A trait-based framework for assessing the vulnerability of marine species to human impacts

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Abstract

Marine species and ecosystems are widely affected by anthropogenic stressors, ranging from pollution and fishing to climate change. Comprehensive assessments of how species and ecosystems are impacted by anthropogenic stressors are critical for guiding conservation and management investments. Previous global risk or vulnerability assessments have focused on marine habitats, or on limited taxa or specific regions. However, information about the susceptibility of marine species across a range of taxa to different stressors everywhere is required to predict how marine biodiversity will respond to human pressures. We present a novel framework that uses life-history traits to assess species' vulnerability to a stressor, which we compare across more than 33,000 species from 12 taxonomic groups. Using expert elicitation and literature review, we assessed every combination of each of 42 traits and 22 anthropogenic stressors to calculate each species' or species group's sensitivity and adaptive capacity to stressors, and then use these assessments to derive their overall relative vulnerability. The stressors with the greatest potential impact were related to biomass removal (e.g., fisheries), pollution, and climate change. The taxa with the highest vulnerabilities across the range of stressors were molluscs, corals, and echinoderms, while elasmobranchs had the highest vulnerability to fishing-related stressors. Traits likely to confer vulnerability to climate change stressors were related to the presence of calcium carbonate structures, and whether a species exists across the interface of marine, terrestrial, and atmospheric realms. Traits likely to confer vulnerability to pollution stressors were related to planktonic state, organism size and respiration. Such a replicable, broadly applicable method is useful for informing ocean conservation and management decisions at a range of scales, and the framework is amenable to further testing and improvement. Our framework for assessing the vulnerability of marine species is the first critical step towards generating cumulative human impact maps based on comprehensive assessments of species, rather than habitats.

Key words

Trait-based vulnerability; anthropogenic threats; anthropogenic stressors; marine conservation planning; conservation decision-making; climate change; pollution; fishing; ocean.

Introduction

The vast majority of the ocean is impacted by multiple stressors associated with human activities (Halpern et al. 2019). Some stressors, such as those associated with climate change, have widespread impacts, where other stressors, such as those related to destructive fishing, are more localized. As human activities driving these stressors continue to expand, so do their impacts on marine ecosystems and species.

There are multiple anthropogenic activities that impact marine species and ecosystems (Halpern et al 2007; 2019), including energy production and consumption, agriculture, watershed development, shipping, commercial and non-commercial fishing, ocean mining, and aquaculture. The stressors resulting from these activities include increasing sea surface temperature and eutrophication, chemical pollution, entanglement from fishing gear, ocean acidification, and destruction of marine habitat (Table S3; e.g., Halpern et al. 2019; Olden et al. 2007; Brooker et al. 2014; Stelfox et al. 2016; Laist 1997; Vaquer-Sunyer 2008).

Species typically respond to stressors. We define a species' vulnerability to a stressor as a function of its sensitivity (the degree to which it is affected by a stressor), and adaptive capacity (ability to adapt to or recover from a stressor). Ultimately, the impact of a stressor (Figure 1) will depend on these intrinsic factors, determined by biological characteristics, or traits (Dawson et al. 2011; Butt et al. 2016; Butt & Gallagher 2018), combined with the degree of exposure to the stressor, an external factor. Thus, even though exposure to a stressor may be consistent across species, varying sensitivity and adaptive capacity among species means that vulnerability also varies. Hundreds, if not thousands, of studies have assessed the vulnerability of species to stressors (both inclusive and exclusive of exposure), but they are focused on individual populations or particular species and/or rarely consider multiple stressors. We lack comprehensive information about the vulnerability of all marine species to the full range of stressors affecting the ocean (O'Hara et al. 2021). Such comprehensive information will be critical for assessing and comparing different species, as well as new species as they are discovered, and in turn enabling strategic and effective management of the ocean.

Although there is a strong foundation for trait-based approaches to assessing species' vulnerability to a range of stressors, a framework applicable to marine species globally does not exist. Trait-based vulnerability assessments have been used to estimate extinction risk (Pearson et al. 2014), to estimate vulnerability of selected taxonomic groups (Foden et al. 2013) and of nationally listed threatened species (Lee et al. 2015), and for predicting the conservation status of data-deficient species (Walls & Dulvy 2020). However, these previous assessments focused on narrow suites of traits (Comte & Olden 2017; Estrada et al. 2016; González-Suárez et al. 2013; Hobday et al. 2011; Juan-Jordá et al. 2012), specific taxa and places (Bender et al. 2013; Chessman 2013; Gallagher et al. 2014; Sunday et al. 2015; Ormseth & Spencer 2011; Taylor et al. 2014; Stelzenmuller et al. 2010; Laidre et al. 2008; Markovic et al. 2017; Jorgensen et al. 2015; Certain et al. 2015; Fabri et al. 2014; Maxwell et at. 2013; Williams et al. 1995), or on terrestrial species (Estrada et al. 2016).

The only global marine vulnerability assessment that has been conducted focuses on habitats (Halpern et al. 2007), however species respond to stressors differently than do habitats. Although many habitats have a foundation species at their base (e.g., kelp forests, oyster reefs, salt marshes), others do not (e.g., rocky reef, beach). Thus, a habitat exposed to a stressor might persist, but the composition of species and thus ecosystem function might be lost, or vice versa. Species have often not been considered in global analyses as distribution data are limited, and most species and the important ecological roles they play have been overlooked in management. In addition, previous assessments were often limited as they focused on particular regions or taxa.

We developed a comprehensive traits-based framework for assessing species vulnerability (defined here as sensitivity and adaptive capacity) that can be applied across any marine invertebrate and vertebrate taxonomic group, allowing for broader investigation of the impacts of anthropogenic stressors; the first such framework to our knowledge. Importantly, the flexibility and wide applicability of the framework allows for it to be tested and improved. To develop this framework, we: 1) determined a list of life-history traits relevant for estimating species' vulnerability to pressures, based on traits related to species' sensitivity and adaptive capacity; 2) assigned life-history traits to more than19,250 species; (more than 33,000 with gapfilling/extrapolation to higher taxonomic levels) across a wide range of species and taxonomic groups, and; 3) developed and applied a model to translate these traits into a score describing the relative vulnerability of these species to a range of stressors.

Methods

There were two primary components to the work (Figure 2). Firstly, we created a framework for assessing the vulnerability of species to anthropogenic stressors based on life-history traits. Secondly, we applied the framework to predict the vulnerability of as many species as possible to anthropogenic stressors.

1. Traits framework

Our framework for assessing species' vulnerability based on species traits was developed using expert elicitation, a literature review, and IUCN Red List guidelines. Expert elicitation was conducted in a working group format, through one-on-one meetings, and over email (Martin et al. 2012), where each person had expertise in a particular group of marine species, including coral, cephalopods and other molluscs (bivalves and gastropods – referred to throughout as ‘molluscs’), echinoderms, seabirds, elasmobranchs, marine arthropods, marine reptiles and a range of bony fish groups. Expert knowledge, when meticulously collected and applied, can be as robust as empirical data (Drescher et al. 2013). First, as part of the expert group (coauthors), we derived an initial list of life-history traits that likely determine a species’ vulnerability to stressors from multiple anthropogenic activities, either by conferring sensitivity to specific stressors or limiting adaptive capacity (Butt & Gallagher 2018). In developing this list, we considered the following trait groups hypothesized to be important factors in determining species’ vulnerability to stressors (Polidoro et al. 2020; Chessman 2013; Comte & Olden 2017; Foden et al. 2013; Lee et al. 2015): movement, reproduction, specialization, spatial scale metrics, and biophysical traits.

The five trait groups are associated with species’ vulnerability in different ways. Movement traits incorporate dispersal ability and determine a species' adaptive capacity by allowing individuals to track optimal conditions for growth and survival and shift their distribution in response to stressors (Comte & Olden 2017; Laidre et al. 2008). Reproductive traits relating to population turnover, such as fecundity and age to first reproduction, partly determine the capacity of populations to adapt to or recover from anthropogenic stressors and pressures at their location. Some species have specializations that make them highly adapted to the specific habitats they live in, and those with narrowly-defined niches are more likely to be ecological specialists, with a higher sensitivity to stressors that drive changes in habitat conditions (Slatyer et al. 2013). Conversely, species with broader niches are more likely to have a lower sensitivity. Species’ with spatial distributions that are relatively small and/or with low connectivity among populations have less adaptive capacity, and this trait is often used as a proxy for vulnerability, such as extinction risk (Mace et al. 2008). Species with small distributions are more likely to be at risk from anthropogenic stressors as a large proportion, or even all, of the population could be impacted by a single stressor; species with broad ranges are more likely to have some portion of the population unimpacted by the stressor (IUCN 2016). For anthropogenic stressors, species' biophysical traits are important indicators of sensitivity. Species that can fly are able to disperse more easily and widely than those that cannot, but are also vulnerable to stressors that do not affect species without flight, such as those posed by infrastructure (oil rigs, wind turbines). Maximum body size, length, or mass is frequently used in assessments of vulnerability (González-Suárez et al. 2013; Jørgensen et al. 2015; Juan-Jordá et al. 2012; Ormseth & Spencer 2011; Sunday et al. 2015; Chessman 2013; Bender et al. 2013; King & McFarlane 2003; Taylor et al. 2014). Large-bodied species are generally more vulnerable to many stressors (Bender et al. 2013, Davidson et al. 2012), although this varies with stressor and taxon.

To score each trait, we first determined whether it was most appropriately assessed as a categorical (high/medium/low/none) or binary (yes/no) class, and then defined classes to best distinguish vulnerability among species (Table 1). We also included 'NA (not applicable)'. Assessing a species as NA to a particular trait was important as we aimed to include a wide range of marine species, and including this category ensured that vulnerability assessment was not skewed for traits that were not relevant to a species (e.g., salinity in relation to diadromous fish). Where data were lacking, we used 'unknown'.

Following the workshop, we identified experts in taxonomic groups not included in the workshop, including sea snakes, sea spiders, additional bony fish taxa, sponges, plankton, marine mammals (including cetaceans and pinnipeds), annelid worms, and sea turtles. In addition, we consulted with plant and algal taxonomic experts, but omitted these groups from the final analysis. We elicited information from individual experts over email, calls, or in-person meetings to refine both the trait list and the categories for each trait. Finally, we conducted a literature search to collate life-history trait data for each taxonomic group and to ensure our list of traits was comprehensive. We used the snowball method (Wohlin 2014) to review the literature, using search terms "marine", "marine species", "vulnerability assessment", "traits", "life-history traits" to further support and guide the development of the framework. In total, 25 marine taxonomic experts covering 38 taxonomic groups (Table S1) provided data and insight to develop our framework. These experts provided trait information at various taxonomic ranks when traits were broadly applicable across an entire genus, family, order, or class; in other cases, experts scored traits for individual species that they considered broadly representative of their genus, family, or order.

2. Traits-stressors matrix

Building on the anthropogenic stressors to marine ecosystems identified in Halpern et al. (2019), we identified 22 stressors to marine species, and determined if each species trait conferred vulnerability to individual stressors. The stressors, their explicit pathways, and drivers are described in Table S3.

We determined whether or not, and quantified how, each trait conferred vulnerability to each stressor through a literature review and expert knowledge, including experts on particular stressors. For each trait category-stressor combination (n=2550 individual scores), 3-7 experts assigned sensitivity and adaptive capacity values based on their knowledge and the literature (Table S4), and we further consulted experts for specific stressors (e.g., pollution stressors) and trait categories (e.g. traits relating to calcium carbonate) where required. We compiled these and identified any discrepancies across the inputs with cross-checking and calibration (Martin et al. 2012; McBride et al. 2012). We split the traits into stressor-specific sensitivity, stressor-specific adaptive capacity, and general adaptive capacity, based on the intrinsic components of vulnerability (Figure 1). The allocation of traits to the three groups is given in Table S2.

We assigned traits to the general adaptive capacity group when their adaptive capacity is linked to resilience at the level of population recovery from the impact of a stressor, and not explicitly linked to individual stressors. For general adaptive capacity, if a species has a large global population, or many subpopulations, or a large distributional range, or very responsive reproductive strategies (such as high fecundity, short generation time, and so on), the species would be expected to be more able to recover from exposure to a regional stressor. For the general adaptive capacity traits, we assigned a value based on how likely it was to confer adaptive capacity to each stressor.

The second group included traits relating to specific adaptive capacity, which include traits that allow an organism or species to avoid or mitigate exposure to a stressor, and are stressor-specific, as stressors vary in terms of spatial and temporal characteristics. These traits included adult mobility and planktonic larval duration. When assigning values to these traits, we assessed whether a particular trait category was likely to confer more adaptive capacity than another (to each stressor). For example, for adult mobility, horizontal migration and nomadism confers high adaptive capacity to eutrophication and nutrient pollution, but low adaptive capacity to entanglement.

The third group comprised traits related to sensitivity, which determine whether, and how, an organism is physiologically sensitive to a given stressor, largely related to tolerance limits and specializations. These traits include thermal and salinity tolerance ranges and several life cycle specializations and biophysical traits. When assigning values to these traits, we asked whether a particular trait category was likely to confer more sensitivity than another (to each stressor).

We then used a simple scale and assigned a value of ‘none/NA’, ‘low’, ‘medium’ or ‘high’ to each trait-stressor combination, in line with previous assessments of species’ vulnerability to various stressors (e.g., Jorgensen et al. 2013 for marine species’ vulnerability to bottom trawling; Laidre et al. 2008 for marine mammal vulnerability to climate change; Estrada et al. 2016 for bird and plant vulnerability to climate change; Ormseth & Spencer 2011 for groundfish vulnerability to overfishing).

Although there are also other types of interactions between stressors and traits, such as the mechanistic relationship between temperature and salinity, we took the parsimonious approach of considering only the direct effect of a stressor. For planktonic larval duration (a movement trait), we assumed that longer larval duration resulted in decreased adaptive capacity due to increased exposure to potential stressors during the developmental period, rather than assuming that increased time in the planktonic larval stage gave the organisms more opportunity to disperse away from the stressor.

3. Vulnerability model

We developed a model to estimate the vulnerability of a given species to a given stressor as a function of its sensitivity, adaptive capacity, and potential exposure (defined below) based on species-level traits and habitat preferences.

As above, sensitivity of a given species to a given stressor is determined by the degree to which the life history traits of the species make it physiologically sensitive to a given stressor. These sensitivity-related traits are largely related to tolerance limits and specializations, e.g., thermal and salinity tolerance ranges, life cycle specializations, or biophysical traits. For each stressor, we scored each of 85 trait categories (from the 42 traits) as conferring high, medium, low, or no sensitivity (or NA), which were weighted as 1.00, 0.67, 0.33, and 0 respectively (We also carried out a sensitivity analysis to test how vulnerability scores changed when the high/medium/low/none scoring changed – see S2.1). For the specialization trait habitat dependence, we combined a value of 1 for each 'within-stage and/or across stage habitat dependence' 'yes', with the scores for dependent interspecific interactions (0 if 'no', 0.33 if 'yes'), to give an overall sensitivity value. Sensitivity of a given species i to a given stressor j was calculated as the sum of sensitivity weights based on the species' trait category k:

$$\text{sensitivity score } S_{ij} = \sum_k s_{jk} t_{ik} \qquad (1)$$

where s_{jk} represents sensitivity to stressor j based on trait k, and t_{ik} represents the presence (0 or 1) of trait k in species i. For example, a bony fish would score 1 for trait "respiration structure- gills" and 0 for "respiration structure-lungs", while a seabird would score 0 and 1, respectively.

Adaptive capacity of a given species to a given stressor is determined in a similar manner to sensitivity. We considered stressor-specific adaptive capacity as the degree to which an organism or population is able to respond adaptively to a particular stressor, generally by mitigating exposure or through reproductive or other traits related to population resilience. As for sensitivity, for each stressor we scored each of 28 trait categories across five traits as conferring high, medium, low, or no adaptive capacity (weighted 1.00, 0.67, 0.33, and 0 respectively - Table S2; see S2.1 for sensitivity analysis). The specific adaptive capacity of a given species *i* to a given stressor *j* is the sum of adaptive capacity weights based on the species' traits:

$$\text{specific adaptive capacity score } A_{ij} = \sum_k a_{jk} t_{ik} \qquad (2)$$

where a_{jk} represents specific adaptive capacity to stressor *j* based on trait *k*, and t_{ik} represents the presence of trait *k* in species *i*.

In addition to stressor-specific adaptive capacity, we considered general adaptive capacity as traits which broadly improve a species' resilience at the population level, generally by having a favorable reproductive strategy, multiple subpopulations or metapopulations, or an extensive global distribution. General adaptive capacity of a given species *i* is calculated as the sum of general adaptive capacity weights based on species' traits:

$$\text{general adaptive capacity score } G_i = \sum_k g_k t_{ik} \qquad (3)$$

where g_k represents general adaptive capacity (stressor independent) based on trait *k*, and t_{ik} represents the presence of trait *k* in species *i*.

Importantly, vulnerability also depends on potential exposure to a stressor. To ensure sensible results, we placed a binary constraint (presence/absence) on exposure potential for each stressor, limiting exposure potential to particular depth zones or ocean zones. For example, a species that only inhabits the mesopelagic depth zone, below 200 m, will never be exposed to ship strikes. If a species cannot be found in any of the spatial or depth zones typically associated with that stressor, exposure potential is zero, eliminating vulnerability:

$$\text{exposure potential modifier } E_{ij} = 1 \text{ when } \sum_z e_{jz} p_{iz} > 0, \text{otherwise } E_{ij} = 0 \qquad (4)$$

where e_{jz} represents possible occurrence of stressor *j* in zone *z*, and p_{iz} represents the possible occurrence of species *i* in zone *z*.

Finally, vulnerability of species i to stressor j depends on its sensitivity S_{ij}, moderated by its specific and general adaptive capacity A_{ij} and G_i, and constrained by its exposure potential E_{ij}. To account for some stressors having more associated traits, we normalized each component by the maximum value for that component, for that stressor, observed across all species. For example, the sensitivity of species i to stressor j is normalized by $S_j' = \max\_\{i = 1, \ldots, n\}(S_{ij})$.

$$\text{vulnerability } V_{ij} = \frac{S_{ij}/S_j'}{1+G_i/G'+A_{ij}/A_j'} \times E_{ij} \qquad (5)$$

The resulting vulnerability score $V_{ij} \in [0, 1]$ is increasing with sensitivity $S_{ij}/S_j' \in [0, 1]$, decreasing with adaptive capacity G_i/G' and $A_{ij}/A_j' \in [0, 1]$, and constrained by exposure potential $E_{ij} \in \{0, 1\}$. Scores were normalized to enable comparison across and between taxa and stressors.

Fishing pressure is treated differently in this analysis because fished species are directly targeted by humans for reasons that do not necessarily align with intrinsic life history traits: and humans have the capacity to efficiently exploit any species that has a value. Consequently, we classified all taxa as sensitive to this stressor, but vulnerability was moderated by traits related to a species' general adaptive capacity. For this stressor, sensitivity was set to 1 and stressor-specific adaptive capacity to 0 for all species, and then vulnerability was calculated according to equation 5 as for all other stressors.

4. Gap filling

To enable the representation of as many species as possible, we used trait data to 'gap fill' up to the family level for the taxa included in our analysis. We calculated means and standard deviations for known species' traits, and then applied those values to impute vulnerability of congeneric and confamiliar species, allowing us to expand our representation from 30,712 to

44,116 species. We were then able to identify which traits/categories are related to a species' vulnerability to particular stressors, and identify patterns of vulnerability across taxonomic groups and stressors. In addition, we carried out a cross-validation analysis to assess how well the gap filling process worked in terms of predicting vulnerability (S2.2).

Analyses were carried out using R statistical software version 4.0.4 (R core team, 2021) and the tidyverse R package version 1.3.0 (Wickham et al. 2019). We accessed the World Register of Marine Species database (WoRMS: www.marinespecies.org) using taxize R package (Chamberlain & Szocs 2013).

Results

1. Traits framework

We compiled data on 42 traits related to movement, reproduction, specialization, spatial scale, and biophysical information (Table 1) across 12 broad taxonomic groups. The experts provided data for both individual species and genus- and higher-level trait values, with thermal preference data from Aquamaps, resulting in a total species count for direct matches (matches driven by traits at a representative rank), as well as those driven by denoting certain species to be representative of a higher rank, of 30712. In total, the trait data represented: cephalopods (*n*=810 species), corals (*n*=319 species), echinoderms (*n*=7901 species), elasmobranchs (*n*=1243 species), marine arthropods (*n*=2094 species), marine mammals (*n*=122 species), molluscs (*n*=184 species), polychaetes (*n*=2008 species), sponges (*n*=7718 species), reptiles (*n*=91 species), bony fishes (*n*=7886 species), and seabirds (*n*=336 species). With subsequent gapfilling and species matching using WoRMS we were able to cover more than 44,000 species across these taxonomic groups.

Movement traits

We identified two key movement categories: adult mobility and planktonic larval duration (PLD), both associated with the ability for high range shift velocity. Species with a limited movement capacity will likely be more vulnerable to locally acting stressors as they cannot move to avoid the stressor. Species were allocated into seven categories of movement, from sessile to nomadic (Table 1). Sedentary species include those that remain in place but can right themselves after disturbance, such as after being overturned by a wave, or dig themselves out of sediment. Passive species include those who move in an undirected manner, such as some groups of jellyfish and planktonic larvae. Vertical residents are those species that move up and down through the water column but remain in one location (such as some species of squid, plankton, and larvae). Species with a shorter PLD will likely be less vulnerable to local stressors, while more vulnerable to global stressors, in terms of sensitivity, as they lack adult levels of protection from stressors such as high temperature or UV exposure (Hernández Moresino & Helbling 2010; Hobday et al. 2006).

Reproductive traits

We identified eleven reproductive traits that relate to population turnover, which partly determines species' ability to respond to anthropogenic pressures at their location (Table 1). Reproductive traits important for adaptive capacity include: 1) reproductive strategy (Juan-Jordá et al. 2012; Sunday et al. 2015; Stelzenmuller et al. 2010; Bender et al. 2013; Ormseth & Spencer 2011); 2) fecundity (King & McFarlane 2003; Gallagher et al. 2014; Juan-Jordá et al. 2012; Ormseth & Spencer 2011; Williams et al. 1995; González-Suárez et al. 2013), defined as the number of offspring per year, where species with fewer offspring would be expected to be more vulnerable (Chessman 2013); 3) lifetime reproductive opportunities (Taylor et al. 2014; Juan-Jordá et al. 2012; Ormseth & Spencer 2011; King & McFarlane 2003), as species that reproduce only once or rarely within their lifetimes are considered less resilient to disturbances; 4) maximum age, as species with longer-life spans are slower to recover from disturbance, as turnover rates are slower than for shorter-lived species (Mace et al. 2008); 5) age at maturity/first reproduction, generation length, following IUCN Red List categories, known to be an important trait for predicting reproductive capacity (Chessman 2013; Taylor et al. 2014; Gallagher et al. 2014; González-Suárez et al. 2013; Juan-Jordá et al. 2012; Ormseth & Spencer 2011).

Species with shorter generation lengths (time to maturity) are expected to have a faster population turnover and therefore more opportunities for evolutionary or epigenetic changes in response to stressors (Bush et al. 2016). Conversely, species that reproduce late (e.g., orange roughy fish) would be considered to be more vulnerable to certain stressors than those that reproduce early due to reduced adaptive capacity; 6) parental investment, in terms of type of birth and parental care; 7) post birth/hatching parental dependence, in terms of the length of this care, as species requiring post birth care, or with high maternal dependence, are more likely to be vulnerable to some stressors than those with no such requirement (Chessman 2013; King & McFarlane 2003); 8) population size, following IUCN Red List categories, where smaller populations tend to be more vulnerable to stressors; 9) number of (geographically defined) sub-populations known to be linked to adaptive capacity, where low numbers are associated with greater vulnerability (Comte & Olden 2017; Williams et al. 1995; Fabri et al. 2014), and; 10) feeding larva (post-hatching metamorphosis) as related to a species' sensitivity, especially in terms of whether larvae are calcifiers or non-calcifiers (Byrne et al. 2018).

Specialization traits

To assess the vulnerability of species in relation to their habitat specialization and sensitivity, we identified a range of traits important for sensitivity relating to physiological tolerance breadths, including: thermal range (Chessman et al. 2013; Comte & Olden 2017) based on sea surface temperatures, salinity, pH, dissolved oxygen, and sensitivity to wave energy (Table 1).

Habitat dependence and condition (Williams et al. 1995; Laidre et al. 2008; Markovic et al. 2017; Jørgensen et al. 2015; González-Suárez et al. 2013), accounting for both within one life-stage (e.g., adult) and across all life-stage (e.g., larvae through to adult) requirements, was also selected. As different habitats are likely to have varying levels of vulnerability to different stressors themselves (*cf.* Halpern et al. 2015), a species' vulnerability will also likely vary across habitats, differentially according to life-stage. Whether species live at the air-sea interface, and have both terrestrial and marine life stages, informs both sensitivity and exposure and thus vulnerability to stressors that operate at these interfaces: for example, species in intertidal habitats have a higher potential to be impacted by land-based pollution or shore-line alteration. Diet breadth (Laidre et al. 2008; Stelzenmuller et al. 2010; Sunday et al. 2015; González-Suárez et al. 2013; Bender et al. 2013), and interspecific interactions (Bender et al. 2013; Markovic et al. 2017) also provide information on specialization. Breeding and foraging ranges, which relate to a species adaptive capacity, are measured using number of sites, following IUCN Red List categories, and whether or not a population is dependent on a particular site (Laidre et al. 2008).

Spatial scale traits

We selected spatial range metrics (Laidre et al. 2008; Stelzenmuller et al. 2010; Fabir et al. 2014; Markovic et al. 2017), based on those used in IUCN Red List assessments, as well as five depth and habitat zones. In general, species with distributions <100 km^2 and those living in the intertidal zone or coastal estuaries will be more vulnerable than species with larger distributions away from the coast, as they will have a limited capacity to move away from potential stressors. Small ranges may also be linked to high habitat specificity, and intertidal and coastal habitats are often discontinuous and relatively small.

Biophysical traits

We based our size categories on broad definitions for microfauna (<0.4 mm), macrofauna (0.5-49 mm) and megafauna (>50 mm) (Watling 2019), and added a larger category (>1000 mm). Calcium carbonate, $CaCO_3$, is a critical component of many species' bodies and life cycles. Species with external $CaCO_3$ structures, and those that have them at both larvae and adult stages are more sensitive to certain stressors, such as ocean acidification (OA). Biomineral vulnerability is related to OA, and different biomineral compositions will confer different vulnerabilities: species with high-Mg calcite structures are more sensitive due to higher solubility than aragonite and calcite-based structures (Morse et al. 2007; Byrne & Fitzer 2020; Fitzer et al. 2019). Disruptions to sound, light, or magnetic fields will affect species that use them for communication or navigation, and pressure wave sensitivity is important for species' sensitivity (Carroll et al. 2017; Peng et al. 2015). We determined six main categories of respiration structures (Table 1), which confer sensitivity according to the specific stressor.

2. Species vulnerability

Across all 12 taxonomic groups, the stressor associated with the highest vulnerability scores was biomass removal, followed by organic pollution, and inorganic pollution and sedimentation (Figure 3). In terms of relative vulnerability across taxa, elasmobranchs had the highest vulnerability to biomass removal, (non-cephalopod) molluscs to organic pollution, marine mammals and reptiles to bycatch (defined as non-targeted biomass removal and discard), and molluscs and echinoderms had the highest vulnerability to inorganic pollution.

Across all stressors, the taxa with the highest vulnerability were molluscs, corals and echinoderms, which were highly sensitive to ocean acidification due to their calcium carbonate structures. Seabirds also had high vulnerability scores, as they are affected by both land-based and ocean-based stressors. While all groups were sensitive to most stressors; polychaetes were more robust on average and thus had the lowest vulnerability scores overall (Fig 3).

For larger, mobile marine vertebrates (elasmobranchs, bony fish, marine mammals, and reptiles), after biomass removal, bycatch, entanglement, and organic pollution were important stressors. Small, sessile invertebrates (corals, echinoderms, sponges, polychaetes) had the highest vulnerability to eutrophication and microplastic pollution, while more mobile invertebrates (marine arthropods and molluscs) were most vulnerable to ocean acidification, organic and inorganic pollution, and eutrophication (Table S6; Figure 3; Figure 4).

Vulnerability to anthropogenic stressors varied according to broad trait groups. Biophysical trait categories (within each of the traits) were linked to sensitivity to 16 of the 22 stressors. Specialization trait categories were linked to sensitivity and general adaptive capacity to 18 of the 22 stressors. Reproduction trait categories were linked to 13 of the stressors, mostly through the general adaptive capacity pathway (but some cases of sensitivity and specific adaptive capacity). Both traits in the movement group (adult mobility and planktonic larval duration) were linked to specific adaptive capacity; the three traits in the spatial scale trait were linked to specific adaptive capacity and general adaptive capacity (depth and zone, and range, respectively).

For the two largest stressor categories (climate change and pollution), many trait categories conferred sensitivity to water temperature (*n*=33) and air temperature (*n*=26), and inorganic (*n*=41) and organic pollution (*n*=31) (Figure 5). The key traits conferring vulnerability to climate change-related stressors are related to the presence of calcium carbonate structures, larval feeding traits, thermal sensitivity, and whether a species exists across the interface of marine and other realms. For pollution-related stressors, planktonic state, size and respiration traits were most important. Combined with limited adaptive capacity in terms of mobility, small invertebrates were most vulnerable to this group of stressors.

Species' vulnerability to bycatch and entanglement was related to body size (with large animals being more vulnerable) and whether a species was found at the air-sea interface. Eutrophication can cause coastal acidification, a function of freshwater runoff, which reduces the pH of seawater. Traits associated with vulnerability to this stressor were mainly related to physiological tolerance (to salinity, pH and dissolved oxygen) and biophysical (calcium carbonate and respiration structures).

Discussion

Solutions to sustainable ocean management are typically informed by data on the distribution of habitats (e.g., coral reefs) and human activities (e.g., fishing, pollution). Cumulative impact maps, for example, have been a critical source of information for answering a diverse array of ocean conservation questions, including: what is the state of our ocean and how is it changing? (Jones et al. 2018; Halpern et al. 2015; 2019); where are the most effective places for implementing area-based management? (Klein et al. 2013; Halpern et al. 2007); and in which places are land-based conservation measures more effective than marine-based conservation measures at protecting marine biodiversity? (Klein et al. 2010; Halpern et al. 2009). However, cumulative impact mapping efforts based on habitat data rather than species data pose important limitations when applied to many classes of conservation problems because stressors impact species differently than habitats.

As there has been rapid growth in the availability of species range maps (www.aquamaps.org), we have a unique opportunity to assess the vulnerability of marine species to human activities. Our framework for assessing the vulnerability of marine species is a first critical step towards generating cumulative human impact maps focused on species, rather than habitats alone. One of the advantages of evaluating sensitivity and adaptive capacity separate from exposure is that it allows for much clearer assessment and understanding of what causes vulnerability, and easy updating when stressor location, magnitudes, and other, characteristics change.

Our analysis of marine species' vulnerability provides assessment of potential impacts from human activities at the species level. As the results are independent of exposure to a stressor, they can predict impacts when severity or duration of exposure increases, thus setting the context for targeted management intervention. Where vulnerability is greatest, avoiding or reducing exposure for a species will have a greater conservation outcome than for a species with lower vulnerability and the same exposure.

It is important to note that increased vulnerability does not always directly transfer to increased impact. To clarify the difference between vulnerability and impact, for example, biomass removal scored highest in terms of vulnerability for marine mammals, but that is not currently the greatest threat to their persistence, as they are not exposed (targeted) to this stressor to the degree that sea cucumbers are, for example. When marine mammals were previously exposed to extensive biomass removal, populations of many species were devastated and some are only now recovering (e.g., Wedekin et al. 2017).

Our results show that, contingent on exposure to these stressors, fishing-, climate change- and pollution-related stressors are those with the greatest potential impact (i.e., they score the highest for vulnerability across the taxa). Stressors related to climate change will become more of a problem over time in relation to species' distributions, and in turn their population dynamics, interspecific interactions and dependencies, and so on. Species distribution shifts are already happening in response to temperature increase (Pecl et al. 2017). Larger, mobile vertebrates (elasmobranchs, marine mammals, reptiles and bony fish) were potentially most at risk from fishing-related stressors (including bycatch and entanglement), and seabirds were also especially potentially vulnerable to these stressors. Incidental capture of non-target taxa such as elasmobranchs, marine mammals, reptiles and seabirds is a large threat to many populations of conservation concern, and understanding when and where this is likely to occur can guide management actions such as fisheries regulations, monitoring programs and moveable protected areas, or reserves, in time and space.

Our finding that terrestrial invasive species and biomass removal are the stressors with the lowest associated response capacities in seabirds (Figure 3) reflect those from a previous global analysis (Dias et al. 2019). Assuming exposure, seabirds are vulnerable to human pressures related to fishing, resource consumption and human-associated invasive species due to a reliance on both land and sea habitats. While their high mobility and large geographic range moderate their exposure to stressors in some cases, their navigation and communication requirements mean that they are also sensitive to noise pollution and storm disturbance, and that they nest on land makes them, along with reptiles, more sensitive to light pollution and sea level rise than other groups.

As the current assessment does not incorporate the geographic extent or severity of stressor exposures, the next step for future research is to combine the spatial distribution of stressors and species with our framework. Doing so will additionally enable us to take into account endemism, phylogenetic uniqueness, diversity and species rarity, especially within the context of risk of extinction. Recently, there has been rapid growth in mapping species ranges (over 33,000 marine species have been mapped, and the number is rapidly growing through use of computer algorithms and machine learning), creating a unique opportunity to drastically improve our ability to inform conservation problems. Creating these maps will enable us to address questions such as how much of the ocean will be required to achieve international marine conservation goals (e.g., Convention on Biological Diversity and United Nation's Sustainable Development Goals), and which conservation actions will most effectively achieve these goals.

Our framework and analysis can help conservation planners and managers, policy makers, and stakeholders identify and assess how various stressors act differently across taxa and can thus help inform more effective management decisions. While previous ocean impact assessments were used to inform protected area design (Jones et al. 2020; Klein et al. 2013) and guide decision-making around which management activities were most cost-effective (Klein et al. 2010), trait-based vulnerability assessments can provide improved information for species-level conservation, which is often the scale at which managers operate. For example, such assessments will be critical for prioritising actions for species conservation, whether focused on a species that has different and multiple stressors operating at different life-history stage

(Hazlitt et al. 2010; Hamilton et al. 2017; Klein et al. 2017), or on determining which management actions would secure the most threatened species (Joseph et al. 2009).

Where habitats or ecosystems are the focus of protection, they may persist while ecosystem function is lost, or individual species populations decline severely (Hamilton et al. 2017). The implications of coarse habitat-level data include poor location-specific management actions to mitigate certain stressors that cause uneven and varied pressures within an ecosystem. While protected area design based on ecosystem vulnerability (Jones et al. 2020; Trew et al. 2019; Klein et al. 2010) can offer broad habitat protection, using trait-based species assessments can allow for much more precise targeting of protection, thus avoiding potential conflicts over where to locate conservation areas while still balancing human dependence on marine resources that are sustainable.

Similarly, where stressors cross ecosystem and political boundaries, such as land-based run-off, species-level assessments can guide co-management of stressors in relation to particular species that are affected. For example, molluscs, echinoderms and marine arthropods showed the highest vulnerability to sedimentation, eutrophication and nutrient pollution, in coastal or littoral areas. Conservation actions aimed at promoting the persistence of species populations of these groups can target management of runoff to reduce its impacts on these taxa.

While we developed our framework to be as flexible and broadly applicable as possible, it does not capture temporal aspects of a species' vulnerability – it is not able to differentiate between ongoing or temporary sensitivity, or cumulative sensitivity, nor capture the relative severity or spatial extent of stressors to which species may be exposed. It is possible therefore that ongoing stressors, such as those related to climate change, for example increasing ocean temperature and ocean acidification, may be underestimated in comparison with one-time factors, such as entanglement. The ongoing stressors are likely to increase over time and cause more deaths, in marine mammals for instance, compared to other more temporary stressors. This may confound understanding of which stressors are more important to address in some cases. For example, although biomass removal may be the most prominent stressor impacting a marine species now, climate change may have long-term impacts that have not yet affected that species' vulnerability and overall impact (e.g., Beaugrand et al. 2003). Similarly, we could not capture how vulnerability to a stressor may vary with life stage, so a temporary stressor may not have an impact on adults, for example, but may affect larval stages, which may display different life history traits to adults, such as in relation to which oceanic zone they inhabit (e.g., Hamilton et al. 2017).

While we were able to collate and analyse data for a broad range of invertebrate and vertebrate taxa, there are more than 237,000 marine species listed in WoRMS, and inevitably it was not possible to include everything. Although we were able to generalize the available species-level datasets to higher taxonomic levels to represent more species/groups, the current analysis does not cover marine plants, algae, and phytoplankton, and these could be promising targets for future trait-based research. We included plants and algae early on in the process, however deriving universal response capacities for plants and animals was problematic with some traits. For example, body size in animals and in plants confer completely different response capacities to the same type of stressor: plants could therefore not be meaningfully included in the current analysis. However, there are macroalgal traits that may confer comparable response potential to a stressor, for instance, in the case of ocean acidification and biomineralization, where calcifying (coralline) red algae with high-Mg calcite skeletons are quite sensitive to low seawater pH (Diaz-Pulido et al 2012). Similarly, temperate and cold-water kelp species that have restricted habitat distributions are more vulnerable than species with larger distributions (Wernberg et al., 2016).

Our vulnerability assessment framework is ambitious, in that it was designed to apply to any marine invertebrate or vertebrate species. This generality is important, as new species are increasingly discovered and the use of computer algorithms and machine learning has increased our capacity to accurately map the distribution of more species: the framework can be tested and improved as new data are available. While this assessment allows us to measure relative vulnerability among taxonomic groups, anthropogenic stressors are complex, and the selected traits are necessarily broad: it is not possible to capture all nuances and details at all levels (e.g., indirect impacts such as stressors impacting a target species' food species were not accounted for), but represents a reasonable trade-off between tractability, data availability, and accuracy. Given data limitations in most situations, and especially in our rapidly changing world, realistic approaches to assessments of vulnerability are needed, and our framework represents such an approach.

Species are exposed to multiple threats, but extinction risk is not linearly related to the number of threats they face: it is not a simple question of a species being more at risk the more threats it faces (Greenville et al. 2020). Our novel global trait framework captures adaptive capacity and sensitivity for a species, and allows us to identify patterns across traits and taxa, providing knowledge of species' vulnerability to a range of anthropogenic stressors, which can guide effective conservation management action, especially in the absence of comprehensive information on the direct impact of stressors on the vast majority of marine organisms. In particular, our framework will be useful for conducting a range of global marine assessments used to inform international conservation policies and agreements (e.g., Convention on

Biological Diversity, UN Sustainable Development Goals), which form the foundation for many national conservation and management actions.

The most prevalent 11 of our 22 anthropogenic stressors are linked with either removal (targeted fishing and bycatch), substance pollution (nutrient, inorganic, organic, microplastic, poisons, sedimentation), or global heating (ocean acidification, salinity, water temperature). Thus, management of these stressors in particular can protect the greatest number of marine species. Trait-based vulnerability assessments can provide improved information for species-level conservation, which is often the scale at which managers operate, and our novel framework can be applied to specific taxa, management units, regions, or threats. Such assessments will be critical for prioritising actions for species conservation, whether focused on a species that has different and multiple stressors operating at different life-history stage, or on determining which management actions would best protect marine biodiversity. In the absence of species-based vulnerability data, decision makers are forced to use poor and outdated information, leading to potentially ineffective or inadequate responses to threats to protect marine biodiversity.

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Table 1: Species traits used for assessing the vulnerability of any marine species to stressors, as related to sensitivity and adaptive capacity. For each trait, we list categories used in the assessment. See Table S2 for full category definitions and summaries for sensitivity and vulnerability in relation to the trait, details on the habitat types, depth and zones.

Trait	**category/units**
Movement (Range shift velocity)	
adult mobility	sessile; sedentary; passive; vertical migrator; mobile resident; horizontal migrator; nomadic
planktonic larval duration (PLD)	log scale (<1 day; <1 week; <1 month; <4 months; 4 months -1yr; >1yr; no larvae)
R (Reproductive Traits)	
reproductive strategy	sexual dioecious; sexual hermaphrodite; asexual; colonial
fecundity	<1/per year; 1-2; 2-5; 5-10; 10-20; 20-50; 50-100; 100-1000; 1000-10,000; >10,000
number of lifetime reproductive opportunities	1; 2-10; 11-25; 26-50; 51-100; 100+
age to 1st reproduction/generation time	>20yrs; 10-20yrs; 5-10yrs; 1-5yrs; <1yr
max age	>100yrs; 20-100yrs; 10-20yrs; 5-10yrs; 1-5yrs; 3months-1yr; <3months

parental investment	live birth/ egg care; spawner; egg-layer (unattended)
post-birth/hatching parental dependence	>year; month-year; week-month; <week; NA
global population size	<1000; 1K-10K; 10K-100K; 100K-1M; >1M
Are there sub-populations?	yes; no
feeding larva (post-hatching metamorphosis)	Larval type: feeding; non-feeding; no larva; NA
can the sex ratio be altered by temperature?	yes; no

Specialization

physiological tolerance breadths	
thermal – preferred tolerance range (°C)	0-2.5; 2.5-5; 5-7.5; 7.5-10; 10-15; >15
thermal - sensitivity to heat spikes/heat waves	yes; no
Salinity	stenohaline; euryhaline; NA
pH	<7.4; 7.5-7.7; 7.8-8.2 pH categories - use change over the year to derive tolerance
dissolved oxygen (changes in)	low tolerance; medium tolerance; high tolerance; air breathers
sensitivity to wave energy (physical forcing)	sensitive; not sensitive; NA (e.g. sea grass/limpet/whale)
photosynthetic	yes; no
air-sea interface	floating; yes; no
dependent habitats + condition	yes; no (across and within stage)
habitat forming	yes; no
terrestrial and marine life stages	yes; no
extreme diet specialization	specialist; generalist; NA
dependent interspecific interactions	yes; no
breeding/nesting range/number of spawning aggregations (fish)	one; few; many; does not aggregate; NA
sub-population dependence on particular sites	yes; no
foraging range no. of sites, incl. terrestrial wetlands	one; few; many; NA
sub-population dependence on particular sites	yes; no

Spatial Scale of species

Extent of Occurrence (EOO) (range)	<99km^2; 100-4999; 5000-19,999 >20,000
depth (min/max)	air, epipelagic; mesopelagic; bathypelagic; abyssopelagic; hadopelagic
zone	intertidal; neritic; oceanic; demersal; benthic

Biophysical Traits

adult body mass/body size	>1000 mm; 50 mm-999 mm; 0.5-49 mm; <0.4 mm
calcium carbonate structure location	none; internal; external with a cover; external; in external; protein matrix/in cellulose cell wa

calcium carbonate structure stages	none; larvae; adult; both
biomineral	aragonite; High-Mg calcite; calcite; chitin/$CaCO_3$ mix; silicate; other
flight	yes; no
communication requirement (sound)	yes; no
navigation requirements (sound or light, or magnetic)	Light; sound; magnetic; none
extreme pressure wave sensitive structures	high; medium; low sensitivity
respiration structures	lungs; gills; skin; diffusion; pneumatophores; filter feeders

Figure legends

Figure 1: A species' vulnerability to a stressor is made up of its sensitivity and adaptive capacity (intrinsic factors, determined by biological characteristics, or traits), which combine with exposure (to the threat, an external factor), to give the overall impact of the stressor (Source: Butt et al. 2016).

Figure 2: Overview of the different steps in the analysis, including expert elicitation to develop the traits framework (left), and development of the traits-stressor matrix from which the vulnerability scores were derived (right).

Figure 3: Relative vulnerability scores across all stressors and taxa. Boxplot mid-line indicates median; red point indicates mean; boxes are the interquartile range and whiskers indicate the furthest point within 1.5x interquartile range; dots represent outliers outside that distribution. The taxa are grouped into vertebrates and invertebrates, ordered by decreasing overall vulnerability. The stressors are ordered by decreasing impact: biomass removal; organic pollution; inorganic pollution; sedimentation; microplastic pollution; poisons & toxins; eutrophication & nutrient pollution; bycatch; increasing water temperature; changes in salinity; ocean acidification; habitat loss & degradation; light pollution; increasing storm disturbance; oceanographic processes; macroplastic pollution; increasing ultraviolet radiation; sea level rise; increasing air temperature; noise pollution; wildlife strike; invasive species.

Figure 4: Mean vulnerability for the top three stressors for each broad threat (pollution, fishing, climate change), and the top four vulnerable taxa.

Figure 5: Proportion of trait categories conferring sensitivity to a) pollution-related stressors (top, in dark blue), and b) climate change-related stressors (bottom, in turquoise).

Figures

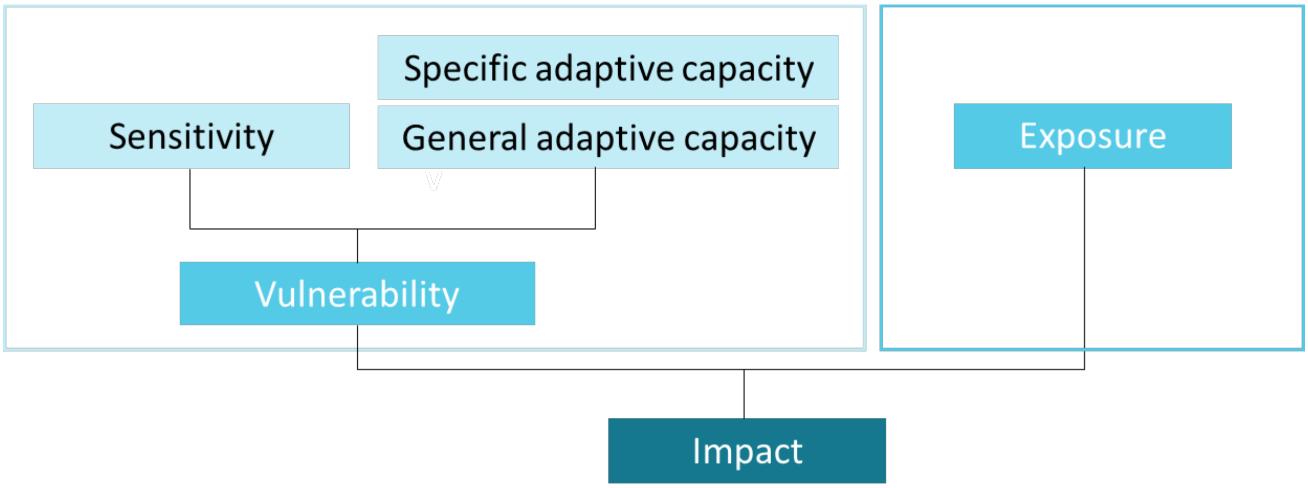
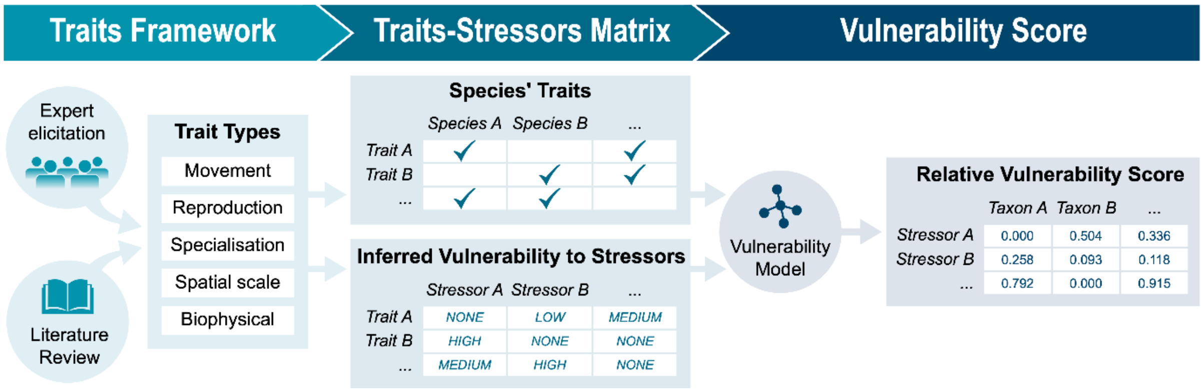

Specific adaptive capacity
Sensitivity
General adaptive capacity
Exposure
Vulnerability
Impact

Figure 1

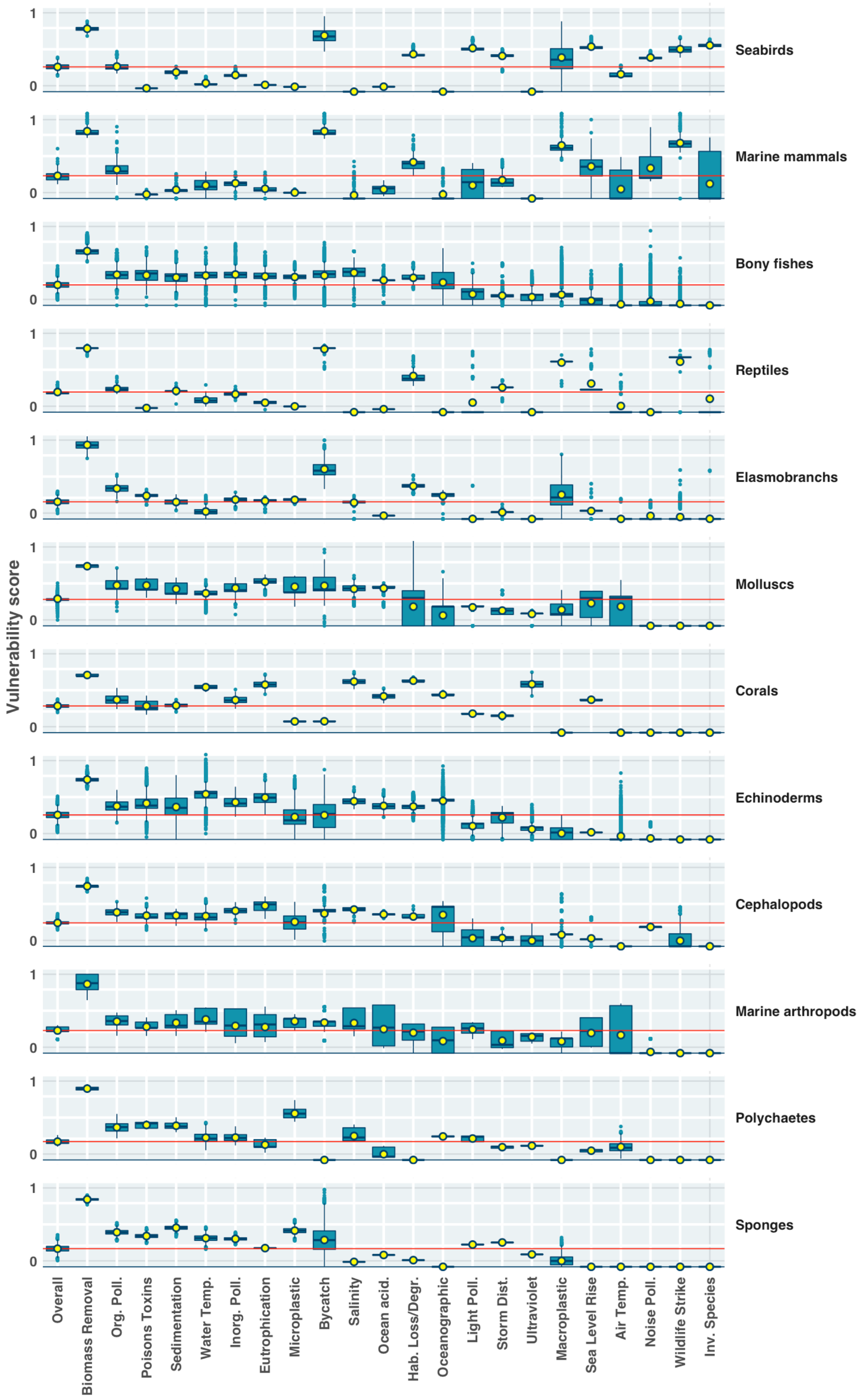


	Species A	*Species B*	...
Trait A	✓		✓
Trait B		✓	✓
...	✓	✓	

	Stressor A	*Stressor B*	...
Trait A	*NONE*	*LOW*	*MEDIUM*
Trait B	*HIGH*	*NONE*	*NONE*
...	*MEDIUM*	*HIGH*	*NONE*

	Taxon A	*Taxon B*	...
Stressor A	0.000	0.504	0.336
Stressor B	0.258	0.093	0.118
...	0.792	0.000	0.915

Figure 2



1129

1130 Figure 3

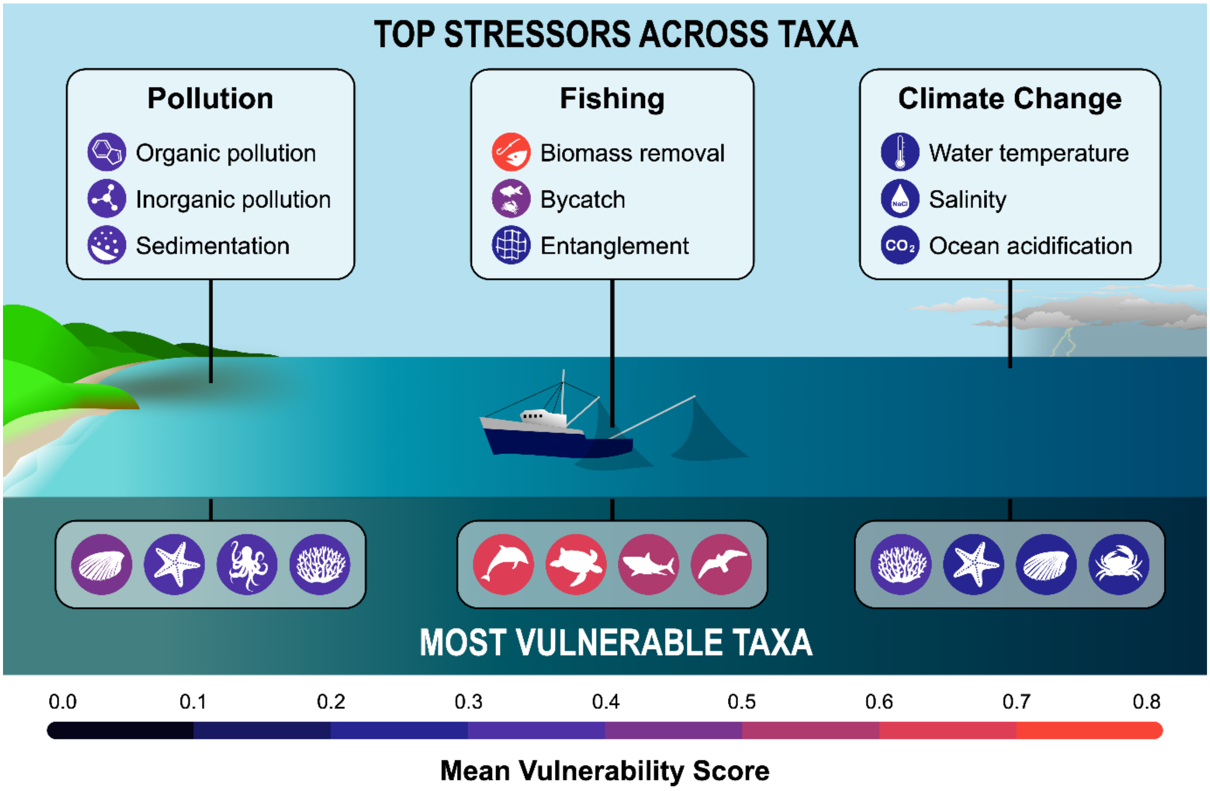

TOP STRESSORS ACROSS TAXA
Pollution
Organic pollution
Inorganic pollution
Sedimentation
Fishing
Biomass removal
Bycatch
Entanglement
Climate Change
Water temperature
Salinity
Ocean acidification
MOST VULNERABLE TAXA
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Mean Vulnerability Score

Figure 4

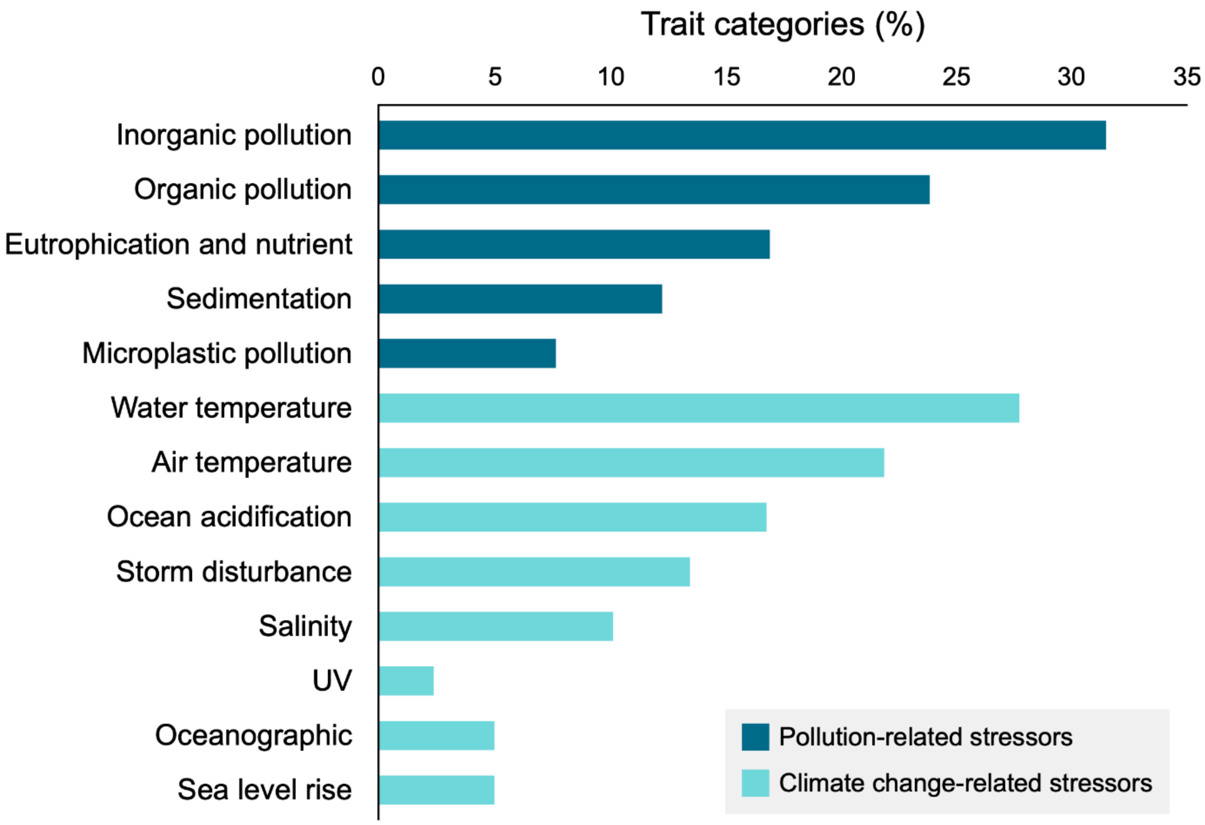

Trait categories (%)
0
5
10
15
20
25
30
35
Inorganic pollution
Organic pollution
Eutrophication and nutrient
Sedimentation
Microplastic pollution
Water temperature
Air temperature
Ocean acidification
Storm disturbance
Salinity
UV
Oceanographic
Sea level rise
Pollution-related stressors
Climate change-related stressors

Figure 5

Supplementary Information Section 1

Table S1: Taxonomic groups used to develop trait framework

Table S2: Species traits used for assessing the vulnerability of any marine species to stressors, as related to sensitivity and adaptive capacity, including full category definitions and summaries for sensitivity and vulnerability in relation to the trait, details on the habitat types, depth and zones. For each trait, we indicate which categorical or binary category was used in the assessment.

Table S3: 22 anthropogenic stressors used in the analysis: explicit pathways, activities, and drivers.

Table S4: Reference database for literature used inform vulnerability values, listing stressors and trait categories.

Table S5: Full references for Table S4.

Table S6: Vulnerability scores for each taxon and stressor.

Supplementary Information Section 2

S2.1. Sensitivity testing of scaling and ranking of vulnerability

Figure S2.1. Sensitivity testing of scaling and ranking of vulnerability

Figure S2.1.2: Distribution of vulnerability scores by taxon for three scoring functions. Distributions represent average vulnerability across all stressors.

Figure S2.1.3: RMS shift in normalized rank by stressor, across all assessed species.

Figure S2.1.4: RMS shift in normalized rank across all stressors, by taxon.

S2.2 Gap-filling sensitivity analysis

Figure S2.2.1: RMSE of imputed vulnerability score using leave-one-out cross-validation, for each stressor and taxon at various taxonomic ranks.