat (temperature extremes), whereas the only critically endangered cetacean in this study (North Atlantic right whale [*Eubalaena glacialis*]) had only medium vulnerability across all threats. This result was surprising because sei whale populations are considered to be increasing and their endangered status is largely the result of historical commercial whaling (Cooke, 2018). However, there is some evidence linking El Niño conditions to mass sei whale mortality (Häussermann et al., 2017), which may have resulted in regional biases among experts providing input.

In contrast, the North Atlantic right whale is highly threatened by entanglement in fishing gear (Knowlton et al., 2022), vessel strikes (Sharp et al., 2019), and climate change (Meyer-Gutbrod et al., 2021), which have resulted in a declining population trend (Runge et al., 2023) and a current population estimate of fewer than 400 individuals (Pettis et al., 2021). The severity of this population decline was, however, not captured by our scores because the species did not receive above medium vulnerability for any fishing threat. This might have happened because experts were not required to rate more than one species, meaning that a sense of comparison of vulnerabilities might not be reflected in all scores provided. In future work, including an explicit comparison of scores could reduce the potential for inconsistent results.

Our result showing higher vulnerability of turtles to temperature extremes than elasmobranchs and bony fishes contrasts with the results obtained by Boyce et al. (2022). This difference may have resulted from the inclusion of large numbers of nonmigratory fishes with restricted range sizes in Boyce et al.'s (2022) index, which could have inflated the contribution of the variables they used (e.g., thermal habitat variability and thermal safety margins). Our results align with known impacts from high temperatures on turtle hatchlings, leading to female-biased populations (Bentley et al., 2020) and potentially leading to turtle population declines through reduced hatching success (Saba et al., 2012). Although impacts from climate change on elasmobranchs and bony fishes are still not fully understood, most published results point to changes in distribution and habitat use, including poleward shifts (e.g., Sequeira et al., 2014) and changes associated with deoxygenation (Vedor et al., 2021). Regardless, the diverse range of threats affecting fishes underscores the importance of comanaging multiple threats to better support the sustainable exploitation of fisheries resources. Further, these inconsistencies likely resulted from our vulnerability framework being based on scores for expected timing, scope, and severity of impacts of threats to populations (which implicitly includes knowledge of species' environmental tolerances and current level of exposure to threats) rather than solely on species-specific traits or species' known extinction risk status.

Ours was a broad analysis of at-sea threats to highly mobile and wide-ranging marine megafauna globally based on scores provided by experts. Although we tried to address inherent biases from the expert scoring processes, particularly those due to the level of expert certainty and number of expert contributions per species–threat combination, it is possible that some other biases remained. For example, the threat vulnerability of species that are difficult to track or that interact with threats in remote regions may have been underestimated. When using our vulnerability scores, we suggest the certainty scores for species–threat combinations (Appendix S9) be consulted. We also recognize that globally mapped threats may not align with local threats, and we encourage the development of region-specific studies, particularly in regions from which we received fewer contributions (e.g., Africa and Asia). Where possible, we recommend cross-referencing our results with empirical data, such as documented vessel strikes and injuries or deaths resulting from threats. The IUCN's method of summing ordinal variables has drawbacks, which might be why the calculation of impact scores has been paused (see https://www.iucnredlist.org/resources/threat-classification-scheme [accessed December 2023]). An alternative to the IUCN's variables has yet to be proposed, but we recommend future researchers using these variables adapt the IUCN's impact scoring system to ensure compatibility with available data.

Because we aimed to specifically assess at-sea threats that can be spatially mapped, we restricted our selection to threats with available spatial datasets and did not consider threats with limited spatial data (e.g., driftnets) or some land-based threats (e.g., invasive species). Despite our recognition that it is important to understand the separate effects of targeted versus unintentional fisheries, because these threats are mapped using the same spatial datasets, we were unable to separate them. The delineation between artisanal and industrial fisheries is also blurred in some regions (Belhabib et al., 2018), meaning that our grouping of artisanal fisheries into one threat rather than by gear type may have resulted in an underestimate of species' vulnerabilities in those regions. Further studies should aim to evaluate these threats as spatial datasets for them become available. Nevertheless, our expansion of industrial fishing threats into 6 gear types provides the most comprehensive analyses of marine megafauna vulnerability to fishing globally. Together with our expansion of individual threats for climate change, our vulnerability scores will facilitate spatial risk assessments and the planning of mitigation measures to promote species recovery. Our results and transparent methods that build on existing IUCN Red List scores will allow evaluation of risk from at-sea threats to marine megafauna over various spatial and temporal scales and help identify key species and threats on which to focus and prioritize conservation actions in response to global initiatives to protect biodiversity under the Kunming–Montreal Global Biodiversity Framework.

AUTHOR CONTRIBUTIONS

Ana M. M. Sequeira and Michelle VanCompernolle conceptualized the study, acquired funding, conducted formal analyses, and wrote the original draft. Michelle VanCompernolle, Ana M. M. Sequeira, Víctor M. Eguíluz, and Jorge P. Rodríguez developed the methodology. Michelle VanCompernolle, Juliet Morris, Hannah J. Calich, Sarah A. Marley, and Jessica R. Pearce curated the data. Michelle VanCompernolle, Juliet Morris, Hannah J. Calich, and Jessica R. Pearce created the visualizations. All coauthors contributed data, assisted with validation of data, and reviewed, edited, and approved the manuscript.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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