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## Abstract

Under climate change, species composition and abundances in high-latitude waters are expected to substantially reconfigure with consequences for trophic relationships and ecosystem services. Outcomes are challenging to project at national scales, despite their importance for management decisions. Using an ensemble of six global marine ecosystem models we analyzed marine ecosystem responses to climate change from 1971 to 2099 in Canada's Exclusive Economic Zone (EEZ) under four standardized emissions scenarios. By 2099, under business-as-usual emissions (RCP8.5) projected marine animal biomass declined by an average of −7.7% (±29.5%) within the Canadian EEZ, dominated by declines in the Pacific (−24% ± 24.5%) and Atlantic (−25.5% ± 9.5%) areas; these were partially compensated by increases in the Canadian Arctic (+26.2% ± 38.4%). Lower emissions scenarios projected successively smaller biomass changes, highlighting the benefits of stronger mitigation targets. Individual model projections were most consistent in the Atlantic and Pacific, but highly variable in the Arctic due to model uncertainties in polar regions. Different trajectories of future marine biomass changes will require regional-specific responses in conservation and management strategies, such as adaptive planning of marine protected areas and species-specific management plans, to enhance resilience and rebuilding of Canada's marine ecosystems and commercial fish stocks.

**Key words:** climate change, ensemble modeling, marine ecosystem models, Canada Exclusive Economic Zone, Fish-MIP, projection uncertainty

## Introduction

Climate change is already altering the physical and biogeochemical properties of the ocean, with impacts on species abundances, distributions, ecosystem functioning, and the provision of ecosystem services (Cheung et al. 2016; Worm and Lotze 2016). Rising temperatures and enhanced stratification alter primary productivity, changes which can then amplify through food webs with consequences for higher trophic levels (Kwiatkowski et al. 2018; Lotze et al. 2019). Other stressors, such as ocean acidification and oxygen declines, are impacting ocean productivity, nutrient and carbon cycling, leading to metabolic consequences and behavioural changes in many species (Doney et al. 2009; Keeling et al. 2010). Species range shifts are already occurring and expected to continue into the future, particularly in high-latitude and polar waters, resulting in reconfigurations of ecological communities (Cheung et al. 2010; Poloczanska et al. 2013). Therefore, projections of climate-change impacts in the fast-changing oceans of high-latitude countries such as Canada, where commercial and subsistence fisheries are economically, nutritionally, and socially valuable, are urgently needed to inform fisheries management and marine conservation.

Canada has one of the longest coastlines in the world and borders three different oceans—the Atlantic, Pacific, and Arctic—making it a pertinent case study for investigating marine biomass responses to climate change within its Exclusive Economic Zone (EEZ). To do so requires the use of coupled physical, biogeochemical, and ecological models. Using outputs such as water temperature, primary production, and other physical and biochemical variables from Earth System Models (ESMs) as forcing variables, marine ecosystem models can be used to project changes in animal biomass, species distributions, and food webs (Bopp et al. 2013; Lefort et al. 2015; Tittensor et al. 2018a). Individual ecosystem models are based on model-specific building blocks, such as species types, size classes, or functional groups, and ecological processes considered are unique to each model, hence they vary in their response to changing ocean conditions (Tittensor et al. 2018a). Past studies have typically used single marine ecosystem models, forced by one or several ESMs to derive patterns of biological changes on multiple scales (Blanchard et al. 2012; Barange et al. 2014; Jones et al. 2015), which can underrepresent the variety of underlying ecosystem processes and underestimate the range of projection uncertainty (Bryndum-Buchholz et al. 2019). Combining projections from multiple ecosystem models into ensembles allows the quantification of mean trends and an assessment of variation in projections due to differing model structures, parameters and processes (Tittensor et al. 2018a). Such model intercomparison projects (MIPs) are commonly used in climate impact research and have proven invaluable in the understanding of physical climate-change projections (e.g., Bopp et al. 2013), yet they have only recently been adopted for global ocean ecosystems (Tittensor et al. 2018a; Lotze et al. 2019).

We used ensemble projections from the Fisheries and Marine Ecosystem Model Intercomparison Project (Fish-MIP; Tittensor et al. 2018a) to quantify spatio-temporal changes in marine animal biomass within the Canadian EEZ under multiple climate-change scenarios over the 21st century. We analyzed outputs from six global marine ecosystem models forced with standardized outputs from two ESMs under four emissions scenarios (Tittensor et al. 2018b). We compared mean trends and variation in total marine animal biomass due to changing climate conditions; quantified responses to differences in projected climate-change mitigation efforts in Canada's Pacific, Atlantic, and Arctic oceans; and examined the policy and management consequences of our findings.

## Materials and methods

### Data sources

We extracted historical (1970–2005) and future (2006–2099) spatially explicit projections of marine animal biomass (total marine animal biomass; including all vertebrates and invertebrates of trophic

level >1, excluding zooplankton) from six global marine ecosystem models included in Fish-MIP simulation round 2a: APECOSM (Maury 2010), BOATS (Carozza et al. 2016), DBEM (Cheung et al. 2010), DPBM (Blanchard et al. 2012), EcoOcean (Christensen et al. 2015), and Macroecological (Jennings and Collingridge 2015; Tittensor et al. 2018b; Table S1). Each ecosystem model was forced with standardized outputs from two ESMs (GFDL-ESM2M and IPSL-CM5A-LR; APECOSM and DPBM runs were only available for IPSL-CM5A-LR in Fish-MIP simulation round 2a) provided by the Coupled Model Intercomparison Project Phase 5 (CMIP5, https://esgf-node.llnl.gov/search/cmip5/) under four contrasting greenhouse gas (GHG) concentration scenarios (representative concentration pathways (RCPs), further referred to as emissions scenarios; DBEM runs were only available for RCP2.6 and 8.5 in the Fish-MIP simulation round 2a). One of the ESMs, GFDL-ESM2M, projects moderate changes in variables such as sea surface temperature (SST) and oceanic net primary productivity (NPP) over the 21st century, whereas IPSL-CM5A-LR projects stronger SST warming and NPP declines (Bopp et al. 2013). The four RCPs were: RCP2.6, a low emissions and strong mitigation scenario, assuming peak emissions by 2010–2020 with a substantial reduction until 2100 (van Vuuren et al. 2011); RCP4.5 and 6.0, two stabilization emissions scenarios that level off at intermediate GHG concentration levels by 2100 (Masui et al. 2011; Thomson et al. 2011); and RCP8.5, a high business-as-usual emissions pathway, assuming continuous emissions increase until 2100 (Riahi et al. 2011). In this study, we focus on Fish-MIP model runs under no-fishing scenarios, since spatially explicit future projections of fishing at global scales are as of yet unavailable, and outputs that include a simplified fishing projection (using an assumption of constant and spatially unchanged fishing pressure at 2005 levels to 2100) are only available for three marine ecosystem models (Tittensor et al. 2018a, 2018b). Therefore, our analysis isolates the climate-change signal on marine animal biomass.

## Study area

Our study area spanned the entire Canadian EEZ across three oceans (Fig. 1). The Canadian Pacific along the coast of British Columbia is characterized by warm waters carried onshore by the North Pacific Current (Okey et al. 2014). Canada's Atlantic Ocean ranges from the Gulf of Maine to northern Labrador and is influenced by the warm Gulf Stream and cold Labrador Current (Saba et al. 2016). The Canadian Arctic spans the entire northern Canadian coast and is characterized by cryospheric elements sensitive to warming (Prowse et al. 2009a, 2009b; Dufresne et al. 2013).



**Fig. 1.** Delineations of the Arctic, Atlantic, and Pacific oceans in Canada's Exclusive Economic Zone (EEZ). Country shapefile retrieved from www.diva-gis.org. EEZ outline modified from Flanders Marine Institute (2018).

## Data analysis

### Temporal changes in total marine animal biomass, SST, and NPP

Historical and future projected time series of total marine animal biomass were extracted on a common 1° × 1° grid for the Canadian EEZ from each marine ecosystem model, ESM, and emissions scenario combination. Biomass projections by DBEM, the only model with a 0.5° × 0.5° grid resolution, were averaged over each 1° × 1° grid cell. To analyze climate-driven biomass changes in each area of the EEZ, we first calculated the annual spatially weighted (by latitude–longitude grid cell size) mean biomass across each of Canada's three oceans (Pacific, Atlantic, Arctic) for each ecosystem-ESM combination and emissions scenario. Next, we derived time series of the annual percent biomass change from 1971 to 2099 relative to the average of 1990–1999 (defined as the historical reference period) for EEZs and grid cells. Defining the 1990s as the historical reference period allowed us to compare future projected biomass changes over the course of the 21st century and its last decade (2090s) to the last decade of the 20th century. Lastly, we calculated the ensemble mean relative biomass change (in percent for each model; different ecosystem models include different components, hence they are not directly comparable in absolute terms) and model spread, expressed as one inter-model standard deviation of the ensemble mean, over all ecosystem–ESM combinations for each grid cell and ocean. A similar approach was used to derive projected changes in SST (in °C) and NPP (in percent) forcing data for GFDL-ESM2M and IPSL-CM5A-LR. In addition to mapping the ensemble mean and the inter-model standard deviation, we also mapped the model agreement, defined as the percentage of model projections agreeing on the direction of change, ranging from 50% (half of models indicate a decline, half indicate an increase) to 100% (all models agree on direction of change).

We then assessed the climate-change mitigation effect for the model ensemble by subtracting the annual mean biomass change per grid cell under the high-mitigation pathway (RCP2.6) from the no-mitigation pathway (RCP8.5). The obtained values represent the climate-change mitigation effect in terms of the difference between the projected biomass changes under the two contrasting emissions scenarios.

## Results

### Temporal changes in total marine animal biomass, SST, and NPP

The climate-change effects on marine animal biomass varied across Canada's three oceans. In the Canadian Arctic, ensemble mean total marine animal biomass increased over the 21st century relative to 1990–1999 (**Fig. 2a**). The greatest magnitude in projected biomass change and largest inter-model standard deviation was found under RCP8.5 (26.2% ± 38.4% in 2099 relative to 1990s), while projected changes under RCP4.5 (8.2% ± 11.4%) and 6.0 (7.2% ± 19.7%) were smaller, and those under RCP2.6 (9.6% ± 18%) intermediate (**Fig. 2a**). Projections under RCP4.5 and 6.0 were influenced by the lack of projections from DBEM in the ensemble (see Methods), an ecosystem model which otherwise showed some of the strongest changes under RCP8.5 and 2.6 in the Arctic area (see **Fig. S1a**). Biomass projections under both RCP2.6 and 8.5 decreased by 3%–4% between 2070 and 2090 relative to the 1990s before showing an increasing trend during the 2090s. For all emissions scenarios, the variation around the projected biomass increase was greater than the ensemble mean, indicating high uncertainty in projecting biomass changes in this polar region (**Fig. 2a**). Comparing individual model runs under RCP8.5 (**Fig. S1a**) revealed that two ecosystem–ESM combinations (Macroecological IPSL-CM5A-LR, DPBM IPSL-CM5A-LR) showed biomass declines, while all other combinations projected biomass increases.

In contrast to the polar region, the projected ensemble mean animal biomass in the Canadian Pacific and Atlantic areas decreased over the 21st century. In the Canadian Pacific, total projected biomass declines ranged from −8% (±9.5%) under RCP2.6 to −24% (±24.5%) under RCP8.5, with projections
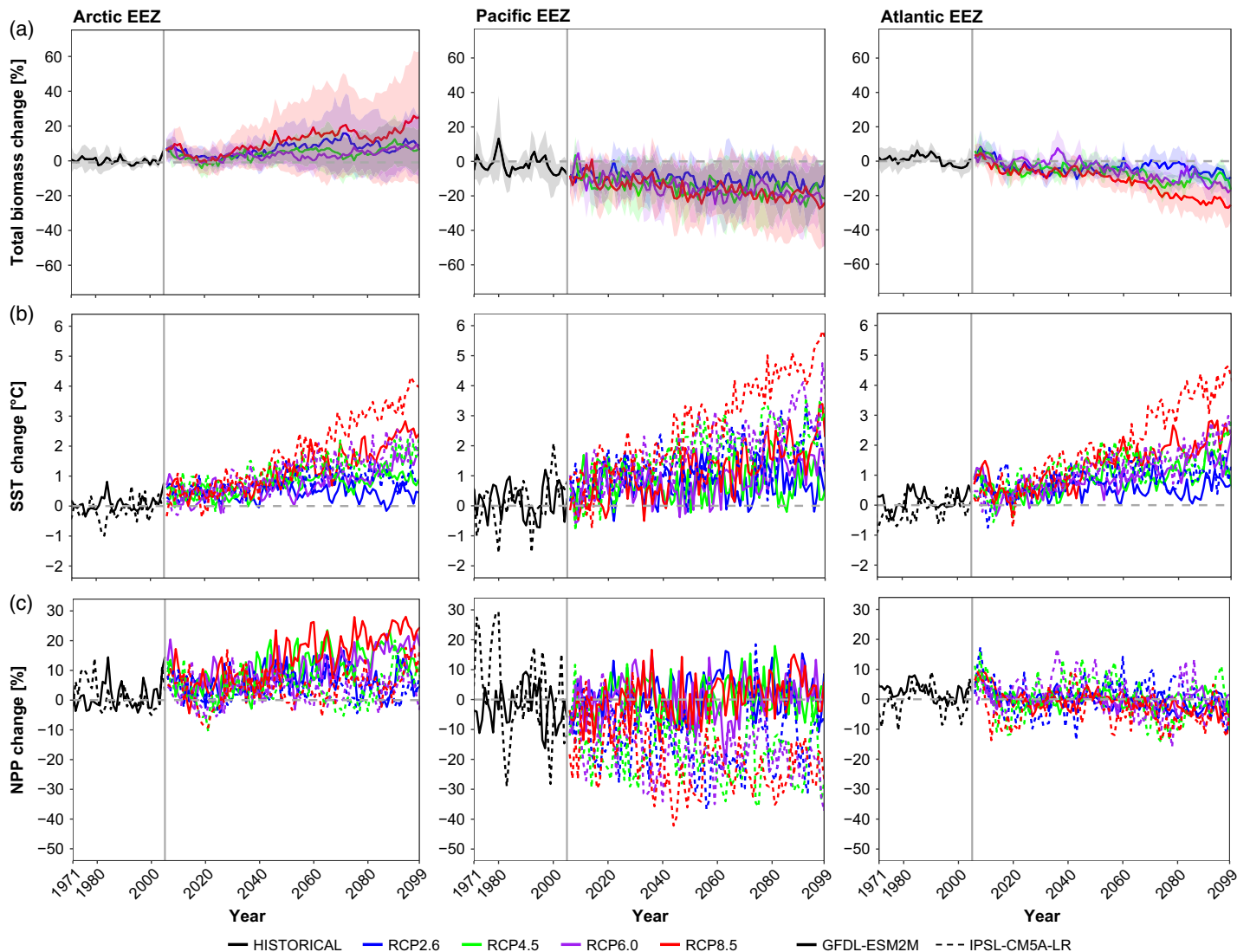
**FACETS**



**Fig. 2.** Model projections of (a) total marine animal biomass, (b) sea surface temperature (SST), and (c) net primary production (NPP) in Canada's three oceans from 1971 to 2099 under four emissions scenarios (RCP2.6, RCP4.5, RCP6.0, RCP8.5). Trends are depicted as the projected annual mean change relative to 1990–1999 with total marine animal biomass and NPP as percent change and SST in °C. (a) Ensemble model projections with one inter-model standard deviation (SD, shading). Ensemble results in (a) are averaged across marine ecosystem model-Earth System Model combinations (total marine animal biomass, $n = 10$). In (b) and (c) solid lines are GFDL-ESM2M projections; dashed lines area IPSL-CM5a-LR projections. The vertical solid grey line denotes the separation of historical and future projections. Note different $y$-axes values among figure panels. EEZ, Exclusive Economic Zone.

from RCP4.5 (−21.5% ± 20%) and 6.0 (24.5% ± 24.8%) showing intermediate declines by 2099 (**Fig. 2a**). The variation around projected biomass decreases was slightly greater than the mean for all RCPs (**Fig. 2a**), with all ecosystem–ESM combinations showing biomass declines under RCP8.5 (**Fig. S1b**) except for two (DBEM GFDL-ESM2M, EcoOcean GFDL-ESM2M). Projected total biomass in the Canadian Atlantic declined by −9.3% (±4.2%) under RCP2.6 and −25.5% (±9.5%) under RCP8.5 and showed intermediate declines under RCP4.5 (−16.5% ± 8%) and 6.0 (−16.7% ± 6.8%) by the end of the 21st century (**Fig. 2a**). Here, the variation (SD) was lower than the ensemble mean for all scenarios, indicating higher consistency across individual projections in

the Canadian Atlantic, with all ecosystem–ESM combinations showing biomass declines (**Fig. S1c**). Overall, the model spread of biomass projections was largest in the Arctic area and lowest, and thus most consistent, in the Atlantic area, and in general variability was greater under higher emissions scenarios (**Fig. 2a**).

The projected increase in biomass under all four emissions scenarios in the Canadian Arctic was concurrent with a projected increases in SST and NPP under both ESMs (**Figs. 2b** and **2c**). GFDL-ESM2M projected SST increases of 0.45 °C (RCP2.6) and 2.4 °C (RCP8.5), where IPSL-CM5A-LR projected larger SST increases, reaching 0.7 °C (RCP2.6) and 4 °C (RCP8.5) by 2099 (**Fig. 2b**). NPP projections increased between 4.5% (GFDL-ESM2M) and 8% (IPSL-CM5A-LR) under RCP2.6; under RCP8.5 NPP increased between 16% (IPSL-CM5A-LR) and 24% (GFDL-ESM2M by 2099 (**Fig. 2c**). In the Canadian Pacific and Atlantic oceans SST was projected to increase in similar magnitude compared with the Arctic SST projections for both ESMs under all four emissions scenarios; however, NPP projections decreased for IPSL-CM5a-LR in the Pacific EEZ (−5.6% under RCP2.6; −26.5% under RCP8.5) and for both ESMs in the Atlantic EEZ (IPSL-CM5a-LR: −5% under RCP2.6; −4.7% under RCP8.5; GFDL-ESM2M: −0.45% under RCP2.6; −5.6% under RCP8.5) (**Figs. 2b** and **2c**). Projections of the two ESMs were generally more consistent in the Atlantic and Arctic compared with the Pacific, and they were more variable under higher emissions scenarios.

## Spatial patterns of change in total marine animal biomass

Within the Canadian Arctic, projected animal biomass under RCP2.6 increased moderately in the Hudson Bay by the end of the 21st century, whereas greater increases were observed throughout other areas within the Arctic EEZ, in particular around the islands of the central Arctic Ocean and the Beaufort Sea (**Fig. 3a**). Similarly, under RCP8.5, projected animal biomass increased in many regions of the Canadian Arctic; however, it decreased along the western coast of the Hudson Bay, the northern Beaufort Sea, and in some parts of the central Arctic Ocean (**Fig. 3b**). Within the Pacific and southern regions of the Canadian Atlantic Ocean, projected biomass consistently declined by the end of the 21st century, with stronger declines under RCP8.5 than RCP2.6 (**Figs. 3a** and **3b**). In contrast, projected biomass in the northern Atlantic regions of the EEZ increased under both emissions scenarios (**Figs. 3a** and **3b**).

Reduced emissions through climate-change mitigation would lead to a dampening of projected biomass changes under the current GHG emissions trajectory (RCP8.5) across Canada's three oceans (**Fig. 3c**). This climate-change mitigation effect (RCP8.5-RCP2.6) was the weakest in the Pacific area of the EEZ, where projected biomass decreases were only slightly reduced (light yellow (**Fig. 3c**) = <0% to −10%) compared to projected decreases under RCP8.5 (**Fig. 3c**). In the Canadian Atlantic, climate-change mitigation consistently reduced projected biomass decreases under RCP8.5 from <0% to −20% (**Fig. 3c**). Climate-change mitigation had the strongest effect across the Canadian Arctic, especially in the Arctic Archipelago (**Fig. 3c**), where climate-change mitigation would result in lower biomass increases (−30% to −70%) across the region.

Model spread (inter-model standard deviation of the ensemble mean) was generally higher in projections under RCP8.5 than RCP2.6; however, it was spatially consistent in terms of areas with high and low standard deviations (**Figs. 4a** and **4b**). Under both emissions scenarios, standard deviations were lower in the Pacific and Atlantic than the Arctic area of the EEZ, with the exception of the Hudson Bay, which showed similar standard deviations (**Figs. 4a** and **4b**). Model agreement on the direction of projected biomass changes across ecosystem models was also higher under RCP2.6 than RCP8.5 (**Figs. 4c** and **4d**). Under RCP2.6, model agreement was more consistent at the southern latitudes of the study area (i.e., the Atlantic and Pacific areas of the EEZ) and in the central Arctic Ocean, whereas
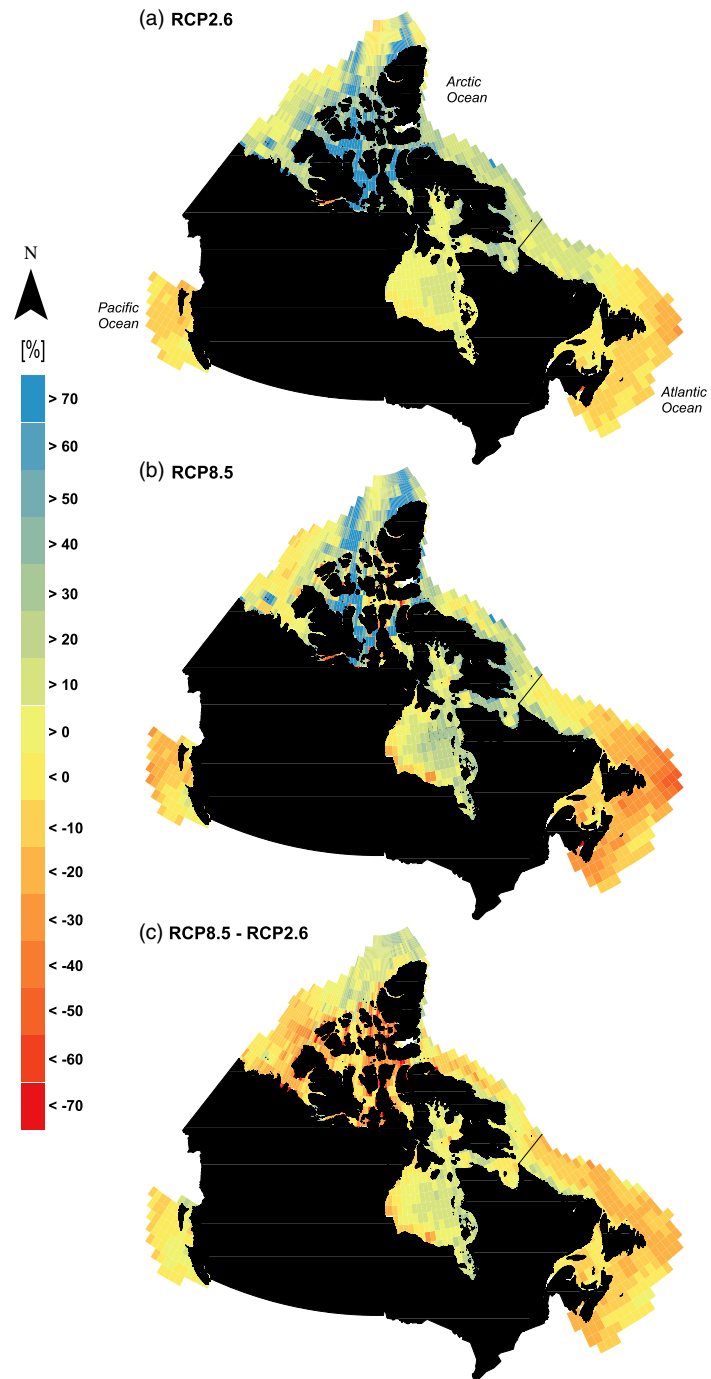
**Fig. 3.** Spatial patterns of ensemble projections of total marine animal biomass for (a) RCP2.6, (b) RCP8.5, and (c) climate-change mitigation effect (RCP8.5-RCP2.6) in Canada's three oceans. Ensemble biomass projections represent a mean percent change in total marine animal biomass in 2090–2099 relative to 1990–1999 (a and b). Values in (c) represent the climate-change mitigation effect in terms of the difference between the projected biomass changes under the high-mitigation scenario (RCP2.6) and no-mitigation effect (RCP8.5). For better visualization of patterns, percent biomass change values were capped at ±75%. Black line separates Canadian Arctic and Atlantic oceans. Country shapefile retrieved from www.diva-gis.org. Exclusive Economic Zone outline modified from Flanders Marine Institute (2018).
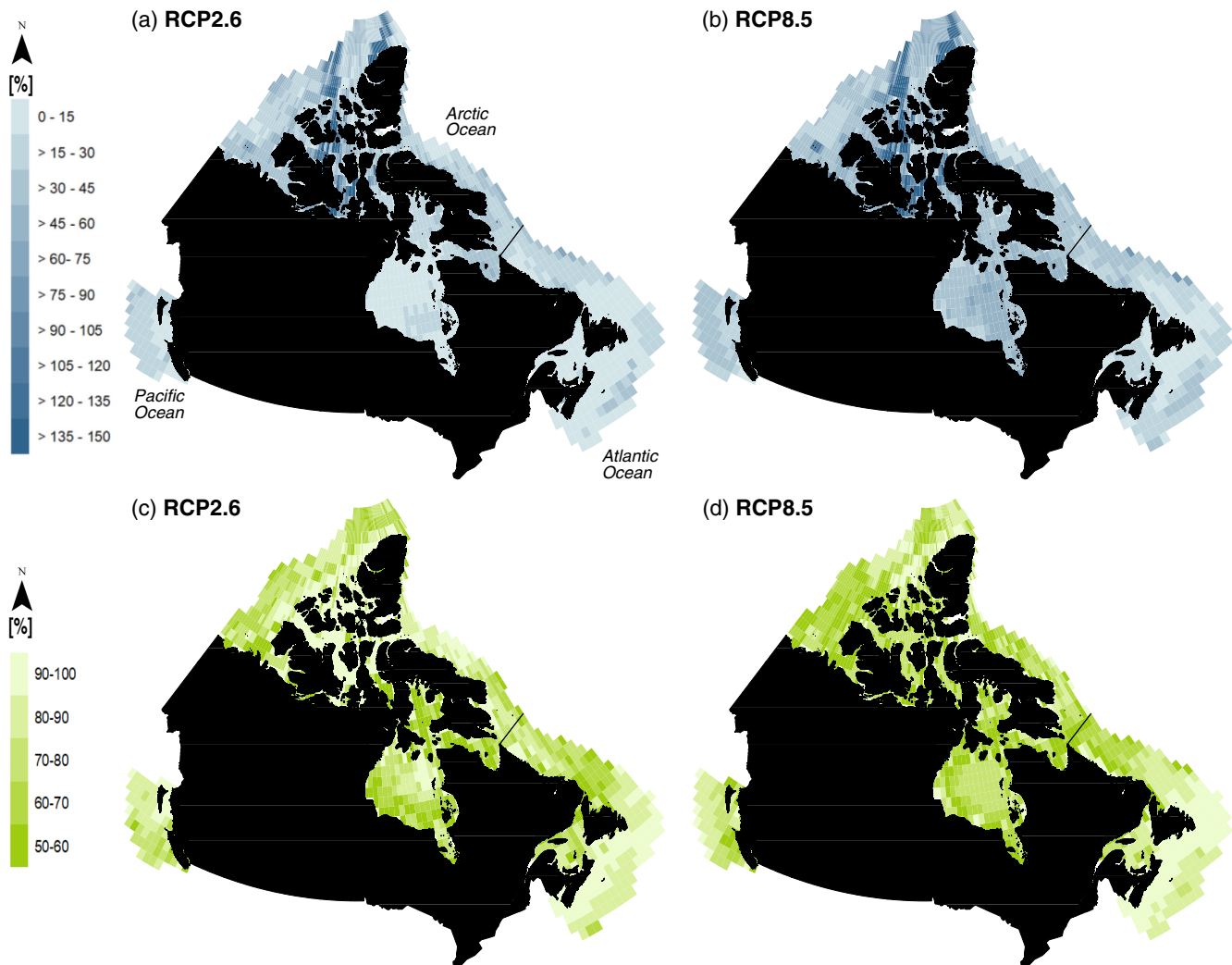
**Fig. 4.** Model spread and model agreement of the ensemble mean biomass change in 2090–2099 relative to 1990–1999 under RCP2.6 and RCP8.5 in Canada's Exclusive Economic Zone (EEZ). The model spread is depicted as one inter-model standard deviation (%) of the ensemble mean for (a) RCP2.6 and (b) RCP8.5. Model agreement (%) represents the percentage of models agreeing in the direction of projected biomass change for (c) RCP2.6 and (d) RCP8.5. For better visualization of patterns, percent inter-model standard deviation values were capped at 150%. Black line separates Canadian Arctic and Atlantic oceans. Country shapefile retrieved from diva-gis.org. EEZ outline modified from Flanders Marine Institute (2018).

ecosystem models agreed less on the direction of projected biomass changes in the Hudson Bay, the Beaufort Sea, and the northern regions of the Canadian Arctic Ocean (**Fig. 4c**).

## Discussion

Findings from this study support the expectation that climate change is having and will continue to have large impacts on marine ecosystems in mid- to high-latitude shelf seas, such as those in Canada. However, there are regional differences in the direction and magnitude of the projected marine animal biomass changes and hence consequences for management and policy. These are largely driven by the differences in projected changes in oceanographic drivers amongst the different regions as well as differences in the representation of the regional ecosystem structure by the models.

In the Canadian Arctic Ocean, our results suggest an overall increase in mean total marine animal biomass over the 21st century under the high-emissions scenario (RCP8.5); however, high uncertainty around the ensemble mean indicates a broad range of potential future trajectories. Some areas of projected biomass declines under RCP8.5 include parts of the central Arctic and along the coasts of Hudson Bay and the northern Beaufort Sea. The high variability of biomass projections in the Arctic compared with the Atlantic and Pacific areas may be partly explained by an underrepresentation or divergent representation of key structures and dynamics in existing ecosystem models. It may also be due to a general lack of available data for parameterisation, a limited structural understanding of the Arctic ecosystem, or to general global models not being tailored to these polar ecosystems, e.g., not adequately accounting for the effects of seasonal ice coverage (Steiner et al. 2015). This is consistent with global ensemble studies suggesting a higher uncertainty of projected future changes in polar regions (Bryndum-Buchholz et al. 2019; Lotze et al. 2019).

Comparing across ecosystem models, most models projected biomass increases in the Canadian Arctic Ocean, with DBEM projecting the largest biomass increases under both RCP2.6 and RCP8.5 (Figs. S1 and S2). DBEM represents the distribution of commercial species only, which have relatively low initial biomass levels in the Arctic compared with the broader biomass compositions simulated by the other five ecosystem models (APECOSM, DPBM, BOATS, EcoOcean, and Macroecological) in our ensemble. These represent a range of different size-classes and functional or trophic groups, including commercial and noncommercial groups with higher initial biomass levels (Table S1; Bryndum-Buchholz et al. 2019). Because many commercial species in DBEM are projected to invade the Arctic over the course of the 21st century, relative changes in biomass are amplified compared with other ecosystem models (Cheung et al. 2009, 2016; Bryndum-Buchholz et al. 2019). Starting with higher initial biomass levels (i.e., including commercial and non-commercial groups) may lead to relatively lower future biomass changes in other models in comparison with DBEM (Bryndum-Buchholz et al. 2019), and these aspects should be borne in mind when interpreting the results in this region.

Overall, our multi-model mean of projected biomass trends in the Canadian Arctic is strongly influenced by DBEM and EcoOcean, which are the only models that are spatially resolved within the Canadian Arctic Archipelago (Figs. S2 and S3). Projections of coastal dynamics within the Arctic Ocean are still very uncertain and ESMs diverge in their projections of primary production and other physical and biochemical factors within the region (Vancoppenolle et al. 2013; Steiner et al. 2015).

Another interesting observation is the projected biomass declines between the 2070s and 2090s under both RCP2.6 and 8.5 in the Arctic Ocean (Fig. 2a), which are concurrent with declines in NPP (Fig. 2c) and may represent the onset of a projected long-term decrease in ocean productivity within the Arctic Ocean over the next centuries (Moore et al. 2018). Moreover, the strong response in biomass changes after the 2070s observed in DBEM-GFDL-ESM2M (Fig. S1a) could be due to few commercial species reacting strongly to changing ocean conditions and driving the projected mean trend. In contrast, five out of six ecosystem models are not species-specific and may respond less drastically to future changes in the Canadian Arctic.

Spatially, areas of biomass changes in the Arctic are projected to expand or intensify in magnitude under RCP8.5 compared with RCP2.6. Only BOATS projected biomass increases for the majority of the Arctic under both emissions scenarios. DBEM's Arctic projections shifted from large biomass increases under RCP2.6 to declines under RCP8.5, particularly in the northern and central Arctic areas of the EEZ and the Hudson Bay. EcoOcean projected biomass increases across the Arctic area of the EEZ, except for some declines in northern regions under both emissions scenarios. Importantly, in our study, only the DBEM and EcoOcean models directly incorporate changing ice cover into their biomass projections, which might lead to an underrepresentation of ice-cover related dynamics in the entire Arctic ecosystem within the model ensemble (Tittensor et al. 2018a).

The further incorporation of sea ice cover, thickness, seasonality, or other physical attributes specific to polar oceans as forcing factors into marine ecosystem models may help refine projections of ecosystem changes in the Canadian Arctic Ocean. Model development in this direction is paramount, given the drastic changes already being observed within the Arctic Ocean. Arctic mean summer surface water temperatures have increased by +1 °C per decade from 1982 to 2018, with drastic changes in seasonal sea ice cover and associated phytoplankton communities and primary production (Tremblay et al. 2012; Timmermans and Ladd 2018). In response to warming waters, sea ice has been decreasing in all regions of the Arctic over the past three decades (Meier et al. 2014). Consequently, plankton communities and overall marine productivity is changing. For instance, in coastal areas such as the Canadian Arctic Archipelago, primary production is increasing in response to enhanced upwelling due to more favorable winds and deeper seaward retreat of ice (Tremblay et al. 2012). Pelagic phytoplankton communities, on the other hand, are shifting towards small picophytoplankton due to warming and freshening of surface layers, potentially impacting the entire Arctic marine food web (Tremblay et al. 2012).

In the Atlantic and Pacific areas of the Canadian EEZ, our model ensemble projected consistent decreases in total marine animal biomass over the 21st century under all four emissions scenarios. These results are in line with findings showing that ocean warming increases biological energy dissipation in ecosystems and enhances water column stratification thus reducing primary production. Both processes can cause a strong decrease of marine animal biomass (Lefort et al. 2015; Cheung et al. 2016; Guiet et al. 2016; Worm and Lotze 2016) that amplifies along food chains (Lefort et al. 2015; Lotze et al. 2019). Compared with the Canadian Arctic, biomass projections in the Canadian Atlantic and Pacific oceans were more consistent among ecosystem models and the variability in the ensemble mean was smaller both temporally and spatially. The size-structured ecosystem models BOATS, DPBM, and Macroecological projected the strongest biomass decreases within the Atlantic and Pacific areas of the EEZ. These models focus on metabolic rates and biomass flow, with biomass projections primarily responding to changes in primary production and SST (Blanchard et al. 2012; Jennings and Collingridge 2015; Carozza et al. 2019). EcoOcean, a trophodynamic ecosystem model, and APECOSM, a composite 3-D ecosystem model, projected overall weaker biomass declines.

Under the high-emissions scenario, NPP increased strongly within the Arctic area of the EEZ yet decreased in the Canadian Atlantic Ocean and was highly variable in the Pacific area of the EEZ by the 2090s. The higher variability in projected NPP within the Canadian Pacific could partly be attributed to the influence of inter- and intra-decadal climate variations, such as the Pacific Decadal Oscillation and the El Niño Southern Oscillation (Talloni-Álvarez et al. 2019). The variability of both climate phenomena has increased in recent years, impacting SST in the Canadian Pacific with consequences for marine productivity (Hunter and Wade 2015).

On the timescale examined in this study, the ocean, land, atmosphere, and their coupling control the supply of nutrients to coastal waters and therefore phytoplankton growth and NPP (Blanchard et al. 2012). Warming waters can enhance ocean stratification, leading to nutrient limitation in the euphotic zone and reduced NPP (Cabré et al. 2015), while loss of sea ice in the Arctic can enhance NPP due to a longer growing window (Boyce and Worm 2015; Worm and Lotze 2016). The evolution of NPP dynamics plays a critical role in model projections of upper trophic levels as primary production is the only source of energy fueling the entire upper ocean food web (Kwiatkowski et al. 2018; Tittensor et al. 2018a; Lotze et al. 2019).

SST was projected to increase throughout the Canadian EEZ over the 21st century under RCP2.6 and RCP8.5. Under RCP8.5, Bopp et al. (2013) found a global mean SST increase of 2.73 °C (±0.72 °C) by 2100 based on 10 ESMs, slightly lower than the average trends we found in the Canadian EEZ (3.6 ± 0.5 °C). Changes in SST affect the physiology; the dissipative processes of metabolism including

food intake, growth, reproduction, maturation and maintenance (Guiet et al. 2016); survival, abundance, and distribution of marine species (Sarmiento et al. 2004; Brander 2010; Grady et al. 2019) with overall impacts on ocean biomass (Lefort et al. 2015; Cheung et al. 2016; Lotze et al. 2019).

SST and NPP were the main forcing variables considered in all six ecosystem models used in this study (Tittensor et al. 2018a). Several other physical and biochemical factors are also influenced by climate change, such as pH, oxygen content, light penetration, marine currents, vertical distribution of primary production, or sea ice cover (see above, Bopp et al. 2013). However, not all the ecosystem models in our analysis use these variables and represent the corresponding processes (Tittensor et al. 2018a). This heterogeneity in ecosystem model configuration is reflected in the varying individual biomass projections. Some marine ecosystem models in our ensemble respond strongly to temperature changes affecting metabolic rates in the modelled higher trophic levels (BOATS, DPBM, Macroecological), other models, such as EcoOcean, respond strongly to NPP changes. DBEM considers pH, oxygen, and sea ice cover as additional drivers to determine evolving habitat niches and species distribution (Tittensor et al. 2018a; Bryndum-Buchholz et al. 2019).

## Study limitations and future research

Notwithstanding the aforementioned points on incorporation of ice dynamics and differing biotic community compositions in the individual marine ecosystem models, there are other aspects that need to be recognized when interpreting our results. A challenge in mapping ensemble mean biomass changes was the inconsistent spatial coverage among ecosystem models due to different ecosystem models using their own specific grids and land/sea masks (**Figs. S2** and **S3**). Open ocean regions had greater coverage (≥5 models) than coastal and island regions (2–3 models). Low model coverage in some Arctic grid cells (e.g., the central Arctic Archipelago) reduced the number of ecosystem models incorporated into the ensemble mean, yielding some results being dominated by EcoOcean and DBEM (**Figs. S2** and **S3**).

Further, our study relied on outputs of global ESMs and global marine ecosystem models to represent all of Canada's EEZ across the three oceans, because there are no consistent regional climate and ecosystem models that could be used for such an ensemble approach. Generally, global ESMs provide limited resolution of processes in coastal or polar regions (Bonan and Doney 2018; Derksen et al. 2018). Advancements in ESM representation and resolution of high-latitude coastal zones and relevant processes, especially in the context of the complex Canadian Arctic Archipelago, will help to improve projections for those regions. Additionally, environmental changes (i.e., dramatic changes in water temperature and oxygen concentration) occurring in shelf ecosystems, as found within the Atlantic area of the Canadian EEZ, may only be resolved by high-resolution ESMs (Claret et al. 2018). Improving ESM projections will be crucial to understanding changes in polar regions such as the Canadian Arctic, given their importance for fisheries and other ecosystem services, and for the conservation of marine and polar biodiversity.

The approach of regionally downscaling global ESMs can potentially help to incorporate climate and ecosystem dynamics at a higher resolution (Holt et al. 2017). However, regional downscaling can be problematic, as changing resolution within models can introduce additional uncertainty, giving less confidence in projected outcomes (Bopp et al. 2013; Holt et al. 2017; Tittensor et al. 2018a). As such, our results should be considered with broad spatial and temporal trends in mind, as opposed to seeking highly specific regional insights, and we caution that these projections may fail to capture important potential changes that might threaten the coastal oceans in the future. Developing standardized, high-resolution regional models that are specifically tailored to deal with the abovementioned issues is paramount to push forward our understanding of climate-change impacts in complex coastal marine ecosystems and the societies that depend on them.

Another limitation of our analysis is that it represents ecosystem responses to climate change in an unfished ocean; however, fisheries exploitation is strongly altering the structure of populations and ecosystems leading to modified responses to future climate, in terms of reduced capacity to buffer the perturbations and exacerbated climate effects on marine ecosystems (Planque et al. 2010). Hence, our ensemble results may be conservative, especially in regions of current high fishing intensity within the Canadian EEZ, such as the Canadian Maritimes. Yet, a recent study by Lotze et al. (2019), using the reduced Fish-MIP model ensemble that includes a fishing effect, suggested that under current levels of fishing pressures, fishing might not substantially alter the relative effect of climate change on a global scale. How the fishing effect might play out more precisely, both globally and regionally, requires improved integration of fishing scenarios into marine ecosystem models, as currently under development in the Fish-MIP's second simulation round.

## Implications and conclusions

Our ensemble projections suggest that ecosystem productivity in the Canadian Pacific and Atlantic Oceans will be negatively impacted by climate change over the 21st century, which may have substantial consequences for fisheries, socio-ecological systems, ecosystem management, and biodiversity conservation in these regions. In contrast, new economic opportunities as well as potential conflicts and challenges to resource management and marine conservation may develop in the Canadian Arctic. Our results can help inform several aspects of long-term planning and policy development in the Canadian EEZ.

First, planning for national climate-change adaptation and mitigation, such as efforts by Environment and Climate Change Canada (ECCC 2016a), requires a solid understanding of the expected changes, including their timelines, spatial patterns, and uncertainties. Moreover, as Canada is committed to international agreements (ECCC 2016a) including the United Nations Sustainable Development Goals (notably SDG 13, climate action, and SDG 14, life below water), understanding projected changes in Canada's three oceans is essential. Additionally, we clearly demonstrate the benefits to be gained from climate-change mitigation in Canada's Atlantic and Pacific Ocean, where our strong mitigation scenario (RCP2.6) lessened the projected declines in marine animal biomass. Considering Arctic ecosystems in Canadian climate-change mitigation efforts is essential, as unmitigated changes within the Arctic will have dramatic consequences that reach far beyond regional ecosystems and socio-economic systems (Whiteman et al. 2013; Flato et al. 2019). Changes due to a warming Arctic Ocean include sea ice loss, permafrost melting, ocean acidification, and altered ocean and atmospheric circulation. These changes are impacting Arctic marine and terrestrial ecosystems at a rate faster than most ecosystems could adapt to naturally (Wassmann et al. 2011). Beyond these regional impacts, changes in the Arctic are also affecting the functioning of the Earth System at the global scale (Whiteman et al. 2013).

Second, the study highlights potential risks and vulnerabilities within different marine regions in the Canadian EEZ, which is an essential component of developing ocean management that is adaptive to climate change. Our results could support Fisheries and Oceans Canada in their efforts to adapt fisheries and marine ecosystem management for a changing environment over the 21st century. For example, planning for potential fish biomass declines in the Atlantic and Pacific may necessitate measures to avoid further overexploitation, support rebuilding, and enhance ecosystem resilience, with differing levels of change requiring differing responses. Despite these general ecosystem changes, individual fish stocks may show varying responses to climate change, including impacts on their distribution, reproduction and biomass production (Pinsky et al. 2013; Stortini et al. 2015; Britten et al. 2016; Free et al. 2019), which will need to be considered in species-specific management plans.

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Third, given Canada's commitment to increase its marine protected areas and to biodiversity conservation as a Party to the Aichi Biodiversity Targets (ECCC 2016a, 2016b), an understanding of when and where changes in marine animal biomass and productivity will occur is critical, particularly to future-proof current conservation and management actions. For example, our results projected strong latitudinal changes in Atlantic and Arctic marine ecosystems, which will require long-term and dynamic planning and management of marine protected areas given the likelihood that many species will shift towards polar waters over time.

Finally, our analysis represents an important case study for climate-change impacts on a northern high-latitude country and its oceans. Based on our model ensemble, we highlight potential climate-change impacts on marine biomass in the Canadian EEZ, which could be dampened by implementing effective climate-change mitigation strategies. While our study does not explicitly simulate mitigation pathways of global GHG emissions, our results based on the difference between RCP8.5 and RCP2.6 suggest that strong mitigation policies can lower the magnitude of climate-change impacts on marine animal biomass across Canada's three oceans. These impacts need to be recognized to proactively respond to ecosystem reconfigurations in the face of climate change, especially given the additional impacts of exploitation and other stressors that will be overlaid. Overall, our high model agreement in projecting marine biomass changes indicates broad confidence in the expected direction of change, while the high variability around the ensemble mean highlights uncertainty in the magnitude of projected changes and points to the potential for improvements of model projections, especially for the Canadian Arctic Archipelago.

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## Author contributions

AB-B, FP, and HKL conceived and designed the study. AB-B and FP analyzed and interpreted the data. JLB, WWLC, VC, EDG, and OM contributed resources. AB-B, FP, DPT, JLB, WWLC, VC, EDG, OM, and HKL drafted or revised the manuscript.

## Competing interests

The authors have declared that no competing interests exist.

## Data availability statement

All relevant data are within the paper and Supplementary Material.

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## Supplementary material

The following Supplementary Material is available with the article through the journal website at doi:10.1139/facets-2019-0035.

Supplementary Material 1

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