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RESEARCH ARTICLE

Climate models drive variation in projections of species distribution on the Grand Banks of Newfoundland

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Abstract

Species Distribution Models (SDMs) are tools for understanding climate-induced habitat changes, yet their outcomes depend heavily on climate model selection. This study compares biomass projections for three key species on the Grand Banks of Newfoundland that are known to be sensitive to warming—snow crab, yellowtail flounder, and Atlantic cod. We use Earth system models (GFDL-ESM4, IPSL-CM6A-LR) and a regional ocean model system (Atlantic Climate Model (ACM)) under varying climate change emissions scenarios to assess long-term biomass trends and distributional shifts driven by future ocean warming on the Grand Banks. Projections indicate declining biomass for snow crab and yellowtail flounder with rising temperatures, whereas Atlantic cod is anticipated to exhibit biomass gains, particularly in the southern Grand Banks. Variations in biomass projections among climate models were noticeable, with IPSL forecasting the most drastic decline. ACM and GFDL biomass projections were more similar to each other than GFDL and IPSL projections, likely because ACM was downscaled from GFDL. Differences between GFDL and ACM likely arise from the coarse spatial resolution of ESMs, leading to insufficient resolution of the bathymetry and incorrect current patterns, in turn affecting the bottom temperature field. These findings underscore the important role of climate model selection in SDM-derived biomass projections. We partitioned uncertainty by source and found that the relative contribution of variability by component changes by species. As temperatures continue to rise, the urgency of implementing adaptive management strategies to minimize impacts on Newfoundland and Labrador fisheries becomes increasingly evident. SDM outputs can aid in strategic decision making, providing valuable insights for medium and long-term planning in fisheries management.

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Data Availability Statement: The data that support the findings of this study are available from Fisheries and Oceans Canada- Newfoundland and Labrador region. Restrictions apply to the availability of these data, which were used under license for this study. Data are available under formal request to the regional headquarters [contact info: https://www.dfo-mpo.gc.ca/contact/regions/newfoundland-terreneuve-eng.html]. The request process involves filling out a form specifying the data of interest [file name: 7B_KG-PER-

SET_DATA_FOR_GIS_MAPPING_9_Feb_2021]. Please, specify the following queries: [Division: 3L, 3N and 3O]; [Season: spring]; [Gear name: Campelen] and [Year: 1996-2019] to ensure accurate retrieval. Our research involves sensitive information for the Newfoundland fishing sector, and public deposition would breach compliance with the protocol approved by our research ethics board. We believe that by directing interested parties to the official channel at DFO, we can balance the need for transparency with the necessity of adhering to legal and ethical obligations. The code employed for the data analysis is publicly accessible on Zenodo: DOI: 10.5281/zenodo.13819714.

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Introduction

Species distribution models (SDMs) have become increasingly important as the marine environment changes rapidly. Distributions of species in space and/or time are modelled as a function of a range of physical, environmental, and ecological variables. SDMs have been implemented with a diverse range of statistical tools, including classic regression models (e.g., generalized linear models- GLMs, generalized additive models- GAMs, and generalized linear mixed models GLMM) [1], machine learning algorithms (e.g., random forest and artificial network analysis) [2], climatic envelope methods (e.g., dynamic bioclimatic envelope models) [3, 4] and decision tree methods (e.g., boosted regression trees) [5]. To forecast climate change impacts on species distributions, environmental outputs from Earth system models (ESMs) and regional ocean modelling systems (ROMS) are commonly used as SDM inputs [4, 6]. ESMs simulate the Earth's entire climate system, focusing on global-scale interactions between the atmosphere, oceans, land surfaces, and ice. They provide insights into long-term climate trends and variability [7, 8]. Variation in ESM projections can arise due to differences in forcing, process configuration, feedbacks, and horizontal and vertical resolutions [9, 10]. In contrast, ROMS concentrate on specific regions or domains of the ocean, offering higher spatial resolution to study fine-scale processes such as coastal dynamics, boundary currents, and mesoscale eddies [11, 12]. The low spatial resolution of ESMs can make it challenging to adequately represent regional processes, as they are primarily designed to emphasize global-scale dynamics [7]. ESMs also do not appropriately represent depths less than 50 m [7]. However, in many cases these models are the only available information to project species distribution under climate change scenarios [9].

Newfoundland and Labrador, located on the east coast of Canada, is a dynamic region that undergoes significant climatic variations, oscillating between warm and cold periods on decadal scales [13]. Within it, three major geographical subunits characterized by distinct productivity and a reasonably well defined major marine community (ecosystem production units), have been identified: Newfoundland Shelf (North Atlantic Fisheries Organization (NAFO) divisions 2J3K), Grand Banks (3LNO) and Flemish Cap (3M) [14, 15]. A key feature of the Newfoundland system is the cold intermediate layer (CIL), consisting of a water layer below 0˚C. It forms during winter as a cold surface layer and remains as an intermediate layer separate from the surface (roughly 0–50 m) when waters warm in spring [13]. The presence of the CIL heavily impacts the Grand Banks because of the shallow depth of the oceanic plateau. This creates distinct temperature patterns within the Banks. Moreover, recent observations suggest a trend of warming ocean temperatures on the Grand Banks [16]. This warming may be influenced not only by warmer air temperatures that increase the heat transfer to the upper layers of the oceans, but also by a slowing down of the shelfbreak jet, which reduces the supply of the fresh, cold and nutrient-rich waters of the Labrador Current to the Grand Banks slopes [17–19].

In the Newfoundland and Labrador region, a shift from a warm to cold phase in the 1990s, coupled with intensive fishing, triggered alterations in ecosystem productivity, leading to a substantial decline in most groundfish stocks and a surge in invertebrate biomass on the Newfoundland Shelf [20] and the Grand Banks [21]. Responding to the groundfish collapse, several fishing moratoria were imposed in 1992 and 1994 on the Newfoundland Shelf and the Grand Banks respectively, to facilitate the recovery of groundfish stocks (e.g., Atlantic cod, yellowtail flounder, haddock, among others). The impact of the collapse was profound, affecting both harvesters and plant workers in the province, with over 35,000 individuals losing their source of livelihood [22]. In the present study, we focused on three key fisheries species of the Grand Banks that exhibited distinct responses to the collapse: yellowtail flounder (*Limanda ferruginea*), Atlantic cod (*Gadus morhua*) and snow crab (*Chionoecetes opilio*).

The yellowtail flounder fishery in the 3LNO division was closed from 1994 to 1997 and rebounded, currently operating as a Marine Stewardship Council (MSC) certified fishery [23, 24]. Yellowtail flounder inhabits the east coast of North America, from Newfoundland to the Chesapeake Bay [23], with biomass peaking on the Grand Banks at approximately 3˚C, tolerating a temperature wide range [25]. In contrast, Atlantic cod stocks (3NO and 2J3KL) remain at low levels compared to historical baselines, with only a modest increase in biomass observed in the 2J3KL stock, primarily driven by the 2J3K divisions [26]. This situation resulted in the persistent closure of the directed commercial fishery for both stocks over 30 years, although a stewardship fishery has been allowed in the 2J3KL division [26, 27]. In 2024, the 2J3KL Atlantic cod commercial fishery opened again. Atlantic cod is found across the North Atlantic Ocean, avoids temperatures exceeding 12˚C [28], and shows higher biomass at 5–6˚C on the Grand Banks [15].

Following the collapse, Newfoundland and Labrador's fishing industry diversified its target species, focusing on invertebrate like snow crab. Snow crab has become the province's most valuable species, with a value of $761 million CAD in 2022, representing 58% of the total landed value of all fisheries resources in NL [22, 29]. A recent study found that the species is moving from subArctic to Arctic environments [30]. This suggests that with future warming, the species may experience biomass losses on the Grand Banks, where most of the Newfoundland and Labrador quota (59%) is currently allocated (https://www.dfo-mpo.gc.ca/fisheries-peches/decisions/fm-2023-gp/atl-14-eng.html).

The climatological changes mentioned above may present a pressing issue for Newfoundland and Labrador's fishing sector, which in 2022 contributed $1.4 billion CAD to the local economy and currently employs over 17,000 people across 400 communities [29]. Thus, the objectives of this study were: i) to produce and compare biomass projections for three contrasting species on the Grand Banks of Newfoundland under two climate change emissions scenarios; and ii) to evaluate the importance of climate model choice in these types of projections. In particular, we compared species biomass projections using the Coupled Model Intercomparison Project (CMIP) 6 earth system models IPSL-CM6A-LR [31] and the GFDL-ESM4 [32] under low (SSP1-2.6) and high (SSP3-7.0) emissions scenarios, and the ROMS Atlantic Canada model (from now on referred as ACM) [19, 33] as climate forcings. While these projections should be interpreted with caution, they provide valuable guidance for fisheries management strategies by detecting changes in habitat suitability and anticipating future biomass trends. In assessing variation in biomass projections, we specifically analyzed the influence of climate model and emissions scenario choice, including variations in bottom temperature under low (SSP1-2.6) and high (SSP3-7.0 and SSP4-6.0) emissions pathways.

Materials and methods

General approach

We used SDMs to characterize current species distributions, with temperature and depth as key drivers. These models aim to capture the general changes associated with climate-driven shifts in temperature. To achieve this, we defined temperature fields for the Grand Banks using various emissions scenarios (low—SSP1-2.6 and high–SSP3-7.0 and SSP4-6.0-) generated by multiple climate models (IPSL, GFDL and ACM), thereby capturing uncertainty surrounding these projections. Subsequently, we utilized the SDMs and the projected temperature fields to forecast the expected distributions of the focal species between the present and 2100 under different climate change scenarios. Finally, we assessed variability in projections as a function of climate models and emissions scenarios.

Oceanographic and biological survey data

Fisheries and Oceans Canada (DFO) has been conducting annual random stratified multispecies trawl surveys in Newfoundland and Labrador since 1971, with these surveys experiencing important modifications in survey design, coverage, species recorded, and gear over time [34]. One major change in these surveys was the transition from the use of the Engels trawl to the Campelen trawl gear (i.e., 1800 shrimp trawl) in 1995–1996 [34]. This change improved catches of small-sized fishes and marked the start of the time series for commercial shellfish species being recorded. Georeferenced data on presence/absence and biomass for the focal species of this study as well as water temperature and depth comes from DFO spring surveys on the Grand Banks between 1996 and 2019. To predict biomass, we created grids with a 5 x 5 km spatial resolution which included gridded bathymetry information with a 15 arc second spatial resolution from the general bathymetric chart of the oceans project (GEBCO) (https://www.gebco.net). Spring bottom temperature data were interpolated over the Grand Banks with a spatial resolution of 0.1˚ x 0.1˚ [16] (Fig 1). Bathymetry data represented depths from 35 to 750 m since those were the depths sampled in the RV trawl survey.

Climate models and emissions scenarios

We considered both low and high emissions scenarios to assess their impacts on snow crab, yellowtail flounder, and Atlantic cod distributions on the Grand Banks. We used three models to characterize these scenarios. The ACM uses ROMS version 3.5, a terrain-following, free-surface, primitive equation ocean model [33, 35]. It was configured with 30 vertical levels (layers are thinner in shallower water and thicker in deeper water), with a minimum water depth of 10 m, and an approximate horizontal resolution of 10 km (240×120 horizontal grid cells). The model encompasses the Gulf of Maine, Scotian Shelf, East Newfoundland Shelf, Grand Banks, and the Gulf of St. Lawrence, and has been demonstrated to accurately capture regional circulation patterns [36], and represent biogeochemical properties well [33]. The ACM was calibrated to observed values [33] and forced by anomalies from the GFDL high-resolution coupled model, CM2.6, with a rapid increase in CO_2 that resembles the SSP4-6.0 scenario [18]. In comparison, IPSL-CM6A-LR [31] and GFDL-ESM4 [32] are ESMs with a coarser spatial resolution of approximately 100 km. These models produce a much poorer agreement with observed temperatures, salinity, nitrate, and chlorophyll observation in the Grand Banks than the ACM [33]. ESMs also do not appropriately represent depths less than 50 m [7].

For biomass projections, we used annual average sea bottom temperature (potential temperature on bottom–thetao_bot) sourced from the Coupled Model Intercomparison Project (CMIP) 6 ESMs IPSL-CM6A-LR [31], GFDL-ESM4 [32] and the ROMS ACM [19, 33]. We used the shared socioeconomic pathway (SSP) and representative concentration pathway (RCP) scenarios SSP3-7.0 for IPSL and GFDL, and SSP4-6.0 for ACM as the high emissions scenarios due to availability, and the low emissions scenario SSP1-2.6 [37]. Unfortunately, the low emissions scenario was not available for ACM (Fig 2A and 2B). Note that while the specifics of the high emissions scenarios do not align perfectly among models (SSP3-7.0 and SSP4-6.0), they are similar enough in their warming trends, allowing for general comparisons. Additionally, the ACM outputs have been smoothed [18], whereas the ESMs have not, explaining the differences in the variability of the temperature field. Finally, we bias-corrected annual bottom temperature projections of the climate models to the local spring observations since they were consistently higher. To align our projections with observed baseline conditions, we calculated the mean temperature from the climate model and the mean observed temperature values from 2015 to 2019 (we selected these years because the projections and observations overlapped). The bias was then determined as the difference between these means and used to

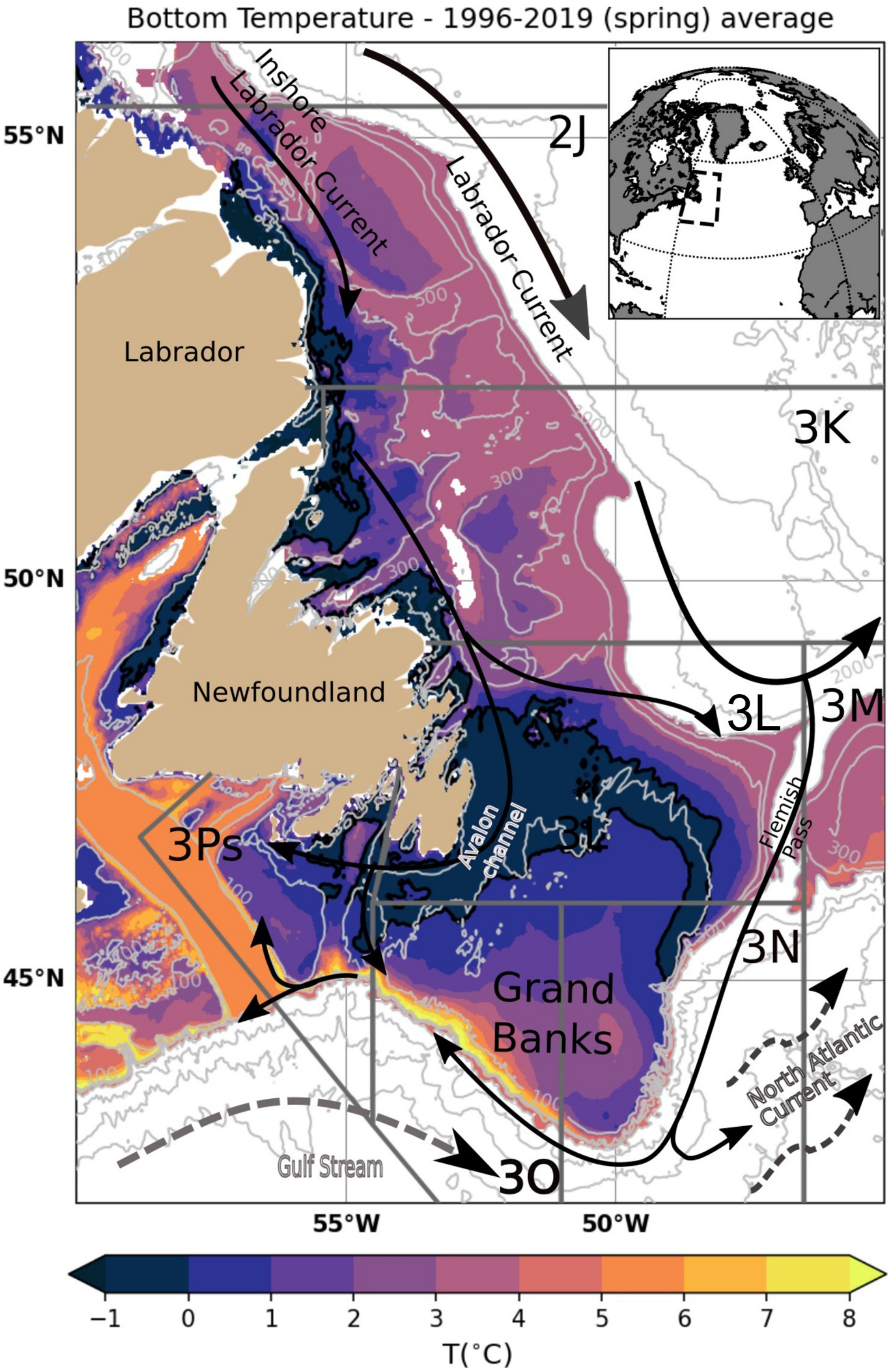

Fig 1. Map of the average spring bottom temperature during the historical period (1996–2019) interpolated over the Grand Banks. Isobaths indicated in light grey; Northwest Atlantic Fisheries Organization NAFO divisions boundaries are indicated with grey rectangles. Black arrows show the main currents of the region. Base map layer from Natural Earth (https://www.naturalearthdata.com/about/).

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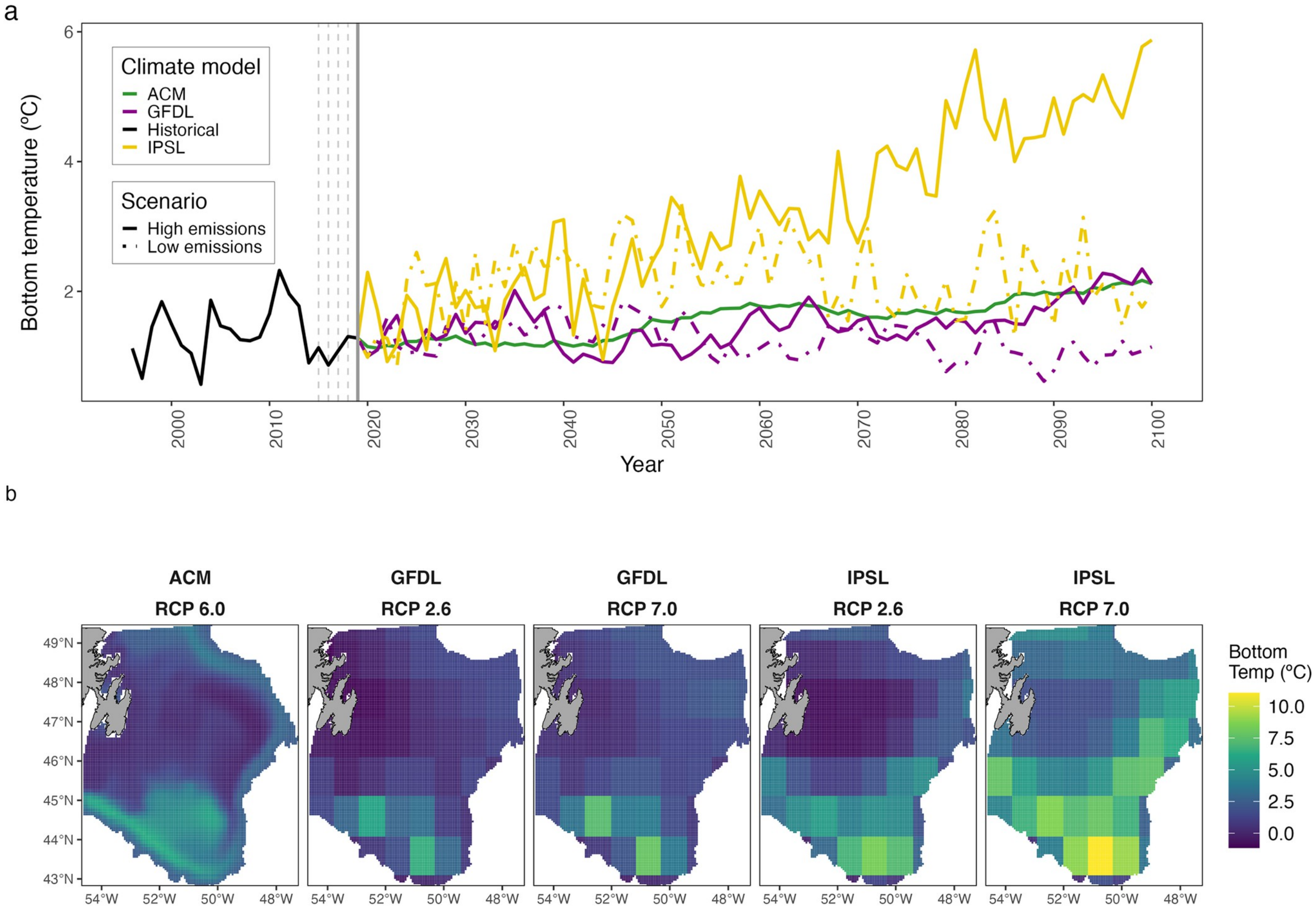

Fig 2. Maps and time series of average annual bottom temperature projection on the Grand Banks. a, Time series of average annual bottom temperature for the model domain. The historical period is represented by a black line, while the IPSL-CM6A-LR, GFDL-ESM4, and ACM models are indicated by yellow, purple and green lines, respectively. Dashed lines represent the low emissions scenario (SSP1-2.6), and solid lines depict the high emissions scenario (SSP4-6.0 for ACM, and SSP3-7.0 for GFDL and IPSL). b, Maps of mean annual bottom temperature projections by climate model (GFDL, IPSL and ACM) and RCP scenarios at the end of the century (period 2071–2100). Base map layer from Natural Earth (https://www.naturalearthdata.com/about/).

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adjust the model output (Figs I and J in S1 Text). This adjustment aligns the model temperatures with observed conditions.

Modelling approach

Species distribution models. To build species distribution models, we used the R package *sdmTMB* [38]. *sdmTMB* fits models with maximum marginal likelihood through template model builder (TMB) [39] and incorporates the stochastic partial differential equation approach (SPDE) [40] for approximating spatial Gaussian random fields [41, 42].

Two population variables were used as response variables to characterize the species distribution. Firstly, a presence/absence variable was considered to measure probability of species occurrence. Secondly, species biomass was used as an indicator of the conditional-to-presence-biomass, which are observations with positive biomass values (i.e., biomass > 0). Abiotic explanatory variables were bathymetry (here called depth) and bottom temperature. After preliminary analysis, covariates were added to the model as curvilinear effects to account for their non-linear relationships. Finally, we included swept-area by the survey gear (log-transformed) as an offset in the model to account for sampling effort [38].

The general form of the SDM is a delta (hurdle) generalized linear mixed effects model (GLMM). We test two different families, delta_gamma and delta_lognormal. We considered $Z(s, t)$ to be the occurrence and $Y(s, t)$ the conditional-to-presence biomass at location s and time t. The model formulation can be written as (Formula 1):

$$Z(s,t) \sim Bernoulli(\pi(s,t)) \tag{1}$$

$$Y(s,t) \sim Gamma(\mu(s,t),\ \phi)\ or\ Y(s,t) \sim Lognormal(\mu(s,t),\ \sigma^2)$$

$$logit(\pi(s,t)) = \beta_z + \sum_{i=1}^{I} f_i(X_i(s,t)) + \mathrm{V}_z(s,t)$$

$$log(\mu(s,t)) = \beta_Y + \sum_{i=1}^{I} f_i(X_i(s,t)) + \mathrm{V}_Y(s,t)$$

Where π (s, t) represents the probability of occurrence at location s and time t; μ (s, t) is the mean; and ϕ and σ are the variance of the conditional-to-presence biomass for the gamma and lognormal distribution, respectively. The linear predictors, which represent the intercept of each variable associated to the parameter π (s, t) and μ (s, t), are represented by β_z and β_Y, respectively. $f()$ represents any function applied to the covariate (X_i), which in the present study was a second-degree polynomial function. $V_z(s,t)$ and $V_y(s,t)$ refer to the spatial structure of the occurrence and conditional-to-biomass model, respectively.

Our model aims to identify the optimal average spatial relationships that describe the distribution patterns, treating individual years as replicates. We created a mesh with a cutoff of 15 km, which resulted in 761 nodes. We refrained from incorporating spatiotemporal variations (i.e., autoregressive model of order one (AR1) and random walk (RW)) as well as fixed temporal covariates (i.e. year as fixed effect) into the model because of challenges in projecting these effects over an extended period into the future [43].

Model selection. We compared four different model configurations (Tables A-C in S1 Text). To select the best fitting model, we used the Akaike information criteria (AIC), an estimator of model prediction error commonly used in model selection [44]. We also quantified the percent deviance explained when comparing model configurations to an intercept-only null model, using relative log-likelihood between models [43]. Finally, we visually inspected the quantile residual plots (see Figs A, C and E in S1 Text).

Additionally, we assessed model predictability during the historical period by comparing mean biomass values observed to those predicted and calculated the area under the curve (AUC) and the Pearson correlation (R). We also assessed future predictability by implementing the leave future out strategy in which we trained our model with data from 1996 to 2016 and tested it against the last 3 years of the time series (2017–2019).

Biomass projections to 2100. We analyzed time series projections of biomass as percent change between the historical period (1996–2019) and each future year. Then, we compared projections among climate models and low (SSP1-2.6) and high (SSP4-6.0 for ACM, and SSP3-7.0 for IPSL and GFDL) emissions scenarios. We ran simulations to the end of the century because temperature projections from the SSP-RCP scenarios increasingly diverge after 2050 [45, 46]. Changes in spatial patterns of species biomass were assessed by calculating the difference between projections and historical period as follow:

$$B_{CM_k}(i, j) - B_{Hist}(i, j) \tag{2}$$

Where B_{CM} represents the biomass at the grid cell (i, j) for the end of century period (2077–2100) under the high emissions scenario for climate model K; $B_{Hist}(i,j)$ is the biomass at the same grid cell for the historical period (1996–2019).

We called this difference in biomass: ΔBiomass. To enhance visual clarity, distributions in the figure were constrained between the 0.1 and 99.9th percentiles range due to the presence of a few extreme values in ΔBiomass.

Biomass uncertainty evaluation

We assessed point-wise prediction uncertainty of species distribution models during the baseline period (1996–2019) by conducting 100 simulations based on the joint precision matrix of our model [47]. The precision matrix, often referred to as the inverse covariance matrix, characterizes the relationships between variables assuming a multivariate normal distribution [38]. The variability in these simulations, and hence the level of prediction uncertainty, is directly influenced by the precision matrix. High variability in biomass at each grid point reflects greater uncertainty in the model's predictions. We repeated this approach to assess biomass projections from each climate model under the high emissions scenarios at the end of the century (period 2077–2100). Finally, we partitioned uncertainty in the biomass estimates among climate models and RCPs by fitting a linear model, with annual biomass estimates as a response variable and climate models (GFDL, IPSL and ACM) and scenarios (low and high emissions) as covariates, allocating residual error to parameter uncertainty (e_i) as in formula 3.

$$Biomass_i = \beta_0 + \beta_1 X_{1i} + \beta_2 X_{2i} + e_i \tag{3}$$

$Biomass_i$ represents the annual biomass estimate for the *ith* observation; β_0 is the intercept term; β_1 and β_2 are coefficients corresponding to the predictor variables X_1 (climate model) and X_2 (emissions scenario), respectively. Finally, e_i represents the residual error term, capturing unexplained variation in the biomass estimates.

Dominance analysis is a statistical technique used to assess the relative importance of predictor variables in explaining variance in a dependent variable, and was applied to evaluate the relative importance of each component [48, 49]. We smoothed the results by computing 10-year averages to mitigate noise and highlight the underlying trends. We acknowledge that having three climate models and only two scenarios–only one in the case of the ACM model–may induce bias in assessing predictor importance.

Results

For all species, models that best explained spatial patterns of biomass distribution included depth and temperature as fixed effects and the spatial random field (Tables A-C in S1 Text). The spatial random field represents biomass deviations in space that are not accounted for by covariates. Its inclusion substantially improved model performance, especially for yellowtail flounder and Atlantic cod. Model estimates are available in Table D in S1 Text.

We used the model fit to predict biomass estimates of the focal species on the Grand Banks of Newfoundland during 1996–2019. Then, we forecasted to 2100 under the low and high emissions scenarios. The predictive capacity of the models varies among species, with yellowtail flounder having the highest predictability (R = 0.74; AUC = 0.97), followed by snow crab (R = 0.55, AUC = 0.89) and Atlantic cod (R = 0.55, AUC = 0.82) (Fig G in S1 Text). We also assessed the out-of-sample predictability, training our model with data from 1996 to 2016 and

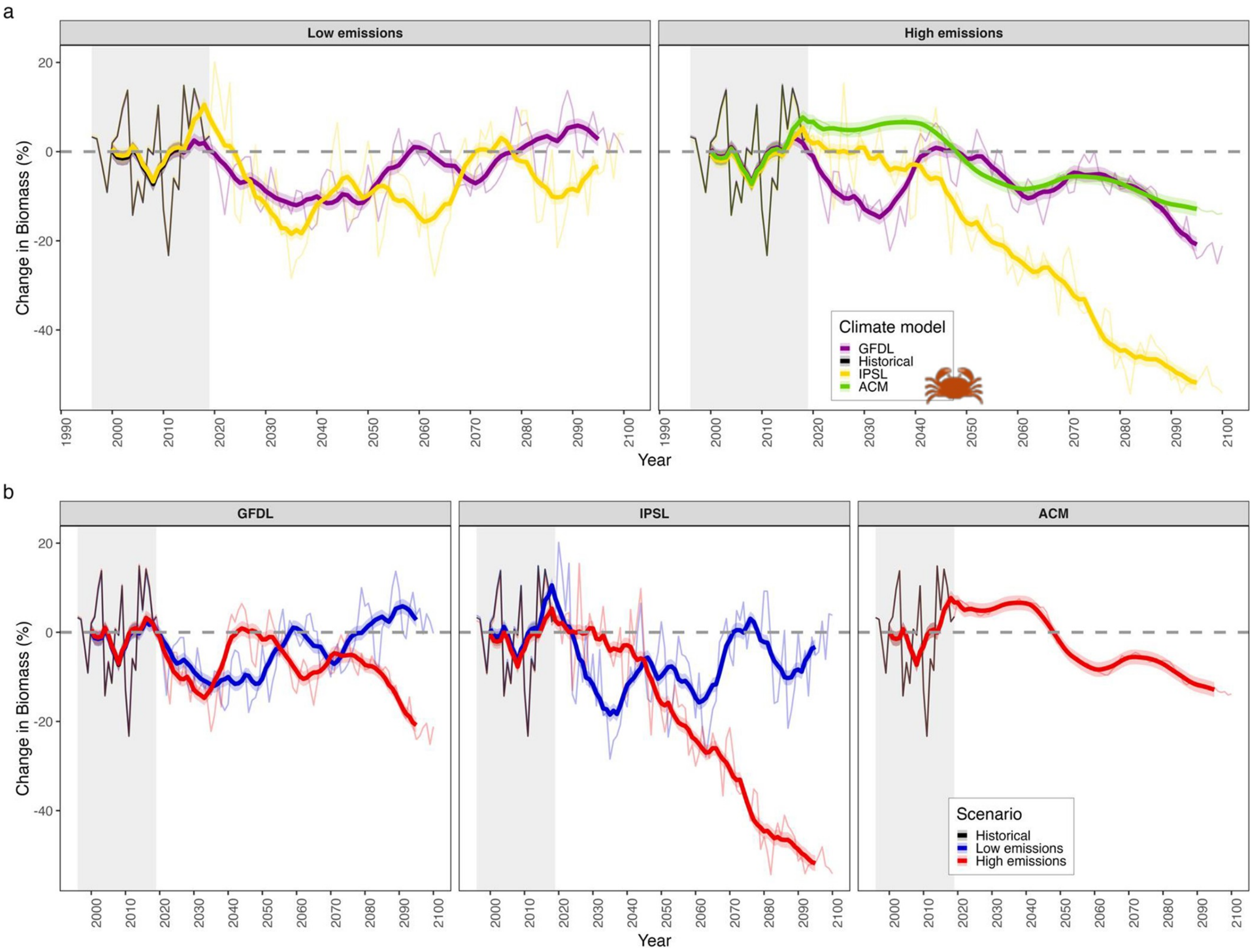

Fig 3. Projections of snow crab biomass by climate model and emissions scenario. a, Projections under low emissions (SSP1-2.6, left) and high emissions scenarios (SSP4-6.0 for ACM and SSP3-7.0 for IPSL-CM6A-LR and GFDL-ESM4 scenario, right). b, Projections by climate models for low and high emissions scenarios. Biomass changes are relative to the predicted values of the reference period (1996–2019), indicated by shaded grey area. Solid colored lines depict average projected biomass, while shaded areas indicate standard deviation. Zero change is represented by a horizontal dashed line.

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testing it for the period 2017:2019. The predictability was (R = 0.7; AUC = 0.97) for yellowtail flounder, (R = 0.41, AUC = 0.89) for snow crab and (R = 0.47, AUC = 0.79) for Atlantic cod (Fig H in S1 Text).

Our findings underscored a long-term decline in the projected biomass of snow crab for all climate models and scenarios except for GFDL under the low emissions scenario (Fig 3). If we focus on the values at the end of the century (2077–2100), greater losses were observed for the high emissions scenario, especially for IPSL model -47% [± 1.67% SD], followed by ACM -10.4% [± 1.59% SD] and GFDL -14.68% [± 1.59% SD]. Under the low emissions scenario, biomass trends fluctuated around the historical average. Values at the end of the century (2077–2100) for IPSL projected biomass losses of -3.8% [± 1.6% SD], whereas GFDL projected biomass gains of 3.7% [± 1.57% SD].

We also observed a long-term decline in yellowtail flounder biomass for the IPSL model under the low and high emissions scenarios -8.4% [± 0.38% SD] and -29% [± 0.36% SD], respectively (Fig 4). Biomass projections at the end of the century (2077–2100) for the GFDL

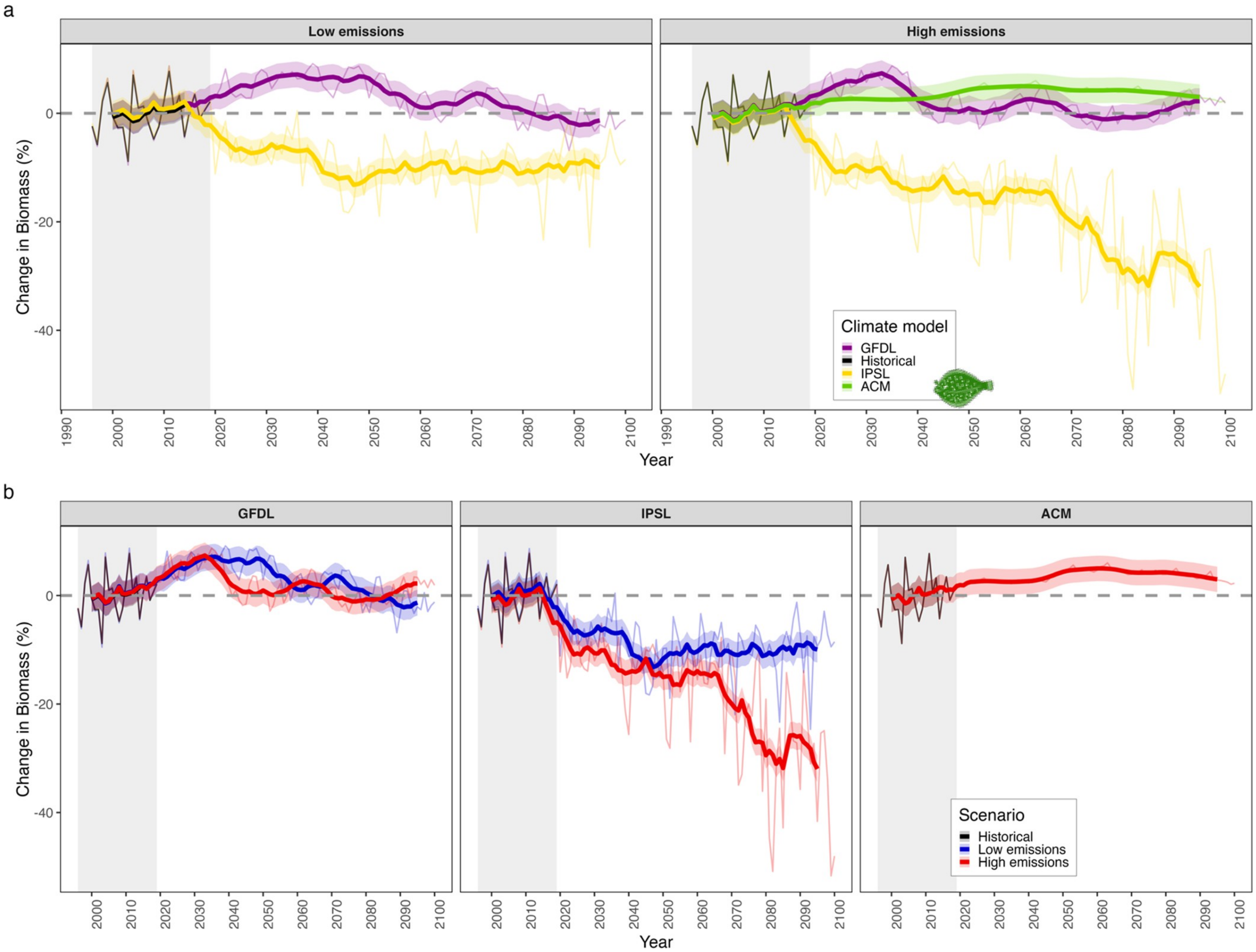

Fig 4. Projections of yellowtail flounder biomass by climate model and emissions scenario. a, Projections under low emissions (SSP1-2.6, left) and high emissions scenarios (SSP4-6.0 for ACM and SSP3-7.0 for IPSL-CM6A-LR and GFDL-ESM4 scenario, right). b, Projections by climate models for low and high emissions scenarios. Biomass changes are relative to the predicted values of the reference period (1996–2019), indicated by shaded grey area. Solid colored lines depict average projected biomass, while shaded areas indicate standard deviation. Zero change is represented by a horizontal dashed line.

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model under both emissions scenarios indicated biomass values close to the historical average, -1.4% [± 0.38% SD] for the low emissions and 0.39% [± 0.38% SD] for the high emissions scenario. Finally, the ACM model suggests a small increase in biomass at the end of the century (period 2077–2100) of 4.45% [± 0.34% SD].

SDMs projected a long-term decline in Atlantic cod biomass for the GFDL-low emissions scenario of -11.5% [± 0.53% SD] at the end of the century (2077–2100), and an increase in biomass for the rest of model and scenarios (Fig 5). The biomass projection for IPSL-low emission scenario indicates a gain of almost 9.8% [± 0.53% SD] at the end of the century. Under the high emissions scenario, GFDL oscillates around the historical average but showed an increase of 3.12% [± 0.53% SD] at the end of the century (period 2077–2100). IPSL and ACM both showed a similar trend of biomass gain at the end of the century, reaching values of 15.21% [± 0.55% SD] and 19.2% [± 0.52% SD], respectively.

The analysis revealed a consensus among earth system models (IPSL and GFDL) regarding the locations with the most pronounced losses in snow crab biomass, specifically at the north

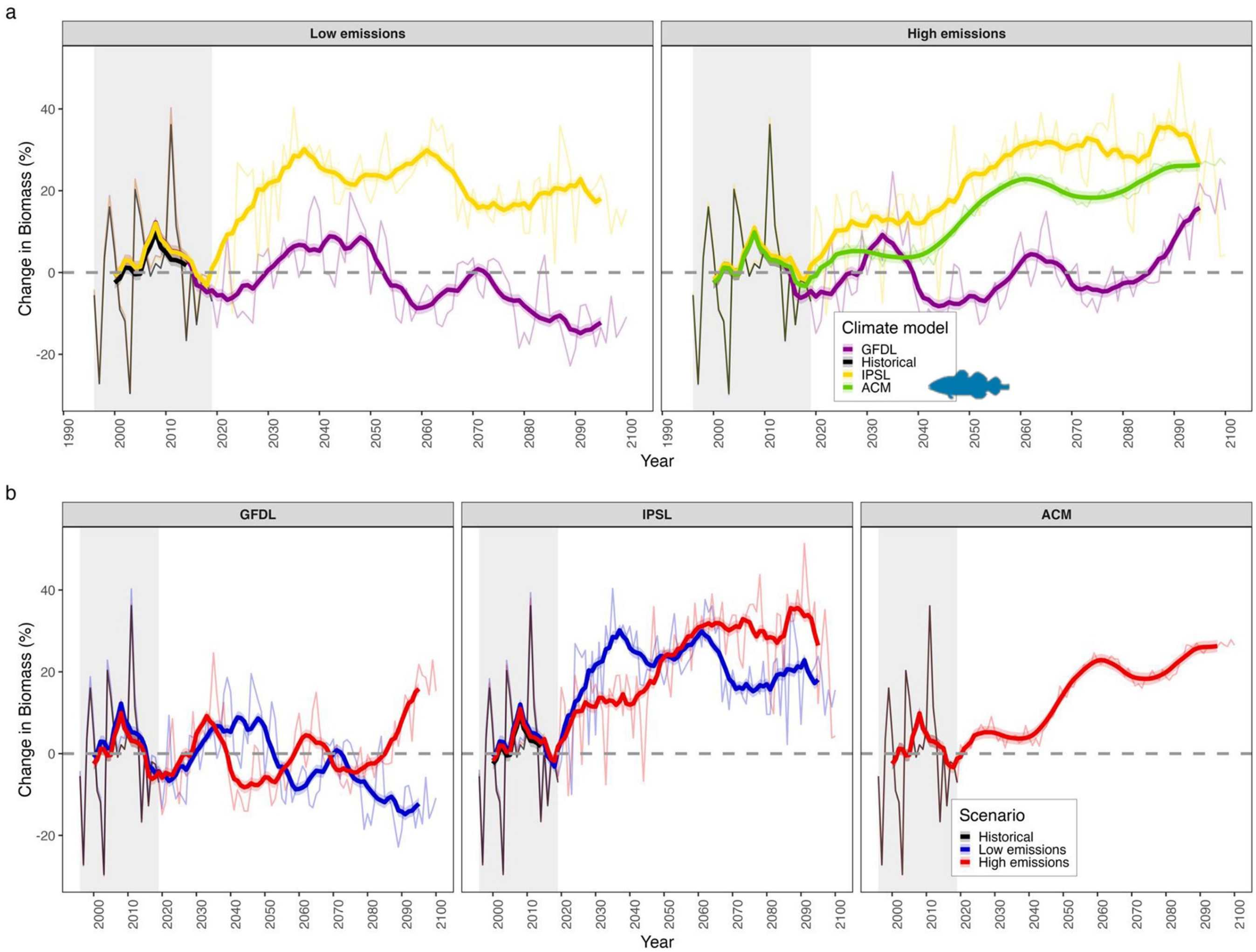

Fig 5. Projections of Atlantic cod biomass by climate model and emissions scenarios. a, Projections under low emissions (SSP1-2.6, left) and high emissions scenarios (SSP4-6.0 for ACM and SSP3-7.0 for IPSL-CM6A-LR and GFDL-ESM4 scenario, right). b, Projections by climate models for low and high emissions scenarios. Biomass changes are relative to the predicted values of the reference period (1996–2019), indicated by shaded grey area. Solid colored lines depict average projected biomass, while shaded areas indicate standard deviation. Zero change is represented by a horizontal dashed line.

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and south of the Grand Banks (Fig 6). However, ACM depicted a less pronounced decline (Fig 6A). The majority of yellowtail flounder biomass changes were observed on the southeast shoal of the Grand Banks. GFDL and ACM mostly agreed for projected spatial biomass changes. In contrast, IPSL suggested a stronger decline in the southern part of the southeast shoal (Fig 6B). Spatial biomass patterns for Atlantic cod showed the biggest disagreement among climate models (Fig 6C). GFDL predicted losses in the north and southern edge, with some gains on the southern shoal. IPSL indicated biomass losses on the southeastern shoal and gains on the rest of the Banks. Finally, ACM projected gains mostly in the south of the Banks.

Uncertainty

We observed marked spatial variability in SDM biomass projections during the historical period (1996–2019), with standard deviations of biomass ranging from 0 to 4 kg/25 km^2 for snow crab, yellowtail flounder and Atlantic cod (Fig 7-SDM). Areas of high variability were

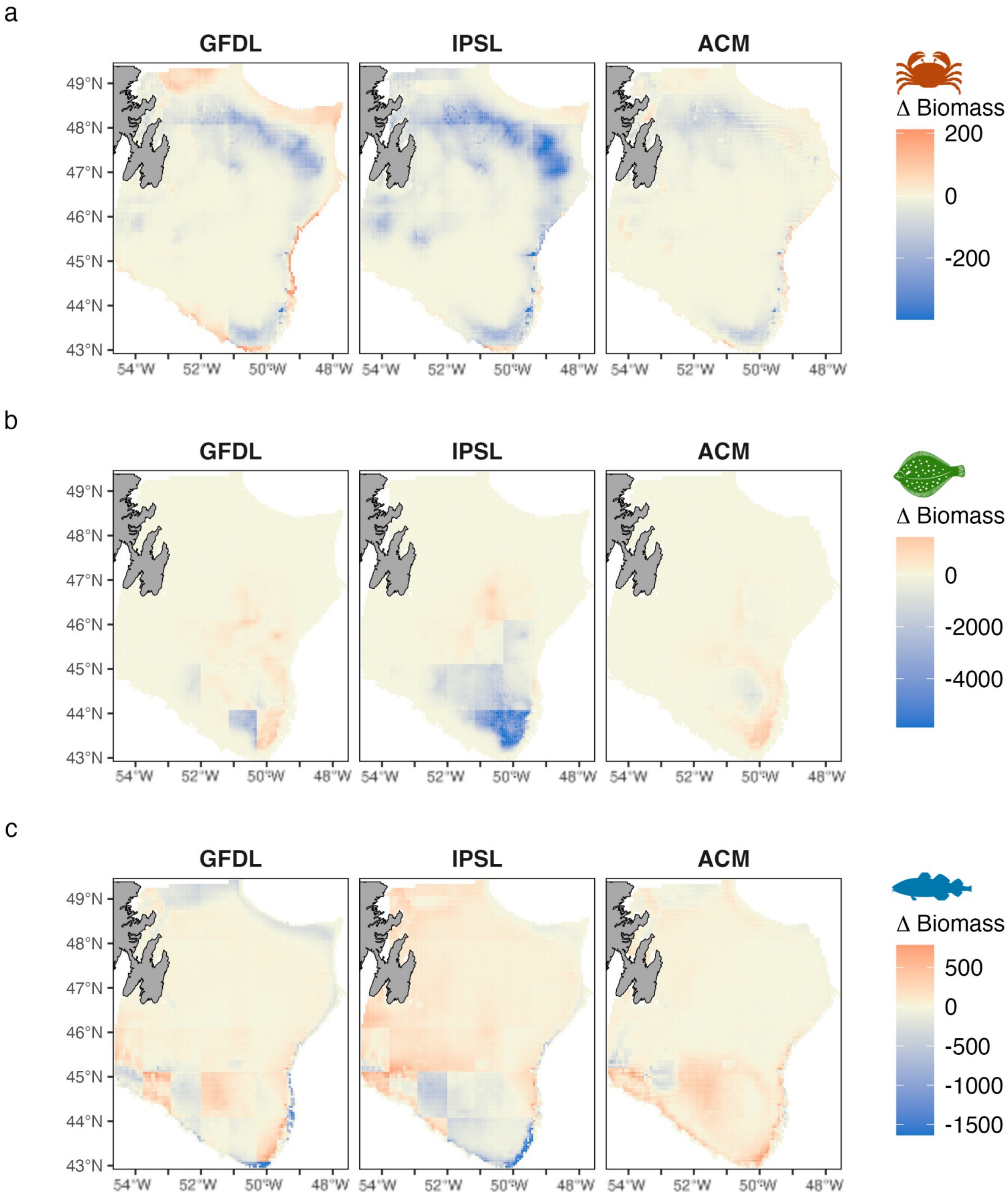

Fig 6. Spatial patterns of species biomass changes (in kg/25 km2) for a, snow crab; b, yellowtail flounder and c, Atlantic cod on the Grand Banks of Newfoundland by climate model (GFDL-ESM4, IPSL-CM6A-LR and ACM) under the high emissions scenarios (SSP4-6.0 for ACM and SSP3-7.0 for IPSL and GFDL) during the 2077–2100 period relative to the historical period (1996–2019). The Avalon Peninsula is the southern piece of land (in grey). Base map layer from Natural Earth (https://www.naturalearthdata.com/about/).

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associated with areas of biomass absence, likely driven by the gamma component of the delta-gamma model (Figs B, D and F in S1 Text). For snow crab, the periphery and the southeast shoal of the Grand Banks showed high variability (Fig 7A). For yellowtail flounder, variability was higher in the northern part of the Banks and on the periphery (Fig 7B). In the case of

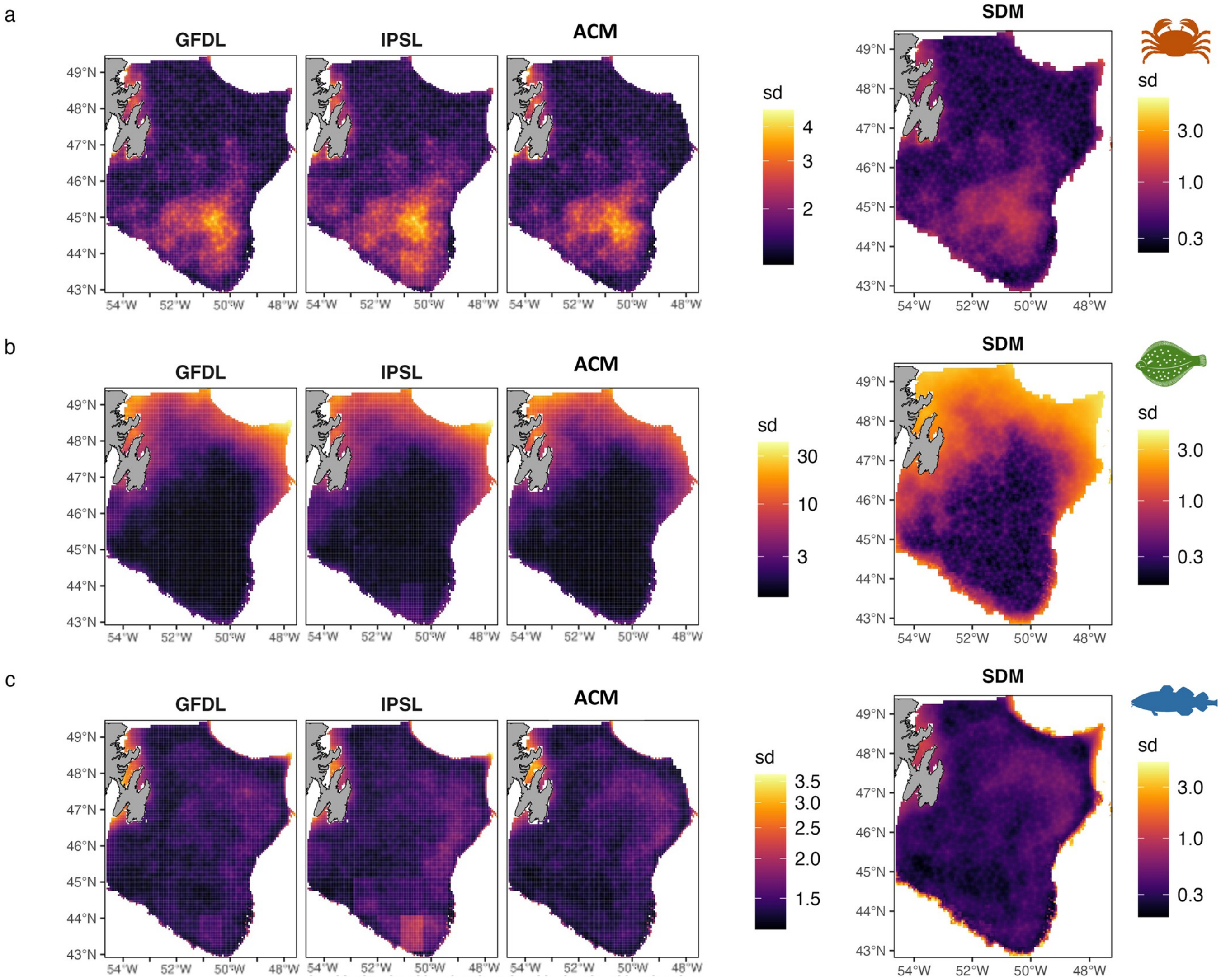

Fig 7. Spatial uncertainty of SDM biomass estimates (historical period; 1996–2019) and climate model projections (GFDL, IPSL and ACM) at the end of the century (2077–2100) measured as the standard deviation from 100 simulation draws for (a) snow crab, (b) yellowtail flounder and (c) Atlantic cod projected biomass. Base map layer from Natural Earth (https://www.naturalearthdata.com/about/).

https://doi.org/10.1371/journal.pclm.0000520.g007

Atlantic cod, variability was pronounced around the Avalon peninsula and on the periphery of the Banks (Fig 7C).

Variability in biomass projections amplified between the historical period to the end of the century (2077–2100), where the standard deviation of the biomass increased, especially for yellowtail flounder (30 kg/25 km^2) (Fig 7).

We partitioned uncertainty to assess the relative contribution of each component: climate model, SSP-RCP scenario and SDM parameters (Fig 8). For all three species—snow crab, yellowtail flounder, and Atlantic cod—climate model uncertainty was the dominant factor contributing to biomass uncertainty across all years, consistently showing the highest influence (above 50%). However, the contribution of SDM parameters and scenarios varied over time. In the three cases, the influence of SDM parameters and scenarios increased slightly after 2050, indicating that uncertainty associated to SDMs parameters and SSP-RCP scenarios become more important as projections extend further into the future.

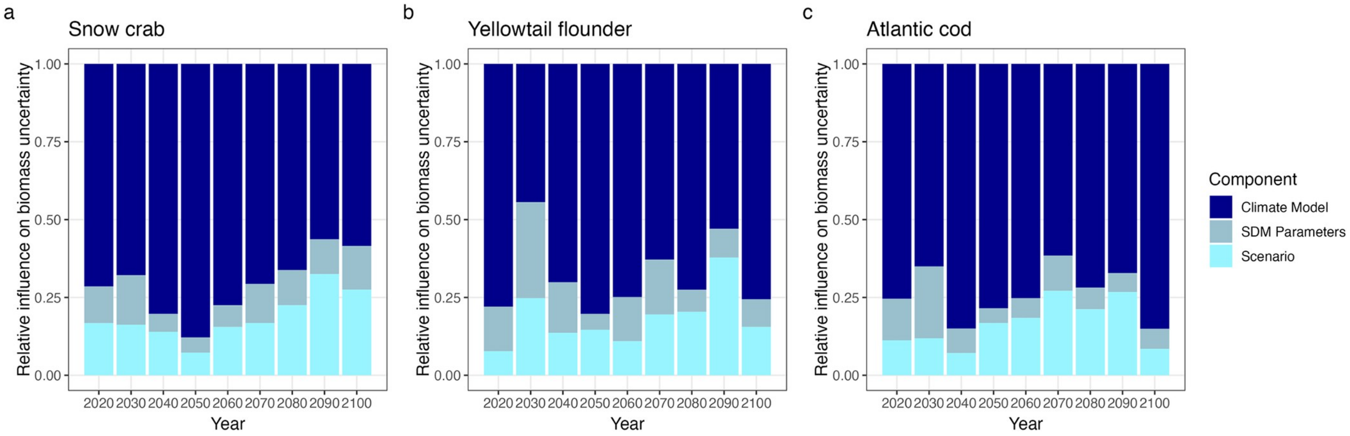

Fig 8. Relative uncertainty in biomass projections for a, snow crab; b, yellowtail flounder and c, Atlantic cod, partitioned across climate models (i.e., IPSL, GFDL and ACM), emissions scenarios (low-SSP1-2.6 and high-SSP4-6.0 & SSP3-7.0) and SDM parametrization.

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Discussion

Depth and temperature are known to be key factors that determine distribution and survival of many species, including snow crab [50], yellowtail flounder [51, 52] and Atlantic cod [28, 53]. As expected, both depth and temperature were relevant variables to explain spatial distribution. The best fitting models also included the spatial random field that explains variability not captured by the covariates.

Projected changes in species biomass to 2100 under low and high emissions scenarios showed an overall decline in snow crab and yellowtail flounder biomass compared to the historical period (1996–2019), whereas Atlantic cod is expected to gain biomass across the 21st century under the high emissions scenario. However, in the GFDL simulation, biomass declines through the mid-century before increasing. While there are differences in the magnitude of biomass projections across climate models, a consensus in the direction of changes was evident in all models except for GFDL-low emissions scenarios. This divergence can be attributed to the GFDL-low emissions scenario forecasting a decline in bottom temperature by the end of the century, in contrast to temperature increases projected by the other models and scenarios. The IPSL model projected the biggest warming on the Grand Banks.

Changes in species geographic distributions can be analyzed by focusing on their range boundaries. At leading edges, species expand into new territories as environmental conditions improve, while at trailing edges, population extirpations lead to range contractions [54]. Marine ectotherm species tend to fully use their potential latitudinal ranges in relation to their thermal tolerance limits [55], and distribution shifts are thought to be higher at the leading edge than at the trailing edge [56], although this is case specific [57]. Snow crab are commonly found in subpolar and Arctic regions, favoring cold water environments below 5˚C [58]. On the Grand Banks of Newfoundland, higher biomass has been observed at temperatures close to 0˚C [25]. Being stenothermic, snow crabs are believed to be highly responsive to changes in bottom temperature, particularly during their juvenile period [59]. Snow crab on the Grand Banks of Newfoundland are at the trailing edge of their distribution. This is because they are near their upper thermal threshold, making them particularly susceptible to ocean warming. A recent study has detected a general shift of snow crab distribution from the Newfoundland region into the Arctic [30]. Here, we found that snow crab biomass on the Grand Banks is expected to decline throughout the 21st century for all models under the high emission scenarios, while remaining close to the historical period under the low emissions scenario.

On the Grand Banks, yellowtail flounder thrive in sea bottom temperatures ranging from 1–6˚C, with biomass peaking at around 3˚C [25]. Despite the species' ability to tolerate a broad range of temperatures, there is evidence that stock productivity declines significantly at both extremes of the temperature range [23]. The case of yellowtail flounder is interesting as uncertainty widely amplifies over time, which was not the case for snow crab and Atlantic cod. Yellowtail flounder distribution is centered around the southeast shoal of the Grand Banks due to the presence of a mild current system, facilitating the retention of eggs and larvae [23]. This region is considered as a nursery ground for yellowtail flounder [51], and is the area in which higher warming is expected on the Grand Banks (Fig 2B). We found that yellowtail flounder biomass projections are expected to remain close to the historical average for GFDL and slightly higher for ACM, but to be negatively impacted for the IPSL model under high and low emissions scenarios.

Atlantic cod tolerates higher temperatures than the other two species, with a peak in biomass found at 5˚C on the Grand Banks [25]. Our analysis indicates that by the end of the century, most climate models (excluding the GFDL-low emissions scenario) predict an increase in Atlantic cod biomass on the Grand Banks. In particular, the ACM showed the greatest biomass gains. These results contrast with findings in the Gulf of Maine, where biomass decrease was noted with ocean warming [60, 61], but are in agreement with forecasted thermal habitat for cod on the Newfoundland and Labrador Shelf [62]. The difference can be attributed to the distinct thermal environments of these regions. The Gulf of Maine has an average bottom temperature of 7.1˚C [60], while the Grand Banks experiences significantly cooler temperatures, averaging 1.34˚C during our historical period (1996–2019). This suggests that Atlantic cod could potentially benefit from moderate warming in the Grand Banks, while those in the Gulf of Maine may be experiencing temperatures beyond their physiological limits, leading to declines in biomass [54]. Gains in Atlantic cod biomass are expected to occur mostly in the southern Grand Banks (3NO stock).

While temperature is a key factor influencing species biomass and distribution, other factors may also play a significant role. In the Grand Banks, the community structure has shifted since the collapse in the early 1990s [63], altering predator-prey interactions and productivity dynamics. Concerns have been raised that fishery-induced changes in these interactions could significantly hinder or even prevent the recovery of depleted populations like Atlantic cod [64]. Moreover, documented changes in life history traits—such as reduced age and size at maturity—and increased natural mortality may complicate recovery, even when thermal habitat conditions are optimal [26, 65, 66]. Continuing fishing and bycatch in low productivity conditions could further delay recovery [67].

Variability in the predictive capacities of the SDMs directly impacts the reliability of biomass projections. For instance, our leave future out cross-validation showed that yellowtail flounder model exhibited the highest predictability ($R = 0.7$; $AUC = 0.97$), indicating more confidence in biomass projections. Conversely, the Atlantic cod model had the lowest predictability ($R = 0.47$; $AUC = 0.79$). Snow crab falls in between with moderate model predictability ($R = 0.41$; $AUC = 0.89$). However, the RV trawl survey has low catchability for this species [68]. Hence, our model may be underestimating the impact of ocean warming on snow crab biomass.

The low spatial uncertainty of the SDMs indicated consistency in the biomass predictions during the historical period (1996–2019). However, projecting to 2100 under the high emissions scenario (SSP3-7.0 for IPSL and GFDL and SSP4-6.0 for ACM) showed increased uncertainty, especially for yellowtail flounder. This finding aligns with other species distribution studies [47, 69], reflecting challenges in extrapolating predictions to novel conditions and/or the model's capacity to capture the underlying mechanisms governing species distributions [49]. In all species, there is a notable overlap between regions with biomass absence and areas of high uncertainty (Figs A, D and F in S1 Text). Furthermore, observation uncertainty, linked to bias in the sampling coverage, can lead to an incomplete depiction of a species' entire environmental niche [70]. While the Grand Banks region has relatively comprehensive sampling coverage, we anticipate observation uncertainty to be more pronounced near the Avalon peninsula, since in this area independent inshore sampling is performed, and at the periphery of the Grand Banks, corresponding to deeper waters that are less sampled [71]. Depth sampling limitation may elucidate the higher uncertainty observed in the biomass predictions for the three species at the periphery of the Grand Banks. Another possible explanation is related to the spatial resolution of the climate models, increasing bias near the slope of the Banks.

Variation in spatial warming among climate models is crucial to understand uncertainty surrounding species distribution projections. In the present analysis, we found greater variation among climate models than among scenarios. We also found differences in the variability of the temperature projections, with ACM temperature increasing steadily, while the ESMs, GFDL and IPSL showed high variability. This is likely due to low spatial resolution of ESMs, leading to incorrect circulation patterns due to inaccuracies in the bathymetry (Figs K and L in S1 Text). In a dynamic coastal region like the Grand Banks, changes in circulation patterns, particularly the strength of the shelf break current, play a crucial role in determining sea bottom temperature [18, 19]. These small-scale circulation features are poorly captured by ESMs, and can even vary among ROMSs [19]. In the same way, the cold intermediate layer is a key feature of the Banks that also affects the temperature pattern distribution, with colder waters prevailing in the northern Grand Banks due to the advection of winter-origin waters from the Labrador Shelf, and warmer temperatures observed in the southern Grand Banks, including the shallow southeast shoal [13]. The CIL falls within a specific depth range (~50–200 m); thus models with high bathymetry bias would likely misrepresent the CIL.

Model caveats and assumptions

The SDMs used here do not capture mechanistic drivers of species distribution based on functional traits and physiological constraints–thus, reducing confidence in the projections. For instance, in the Bering Sea, the recent collapse of the snow crab population has been linked to elevated water temperatures [72]. Despite these temperatures not exceeding the thermal limits of the species, they heightened the crabs' caloric requirements. This, together with a restricted distributional range, resulted in a mass starvation event [72]. Therefore, it is important to acknowledge that ocean warming can trigger unforeseen ecological responses. Moreover, when including the spatial component in our model, we are assuming that the biotic and abiotic conditions (all but temperature and depth) are going to remain the same in the future. This assumption may not be correct. For instance, shifts in species distributions can affect predator-prey dynamics, community structure, and ecosystem structure and functioning [73, 74]. Thus, exploring joint SDMs could help clarify how these species' interactions and environmental changes jointly impact biomass projections [75]. However, neglecting to consider unexplained spatial correlation in species distribution modeling can result in several problems, including an increased likelihood of false positive findings, misinterpretation of the relationships between environmental factors and species distribution, and decreased model accuracy [76]. The inclusion of the spatial random field could impact the estimates of fixed effects due to spatial confounding, which refers to a situation where predictors in the model are correlated with spatial or spatio-temporal effects, potentially leading to bias [77]. When confounding exits, spatial random fields may absorb variability associated with climate variables, potentially leading to an underestimation of the true impacts of climate change on species biomass [47].

In this study, species biomass was estimated across the model domain by predicting biomass values over a 5x5 km grid, allowing for spatial estimates beyond the specific locations where trawl surveys were conducted. This method, which is increasingly used to calculate biomass indices, has been previously applied for our target species in the Grand Banks, comparing it to traditional strata-based biomass estimation methods [25]. There are some uncertainties related to these biomass estimations, associated to trawl survey coverage, low catchability of certain species like snow crab, seasonal limitations from using only spring data, and ontogenic variations in species distribution that are not considered in here (see [25] for further details).

As exploited populations shift, it is important to consider how fisheries management efforts can be adapted to more effectively manage and conserve marine resources [78, 79]. The projections generated by our SDMs can directly inform fisheries management by highlighting future hotspots for species of commercial interest, allowing for the adaptation of fishing zones to ensure sustainable harvests. It is important to note that while these projections indicate expected biomass changes, they should not be interpreted as definitive predictions. Nonetheless, these results hold significant relevance for fisheries management. Firstly, they confirm that changes in habitat suitability are indeed anticipated with warming waters, which could have varying impacts on different fisheries. Secondly, our findings underscore the potential of SDMs to inform medium and long-term planning for fisheries management. By anticipating areas where key species may decline or increase, management can proactively adjust quotas, spatial closures, or gear restrictions to mitigate overfishing or habitat damage [80]. In a socio-economic context, these projections could be used to assess the impacts of distribution shifts on local fishing communities, industry profitability, and food security. For example, fishers who rely on species predicted to decline in their current fishing grounds (i.e., snow crab) might face economic challenges, while others might benefit from newly available species in their region. Understanding these shifts enables better planning for transitions in fisheries-dependent communities, whether by supporting diversification strategies, reallocating fishing rights, or investing in alternative livelihoods [81]. SDMs offer valuable insights into the spatial dimension of these biomass changes, aiding in strategic decision-making.

Supporting information

S1 Text.
(DOCX)

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