Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

Climate vulnerable fish communities are also most exposed to human pressures

Fernanda da Silva

fcads@aqua.dtu.dk

DTU https://orcid.org/0000-0003-2730-9203

P. Daniël van Denderen

DTU aqua https://orcid.org/0000-0001-6351-0241

Antoni Pons

Centre d'Estudis Avançats de Blanes (CEAB-CSIC)

Federico Maioli

DTU

Marcel Solé

CREAF, Cerdanyola del Vallès

Martin Lindegren

Technical University of Denmark https://orcid.org/0000-0002-9185-951X

Biological Sciences - Article

Keywords:

Posted Date: March 26th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-8925690/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Additional Declarations: There is **NO** Competing Interest.

Abstract

The climate crisis has far-reaching consequences on the health and integrity of ecosystems1. More specifically, warming causes shifts in species distributions and interactions, ultimately altering the structure and functioning of ecosystems2–4. The response and sensitivity of marine organisms to climate change have commonly been assessed using temperature-based indices5–8. However, the exclusive focus on temperature overlooks other key environmental stressors affecting marine life, such as deoxygenation and freshening9–11. Here we assess the sensitivity of marine organisms to multiple environmental factors by estimating the single and cumulative Environmental Safety Margins (ESM) of marine fish communities throughout the North Atlantic and Northeast Pacific over the past 30 years. We find ESMs and their underlying stressors to differ between ocean provinces with generally unsafe conditions in lower latitudes and estuarine systems. Furthermore, we demonstrate regional differences in the relative importance of environmental stressors, with temperature, oxygen limitation and low salinities constraining species and communities differently across provinces. The areas deemed most unsafe to climate change are also facing the highest cumulative pressures from fishing, shipping and land-based stressors. These results highlight that climate vulnerable fish communities are also most exposed to human pressures revealing an urgent need for improved conservation efforts.

Introduction

Ecological communities worldwide are exposed to climate change with major implications for the health and integrity of marine ecosystems[12]. Besides ocean warming, higher temperatures reduce oxygen solubility, creating a mismatch between oxygen supply and the metabolic demand of marine organisms[2,4], as well as induce pronounced changes in salinity due to variations in precipitation, ice melting and evaporation[13]. In addition, global change affects ocean acidification, wind patterns, and ocean currents, triggering cascades that alter stratification, nutrient fluxes, and primary production at the base of marine food webs[2,14,15]. Therefore, warming alone is unlikely to fully explain the response and reorganization of communities under climate change.

To better understand and anticipate future responses and impacts of climate change on marine life, a more holistic approach accounting for the joint sensitivity of a changing ocean environment beyond temperature is therefore needed[16]. Here we develop a comprehensive, multi-factor approach to evaluate and compare the overall community sensitivity of marine organisms along multiple climate-related stressors. Because proximity to environmental limits often correlates with population-level responses[17], the difference between upper and lower limits and the *in-situ* conditions experienced can provide an index of a species' tolerance to current and future climate change[8,18,19]. Here we quantify the single and joint Environmental Safety Margins (ESM) between species tolerance ranges relative to the actual set of environmental conditions experienced by communities sampled in both time and space. More specifically, we use an extensive collection of standardized bottom-trawl surveys throughout the North-Atlantic and Northeast Pacific (including >1500 fish species) to assess the upper and lower ESMs of

marine fish to temperature (USM/LSM Temp), as well as the lower ESM for oxygen (LSM O_2) and salinity (LSM S) at each unique sample location (see methods for more detail). Subsequently, we investigate and compare cross-regional patterns and temporal changes in ESMs to past and current climatic changes over the last three decades. We also compare observed ESMs to a null model in which tolerance values are randomly permuted among taxa, thereby distinguishing between patterns in ESM arising from environmental filtering and stochastic (neutral) assembly processes[19,20]. Finally, we provide practical guidance for improved marine management and conservation by identifying particularly vulnerable areas while accounting for other cumulative human pressures such as fishing, shipping and pollution[21], as well as the current global coverage of marine protected areas (MPAs).

ESM differs between ocean provinces

We find pronounced large-scale patterns in the joint ESMs with higher-latitude communities, particularly in the North-east Atlantic exhibiting larger margins and relatively fewer species at risk (Fig. 1a-b). In contrast, a greater proportion of species are experiencing “unsafe” conditions (closer to their tolerance limits) in lower-latitude communities (e.g., the Gulf of Mexico) and semi-enclosed estuarine systems (e.g., the Baltic Sea and Gulf of St Lawrence). The underlying environmental stressors determining the overall degree of safety differ markedly between marine provinces (Fig. 1c). Notably, the higher safety in the Arctic and Northern European Seas is manifested by large margins across all environmental stressors, except for LSM Temp (i.e., low temperatures), while the Warm temperate Northwest Atlantic demonstrates small margins for all stressors. These differences in the overall ESM and their underlying stressors are fairly consistent over time. However, in some regions a slight decline in the overall safety is evident, especially with regards to decreasing USM Temp in more recent decades, likely resulting from warming (Fig. S1- S4). To assess the role and relative importance of the observed community composition in shaping the overall degree of safety, we repeated the analysis while randomizing tolerance ranges from the global pool of species. The results of our null model test show significant standardized effect sizes (SES = (mean ESM – mean ESM_{null}) / standard deviation ESM_{null}) for some environmental stressors and provinces (Fig. 1d), highlighting that ESMs based on the actual species composition differs from a randomly assembled community. Notably, USM Temp was found to be significantly lower in the Arctic and Cold temperate Northwest Atlantic, indicating that communities are closer to their upper thermal limits and thus less safe than expected by chance. This is likely due to the dominance of cold-adapted species with relatively narrow upper thermal tolerance ranges compared to the entire species pool[5,22]. In contrast, the Warm Temperate province exhibited values of USM Temp larger than expected from the null model, likely reflecting the presence and prevalence of more warm-affinity species adapted to higher temperatures. Similarly, greater SES for LSM O_2 was found for the Cold Temperate Northeast Pacific, indicating communities better adapted to low oxygen concentrations, likely resulting from exposure to past and current hypoxia caused by the widespread oxygen minimum zones in this region[23–25].

Taken together, our findings indicate the important role of environmental filtering structuring marine fish communities[19,26] by selecting species with particular traits capable of tolerating the range of physiological and behavioral adaptations that enhance tolerance to environmental stressors[27]. For example, ectotherms exposed to extreme high or low temperatures may produce heat shock or antifreeze proteins to mitigate cellular damage and physiological disruption[27,28]. Similarly, mobile species may simply avoid exposure to such extremes by seeking habitats with more favorable conditions, such as migrating toward higher latitudes or into deep waters[4]. This phenotypic and behavioral plasticity may likely contribute to the persistence of communities even under extreme or generally unsafe conditions, reflected by low ESMs in for instance the Gulf of Mexico and the Baltic Sea. However, the degree to which these, or other communities will continue to persist into the future will be profoundly altered by the rapid rate of climate change globally, both in terms of means and variability. Hence, species and communities showing generally safe margins over the past 30 years may rapidly approach or exceed their physiological tolerance limits with continued warming. This is particularly urgent for more cold-adapted species due to their generally narrower niche widths (Fig S5), at least compared to species adapted to more seasonal environments. Hence, provinces currently displaying "safe" conditions, such as the Arctic will likely be more vulnerable to future environmental changes. While ESMs provide valuable insights into community-level vulnerability, their interpretation should be approached with caution. Especially, since physiological stress can cause impaired growth, reproduction and survival well before safety margins reach zero, while physiological acclimatization or behavioral flexibility may confer greater tolerance than currently estimated[18]. Moreover, safety at the community level does not guarantee protection for individual species, since environmental shifts may disproportionately affect specific taxa, leading to cascading community reorganization if colonizers respond differently to change. Finally, some aspects of species' ecological niches remain poorly characterized, introducing uncertainty that may either over- or underestimate ESMs. For instance, climate change may expose parts of the fundamental niche that are currently inaccessible[29] and incorporating these facets into niche modelling could improve predictions of community vulnerability.

Anthropogenic pressures and conservation

While climate change is recognized as one of the major threats to biodiversity with impacts likely to accelerate during the coming decades[30], other human stressors can strongly limit species' capacity to tolerate and adapt to shifting climatic conditions. Our results reveal a strong negative association between the joint ESM and multiple human pressures[21], including fishing, shipping, and land-based activities such as nutrient and organic chemical pollution (Fig. 2a-c). This emphasizes that communities that are currently most vulnerable to multiple environmental conditions are also those potentially most impacted by other human activities and pressures. Together, these interacting pressures may significantly amplify risks and accelerate ecological decline in marine ecosystems by jointly affecting multiple ecological processes of species related to feeding, growth, reproduction and survival. Finally, we show no relationship between the current coverage of MPAs and the overall degree of climate safety throughout the area (Fig. 2d). Hence, the alleged mitigation potential of MPA as refugia or stepping

stones for dispersal, and safe zones for climate vulnerable species[31] seems currently limited. We believe that our holistic ESM approach, which accounts for the joint sensitivity of species and communities to multiple environmental stressors beyond warming, represents a more robust, precautionary, and broadly applicable framework for climate risk assessment. This framework can inform the designation of MPA networks towards better prioritization of global conservation efforts for biodiversity and overall sustainability under climate change. Integrating our approach into conservation planning could further enhance protection outcomes and help align management actions with global policy targets, such as the Kunming–Montreal Global Biodiversity Framework's goal to protect 30% of the ocean by 2030.

Methods

Bottom trawl survey data

Species and biomass data for marine fish communities were obtained from long-term scientific bottom-trawl surveys across the continental shelves of the Northeast Pacific, Northwest Atlantic, and Northeast Atlantic[32] (Table S1). A total of 1,553 demersal fish species from 227,740 unique hauls covering the time period from 1993 to 2021 were included in the analysis. To evaluate species' tolerance ranges, survey data were standardized across space and time, assigned to hexagonal grid cells, and grouped into three decadal periods (1993–2002, 2003–2012, and 2013–2021).

Sampling effort standardization

Since sampling effort was not uniform across areas, we constructed species accumulation curves (SACs) to assess the completeness of sampling for each cell and decade combination. Subsequently, we fitted a Michaelis-Menten function to each SAC and estimated the asymptotic species richness using the R package *vegan*[33]. For each cell, we then calculated the number of hauls required to reach 75% completeness of the estimated asymptotic species richness. Cells with insufficient sampling to meet this completeness threshold were excluded from the analysis (Fig. S6). To further standardize the dataset, we randomly resampled the estimated number of hauls 99 times (with replacement) and calculated the safety margin metrics (see below) foreach iteration.

ESM calculations

To estimate the environmental safety margins (ESM) we extracted the environmental tolerance limits of each species based on the fitted environmental envelopes from AquaMaps[34,35]. AquaMaps predictions have been validated using independent and effort-corrected survey data[35] and the model performance has been found to be similar to other presence-only species distribution models[34]. Furthermore, we extracted environmental conditions for bottom temperature, salinity and oxygen values by averaging the highest and lowest monthly values within each unique sampling event (by cell and decade). The data were sourced from the ice-ocean model NEMO-Nordic (https://doi.org/10.48670/moi-00013), available through the Copernicus Marine Service (https://marine.copernicus.eu/). Upper (USM) and lower (LSM)

safety margins were calculated for each species (i) per cell per decade and weighted by biomass, following an adjusted version of the method described by Van Der Walt et al. (2021)[8]:

$$\mathrm{USM}_i = X_{\mathrm{max},i} - X_{\mathrm{max,\ env}}$$

$$\mathrm{LSM}_i = X_{\mathrm{min,\ env}} - X'_{\mathrm{min},i}$$

where X denotes the maximum (max) and minimum (min) values of the environment (env) vs the reported species tolerance limits (i). LSM was calculated for all environmental variables, whereas USM was computed only for temperature, as higher concentrations of salinity and oxygen are not expected to limit or increase marine fish species vulnerability. Average USM and LSM values for all variables were then aggregated per grid cell and decade across iterations, resulting in an overall ESM for each community. To enhance visual comparisons of overall ESMs, radar charts were employed to illustrate variations over time and across biogeographic provinces defined by Spalding et al. (2007)[36].

Joint index

The individual ESMs (i.e., USM Temperature, LSM Temperature, LSM Salinity, and LSM Oxygen) were scaled using Min-Max Normalization, ensuring they ranged between 0 and 1. The sum of the four normalized values was then used as a cumulative metric of overall safety margin. In addition, the proportion of species with positive (“safe”) values for at least one ESM metric was estimated, where values near 1 indicate that most species are within their safe environmental conditions.

Anthropogenic pressures

To assess relationships between the estimated joint ESMs and human pressures, we utilized the most up-to-date marine pressure data from Halpern et al. (2019)[21], available at ~1 × 1 km resolution globally. Cumulative impact was calculated by summing raster layers representing 11 stressors, grouped into three categories: (1) Fishing: commercial demersal (destructive, non-destructive high bycatch, non-destructive low bycatch), pelagic (high and low bycatch), and artisanal; (2) Ocean-based: shipping; and (3) Land-based: nutrient pollution, organic chemical pollution, direct human impact, and light pollution. To account for temporal variability, we computed the average value of each group per grid cell over the period 2003–2013. The cumulative safety margins used in the models were aligned with the temporal span of anthropogenic pressures (2003–2013).

Marine Protected Areas (MPA)

Data on MPAs, marine reserves, and other effective area-based conservation measures (OECMs) were obtained from the publicly available Protected Planet database (https://www.protectedplanet.net/en). This database provides the World Database on Protected Areas, a key global resource for area-based conservation efforts. We created a map of protected areas overlaid with hexagonal grid cells containing fish data and calculated the percentage of each cell covered by any type of MPA. The relationship

between cumulative safety margins and MPA coverage was then modeled using Generalized Additive Models, which allow for nonlinear relationships.

Declarations

Data availability

The fish community's data and biomass estimation for all marine provinces are available from FishGlob project https://doi.org/10.1038/s41597-023-02866-w[37], complemented with bottom-trawl survey data from Greenland[38] and Iceland[39] through the EU project B-USEFUL (https://b-useful.eu/), as well survey data from New Foundland[40] kindly contributed by Fisheries and Oceans Canada, Newfoundland and Labrador Region. Environmental tolerances used in this study are publicly available through AquaMaps (https://aquamaps.org/) and can be accessed using the R package "aquamapsdata" at https://raquamaps.github.io/aquamapsdata/articles/intro.html. The satellite data for sea temperature, salinity and oxygen are available from Copernicus Marine Environment Monitoring Service (CMEMS) and are available through http://marine.copernicus.eu/. Data on conservation measures are available at Protected Planet database through https://www.protectedplanet.net/en.

Code availability

The code used to perform the analysis in R is available at ZENODO (https://doi.org/10.5281/zenodo.18350751).

Acknowledgements

We thank D.R. for the inputs and suggestions at the beginning of this project. This research was made possible by the support of the EU Projects B-USEFUL (Grant Agreement 101059823) and ACTNOW (Grant Agreement 101060072). P.D.V.D. was funded by a research grant (VIL60703) from VILLUM FONDEN. A.V.P. was supported by a Juan de la Cierva research grant, funded by MICIU/AEI /10.13039/501100011033 and by FSE+.

Contributions

F.S.: conceptualization, methodology, investigation, project administration, formal analysis, visualization and writing - original draft preparation. D.V.D.: methodology, investigation, and writing - review and editing. A.V.P.: methodology, investigation and writing - review and editing. F.M.: methodology, investigation and writing - review and editing. M.M.S.: methodology, investigation and writing - review and editing. M.L.: conceptualization, methodology, investigation, resources, funding acquisition, and writing - review and editing.

Corresponding author

Correspondence to Fernanda C Silva.

References

1. IPCC. Summary for Policymakers. In: Global Warming of 1.5°C. *Intergovernmental Panel on Climate Change (IPCC)* 7–22 (2018).
2. Doney, S. C. *et al.* Climate Change Impacts on Marine Ecosystems. *Annual Review of Marine Science* **4**, 11–37 (2012).
3. Munday, P. L., Warner, R. R., Monro, K., Pandolfi, J. M. & Marshall, D. J. Predicting evolutionary responses to climate change in the sea. *Ecology Letters* **16**, 1488–1500 (2013).
4. Pinsky, M. L., Selden, R. L. & Kitchel, Z. J. Climate-Driven Shifts in Marine Species Ranges: Scaling from Organisms to Communities. *Annual Review of Marine Science* **12**, 153–179 (2020).
5. McLean, M. *et al.* Disentangling tropicalization and deborealization in marine ecosystems under climate change. *Current Biology* **31**, 4817-4823.e5 (2021).
6. Zarzyczny, K. M., Rius, M., Williams, S. T. & Fenberg, P. B. The ecological and evolutionary consequences of tropicalisation. *Trends in Ecology & Evolution* S0169534723002732 (2023) doi:10.1016/j.tree.2023.10.006.
7. Stuart-Smith, R. D., Edgar, G. J., Barrett, N. S., Kininmonth, S. J. & Bates, A. E. Thermal biases and vulnerability to warming in the world's marine fauna. *Nature* **528**, 88–92 (2015).
8. Van Der Walt, K.-A., Porri, F., Potts, W. M., Duncan, M. I. & James, N. C. Thermal tolerance, safety margins and vulnerability of coastal species: Projected impact of climate change induced cold water variability in a temperate African region. *Marine Environmental Research* **169**, 105346 (2021).
9. Borges, F. O., Sampaio, E., Santos, C. P. & Rosa, R. Impacts of Low Oxygen on Marine Life: Neglected, but a Crucial Priority for Research. *The Biological Bulletin* **243**, 104–119 (2022).
10. Deutsch, C., Penn, J. L. & Lucey, N. Climate, Oxygen, and the Future of Marine Biodiversity. *Annu. Rev. Mar. Sci.* **16**, 217–245 (2024).
11. Salin, K., Auer, S. K., Rey, B., Selman, C. & Metcalfe, N. B. Variation in the link between oxygen consumption and ATP production, and its relevance for animal performance. *Proc. R. Soc. B.* **282**, 20151028 (2015).
12. Rosenzweig, C. *et al.* Attributing physical and biological impacts to anthropogenic climate change. *Nature* **453**, 353–357 (2008).
13. Skliris, N. *et al.* Salinity changes in the World Ocean since 1950 in relation to changing surface freshwater fluxes. *Clim Dyn* **43**, 709–736 (2014).
14. Behrenfeld, M. J. *et al.* Climate-driven trends in contemporary ocean productivity. *Nature* **444**, 752–755 (2006).
15. Boyce, D. G., Lewis, M. R. & Worm, B. Global phytoplankton decline over the past century. *Nature* **466**, 591–596 (2010).
16. Pörtner, H. O., Langenbuch, M. & Michaelidis, B. Synergistic effects of temperature extremes, hypoxia, and increases in CO2 on marine animals: From Earth history to global change. *Journal of Geophysical Research C: Oceans* **110**, 1–15 (2005).

17. Hamblin, A. L., Youngsteadt, E., López-Uribe, M. M. & Frank, S. D. Physiological thermal limits predict differential responses of bees to urban heat-island effects. *Biol. Lett.* **13**, 20170125 (2017).
18. Pinsky, M. L., Eikeset, A. M., McCauley, D. J., Payne, J. L. & Sunday, J. M. Greater vulnerability to warming of marine versus terrestrial ectotherms. *Nature* **569**, 108–111 (2019).
19. Cadotte, M. W. & Tucker, C. M. Should Environmental Filtering be Abandoned? *Trends in Ecology & Evolution* **32**, 429–437 (2017).
20. Keddy, P. A. Assembly and response rules: two goals for predictive community ecology. *J Vegetation Science* **3**, 157–164 (1992).
21. Halpern, B. S. *et al.* Recent pace of change in human impact on the world's ocean. *Sci Rep* **9**, 11609 (2019).
22. Frainer, A. *et al.* Climate-driven changes in functional biogeography of Arctic marine fish communities. *Proceedings of the National Academy of Sciences* **114**, 201706080–201706080 (2017).
23. Moffitt, S. E. *et al.* Paleoceanographic Insights on Recent Oxygen Minimum Zone Expansion: Lessons for Modern Oceanography. *PLoS ONE* **10**, e0115246 (2015).
24. Ross, T., Du Preez, C. & Ianson, D. Rapid deep ocean deoxygenation and acidification threaten life on Northeast Pacific seamounts. *Global Change Biology* **26**, 6424–6444 (2020).
25. Busecke, J. J. M., Resplandy, L., Ditkovsky, S. J. & John, J. G. Diverging Fates of the Pacific Ocean Oxygen Minimum Zone and Its Core in a Warming World. *AGU Advances* **3**, e2021AV000470 (2022).
26. Beukhof, E. *et al.* Marine fish traits follow fast-slow continuum across oceans. *Scientific reports* **9**, 17878–17878 (2019).
27. Fusi, M. *et al.* The predictability of fluctuating environments shapes the thermal tolerance of marine ectotherms and compensates narrow safety margins. *Sci Rep* **14**, 26174 (2024).
28. Kim, H. *et al.* Marine Antifreeze Proteins: Structure, Function, and Application to Cryopreservation as a Potential Cryoprotectant. *Marine Drugs* **15**, 27 (2017).
29. Chevalier, M., Broennimann, O. & Guisan, A. Climate change may reveal currently unavailable parts of species' ecological niches. *Nat Ecol Evol* **8**, 1298–1310 (2024).
30. Bongaarts, J. *IPBES, 2019. Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. vol. 45 681 (2019).
31. Roberts, C. M. *et al.* Marine reserves can mitigate and promote adaptation to climate change. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 6167–6175 (2017).
32. A. Maureaud, A. *et al.* Are we ready to track climate-driven shifts in marine species across international boundaries? - A global survey of scientific bottom trawl data. *Global Change Biology* **27**, 220–236 (2021).
33. Oksanen, J. *et al.* vegan: Community Ecology Package. R package version 2.3-4. https://CRAN.R-project.org/package=vegan (2016).

34. Hodapp, D. *et al.* Climate change disrupts core habitats of marine species. *Global Change Biology* **29**, 3304–3317 (2023).
35. Ready, J. *et al.* Predicting the distributions of marine organisms at the global scale. *Ecological Modelling* **221**, 467–478 (2010).
36. Spalding, M. D. *et al.* Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience* **57**, 573–583 (2007).
37. Maureaud, A. A. *et al.* FISHGLOB_data: an integrated dataset of fish biodiversity sampled with scientific bottom-trawl surveys. *Sci Data* **11**, 24 (2024).
38. Fock, H. O. Driving-forces for Greenland Offshore Groundfish Assemblages: Interplay of Climate, Ocean Productivity and Fisheries. *J. Northw. Atl. Fish. Sci.* **39**, 103–118 (2008).
39. Sólmundsson, J. *et al.* Manuals for the Icelandic bottom trawl surveys in spring and autumn. (2010).
40. Rideout, R., Ings, D. & Koen-Alonso, M. Temporal And Spatial Coverage Of Canadian (Newfoundland And Labrador Region) Spring And Autumn Multi-Species RV Bottom Trawl Surveys, With An Emphasis On Surveys Conducted In 2018. (2022).

Figures

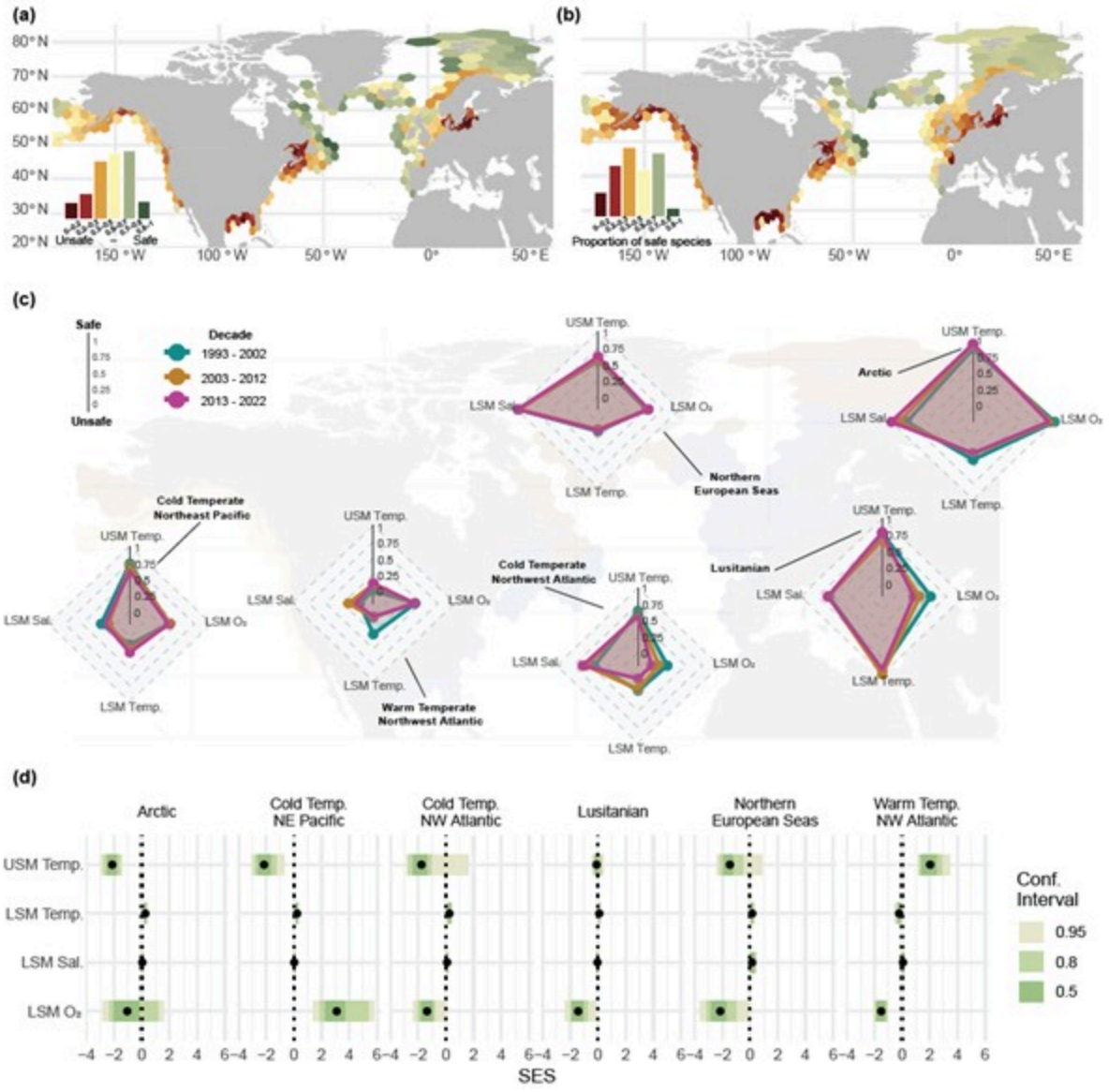


Figure 1

ESMs and their underlying stressors across areas and decades. (a) Spatial distributions of overall ESMs, reflecting the sum of standardized ESM for each environmental stressors (z-transformed and averaged across species and decades by grid cells). (b) The proportion of species within each grid cell displaying ESMs values above zero (i.e., safe conditions). (c) Spatio-temporal patterns of standardized ESMs by marine provinces and decades (colored polygons) ranging from 0 (completely unsafe) to 1 (completely safe). (d) Standardized Effect Size (SES) per ESM and province aiming to distinguish between patterns in ESM arising from environmental filtering from those expected by chance where points represent mean values with corresponding confidence intervals (colors).

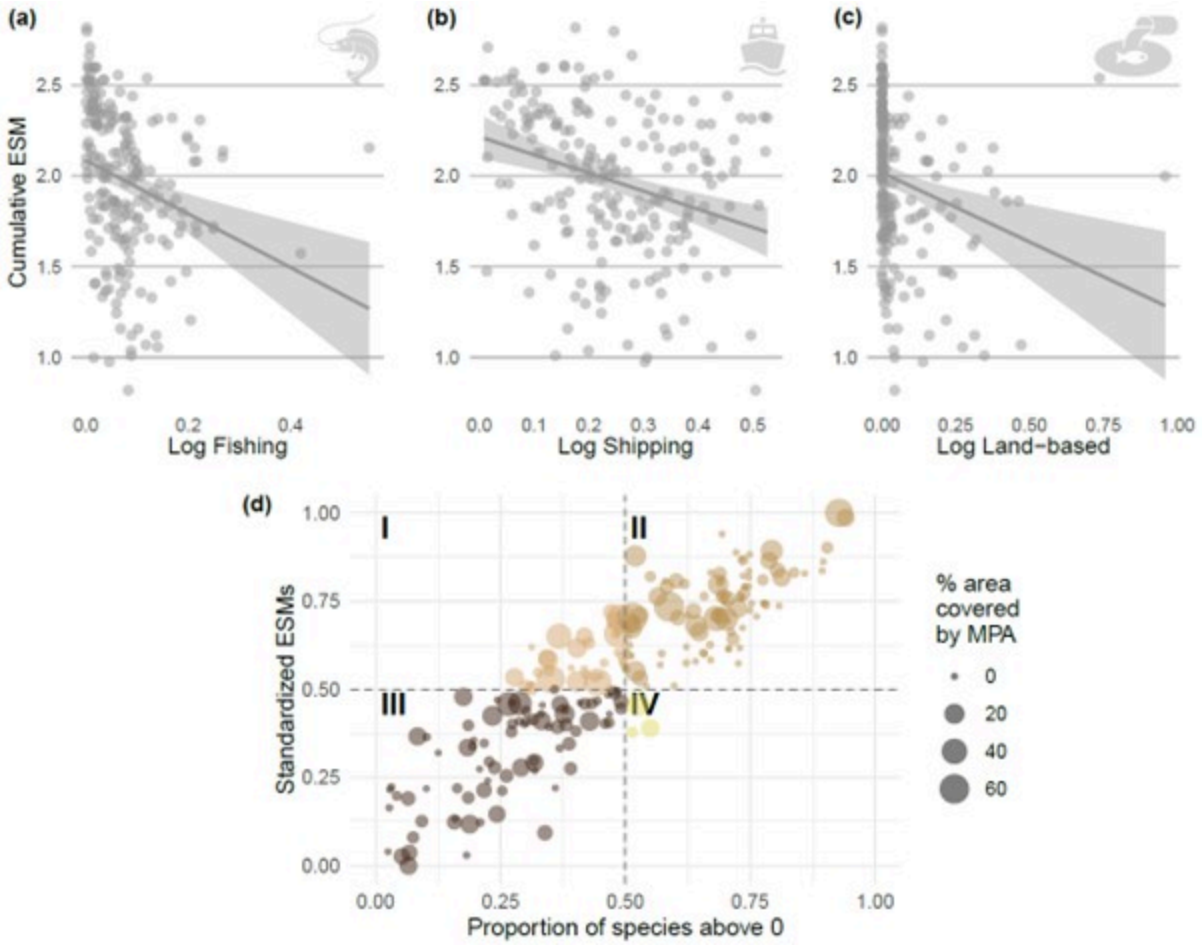


Figure 2

Effects of human pressures and protection on community safety margins.
(a–c) Linear regression models showing consistent negative relationship between cumulative ESM (sum across all ESMs) and human pressures from fishing (industrial tonnes of catch/year), shipping (traffic index/year), and land-based activities (index/km^2). (d) Relationship between standardized ESMs and the proportion of “safe” species (ESM>0). (Values near 0 indicate that most species are living at or beyond their environmental limits, whereas values near 1 indicate that they remain within safe conditions). The colored quadrants represent: (I) high safety maintained by only a few species above zero; (II) high safety with most species above zero; (III) low safety with only a few species above zero; and (IV) low safety with most species still above zero. The size of the points reflects the percentage of each grid cell covered by MPAs.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Extendeddatafigures.docx