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# Operationalizing climate risk in a global warming hotspot

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Climate change is a looming threat to marine life, creating an urgent need to develop climate-informed conservation strategies. The Climate Risk Index for Biodiversity was designed to assess the climate risk for marine species in a manner that supports decision-making. Yet, its regional application remains to be explored. Here, we use it to evaluate climate risk for ~2000 species in the northwest Atlantic Ocean, a marine warming hotspot, to explore its capacity to inform climate-considered fisheries management. Under high emissions, harvested species, especially those with the highest economic value, have a disproportionate risk of projected exposure to hazardous climate conditions but benefit the most from emission mitigation. By mapping critical risk areas for 90 fish stocks, we pinpoint locations likely to require additional intervention, such as in the southern Gulf of St. Lawrence for Atlantic cod. Finally, we demonstrate how evaluating climate risk geographically and understanding how it arises can support short- and long-term fisheries management and conservation objectives under climate change.

Climate change is a major driver of change in marine ecosystems<sup>1</sup>, with critical consequences for ecosystem services<sup>2</sup> and human well-being<sup>3</sup>. It is widely accepted that the successful management and conservation of living resources under climate change will require a comprehensive understanding of the differential vulnerability of species and ecosystems to global warming.

Climate Change Vulnerability Assessments (CCVAs) have been promoted as a critical component of marine management under climate change, particularly in protected areas<sup>4,5</sup> and fisheries management<sup>6–9</sup>. Yet, to be effective within the structured decision-making frameworks of marine conservation and management, CCVAs must provide climate impact knowledge that meets specific criteria. Such criteria include evaluating geographic variation in vulnerability<sup>10–18</sup>, which is critical to developing climate-informed conservation strategies<sup>4,5</sup>; being quantitatively derived from empirical data to ensure reproducibility; assessing all three component dimensions of vulnerability: exposure, sensitivity, and adaptivity<sup>19</sup>; evaluating risk across different levels of biological organization from species to ecosystems; and providing explicit risk assessments on absolute rather than relative scales. Existing CCVA frameworks rarely meet these criteria, which may explain why they are seldom incorporated into management settings despite the benefits they could convey<sup>20–23</sup>. This situation is problematic as

climate change may erode the effectiveness of traditional management approaches<sup>24–26</sup>.

Here, we use the newly-developed Climate Risk Index for Biodiversity (CRIB) framework<sup>27</sup>, which does meet these criteria, to estimate the climate vulnerability and risk for marine species in the northwest Atlantic Ocean under two contrasting greenhouse gas emission scenarios that bracket the range of plausible trajectories (SSP5-8.5: high emissions and SSP1-2.6: high mitigation) to 2100. The CRIB uses surface temperature as the primary measure of climate change to produce empirically rooted estimates that represent climate risk to the local persistence of species and the ecosystems they support. The CRIB does not seek to evaluate climate-driven range shifts; Instead, it assesses the likelihood of adverse consequences<sup>28</sup> at individual locations within species' native geographic distributions to inform conservation and management efforts where they operate. Relative vulnerability is translated into absolute risk using a threshold-based approach comparable to the IPCC Reasons for Concern Framework (RFC) that assesses climate risk to humans<sup>29,30</sup> and the IUCN Red List Index (RLI) of extinction risk for species<sup>31</sup>. However, whereas the RLI provides a single estimate of extinction risk for each species, the CRIB disaggregates climate risk at all locations throughout a species' distribution and evaluates risk for

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species and aggregate ecosystems. Because the CRIB does not consider range expansions, it represents the climate risk to the in situ persistence of species and the biotic intactness of their ecosystems.

The framework was previously applied to ~25,000 species globally at a 1° spatial scale<sup>27</sup>. Here, we apply the CRIB framework to regionally relevant data to produce higher resolution (0.25°) climate risk estimates for 2045 species, three large ecosystems, and 90 fish stocks across Atlantic Canada’s fisheries management areas, hereafter the area of study (AOS; Fig. 1). This area is a global warming hotspot<sup>26,32</sup>, providing an ideal test case to explore how climate risk assessment can support fisheries management and conservation, enhancing traditional management strategies toward climate readiness<sup>33</sup>. We present three example stocks to tangibly illustrate these concepts.

## Results

### The Climate Risk Index for Biodiversity (CRIB)

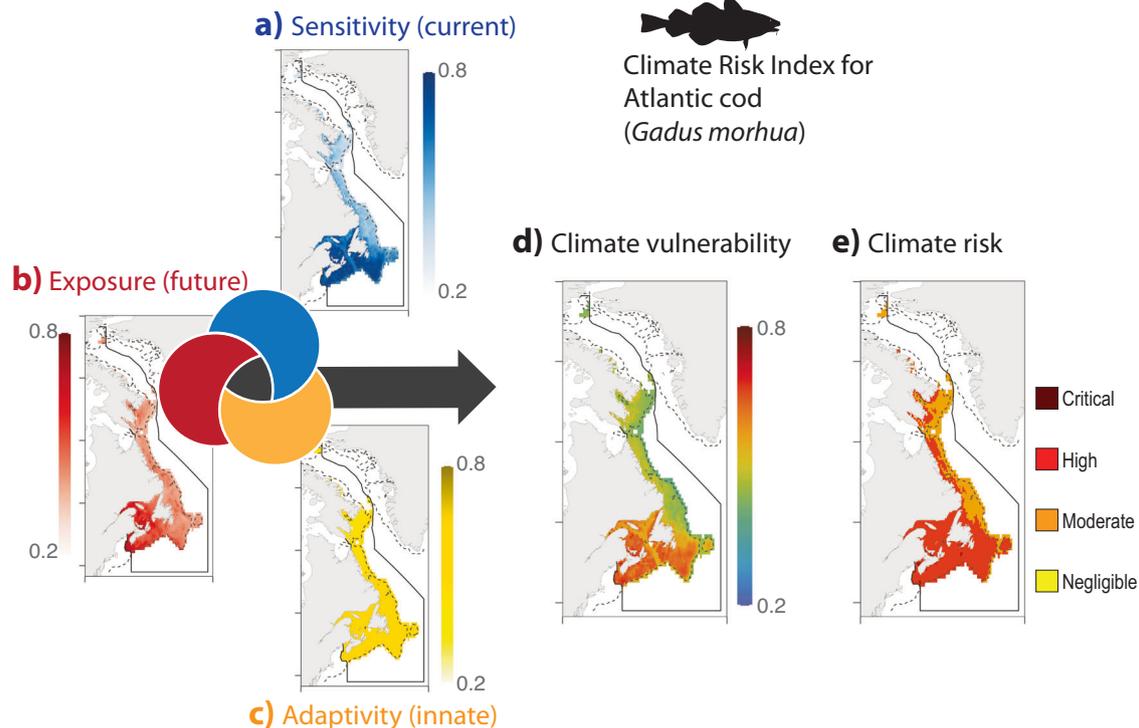
For each species, publicly available and validated data sources were used to calculate 12 climate indices in each 0.25° degree grid cell (~24 km<sup>2</sup> at 40° N) that comprise their native geographic distribution<sup>27,34</sup>; (see Methods for a description and rationale for selecting indices). Figure 1 illustrates how the CRIB framework calculates the spatially explicit indices for a widely known groundfish species, Atlantic cod (*Gadus morhua*), and integrates them to determine climate vulnerability and risk under a high mitigation scenario (SSP1-2.6). Cod experiences substantial variation in climate sensitivity (Fig. 1a), exposure (Fig. 1b), and adaptivity (Fig. 1c) across its geographic distribution. The cumulative climate vulnerability for cod (Fig. 1d) is highest in nearshore and southerly locations (<50° N), where climate sensitivity and exposure tend to be higher and are marginally offset by the higher adaptivity potential. The relative climate vulnerability scores are assessed against four ecologically rooted climate risk categories, enabling them to be interpreted on an absolute scale: negligible, moderate, high, and critical (Fig. 1d). The risk thresholds were established using ecological knowledge (Table S4),

enabling us to determine absolute risk categories for the 12 climate indices, three dimensions, and cumulative risk<sup>27</sup>. This derivation of absolute risk is critical to communicating and applying climate risks in management settings where precise, objective risk determinations are required. Cod predominantly experiences moderate to high climate risk yet is at critical risk at some locations in the southern Gulf of St. Lawrence (GSL; Fig. 1e). In the CRIB framework, cod will almost certainly experience negative climate change impacts at these locations under this scenario. Emissions mitigation reduced the spatial extent of climate vulnerability and risk for cod; under high emissions, cod were at critical climate risk across 4% of their geographic distribution, but this dropped to 1% with high mitigation.

### Climate risk for ecosystems and species

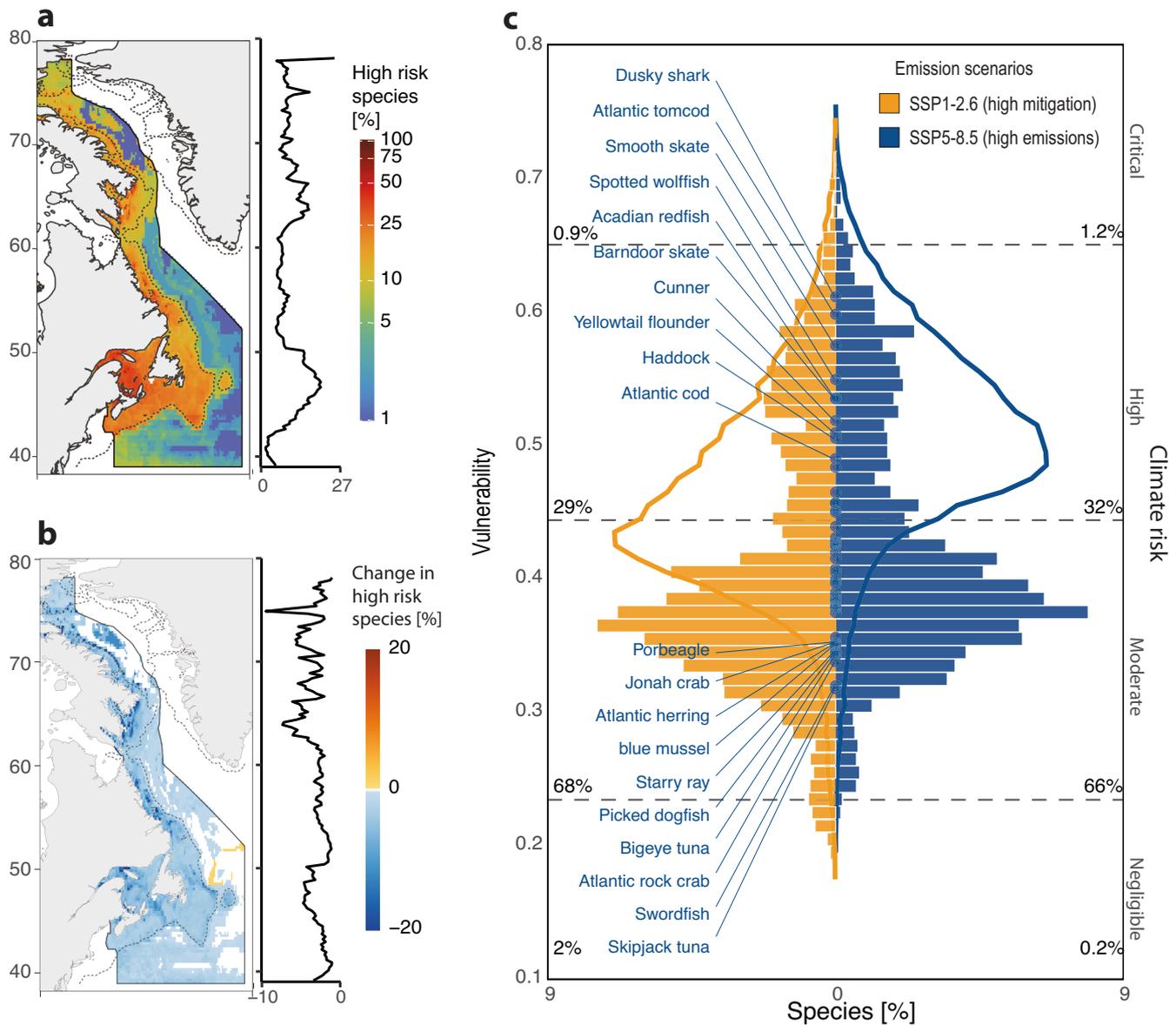
The vulnerability maps for all species were superimposed to evaluate geographic patterns of climate risk for ecosystems. Overall, under both emission scenarios, the proportion of species at high or critical climate change risk tended to be higher closer to coastlines (stepwise increases at <500 m and <2000 m isobaths), particularly in the GSL and on the Grand Banks (Fig. 2a). A larger fraction of species were at risk at high latitudes (>60° N), where the variability in climate risk scores was also higher. Under high emissions, most nearshore ecosystems had between 15% and 50% of their species at high climate risk, with some high latitude nearshore cells having >75% at risk. With emissions mitigation, the proportion of at-risk species declined at almost all locations, with mitigation benefits being most substantial at nearshore and high (>60° N; -4%) relative to low (>60° N; -2%) latitudes (Fig. 2b).

On average, species were at high or critical climate risk across 29% and 33% (ranges: 0–100%) of their native geographic distributions under the low and high emission scenarios, respectively. Regardless of the emission scenario, when species’ vulnerability scores were averaged across their geographic distributions, 0.2–2% were at negligible risk, over two-thirds (66–68%) were at moderate



**Fig. 1 | Spatially explicit assessment of climate vulnerability and risk for a single species, Atlantic cod (*Gadus morhua*).** Within each grid cell (here with a nominal resolution of 0.25°) across the native geographic distribution of cod within the study area, 12 standardized climate indices are calculated and used to define the three dimensions of climate vulnerability, presented here as a conceptual Venn diagram:

present-day sensitivity (a; blue), projected future exposure (b; red), and innate adaptivity (c; yellow). The dimensions are used to calculate cod’s climate vulnerability (d), and the relative vulnerability scores are translated into absolute climate risk categories for cod at all locations across its distribution (e). Maps were made with Natural Earth using the R statistical computing platform (version 4.3.0).



**Fig. 2 | Climate vulnerability and risk for marine ecosystems and species.** **a** The proportion of species at high or critical climate risk under high emissions in each grid cell to 2100. **b** The difference in the proportion of species at high or critical climate risk in each grid cell under the low, relative to high, emissions scenario to 2100. Black lines denote the NAFO divisions, and the dotted line is the 200 m isobath. The variations in high risk species (**a**) and changes in at-risk species (**b**) along latitude are displayed in the right margins. **c** Shading depicts the numerical densities of the

vulnerability scores for all assessed species across the study area under contrasting emission scenarios to the year 2100. Smoothed lines are the vulnerability scores for the global species pool ( $n \sim 25,000$  species) estimated in Boyce et al. (28). Gray dotted lines represent climate risk categories and values are the percentage of species in each risk category and emission scenario. Colours represent the emission scenario (emissions mitigation=yellow; high emissions=blue). Maps were made with Natural Earth using the R statistical computing platform (version 4.3.0).

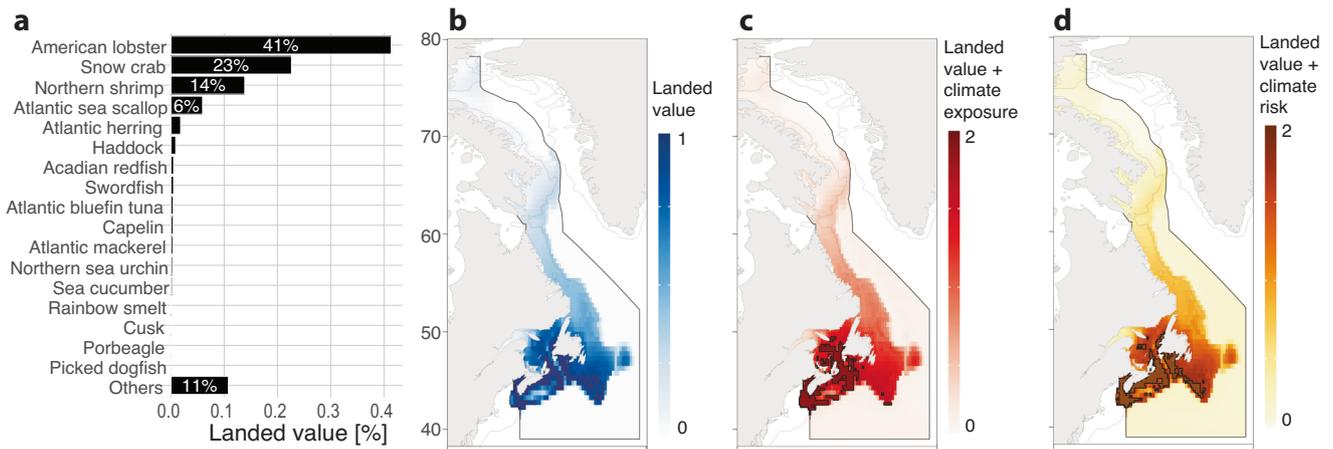
risk of adverse climate change impacts, up to one-third (29–33%) were at high risk, and 0.9–1.2% were at critical risk (Fig. 2c).

### Climate risk in a socioeconomic context

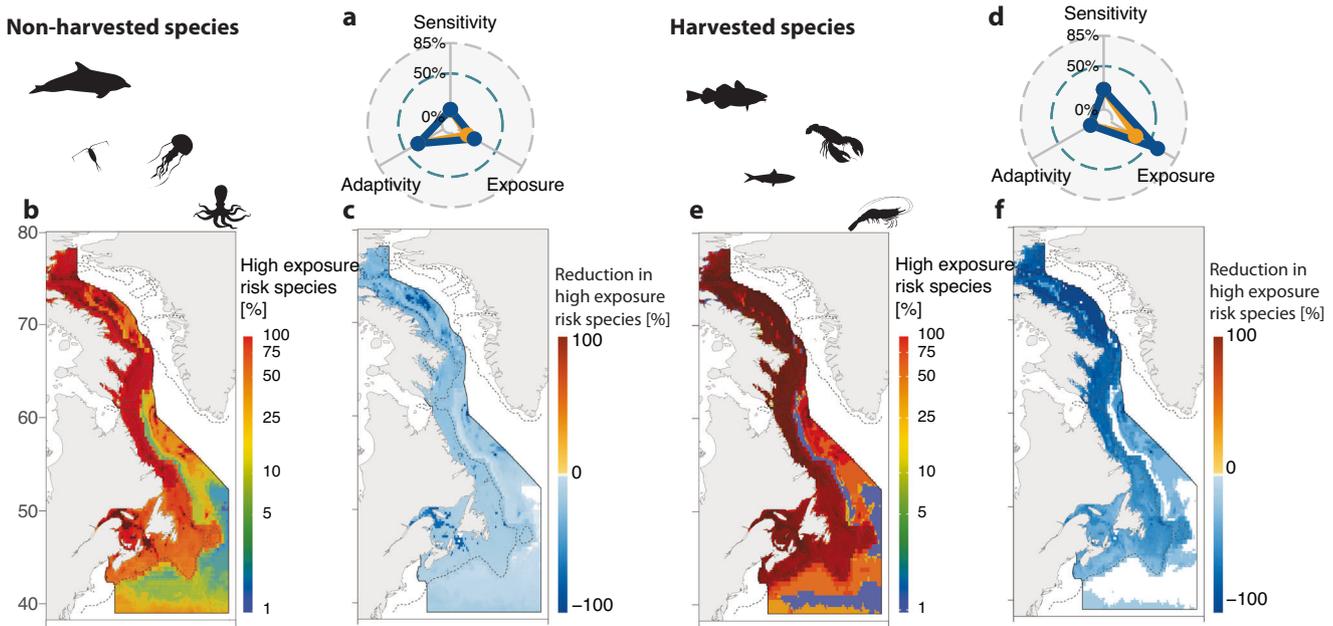
To understand climate risk in a socioeconomic context, we evaluated the risk for (i) 17 commercial species that account for 87–91% of the total landed value in the region (2010–2019); (Fig. 3a) and (ii) 52 harvested species that are fished for subsistence, profit, or cultural reasons (Table S5).

The climate risk for commercial species was first examined spatially by calculating the aggregate (summed) species landed value ( $LV_a$ ; Fig. 3b) and of climate risk and exposure in each grid cell. Intersecting those locations with the highest  $LV_a$  and climate risk identifies priority ecosystems that collectively support many high-value species that are also at climate risk. Climate risk and  $LV_a$  predominantly intersect at lower latitudes ( $<50^\circ$  N), in

nearshore locations, and across known productivity hotspots such as the southern Grand Banks, Georges Bank, the Bay of Fundy, and offshore submarine banks (Fig. 3c), where fishing tends to be concentrated. The intersection of projected climate exposure and  $LV_a$  was similar but was to be more concentrated in the Gulf of St. Lawrence (Fig. 3d). Commercial and non-commercial species have comparable climate risks, but commercial species have a higher climate sensitivity, lower adaptivity, and much higher exposure (Fig. 4a, b, d, e). The proportion of commercial species at risk of projected climate exposure was almost three times higher (62%) than non-commercial species (22%); (Fig. 4a, d). Differences in the spatial extent of climate exposure were also apparent. Non-commercial species were at high exposure risk across 11% of their distributions under low emissions and 23% under high emissions, so mitigation yielded an overall 11% reduction in the spatial extent of their climate exposure risk (Fig. 4c). However, commercial



**Fig. 3 | Climate risk for commercial species.** **a** Contribution of the 17 commercial species to the total landed value of all seafood in Atlantic Canada (2010–2019). **b** Spatial patterns in aggregated landed value across the AOS; Darkest blue show areas where many species exist that collectively have a high landed value. The intersection of aggregated landed value, **c** exposure, and **d** climate risk. **c, d** Darker shading show areas that have many species that collectively have high landed values and climate risk. **b–d** The darkest shading and outlined cells depict the top 5% values. Maps were made with Natural Earth using the R statistical computing platform (version 4.3.0).



**Fig. 4 | Comparative climate risk for harvested and non-harvested species.** **a, d** Points depict the proportions of at-risk species (high or critical) according to their sensitivity, exposure, and adaptivity to climate change, under contrasting emission scenarios. **b, e** The proportion of species at high or critical risk of exposure to hazardous climate conditions under high emissions in each grid cell to 2100. **c, f** The difference in the proportion of species at high or critical climate exposure risk in each grid cell under the low, relative to high, emissions scenario to 2100. **b, c, e, f** Black lines denote the NAFO divisions, and the dotted line is the 200 m isobath. Maps were made with Natural Earth using the R statistical computing platform (version 4.3.0).

species were at exposure risk across 21% of their distributions under low and 65% under high emissions. Thus, the emissions pathway disproportionately impacts the projected climate exposure of commercial species (Fig. 4f); mitigation reduced the geographic area over which species were at high or critical exposure risk by an average of 44%, a reduction four times greater than that experienced by the non-commercial species. The most considerable emission mitigation benefits - reductions in the proportion of their distributions at high exposure risk - were observed in the highest value species, including American lobster (*Homarus americanus*; -98%), Atlantic sea scallop (*Placopecten magellanicus*; -97%), snow crab (*Chionoecetes opilio*; -94%), and northern shrimp (*Pandalus borealis*; -89%); (Fig S12).

Commercial and harvested species' notably higher climate exposure is driven by their interactions with projected emissions-driven climate changes. Harvested species tend to inhabit more southerly areas of rapid projected climate velocity (Fig S16) and experience larger projected losses in their thermally suitable habitat. For example, with high emissions, the average loss of thermally suitable habitat for harvested species was 52%, compared to 20% for non-harvested. Harvested species were also disproportionately climate-sensitive (23%) relative to non-harvested (9%), possibly due to their lower conservation statuses and tendency to inhabit highly impacted nearshore environments. However, the proportion of harvested species at risk in their climate adaptivity was much lower (16%)

than for non-harvested (38%). Harvested species' higher adaptivity may be driven by their broader and more contiguous geographic distributions and greater exposure to climate fluctuations that can enhance climate resilience<sup>35</sup>. Despite the disparities in their climate sensitivity, exposure, and adaptivity, there were no significant differences in the overall range-wide climate vulnerability of harvested and non-harvested species under either emission scenario ( $P > 0.05$ ).

### Operationalizing climate risk for fisheries

Climate vulnerability and risk were evaluated for 90 fish stocks, represented by 29 species. Of these, 75 (83%) are directed fisheries, 14 (16%) are bycatch, and one (2J3KL Winter skate; *Leucoraja ocellata*) is under a fishing moratorium. Each stock's climate vulnerability and risk, as well as its dimensions ( $n = 3$ ) and indices ( $n = 12$ ), were intersected with their spatial management unit areas (e.g., Fig S13) to pinpoint high-risk locations (e.g., Figs S13a, b) or to obtain a single value for each stock (e.g., Fig S13c).

Under high emissions, 38 stocks (42%) were at high climate risk, with 52 (58%) at moderate risk (Fig. 5). With high mitigation, the number of high-risk stocks dropped to 26 (29%), with 64 (71%) being at moderate risk. The elasmobranch stocks ( $n = 7$ ) had the greatest range of vulnerability and risk scores, with smooth skate (*Malacoraja senta*) in the southern GSL (4T) being the most vulnerable and thorny skate (*Amblyraja radiata*) on the Scotian Shelf (4VWXs) being among the least vulnerable, overall. With emissions mitigation, herring stocks (*Clupea harengus*), capelin (*Mallotus villosus*), and northern shrimp emerged as the least climate-vulnerable, although most were still at moderate risk. While emissions mitigation benefited all stocks, some (e.g., northern shrimps and lobsters) benefited greatly, while others (e.g., 4VWX5 silver hake; *Merluccius bilinearis*) only minimally. While evaluating, ranking, and summarizing the climate risk of fish stocks is important, doing so can also obscure geographic differences (Fig S14). For example, under high emissions, the 4RST capelin stock in the GSL is at high climate risk overall, but the risk ranges from moderate to critical across the stock area. This spatial variation in risk can be highly relevant to species conservation in general, particularly for fisheries, which are harvested and often managed spatially explicitly. The notable spatial variation in climate risk within and across stocks emphasizes the importance and value of assessing climate risk taxonomically and spatially to identify both species and locations at risk.

### Discussion

Irrespective of the emissions scenario, and despite the geographic and taxonomic variation, the climate risk for most marine species in Atlantic Canada generally ranged from moderate to high. Species in this study tended to be at lower climate risk when compared to the global species pool<sup>27</sup>, where most of the ~25,000 assessed species were at high climate risk (54–84%; Fig. 2c, coloured lines). Several factors likely drive this difference. While current and projected surface warming rates in the northwest Atlantic are at the upper end of global warming trends<sup>22,26,32</sup>, resident species tend to have broader distribution and hence thermal niches that render them generally less vulnerable to rapid warming when compared to the global species pool which is numerically dominated by tropical species. Furthermore, lower latitude ecosystems also experience rapid warming, and species there tend to possess narrower thermal niches and live close to their upper thermal limit, on average (Fig. S15)<sup>36</sup>, which renders them generally more vulnerable to even slight temperature changes. This result indicates that areas of rapid climate change or velocity may not necessarily be hotspots of ecological climate risk and emphasizes the critical importance of considering how species traits interact with the spatiotemporally dynamic environments they inhabit to define their climate risk robustly.

The overall climate risk was similar between harvested and non-harvested species but manifest differently, with harvested species having a higher climate sensitivity and exposure and reduced adaptivity risk (Fig. 3). The markedly higher exposure of harvested and commercial species to projected hazardous climate conditions is especially notable. The higher climate exposure of harvested species is partly due to their greater projected

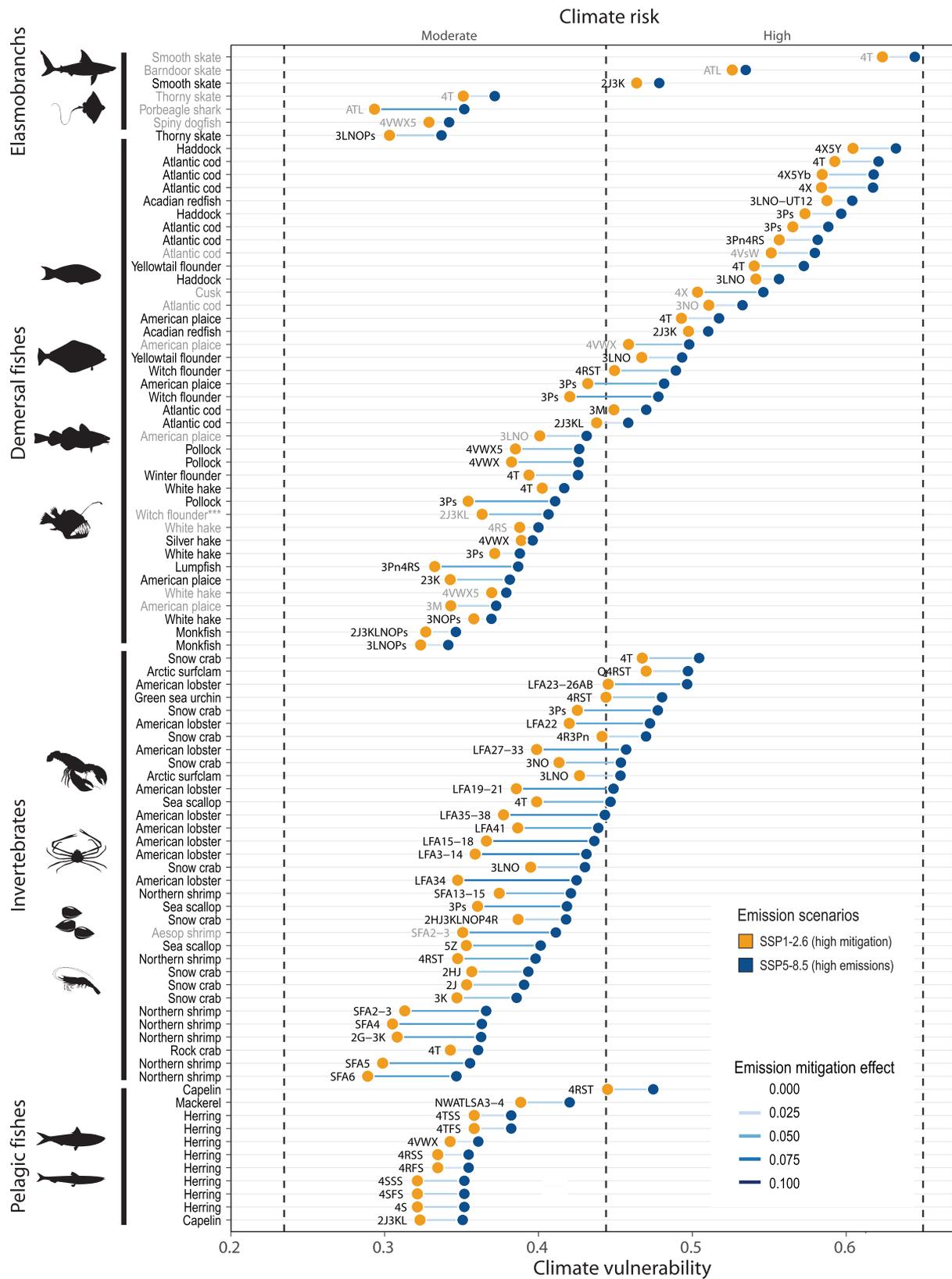
loss of suitable habitat, which implies that they will experience disproportionate geographic displacement across the AOS. Yet, it remains unclear if fisheries will be willing to track such climate-driven geographic shifts in their target species, or if it will be economically feasible to do so. Harvested species also tended to inhabit areas with higher cumulative impacts, which, along with their greater extinction risk and shallower depth distributions, renders them more sensitive to climate change than non-harvested species. The greater exposure and sensitivity of harvested and commercially valuable species could partly be explained by their greater occurrence in the southern portion of the AOS, and particularly in the GSL, relative to non-harvested species, particularly in the western portion (Fig S16), where climate changes and ecosystem stressors are elevated<sup>22,37</sup>. The GSL is a climate change hotspot<sup>22,38</sup>, having experienced rapid surface warming (1900–2019), increased hypoxia (1984–2016) and acidification<sup>38</sup>, declining sea ice extent (1979–2017), and high cumulative human impacts<sup>39</sup>.

The higher climate exposure and anticipated geographic displacement of harvested species, particularly those of high value (Fig S12), is concerning, given that climate change considerations are often not included in fisheries management across the AOS<sup>20,22,23</sup>. There is a similarly low incorporation of climate change considerations into the management of Canadian marine conservation areas (*i.e.*, MPAs) compared to other temperate jurisdictions<sup>40</sup>. This apparent disconnect between climate risk and the management response raises the question of how our assessment of ecological climate risk can be integrated into the management process for sustainable practice in the future. While we can foresee several ways climate risk could be used to support conservation initiatives *e.g.*<sup>27</sup>, our current focus is on fisheries sustainability.

Broadly, fisheries management represents the union of shorter-term (1–5 years) tactical objectives and actions and long-term (>5 years) strategic goals. Although sometimes viewed separately, these two spheres are inextricably linked: short-term tactical objectives centered on setting harvest rates to achieve present-day maximum sustainable yield also need to be set to help meet longer-term strategic goals such as stock recovery, sustainability, and in this case, robustness to climate variability and change. Climate risk information could help support and inform management in both essential domains.

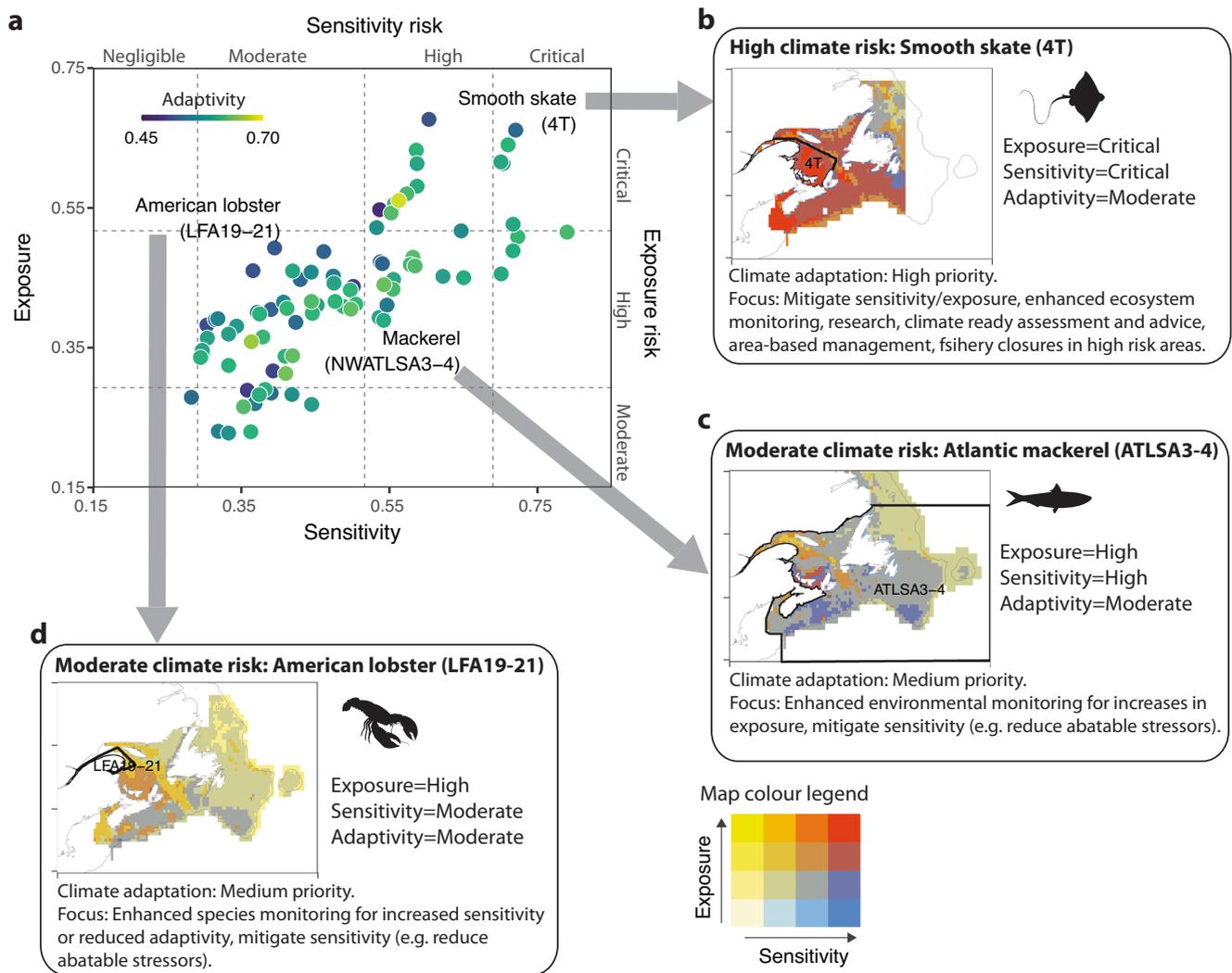
In the strategic planning domain, climate risk can help understand the effect of different emissions pathways on economically valuable species and fisheries and how this might ultimately impact socioeconomically dependent communities. A Scenario Planning Framework<sup>41,42</sup> could allow managers to explore outcomes of management strategies on species or areas of high climate risk. Understanding these tradeoffs between current socio-economic development strategies and future ecological and economic consequences would allow responsible agencies to develop adaptation strategies and inform decisions about setting national strategies for climate mitigation and species-specific action plans. Climate risk can also help determine overarching strategic objectives and directions, such as developing a national climate change strategy for fisheries management *e.g.*<sup>43</sup>. For example, in the Canadian context, establishing an explicit climate change objective in Canada's National Marine Conservation Strategy<sup>5</sup> or explicitly incorporating climate change into legislation such as Canada's Fisheries Act and/or Oceans Act.

In the shorter-term tactical domain, climate risk could support and inform fisheries management and marine spatial planning through several avenues. For instance, the climate risk analysis presented here could help identify the species and locations most urgently in need of climate adaptation and pinpoint steps to support them<sup>44</sup>. In our analysis, the 4T smooth skate stock species of high conservation concern also had the highest climate vulnerability (Fig. 5). This bycatch fishery is at high risk: it is critically exposed to projected climate changes, is critically sensitive to them, and has moderate adaptivity (Fig. 6a, b). This species is globally endangered<sup>31</sup>, and the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has assessed the smooth skate populations in the Laurentian-Scotian region, encompassing the 4T stock, as special concern<sup>45</sup>. This stock would thus be a high priority



**Fig. 5 | Climate risk and mitigation benefits for fisheries.** Points are the average vulnerability scores for 95 stocks in the area of study under contrasting emission scenarios to 2100. Coloured points represent the emission scenario (emissions mitigation = yellow; high emissions = blue). Coloured lines represent the change in the average climate vulnerability of stocks with emissions mitigation, where darker

blue indicates larger emissions mitigation vulnerability reduction. Black labels indicate stocks for which there is a directed fishery and gray those fished as bycatch. \*\* indicates stocks under a fishing moratorium. Species are ranked by their relative climate vulnerability, demonstrating how this approach can be used to triage stocks in a management context.



**Fig. 6 | Operationalizing climate vulnerability and risk for fisheries.**

**a** Relationship between the scores and risk categories for climate sensitivity, exposure, and adaptivity of 95 stocks that operate across the AOS under the high emission scenario to 2100. Colours are the adaptivity scores (dark blue=low, yellow = high). Examples of climate risk scenarios for fish stocks and how they can inform management priorities and decisions. Examples include **b**) Smooth skate (4T), a high-risk species, **c**) Atlantic mackerel (ATLSA3-4), a moderate-risk species but having

higher sensitivity and lower exposure and adaptivity, **d**) Atlantic lobster (LFA19-21), a moderate-risk species, but having higher exposure and lower sensitivity and adaptivity. **b–d** Climate sensitivity and exposure are displayed as colours: blues = high sensitivity-low exposure, yellows=high exposure-low sensitivity, reds = high sensitivity-high exposure. Stock areas are displayed as thick black lines and are labelled; the dotted line is the 200 m isobath. Maps were made with Natural Earth using the R statistical computing platform (version 4.3.0).

for climate adaptation in a climate triage system for fisheries. Resources that would support climate adaptation could include, for instance, pragmatic approaches that integrate climate change considerations into stock assessments, harvest advice, and decision-making<sup>20,22,46,47</sup>. Approaches for doing so range from using climate risk as a modifier to the harvest advice to more detailed quantitative inclusion of climate variables (temperature, oxygen, pH) into the stock assessment process<sup>48,49</sup>. Management strategy evaluations (MSE) can find candidate management strategies that are potentially robust to future climate scenarios, population and ecosystem dynamics, and other uncertainties<sup>50–52</sup>. Dynamic management can set harvest rates based on dynamic climate or ecological forecasts or respond in real-time to changing conditions<sup>53</sup>. Adaptation resources could also include instituting flexible spatial protections where the stock is particularly at risk<sup>4</sup>, targeted ecosystem monitoring for changes in climate vulnerability, and addressing factors affecting the sensitivity and adaptivity of smooth skate (e.g. reducing directed and ecosystem overfishing, bycatch, habitat destruction, pollution)<sup>21</sup>. Since high natural mortality in the GSL, primarily by seals, is also thought to be impairing species

recovery<sup>45</sup>, understanding the influence of bycatch on their mortality and reducing any fisheries-induced mortality through bycatch reduction (e.g. targeted gear regulations and/or seasonal fishery closures, protected areas) could improve the climate adaptivity potential for 4T smooth skate, and species with similar climate risk. For transboundary species and stocks with high climate risk, priority should be placed on ensuring single species-focused fisheries management is broadened to ecosystem-based fisheries management that can both predict and accommodate shifting geographical distributions across jurisdictional boundaries<sup>54</sup>.

While fisheries managers will ultimately determine the specific management strategies for each stock, climate change risk analyses can help identify key overarching priorities, needed resources, and focal actions under climate change. For example, ATLSA3-4 stock for Atlantic mackerel (*Scomber scombrus*) is at moderate climate risk presently and would thus be a medium priority for climate adaptation. However, because the stock is climate sensitive (Fig. 6c), it also has a high latent climate risk – or a high likelihood of becoming at risk, especially if its exposure increases. Mackerel is in the critical zone of Canada’s Precautionary Approach Framework<sup>55</sup> and

is of high ecological importance, supporting many dependent species, including valuable upper trophic fisheries<sup>56</sup>. Thus, taking steps to reduce its latent climate risk would enhance ecosystem resilience. Monitoring the stock's environment for any changes in climate exposure that could push its cumulative climate risk to high or critical would be advisable, for instance, by monitoring species' thermal safety margins over time. Additional actions could be taken to reduce the stock's high climate sensitivity, such as developing and prioritizing interventions that minimize abatable stressors (e.g. directed and ecosystem overfishing, bycatch, pollution, habitat or ecosystem disruption) or through fisheries closures or climate-integrated marine spatial planning<sup>4</sup>. For example, in 2022, commercial and bait fisheries for Atlantic Mackerel and spring-spawning Atlantic herring in the southern GSL were placed under moratorium to permit stocks to recover from decades-long declining trends and current low abundance. These measures can reduce stress and promote the recovery of these species and are one example of interventions that can be applied to reduce stressors. As another example, the lobster stock in Lobster Fishing Areas (LFAs 19-21) is also at moderate climate risk overall (Fig. 5). This species is not a conservation concern<sup>31</sup> but has the highest economic value of any species in the region<sup>8</sup>. This stock also has a high latent risk due to its higher climate exposure (Fig. 6d), and an increase in its sensitivity or decline in adaptivity could shift its climate risk to high or critical. To reduce its latent risk, enhanced lobster monitoring could be conducted to identify increases in the stock's sensitivity (e.g., lower conservation status, narrower thermal safety margins) or reductions in adaptivity (e.g., smaller and more fragmented distribution) to climate change that could trigger climate-relevant management actions.

Spatially resolved risk maps can help inform spatial fisheries management or area-based management tools by identifying locations where the species is particularly at risk or that function as climate refugia<sup>57,58</sup>. This also applies to identifying spatial management units facing extreme climate challenges. Spatially explicit risk knowledge can help evaluate and manage the climate risk for transboundary and highly migratory fish stocks<sup>54</sup>. They could also help pinpoint areas where an exploited species is in double-jeopardy, being at high climate risk at a location that also functions as a critical essential habitat for its population (e.g., reduced recruitment, spawning, summer feeding). Such areas could be priorities for spatial management measures such as seasonal fishery closures, spatial conservation measures (e.g., marine protected areas or other effective area-based conservation measures), or enhanced monitoring.

Aside from cumulative risk, our analysis contains detailed information about the 12 individual aspects that define it. For example, the timing of climate emergence from species' thermal niches<sup>59,60</sup> can provide a chronology of when stock will first become exposed to hazardous climate conditions across its management area. For example, while the 4T smooth skate stock is projected to be exposed to a hazardous climate in 32 years (by 2052) on average (range = 0–80 yrs.), the Atlantic mackerel stock is not expected to be exposed for another 75 years (by 2095) on average (range: 41–80 yrs.). Such information can aid in proactively developing timelines to institute adaptation resources in advance of those impacts and help understand the pace of climate impacts on fisheries.

Climate risk analyses can also help reveal critical knowledge gaps and uncertainties that could erode management effectiveness under climate change. For instance, such knowledge gaps could arise for stocks identified as being at climate risk and thus in urgent need of climate adaptation resources (e.g., climate-considered stock assessments) but for which these cannot be implemented due to resource constraints (e.g., data, technical expertise, knowledge). In such situations, priority would be placed on filling in the missing knowledge or resources to facilitate climate adaptation.

Finally, our climate risk analyses can be used to monitor changing vulnerability and risk of species, ecosystems, and fisheries in a standardized manner over time. The ability to track changing fisheries vulnerability in a spatially explicit, rapid, and cost-effective manner that remains consistent between assessments could provide crucial

information about how fisheries are becoming more or less at risk and anticipate future climate risk outcomes.

The complexity of climate impacts requires any climate risk framework to make assumptions we list here to expose key uncertainties and motivate future work. First, the CRIB uses surface temperature as the primary measure of climate change. Additional factors may affect species' responses, including changes in dissolved oxygen and pH, nutrient flux, total system productivity, differences in warming rates across depths, and modified biotic interactions. While species' responses to such factors are presently less well resolved, the CRIB represents a baseline to build and improve using new data and knowledge. Second, we undertook this analysis using state-of-the-art earth system and species distribution models at the highest spatial resolution permitted by the input data. However, using higher-resolution data as they become available could improve the characterization of species distributions and climate risk, particularly in coastal locations. For instance, 10 km<sup>2</sup> may be an optimal resolution for resolving ocean climate processes across the northwest Atlantic Ocean<sup>32</sup>. Third, CRIB does not consider range expansions into new locations. While range expansions have been evaluated elsewhere, e.g. <sup>61,62</sup> and can be an important aspect of climate adaptation, our approach represents climate risk to the in-situ persistence of species and stocks across their present-day geographic range where fisheries operate. Further, the CRIB does not evaluate risk at different species' life stages<sup>2</sup>, which would be especially valuable for climate adaptation initiatives in fisheries. As fisheries are a coupled socio-ecological system, additional factors not included here could also affect their climate risks, such as how they are managed and operated, the infrastructure supporting them, and other socioeconomic processes and constraints; work is ongoing elsewhere to consider these important factors more fully<sup>63</sup>. Lastly, the validity of the climate risk outputs has not been validated against observed patterns; while such validation is uncommon in the climate risk literature, it would serve to build confidence when seeking to use them in decision-making situations. Notwithstanding these caveats, our climate risk framework builds on existing approaches in several ways, including being spatially and taxonomically explicit, comprehensive, and risk-based. As shown here, the framework is designed to be flexible (e.g., incorporate different data sources and new knowledge) and can potentially overcome some of the listed uncertainties as new information becomes available.

## Conclusions

Our analysis adds to a growing body of evidence outlining how climate change can affect fisheries' productivity, resilience, and sustainability<sup>2,64–66</sup>, with consequences for their management and conservation. Climate and marine ecosystem model projections suggest that this trend will continue into the foreseeable future<sup>5,64,67,68</sup>, with socioeconomic repercussions<sup>3,69</sup>. Such climate-driven changes underscore the critical need to increase the climate readiness of fisheries in Canada, where it lags<sup>20,23</sup>, and elsewhere. This analysis demonstrates how the CRIB framework can further these objectives and supplement traditional fishery assessments. These include prioritizing climate adaptation resources, determining optimal management strategies, enhancing the effectiveness of spatial protections and marine spatial planning, identifying knowledge gaps and uncertainties, and tracking changing climate risk over time. While climate vulnerability and risk analyses are not a panacea to managing fisheries under climate change, our study demonstrates that if carefully undertaken, they can inform and complement existing assessment and management approaches and aid in determining how to prioritize and efficiently deploy limited climate adaptation resources for fisheries.

## Methods

### Overview of CRIB design principles, methodology, and assessed species

The CRIB framework is fully described in Boyce et al.<sup>27</sup>. Briefly, it incorporates information and features that are often required of climate risk assessments in applied settings, including (i) it is spatially resolved, evaluating risk at all sites across species' geographic distributions, (ii) it produces relative vulnerability scores on a standardized scale and translates them into absolute risk

categories, (iii) it uses quantitative, well-validated, and publicly available data, thus ensuring reproducibility, (iv) it is flexible and can be applied at differing spatial scales and biomes and can accommodate different information types, (v) it is comprehensive, evaluating all three dimensions that define vulnerability and risk<sup>29</sup> using multiple assessment types (e.g., trait-based, mechanistic, correlative)<sup>70</sup>, (vii) it assesses the statistical uncertainty (variability) of the vulnerability and risk scores, (viii) it assesses the impacts of anticipated future climate conditions on species to facilitate decisions regarding emission mitigation, and (ix) it is designed hierarchically, thus maximizing its flexibility and the information content (Fig. 2).

The 12 climate indices that define it capture climate change impacts that are generalized across species with varying life histories which are grounded in ecological theory, widely accepted and validated through peer review. The indices maximize parsimony and minimize redundancy and pseudoreplication: those that were easy to interpret and calculate were prioritized. The indices collectively include trait-based, correlative, and mechanistic information and incorporate abiotic, biotic, and human pressures acting across multiple biological organization levels from species to ecosystems. The indices integrate historical, present-day, and projected future information about species' climate vulnerability and are calculated or obtained in their native units. The 12 climate indices are described in Table S1. The climate sensitivity indices include species' thermal safety margins<sup>16–18,71</sup>, vertical habitat variability and use<sup>72–75</sup>, conservation status<sup>76</sup>, and cumulative impacts<sup>25,37,39,77–81</sup>. Climate exposure indices were based on ensemble climate projections and included the timing of climate emergence from species' thermal niches<sup>59,60,82,83</sup>, the extent of suitable thermal habitat loss<sup>61,84,85</sup>, climate-related ecosystem disruption<sup>59,86–89</sup>, and the projected climate velocity<sup>90–92</sup>. Adaptivity indices included the species' geographic range extent<sup>72,90,92–96</sup>, geographic habitat fragmentation<sup>13,97–101</sup>, maximum body length<sup>13,70,99,102–106</sup>, and historical thermal habitat variability and use<sup>13,107–110</sup>. Each index was calculated from environmental or ecological data on a geographic grid across the native geographic distribution of the focal species, defined by the focal species' traits and/or a mix of the two. This produces indices that are taxonomically (e.g., each species) and geographically (e.g., each grid cell) explicit. The indices are transformed to ensure they are on a standardized scale (0–1) across all species and locations. This step ensures that indices with different native units can be compared, normalized, and combined while simultaneously ensuring that vulnerability can be calculated at different spatial resolutions or points in time without losing information. Reference values and scaling functions were used to meet these criteria and are described in Boyce et al.<sup>27</sup>. The 12 standardized climate indices are used to calculate three climate dimensions (sensitivity, exposure, and adaptivity), which ultimately define climate vulnerability and risk.

Species that do not live in the upper 100 m of the ocean are excluded from the analysis, and species with a maximum depth tolerance of more than 1000 m and a preference of more than 600 m are also excluded, as surface temperature may not well define the climate risk of these species. To verify this threshold, a sensitivity analysis was carried out in advance<sup>27</sup>; (Fig S42 in ref. 27). Seabirds were also excluded from the analysis because only a small part of their time is spent in surface water. However, mammals and endothermic fishes (e.g. tunas, billfishes) that can sometimes inhabit depths over 1000 m were not excluded; despite their ability to range into deeper waters, their distribution is often well explained by surface temperatures<sup>111,112</sup>. We excluded species with large freshwater distributions or spending most of their time in freshwater habitats (e.g., sturgeons, salmon, shads, eels). Finally, guided by sensitivity analyses (Supplementary Fig 43 in ref. 27), we restricted our analysis to species and cells containing all 12 indices, and species that lacked at least one climate index in more than 10% of their native range were removed from the analysis.

Almost all (98%) of the assessed species were animals, with Chordates ( $n = 515$ ) and Molluscs ( $n = 506$ ) each comprising ~ one-quarter of the assessed species (25%), while Cnidarians and Arthropods made up 19% and 15%, respectively (Fig S10a). More species were present in coastal regions (<200 m depth) and southern portions of the AOS relative to oceanic and northern locations (Fig S10b).

## Data

All data sources are used in Table S2.

## Climate projections

An ensemble of monthly sea surface temperature (SST; °C) projections (2015–2100) was obtained from three published Global Climate (GCM) or Earth System Models (ESMs) within the coupled model intercomparison project phase 6 CMIP6 archive<sup>27</sup>; (Table S3). All projections were regridded onto a regular global 0.25° grid. SST projections were made under two contrasting IPCC shared socioeconomic pathway (SSP) scenarios representing alternative socioeconomic developments. SSP5-8.5 (Fossil-fueled development; 'taking the highway') represents continued fossil fuel development, and SSP1-2.6 (Sustainability; 'taking the green road') represents an increase in sustainable development<sup>113</sup>. Notwithstanding ongoing discussion on the likelihood of emission scenarios<sup>114</sup>, the two extreme scenarios we evaluated bracket the range of possible outcomes.

## Native geographic distributions

Estimated present-day native geographic distributions for marine species were obtained from AquaMaps<sup>34</sup>. AquaMaps predicts marine species' spatial distribution on a native 0.5° global grid using environmental niche models. The models predict the probability of occurrence for each species as functions of bathymetry, upper ocean temperature, salinity, primary production, and the presence of, and proximity to, sea ice and coasts. AquaMaps geographic distribution estimates have been validated using independent survey observations<sup>115</sup> and evaluated against alternative methodologies and independent species distribution datasets<sup>116</sup>. The native geographic distributions for each species were statistically rescaled to a 0.25° grid using nearest neighbour interpolation.

## Species conservation status

The Wild Species reports<sup>117</sup> assess the conservation status of species in Canada. They are produced by a National General Status Working Group composed of representatives from each Canadian province and territory and of the three federal agencies (Canadian Wildlife Service of Environment and Climate Change Canada, Fisheries and Oceans Canada, Parks Canada). The assessments are completed using the best available knowledge, including museum collections, scientific literature, scientists and specialists, Aboriginal traditional and community knowledge, and conservation and government data centres. Species within the Wild Species reports are assessed regionally and/or nationally and updated every five years. We prioritized Wild Species regional species assessments over National, and for species that were not assessed in Wild Species, their global conservation status, as extracted from the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species<sup>31</sup> in Boyce et al.<sup>27</sup> were used. The full methodology for extracting or calculating species' global extinction risk is described in Boyce et al.<sup>27</sup>.

## Fisheries data

We acquired information on the status of Canadian fisheries from four publicly available sources: (i) fisheries landings reported to the Northwest Atlantic Fisheries Organization (NAFO), (ii) fisheries stock assessments contained in the RAM Legacy Stock Assessment Database<sup>118,119</sup>, (iii) fisheries stock status from within the 2018 DFO Sustainability Survey for Fisheries, and (iv) the landed value of commercial species from DFO.

Annual total fisheries landings for all available species were retrieved from the NAFO Annual Fisheries Statistics Database (21A database) between 1960 and 2019. From this database, we calculated the total landings for each species and NAFO division (tonnes km<sup>2</sup>) and each species across the NAFO area (tonnes) and estimated the time trend in the standardized landings of each species across the NAFO area.

The RAM stock assessment database is a global open-source compilation of stock assessments<sup>118,120</sup>. From the full database, we calculated the climate risk for the 95 stocks that operated within the AOS and had clearly defined and digitized stock management units; 47 stocks also contained

time-series of abundance (spawning stock biomass, total biomass, or numbers).

The annual Sustainability Survey for Fisheries is distributed to DFO scientists and managers who complete the survey for the stocks in their regions. The survey contains information on 179 Canadian stocks. The status of each stock is assigned to one of four categories according to the reported stock biomass level within the DFO precautionary approach framework<sup>121</sup>: critical, cautious, healthy, or uncertain. A stock is critical if its mature biomass is less than the limit reference point (LRP), 40% of the BMSY. A stock is considered cautious if its mature biomass is higher than the LRP but lower than the upper stock limit (USL), 80% of BMSY. A stock is classified as healthy if its mature biomass is above the USL.

The value of Canadian Atlantic coast commercial landings (CAD) for commercial species was acquired from the DFO statistical services unit for each year between 2010 and 2019.

### Thermal niches

The upper and lower thermal preferences and tolerances of marine species were obtained from the AquaMaps niche models. The upper-temperature tolerance values represent the species realized, rather than fundamental, upper thermal tolerances. The veracity of the AquaMaps species' upper thermal tolerances has been evaluated against matching species available in peer-reviewed databases (Supplementary Fig 3 in ref. 27).

### Maximum body lengths

The maximum size (length or mass) reached by species has been commonly used as a proxy for extinction risks, exploitation susceptibility, and species vulnerability to climate change<sup>3,5,58,61-63,81,91</sup>. The maximum size is a proxy for several life-history traits - e.g. generation length, time to maturity, intrinsic rate of population increase - that cumulatively define species' potential reproductive capacity and population growth rate<sup>64,65,81,91,92</sup>. Body size has been used to classify species as *r*- (produce many offspring, high growth rates, and mortality) or *K*-selected (produce fewer offspring, low growth rates, and mortality). For these reasons, the maximum body length was used to indicate species' resilience or adaptivity to climate change, where smaller species that grow and reproduce faster have a higher adaptivity<sup>3,5,58,61-63,81,83,91</sup>.

The maximum body size of species was acquired from Boyce et al.<sup>27</sup>, estimated from the FishBase <http://www.fishbase.org>, and SeaLifeBase, <https://www.sealifebase.ca/> databases. From FishBase, length-length relationships were used to calculate maximum lengths in standard units of total length (TLen). TLen was defined by the shell length and body length of gastropods, bivalves, and some decapods. TLen was determined by mantle length (ML) for cephalopods, carapace length (CL) for some decapods, and shell height (SHH) for some gastropods. Species with missing body length values were imputed in Boyce et al.<sup>27</sup>.

### Vertical habitat

The maximum depth of occupancy and vertical habitat range for each species were retrieved from AquaMaps, SeaLifeBase, and FishBase. The maximum depth of occupancy and vertical habitat range were truncated by the maximum bathymetry present in each grid cell across each species' native geographic distribution.

### Trophic position

The trophic levels (TLs) for each species were acquired from Boyce et al.<sup>27</sup>, where they were retrieved from FishBase and SeaLifeBase or entered manually. The TLs of primary producers not available in FishBase or SeaLifeBase were set at 1 and zooplankton at 2.

### Environmental data

Per almost all CCVAs<sup>8,13,14,19,70,71,122</sup>, sea surface temperature (SST) was used as the primary metric of climate change; it has high spatiotemporal availability, and its effects on species are generally better understood relative to other climate variables (e.g. oxygen, pH). Daily SST estimates were obtained from the NOAA 0.25° daily Optimum Interpolation Sea Surface

Temperature dataset (OISST)<sup>123</sup>. The temperature dataset has been available globally since 1981 at a spatial resolution of 0.25°.

A multivariate index of cumulative human impacts (HI) on ocean ecosystems developed in Halpern et al.<sup>37,39</sup> was used. The HI index represents the integration of 17 global anthropogenic drivers of ecological change, including fishing pressure, pollution, invasive species, eutrophication, climate change, and others. The HI estimates were available at a global 1 km<sup>2</sup> native resolution and were statistically rescaled to a 0.25° grid across the AOS using bilinear interpolation.

Bathymetry values were extracted from the General Bathymetric Chart of the Oceans (GEBCO) on a native 15 arc-second interval grid and were statistically rescaled to a 0.25° grid by taking the mean.

### Analyses

**Climate vulnerability.** The 12 climate indices are used to calculate vulnerability and its dimensions for each species at all locations across their geographic distributions and for each species averaged across their geographic distributions. The following describes these two approaches.

**Spatially explicit vulnerability.** For each species within each grid cell across its geographic distribution that contained sufficient data, sensitivity, exposure, and adaptivity were calculated as the mean of the four indices that define them. The standard deviation of the vulnerability dimensions provided an estimate of their statistical uncertainty and was carried through the subsequent vulnerability calculations using inverse variance weighting. Vulnerability ( $V_{ij}$ ) was then calculated from sensitivity, exposure, and adaptivity while statistically accounting for both the variability and the uncertainty associated with the indices of climate exposure derived from ensemble climate projections.

Discounting was used to statistically account for the uncertainty associated with the model-projected climate exposure of species. Discounting is commonly used to account for the greater uncertainty associated with unknown future states. Its use in vulnerability estimation is comparable: the ESM projected exposure of species to climate change is less well-tested or resolved than their present-day sensitivities or innate adaptive capacities. In the CRIB framework, the reliability of the climate exposure indices scales with the length of the climate projection and the number of ensemble projections, and these are thus used to derive a discount rate  $\delta$ . Exposure indices derived from single ESMs that make longer-term climate projections are perceived as less reliable<sup>3,124</sup> and are thus more heavily discounted. The discount rate was calculated as

$$\delta = \frac{Years}{100\theta} + \frac{Models}{-25\theta} + 0.026, \quad (1)$$

where *Years* is the number of years in the climate projection, *Models* is the number of climate projections in the ensemble, and  $\theta$  is a scaling factor of 40, yielding a maximum possible discount rate of 5%. Our study evaluated climate projections from three models over 80 years, yielding a discount rate of 4.1%. Discounts applied to exposure are credited to sensitivity, such that the maximum total adjustment is 10%, to conserve the vulnerability scaling to between zero and one. For each species within each grid cell across its geographic distribution, the discount rate was applied to the estimated exposure and sensitivity estimates as follows.

$$\check{E}_{s,c} = [(1 - \delta)(E_{s,c})], \quad (2)$$

$$\check{S}_{s,c} = [(1 + \delta)(S_{s,c})], \quad (3)$$

where  $\check{S}_{s,c}$  and  $\check{E}_{s,c}$  are the discounted sensitivity and exposure estimates for species *s* within cell *c*. Through this equation, the future exposure of species to climate change was discounted relative to their current sensitivity and adaptivity. The vulnerability was calculated as a weighted average of

adaptivity and discounted sensitivity and exposure as

$$V_{s,c} = \frac{[\check{S}_{s,c} \times \omega S_{s,c}] [\check{E}_{s,c} \times \omega E_{s,c}] + [(1 - AC_{s,c}) \times \omega AC_{s,c}]}{\omega S_{s,c} + \omega E_{s,c} + \omega AC_{s,c}}, \quad (4)$$

where  $V_{s,c}$  is the vulnerability,  $\check{S}_{s,c}$  and  $\check{E}_{s,c}$  are the discounted sensitivity and exposure, respectively, and  $AC_{s,c}$  is the adaptivity for species  $s$  within cell  $c$ .  $\omega S_{s,c}$ ,  $\omega E_{s,c}$ , and  $\omega AC_{s,c}$  are the statistical reliability weights for the estimated sensitivity, exposure, and adaptivity, calculated from their scaled variances. For example, the weights for estimated sensitivities were calculated as the inverse of their coefficients of variation as

$$\omega S_{s,c} = \left( \frac{\sigma S_{s,c}}{\mu S_{s,c}} \right)^{-1} \quad (5)$$

where

$$\mu S_{s,c} = \frac{1}{n} \sum_{i=1}^n S_{s,c,i} \quad (6)$$

and

$$\sigma S_{s,c} = \sqrt{\frac{\sum_{i=1}^n (S_{s,c,i} - \mu S_{s,c})^2}{NS_{s,c}}} \quad (7)$$

where  $\omega S_{s,c}$  is the reliability weight and  $\sigma S_{s,c}$  and  $\mu S_{s,c}$  are the standard deviation and mean, respectively, of the four indices,  $i$ , that define sensitivity for species  $s$  within cell  $c$ .  $NS_{s,c}$  is the number of climate indices,  $i$ , that define sensitivity for species  $s$  within cell  $c$ .

**Vulnerability of species.** Vulnerability and its variability were calculated for each species,  $s$ , while statistically accounting for geographic differences in its uncertainty. Species' vulnerabilities were calculated as an inverse variance-weighted mean of the vulnerabilities in each grid cell across their geographic distribution as

$$V_s = \frac{\sum_{c=1}^n \omega V_{s,c} V_{s,c}}{\sum_{c=1}^n \omega V_{s,c}} \quad (8)$$

while their variance-weighted standard deviations were calculated as

$$\sigma V_s = \sqrt{\frac{V_1}{V_1^2 - V_2} \sum_{c=1}^N \omega V_{s,c} (V_{s,c} - \mu V_{s,c})^2} \quad (9)$$

where,

$$V_1 = \sum_{c=1}^N \omega V_{s,c} \quad (10)$$

and

$$V_2 = \sum_{c=1}^N \omega V_{s,c}^2 \quad (11)$$

and

$$\omega V_{s,c} = \left( \frac{\sigma V_{s,c}}{\mu V_{s,c}} \right)^{-1} \quad (12)$$

Following this, greater statistical weighting is given to vulnerability estimates in grid cells where their variance (e.g., spread of the indices used to calculate them) is lower and vice-versa. Species estimates will be more variable when the vulnerability is more dissimilar in the grid cells that comprise its geographic distribution and vice-versa.

**Climate risk.** Each of the 12 climate indices was interpreted along ecological gradients to define thresholds that enable climate vulnerability to be translated into risk categories. The risk thresholds are defined in their native units and propagated through the analysis, preserving their meaning and interpretation. This approach allows the vulnerability of species and communities to be translated into absolute risk categories using transparent and, where possible, empirically supported approaches<sup>125–127</sup>. Our definition of climate risk is comparable to the definition of extinction risk used by the IUCN Red List of species<sup>31</sup>, the Reasons for Concern (RFC) framework adopted to define climate risk by the Intergovernmental Panel on Climate Change (IPCC)<sup>28–30</sup>, and to the widespread use of limit reference points to define the status of fish stocks and determine harvest strategies<sup>128</sup>. Details of the risk thresholds used to determine climate risk for species and their justification are listed in (Supplementary Table 4 in ref. 27).

**Quality control and sensitivity analyses.** Our analyses were guided by and validated through extensive sensitivity analyses that were applied to minimize wherever possible uncertainties inherent to each underlying model (described in Boyce et al.<sup>27</sup>). Individual analyses were undertaken to inform our determination of the appropriate species and data to include (Supplementary Figs 42, 44 in ref. 27), the acceptable levels of data missingness (Supplementary Fig. 43 in ref. 27), the impact of the standardizations on the calculations (Supplementary Fig. 45, 47 in ref. 27), the accuracy of the data imputations (Supplementary Fig. 48 in ref. 27), the collinearity of the climate indices (Supplementary Fig. 51 in ref. 27) and the definition of species' native geographic distributions (Supplementary Figs. 49, 50 in ref. 27).

### Data availability

All datasets used in this paper are described and archived at the publicly available sources listed in Table S2. Species vulnerability scores are available through figshare: <https://doi.org/10.6084/m9.figshare.25934329>.

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## Author contributions

D.G.B. conceived and designed the study with input from B.W., D.P.T., and N.S.; K.K., K.S., and S.F. provided data; D.G.B. wrote the computer code and conducted the analyses; D.G.B. drafted the manuscript; all authors reviewed the manuscript and edited subsequent drafts.

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## Competing interests

The authors declare no competing interests.

## Additional information

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